Functional Valuation of Ecosystem Services on Bonaire

-An ecological analysis of ecosystem functions provided by coral reefs -

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ABSTRACT

My thesis research builds on the 'movement' to value nature. This movement as I call it started as early as 1970 with a theory to quantify and monetize nature (Hueting, 1970). References to the concept of ecosystem services date back to the mid 1960s and early 1970s (de Groot et al., 2002) A Phd research into the value of nature by De Groot (1992) emphasized the need to "ecologize" economic valuation of ecosystem services by integrating ecological information. In 2005 the Millenium Ecosystem Assessment (MEA) report used the ecosystem services approach to highlight the importance and drivers of changes of ecosystem service delivery (MEA, 2005). The Economics of Ecosystem services and Biodiversity (TEEB) platform built on the framework of MEA, but specified ecosystems in underlying functions, processes and structures to "ecologize" economic benefits of biodiversity and costs of biodiversity losses (TEEB, 2010a). Valuation of ecosystem services can be done at three levels, monetary, quantitative and qualitative. Qualitative describes benefits in a non-numerical scale, quantitative measures benefits and changes based on numerical data and monetary builds on quantitative value and attaches a monetary value (White et al., 2011).

This research is a semi-quantitative analysis of the functional value of coral reef habitats on Bonaire to support ecosystem services. It is part of an economic valuation study of marine and terrestrial ecosystem services on Bonaire. The economic valuation study estimated a monetary value of selected ecosystem services. My research measured the functional value, defined as the ecological importance of a habitat, on an ordinal scale with four levels (0-3). The TEEB theoretical framework was applied by studying the underlying ecological functions, processes and structures of coral reefs that determine the capacity to deliver coral reef ecosystem services through a literature review. The functional group approach was used as a measure of the importance of habitats based on the level of representation of fish and coral functional groups. The methodology to analyze the functional value was inspired by a study of Harborne (2006) that established the functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. My research applied this method using Bonaire as case study and adapted the method to determine the functional value of habitats to ecosystem services instead of ecosystem processes. This way the study of Harborne has been taken a step further by making the link between the economic analysis focussing on ecosystem services and the ecological analysis focussing on ecosystem functioning. The other adaptations made were the spatial scale, the habitat types and the data collection method. Harborne determined the value by doing a meta-analysis of empirical literature on processes in ten coral reef, seagrass and mangrove habitat types. For my research primary data of fish and benthic functional groups were collected at over hundred locations along the entire leeward coast of Bonaire to value just two coral reef habitat types.

Outcome of this research are matrices presenting relationships between socio-economic services and ecological functions, processes and fish and benthic species representing a functional role. Another outcome are maps presenting the functional value of each location to support twelve ecosystem services based on the primary data collected. These maps were analyzed taking into account resource use on Bonaire and show which area are of high importance for each service. This research is innovative in its attempt to link the economic value of ecosystem services with an ecological value of habitats to support these ecosystem services. In addition the survey of benthic cover and fish biodiversity and abundance has not been done at such a large scale according to our knowledge since the mapping of Bonaire in 1985 (Van Duyl, 1985).

TABLE OF CONTENTS

1 INTRODUCTION

My thesis research for the Institute for Marine Resources and Ecosystem Studies (IMARES) was part of the project “What’s Bonaire nature worth? “, an economic valuation of ecosystem services on Bonaire. For this project IMARES is providing scientific information and understanding of the ecological functioning of those ecosystems. Some background information on Bonaire, the project and IMARES is presented in chapter 1.1.

In my research I studied the functional value of coral reef ecosystems, and the capacity of coral reefs to provide ecosystem services. The rationale for my study to “ecologize” economic valuation of ecosystem services is explained in chapter 1.2, followed by the objectives and research questions of my research in chapter 1.3. The last chapter outlines the structure of this report.

1.1 Background

1.1.1 Bonaire

Bonaire is an island in the Caribbean Sea located 80km north of Venezuela [1] as shown in figure 1. It is part of the Kingdom of the Netherlands. Since the dissolution of the Dutch Antilles on 10 October 2010 Bonaire became a special municipality of Caribbean Netherlands [2].

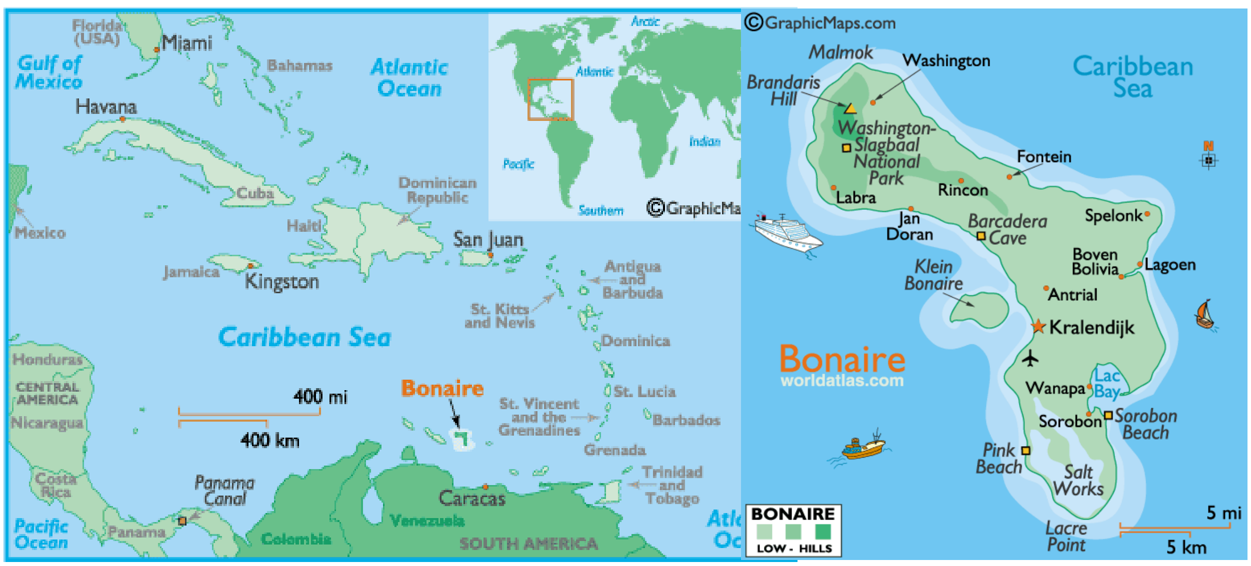


Figure 1. Position of Bonaire in the Caribbean Sea (Source: http://www.worldatlas.com).

The island covers an area of 288 km^2 (RLG, 2009) , 38 km long and between 5 and 11 km wide [1] plus an additional 6 km^2 for the small uninhabited island of Klein Bonaire (Wolfs, 2011). There are both terrestrial and marine protected areas. The Bonaire National Marine Park encompasses the marine protected area of about 27 km^2 along the entire coast of Bonaire from the high water mark to 60 meters depth, and includes coral reef, seagrass and mangroves [3]. The reefs around Bonaire and Klein Bonaire are fringing reefs, starting at the shoreline and extending to a maximum of 300 meters offshore. They provide habitat for about 65 species of stony coral and more than 450 species of reef fish (IUCN, 2011). The seagrass and mangrove habitats are mainly found in Lac Bay, which is not only a local marine protected area, but also a globally recognized wetland and protected RAMSAR area [4]. The topography of the island is diverse, with mountains, dry forest and rocky shores in the north-west and a flat landscape with salt lakes and coral rubble or sandy shores in the south-west. The windward north-eastern coast is characterized by limestone plateaus, rocky shores and difficult access to sea due to high waves, while the leeward coast has generally calm water and easy access to sea.

Bonaire has about 15.000 inhabitants, the majority of them living in Kralendijk [1] and along the leeward western coast. Tourism is the most important source of employment, mainly in dive tourism as Bonaire is known as 'Divers Paradise' [1], in addition to cruise tourism and surf tourism in Lac Bay. Other important industries are the oil storage terminal in the north-west and the salt production industry in the south-west [1].

1.1.2 What's Bonaire nature worth?

The project "What's Bonaire nature worth?" is a socio-economic valuation of ecosystem goods and services and biodiversity of Bonaire. The project is an initiative of and coordinated by Esther Wolfs, an independent consultant living on Bonaire. The objective is to provide information for policy makers to make better-informed decisions and regulatory measures for nature protection (Wolfs, 2011). The rationale for the project is that small island economies in the Dutch Antilles depend heavily on their marine and terrestrial ecosystem services for industries such as tourism, fisheries and sea transportation (Wolfs, 2011). Ecosystem services are the benefits people obtain from ecosystems (MEA, 2005). On Bonaire these services are threatened by coastal development, increased runoff due to grazing by feral livestock, lack of sufficient waste water treatment, increase of visitors, effects of climate change and other environmental pressures (Wolfs, 2011). The aim of the socio-economic valuation study is to get insight in the economic value of direct and indirect ecosystem services and to better understand the socio-economic impacts of changes within ecosystems. Within the scope of the project it is acknowledged that the condition of ecosystems and biodiversity and its underlying ecological processes including drivers of ecosystem change are important to understand in order to determine the economic value of ecosystem services. The key ecosystems on Bonaire selected for the study are coral reefs, mangrove forest, seagrass beds, coastal waters, beaches, coastal vegetation, and dry forest (Wolfs, 2011).

1.1.3 IMARES

IMARES is an independent and objective research institute that is part of Wageningen UR (University & Research centre) and provides knowledge necessary for an integrated protection, exploitation and spatial use of the sea and coastal zones. Erik Meesters, tropical marine ecologist and researcher at the department Ecosystems of IMARES locations Texel and Den Helder, is within the institute responsible for the project "What's Bonaire nature worth?". The role of IMARES in the project is to provide scientific information and understanding of the functioning of selected ecosystems in Bonaire, and to assess the impacts of changes in ecosystem conditions on the provisioning of services.

1.2 Problem definition

The need for "ecologizing" economic valuation of ecosystem services by integrating ecological information was already emphasised by De Groot (1992) in his research into the functions and values of nature. Decades later The Economic of Ecosystems and Biodiversity (TEEB) platform, a global 2-year study of hundreds of experts, reports that knowledge about the role of ecosystem processes and biodiversity in the provision of services for human welfare is still lacking, and that research efforts are needed to get better indicators to measure biodiversity and the provision of services as a basis for economic valuation (De Groot et al., 2010). According to Kremen (2005) ecological understanding of most ecosystem services is still limited. Ecology and economy need to be better linked in order to make informed decisions in the conservation and management of ecosystems. Economic valuation of ecosystem services identifies supply of goods and services and estimates monetary values, but does not measure how ecosystem functioning and biodiversity determine and influence the quantity and quality of goods and services provided (Kremen, 2005). Lack of knowledge about the role of ecosystem processes and biodiversity on human welfare and the role of human actions on environmental change are identified as reasons for large scale and continuous ecosystem degradation and accelerating loss of ecosystem services and biodiversity (De Groot et al., 2010). These complex dynamics might be the reason that ecological processes and ecosystem functioning have not been sufficiently integrated in economic valuation studies. The complex ecological interactions from environmental conditions to biological processes to ecological function delivery (Frid et al., 2008) might be another reason for the research gap in "ecologizing" economic valuation.

The socio-economic valuation study of Bonaire provides the opportunity and framework to address this research gap on a local scale, using the ecosystem services of coral reefs in Bonaire as a case study. The aim of the ecological research within the framework of the socio-economic valuation study is (1) to identify key ecological processes and corresponding process indicators that determine the condition of the ecosystems and (2) to identify indirect and direct drivers of ecosystem change and corresponding indicators of change in the status of the ecosystems (Wolfs, 2011). The focus of my research is on marine ecosystems in general, and on coral reefs in particular. Two interconnected ecosystems, seagrass beds and mangrove forests, are included in this research with respect to those processes that are linked to the services provided by coral reefs. For example, mangroves are nurseries for juvenile species and support fish and invertebrate biomass and diversity on coral reefs, increasing resources available for extractive use in fisheries and non-extractive use in diving tourism.

The quality of ecosystems is the basis for all ecosystem functions and continuous provision of services (Bouma and van der Ploeg, 1975). Well-functioning ecosystems are more likely to provide sustainable delivery of ecosystem services. Sustainable in this context means that the state of the ecosystem meets the needs of the current human population without compromising the ability to meet the needs of future generations (MEA, 2005) to deliver ecosystem services. Well-functioning ecosystems are ecosystems that have developed into – or are in the process of development towards - a steady state ecosystem that is stable at the relative short-term of 50 to 200 years (Bouma and van der Ploeg, 1975). A stable state ecosystem is characterized by the resilience of the ecosystem (Bouma and van der Ploeg, 1975). Resilience is the capacity of an ecosystem to cope with disturbances without shifting into a qualitatively different state that is controlled by a different set of processes (De Groot et al., 2010; Maynard et al., 2010). The stable state of a healthy coral reef is a coral-dominated state (Sheppard et al., 2009). A qualitatively different state is an algae- or even rubble-dominated state (Maynard et al., 2010). These alternative states do not support the biodiversity and structural complexity that coral reefs offer, and such changes in ecosystems will inevitably lead to changes in ecosystem service delivery.

In the case study of Bonaire, most direct and indirect use of ecosystem services of coral reefs depends on the current coral-dominated state. For example, diving tourism relies on the abundance and diversity of corals and reef fish, but also regulating services such as coastal protection require the coral reef structure that dissipates wave energy and provides natural breakwaters. While ecosystem services are dependent on well-functioning and stable ecosystems, at the same time use of ecosystem services can lead to ecosystem disturbances and the use of one service can influence the ecosystem's ability to provide another service. People can function within the stable state conditions of an ecosystem, however frequently ecosystems are unable to cope with and to neutralize the anthropogenic impacts (Bouma and van der Ploeg, 1975). Coral reef resilience is related to functional and structural components of the reef ecosystem. The status of these components can be characterised by indicators that can be measured. Evaluation of these indicators can be used to inform stakeholders on the status of the ecosystem and its functions, the impacts of natural and anthropogenic pressures on the future delivery of ecosystem services and inform management on measures to mitigate impacts.

1.3 Thesis research

1.3.1 Objectives

The overall aim of this research was to analyze for Bonaire how ecosystem services provided by coral reefs and interconnected seagrass beds and mangrove forests are determined by different ecological processes and structures that play a key role in ecosystem resilience and the sustainable delivery of ecosystem services. The approach for "ecologizing" the economic value of ecosystem services is to analyze how these marine habitats represent ecosystem services as well as key ecological processes. The research objectives are twofold:

The first objective is to develop a method to analyze the functional value of coral reef habitats in Bonaire to key ecological processes and structures, by assigning values to habitats where key ecological processes and structures are taking place based on the presence of functional groups of reef fish and corals and their functional role in these ecological processes and structures.

The second objective is to analyze which coral reef habitats and locations in Bonaire contribute most to the ecosystem services provided for in Bonaire, in order to know which marine habitats need to be targeted in conservation management and how to incorporate the sustainable delivery of ecosystem service.

1.3.2 Research questions

What is the functional value of coral reefs in Bonaire to ecosystem services measured as the representation of crucial functional groups that support key ecological processes and biophysical structures that provide ecosystem services (and ultimately support coral reef resilience)?

In order to answer this research question, the following questions need to be answered:

1. Which ecosystem services are provided by coral reefs on Bonaire?
2. What are key ecological processes and structures that determine ecosystem functions (and the capacity to deliver these ecosystem services)?
3. What are crucial functional groups and their functional roles to support these key processes and structures?
4. What is the level of representation of these functional groups in coral reef habitats and locations on Bonaire?

1.3.3 Method overview and scope

This research consisted of two parts: a literature review on coral reef ecosystem services and underlying ecological processes and structures and an analytical study of primary data collected through a snorkel survey.

Not all ecosystems which are included in the project "What's Bonaire nature worth?" were examined, but just the coral reef ecosystem. Furthermore it did not intend to describe the complete and complex functioning of a coral reef ecosystem as a whole, but only those elements that are linked to those functional groups of coral and fish that can be included in a visual census technique. For example the microbial loop that is considered essential in the nutrient cycle on coral reefs is not included as these single-celled organisms are not visible while doing a snorkel survey. Research into the impact of threats to ecosystem functioning and ecosystem service delivery was not included either.

1.4 Structure of report

After this introduction the methodology of the research is explained in chapter 2, including the theoretical framework with existing theories and concepts that resulted in the conceptual model for this research. It also elaborates how each step of the conceptual model is used to answer the research questions.

In chapters 3, 4 and 5 the outcomes of the two components of this research, the literature study and the analytical study, are presented. Chapter 3 answers the first three research questions based on a literature review by providing an overview of ecosystem functions and linking them to (1) ecosystem services that can be delivered by those functions in chapter 3.2 and (2) functional groups that support these functions and the underlying processes and structures in chapter 3.3. In chapter 4 the results of primary data analysis are presented: the selection and representation of functional groups in the coral reef habitats. This answers the fourth research question for fish functional groups in chapter 4.2 and for corals in chapter 4.3. The overarching research question of the functional value of coral reefs on Bonaire is answered in chapter 5, based on the results from chapter 3 and 4.

In the discussion in chapter 6 the caviates of gaps, assumptions and methodological limitations are discussed as well as suggestions how the results can be used in other project deliverables of "What's Bonaire nature worth?". Finally, in chapter 7 the conclusions and summary of the results are presented.

2 RESEARCH METHODOLOGY

The design of this research is summarized in a conceptual model which outlines the approach of the ecological analysis and how it fits in the economical analysis. The model builds on a theoretical framework of existing theories and concepts which is presented in chapter 2.1, followed by the conceptual model itself in chapter 2.2. Chapter 2.3 elaborates on the methods used to collect, process and analyze data.

2.1 Theoretical framework

This research is based on three existing concepts: economic valuation of ecosystem services, The Economics of Ecosystems and Biodiversity framework (TEEB) and functional valuation of habitats. The first concept indicates how ecosystem services can be integrated in decision making through economic valuation. The second concept explains how economic valuation can be improved through integration of ecological processes and biophysical structures to determine ecosystem functions and integration of drivers of change affecting ecosystem functions. The third concept is a method to assess the functional value as indicator of the importance of habitats to ecological processes. The last concept was used in this research for the functional valuation of coral reef habitats on Bonaire, to assess which are important habitats and locations for ecosystem functions that provide the capacity to deliver ecosystem services.

2.1.1 Economic valuation of ecosystem services

Economic valuation of ecosystem services can be used for several purposes. The main aim of valuing natural capital and ecosystem services is to make better informed decisions (Daily et al., 2009) by putting a monetary value on the benefits that ecosystems deliver for human well-being. The Millennium Ecosystem Assessment (MEA, 2005) defines an ecosystem as a dynamic complex of plant, animal, and microorganism communities and their non-living environment interacting as a functional unit. Ecosystem services are defined as the benefits people obtain from ecosystems (MEA, 2005). MEA (2005) classifies them in provisioning, regulating, cultural and supporting services. Provisioning services are the products provided by ecosystems (MEA, 2005) such as fish for food and genetic resources for the pharmaceutical industry. Regulating services are the benefits people obtain from the regulation of ecosystem processes (MEA, 2005), such as climate regulation and water purification. Cultural services are the non-material intangible benefits people obtain from ecosystems (MEA, 2005) such as spiritual enrichment, cognitive development, aesthetic experience and recreation. Supporting services are those that are necessary for the production of ecosystem services (MEA, 2005) such as primary production.
For economic value estimation ecosystem services are classified in direct use, indirect use and non-use value. Direct use refers to use of services that are either extractive, such as fisheries, or non-extractive, such as dive tourism. Indirect use refers to use of services outside the ecosystem itself, for example carbon sequestration from mangrove forests for global beneficiaries. Non-use refers to ecosystem services independent of any present or future use, such as the knowledge that rare species exist or the insurance that future generations can use the service (Van Beukering et al., 2007). Direct use values of provisioning services are easy to estimate (Van Beukering et al., 2007), because services often have a market value. Indirect use values are more difficult to estimate because of the complexity to estimate the level of use in relation to the ecosystem (Van Beukering et al., 2007), but there are also valuation methods to estimate indirect use value of regulating services and even non-use values such as most cultural services. Supporting services are generally not valued as this would result in double counts, because the service they support is already included in the valuation.
The contribution of economic valuation in ecosystem management is that it provides information on the value of nature in a comprehensive way, by including not just direct use benefits with a market value. The total economic value of all benefits represents the costs for society if ecosystem services are lost due to changes in ecosystems.

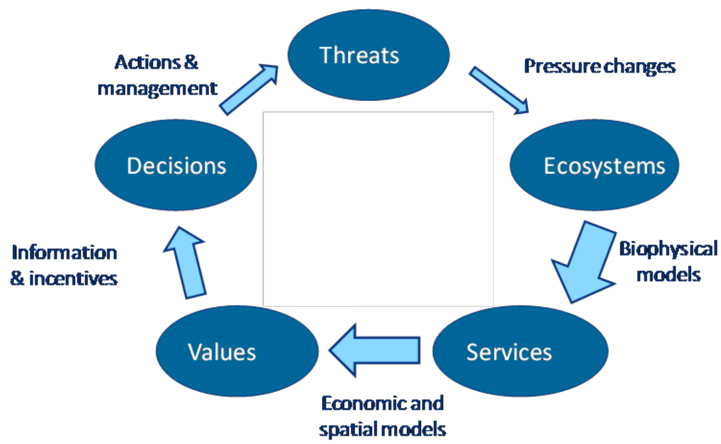


Figure 2. Role of economic valuation in ecosystem management (adapted from Daily et al., 2009).

Furthermore the economic value can be used in cost benefit analyses to compare the benefits with the costs of protecting ecosystems. The framework presented in figure 2 shows that valuation of ecosystem services is not an end in itself, but a way of organizing information and a step in the larger and dynamic process of decision-making (Daily et al., 2000). Ecosystem dynamics including the impact of threats and the effect on provision of services are an important step in this process as well.

2.1.2 The economics of ecosystems and biodiversity

TEEB, The Economic of Ecosystems and Biodiversity platform, is a global 2-year study, in which hundreds of experts from around the world are involved. They have analyzed economic benefits of biological diversity and costs of biodiversity losses and have reported their findings at the Convention for Biological Diversity in October 2010 (TEEB, 2010a). They report that knowledge about the role of ecosystem processes and biodiversity in the provision of services for human welfare is still lacking, and that research efforts are needed to get better indicators to measure biodiversity and the provision of services as a basis for economic valuation (De Groot et al., 2010). TEEB builds on the framework of the MEA, but specifies ecosystems in underlying ecosystem functions, ecological structures and processes, because ‘a lot goes on before services and benefits are provided’ (De Groot et al., 2010). This is shown in the upper-left hand box in figure 3.

Ecosystem functions are defined by TEEB as ‘a subset of the interactions between ecosystem structure and processes that underpin the capacity of an ecosystem to provide goods and services’ (TEEB, 2010b). This is different from ecosystem services, because functions represent the capacity to provide ecosystem services, not the actual use of services. For example the biomass of fish is the function, while the services provided are fish catch and fish biodiversity to enjoy for divers as cultural service. Furthermore ecosystem functions make the link between ecology and economy more distinct, as functions are determined by ecological processes and biophysical structures, while services are determined by the direct and indirect use for economic, social and ecological welfare. Ecosystem processes are defined as any change or reaction which occurs within ecosystems, either physical, chemical or biological (TEEB, 2010b) which include decomposition, production and nutrient cycling. Ecosystem structure is defined as the biophysical architecture of an ecosystem, for which the composition of species making up the architecture may vary (TEEB, 2010b). Finally, drivers of change are affecting ecosystem services through ecosystem changes. Drivers are defined as any natural or human-induced factor that directly or indirectly causes a change in an ecosystem (TEEB, 2010b). Indirect drivers such as demographic shifts, technology innovation and economic development affect the way people directly use and manage ecosystems and their services. Direct drivers are divided in negative, neutral and positive drivers. Negative drivers include habitat destruction and over-exploitation. Neutral drivers can be changes in use. Positive drivers enhance natural capital and include ecosystem conservation and sustainable management (De Groot et al., 2010).

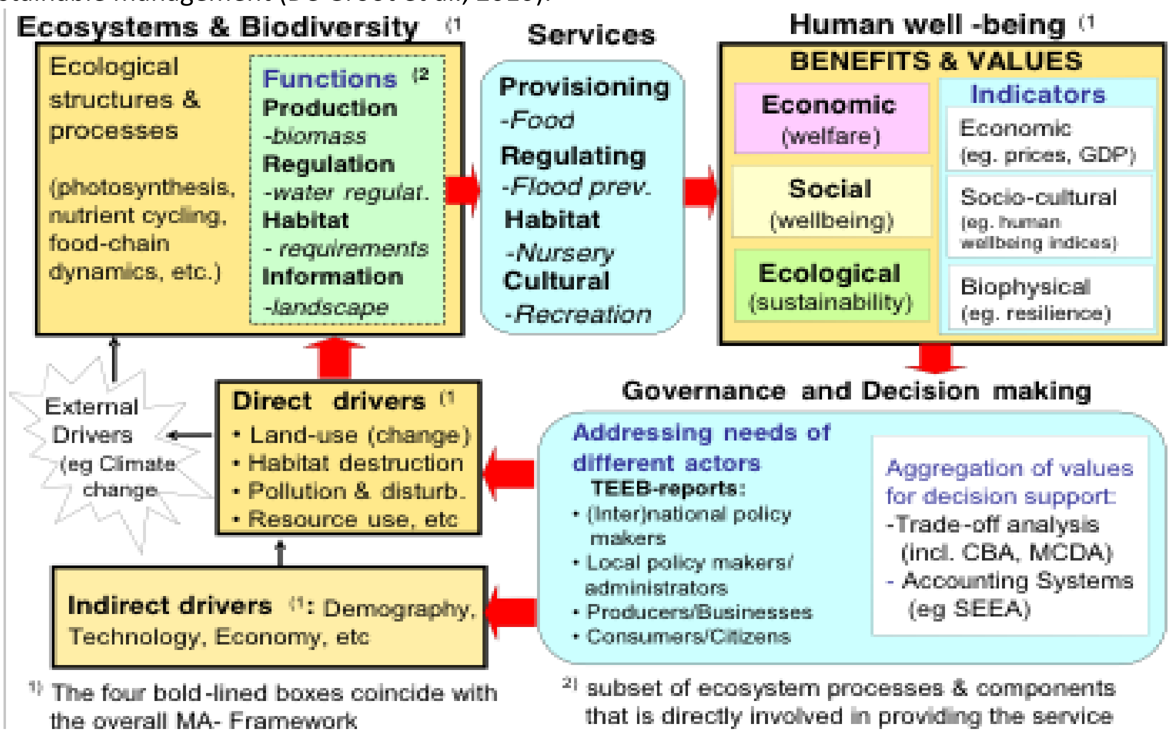


Figure 3. TEEB conceptual framework (De Groot et al., 2010).

Ecosystem function categories distinguished by TEEB are the production function, regulation function, habitat function and information function. They are linked to provisioning, regulating, habitat and cultural services. TEEB omitted the MEA category of supporting services as these are seen as a subset of ecological processes in the TEEB framework (De Groot et al., 2010). This is in line with the principle to avoid double counts in economic valuation. TEEB added habitat service to highlight the importance of ecosystems to provide habitat for migratory species and gene pool protection (De Groot et al., 2010). According to the TEEB classification 22 services are distinguished. For a complete overview of these services, including a comparison of similarities and differences between TEEB and MEA classification is referred to appendix A.

2.1.3 Functional valuation of habitats to ecosystem processes

The third concept on which this research proposal is based is a method designed by Harborne et al. (2006) to assign functional values to ecosystem processes in Caribbean coral reef, seagrass and mangrove habitats. The method is based on an empirical literature review of ecosystem processes across the Caribbean. Harborne et al. (2006) examined the importance of coral reef, seagrass and mangrove habitats in each of these processes, which is defined as the functional value. The functional value is expressed on an ordinal scale in semi-quantitative categories: none, low, medium or high. Categorization is as much as possible based on quantitative empirical data, and otherwise based on a putative functional value according to circumstantial evidence or the authors' observation. When habitat maps are available, functional values can be assigned to the habitat map to create hotspot maps with high functional value or to create process maps with a layer per process to address particular ecological and management questions (Harborne et al., 2006).

Harborne et al. (2006) distinguished ten habitat types and eleven ecosystem processes. Habitat typology is based on geomorphological structure and biotic and abiotic benthic composition (Mumby and Harborne, 1999). The selected scale of habitats is large enough to discriminate habitat types by high-resolution optical remote sensing. Geomorphological zones typically found on Caribbean coral reefs are lagoons, patch reef, back reef, reef crest, spur and groove, fore reef and escarpment. Benthic communities typically found on Caribbean coral reefs are divided in 4 main groups: coral dominated, algal dominated, bare substratum dominated and seagrass dominated.

Table 1. Functional values of Caribbean coral reef, seagrass and mangrove habitats to main ecosystem processes (adapted from Harborne et al., 2006).

Functional value:
- None
- Low
- Medium
- High

		Habitat types									
Ecosystem Process	**Unit of measurement**	**Mangrove**	**Lagoon - seagrass**	**Patch reef - coral**	**Back reef - coral**	**Reef crest - coral *Acropora***	**Forereef - algae+gorgonians**	**Shallow forereef - coral *Montastraea***	**Forereef - sand**	**Deep forereef - coral *Montastraea***	**Escarpment - coral**
1. Wave energy dissipation	**% of energy**	None	None	Low	Low	High	Medium	Medium	Medium	None	Low
2. Nitrogen fixation	**nmol N_2 g afdw^{-1} h^{-1}**	Low	High	Low	Medium	High	Low	Medium	Low	Low	Low
3. Gross primary production	**g O_2 m^{-2} d^{-1}**	Medium	Medium	Medium	High	High	Medium	Medium	Low	Low	Low
4. Density of herbivores	**fish 100 m^{-2}**										
- Stoplight Parrotfish *Sparisoma viride*		Low	Low	High	High	High	Medium	High	None	Medium	Low
- Surgeonfish *Acanthuridae spp.*		Low	Low	High	High	High	Low	Medium	None	Low	Low
- Threespot Damselfish *Stegastes planifrons*		None	None	High	High	Low	Low	Medium	None	Medium	Low
- Sea urchin *Diadema* (<1983)		Low	Medium	High	Medium	High	Medium	High	None	Low	None
- Sea urchin *Diadema* (>1983)		Low	Low	Low	Low	Low	Low	Low	None	Low	None
5. Density of planktivores	**fish 100 m^{-2}**	None	None	Low	Low	Low	Low	Medium	None	High	High
6. Density of invertivores	**fish 100 m^{-2}**										
- White Grunt *Haemulon flavolineatum*		High	High	High	High	High	Low	Medium	None	Medium	Low
7. Density of piscivores	**fish 100 m^{-2}**										
- Nassau Grouper *Epinephelus striatus*		High	Low	High	Low	Low	Medium	Medium	None	Medium	Low
- Spiny Lobster *Panulirus argus*	**individuals ha^{-1}**	High	High	High	Low	Low	Medium	Medium	Low	Medium	High
- Queen conch *Strombus gigas*	**individuals ha^{-1}**	Low	High	Medium	Medium	Low	Medium	Low	High	Low	None
8. Gross calcification	**kg CaCO3 m-2 yr-1**	Low	Low	Medium	Medium	High	Low	High	Low	Medium	Low
9. Community bioerosion	**kg CaCO3 m-2 yr-1**	None	None	High	High	High	Medium	High	None	Medium	Low
10. Coral recruitment	**juveniles m^{-2}**	Low	Low	High	Medium	Medium	Medium	High	None	High	High
11. Coral diversity	**Shannon diversity index**	Low	Low	High	Medium	Medium	Medium	High	None	High	High

Table 1 shows the ten identified habitat types based on their structure and main benthic composition (Mumby and Harborne, 1999). Table 1 also shows the eleven ecosystem processes and their unit of measurement and standardization of quantitative empirical data. The processes are selected based on the framework of major processes described by Hatcher (1997): coral reef accretion, biological production, organic decomposition, biogeochemical cycling and maintenance of biodiversity.

2.2 Conceptual model

To 'ecologize' the economic valuation of ecosystem services in Bonaire, the ecosystems that are part of the dynamic decision making process as shown in figure 2 were analyzed according to the principles of TEEB as shown in figure 3, by examining the underlying ecological processes and biophysical structures that determine ecosystem functions. The conceptual model of this research is presented in figure 4 and shows how the ecological and economical analyses were linked through the functional value as introduced in chapter 1.3.1. Arrows connect the different steps in the research and refer to a relationship that was examined. Dashed arrows refer to relationships with components of the project "What's Bonaire nature worth?" that fell outside of the scope of this research, but are nevertheless included in the conceptual model to show the overall picture of the project. The ecological analysis examined the key ecological processes and biophysical structures based on functional groups of reef fish and corals and their functional roles in these ecological processes and structures. The economical analysis determined the main ecosystem services for beneficiaries in Bonaire and estimated the economic value of each ecosystem service. The economic value can be allocated to specific habitats based on the functional value of each habitat. Each step in the conceptual model is explained in more detail below.

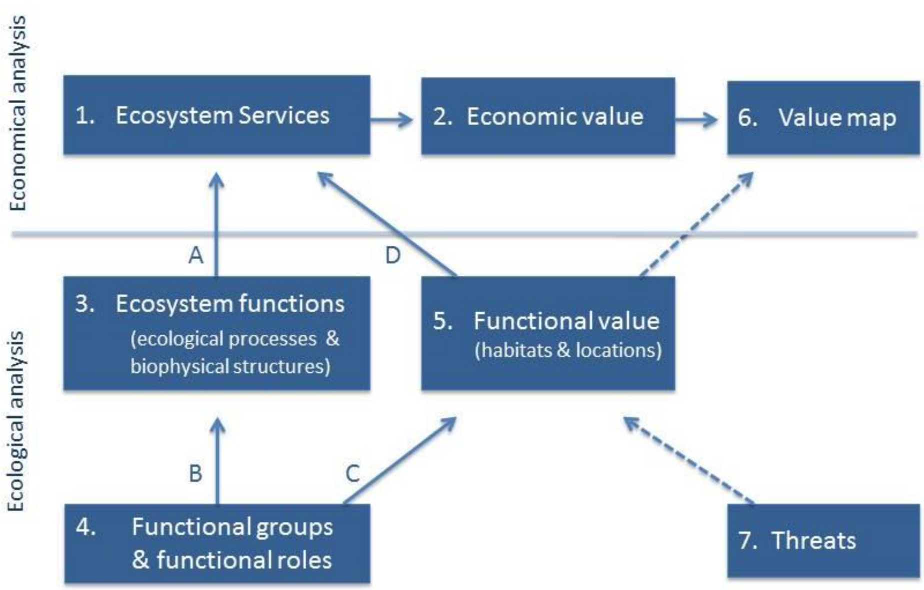


Figure 4. Conceptual model of functional valuation of ecosystems. The numbers refer to subsequent steps in the research: For the economical analysis the steps were 1) identification of ecosystem services 2) estimation of their economic value and 6) mapping of these values. For the ecological analysis the steps were 3) identification of ecosystem functions and 4) functional groups, followed by 5) estimation of the functional (ecological) value of survey sites to support ecosystem services based on the representation of functional groups. Step 7) identification of threats that impact the functional value of sites fell outside the scope of this research. The characters refer to the relationships between components: A) which functions and underlying processes and structures determine the delivery of each ecosystem service, B) which functional groups have a functional role to support each ecosystem function, C) what is the functional value of survey sites, measures as the representation of each functional group at each survey site and D) what is the functional value at survey sites for the potential delivery of each ecosystem service.

2.2.1 Functional group approach

The research method how to collect data and analyze ecosystem functional value was based on a functional group approach. Functional groups are defined as a collection of species that perform a similar function irrespective of their taxonomic affinities (Steneck and Dethier, 1994). This functional group approach has been selected for three reasons: First, it helps to simplify the ecological analysis as it permits an examination of patterns without the need for detailed data collection at species level (Steneck and Dethier, 1994). Second, it provides the basis for managing uncertainty in conservation by maintaining not individual species but the functional groups that support dynamic ecological processes (Bellwood et al., 2004) and sustain ecosystem services (Hughes et al., 2005). Third, it is possible to classify functional groups according to the focus and needs of the research, based on either morphological, physiological, behavioural, biochemical or trophic criteria (Steneck, 2001).

With regards to the second reason, functional redundancy of individual species depends on the response diversity between species in the functional group. Within a functional group species richness determines the functional redundancy, whereby the loss of one species is potentially compensated for by another species (Bellwood et al., 2004). This acts as an insurance against environmental change, however functional redundancy is ineffective if there is low response diversity (Bellwood et al., 2004). Response diversity is the range of responses to environmental change by species within a functional group (Elmqvist et al., 2003) for example differences between coral species in bleaching as response to a rise in sea surface temperature.

With regards to third reason, fish functional groups were selected based on behavioural and trophic characteristics and coral functional groups were selected based on morphological characteristics.

Fish functional groups are generally used synonymously with guilds of species from different trophic levels in the food chain. Guilds are species with similar resource use, like food resources used by herbivores, planktivores, invertivores and piscivores (Blondel, 2003). This also reflects their role in transferring energy to the next level in the food chain (Done et al., 1996). Fish functional groups have also been identified by their roles in ecosystem processes (Bellwood et al., 2004). Herbivores for example are then split in sub-groups of scraping, roving, eroding and browsing herbivores (Bellwood et al., 2004), because these differences in feeding behaviour are important for their functional role in different key ecological processes such as grazing of algae (Mumby, 2006; Mumby et al., 2006) and bioerosion of corals through scraping of coral parts while grazing algae (Hutchings and Kiene, 1986).

Coral functional groups have also been identified by their functional roles in the key ecological processes, such as calcification and construction of reef structure (Bellwood et al., 2004) for coastal protection and provision of habitat and shelter. Selection criteria used for coral functional groups were characteristics that play a role in these processes, such as coral morphology. Morphology is the particular form of an organism (Levin, 2000) so depending on the shape of coral it provides a certain strength and structure.

2.2.2 Step 1, 2 and 6: Economical analysis

Step 1 refers to the identification of ecosystem services on Bonaire that were selected for the estimation of their economic value in step 2, which was input for step 6 to assign economic values at a spatial scale to specific areas on Bonaire in a value map.

Step 1, 2 and 6 are part of the economical analysis carried out by project coordinator Esther Wolfs and researchers of the Institute for Environmental Studies (IVM) of VU University and as such were not part of this thesis research. However, since the aim of my research was to 'ecologize' the economic valuation by analyzing the functional relationships between ecosystem components and how they affect the provision of services, it was important to determine the relationship between services and functions.

Furthermore, the functional valuation of habitats and locations assigned functional values at a spatial scale to areas on Bonaire, which could also be used as input for the value map.
The project coordinator provided, with input from IVM and IMARES, a list of ecosystem services delivered by all key ecosystems on Bonaire as part of the project and specified in chapter 1.1.2, including coral reefs. Only for a selection of these services the economic value was estimated, depending on data availability and feasibility to use appropriate valuation techniques. Ecosystem services of coral reefs as identified in step 1 are reported in chapter 3.2.1. This report does not further elaborate on step 2, the economic valuation methods and results. Step 6 is briefly addressed in chapter 2.2.4 to elaborate how functional values at a spatial scale could be used in the value map.

2.2.3 Step 3, 4 and 5: Ecological analysis

In step 3 key ecological processes and biophysical structures underlying ecosystem functions of coral reefs habitats were identified. This was done by means of a literature review, using as a starting point the eleven ecosystem processes identified by Harborne et al. (2006) as presented in table 1 of the third theoretical concept. Additionally, ecosystem processes and structures which are considered essential for coral reef resilience according to the literature were included.

(A) The relationship between ecological functions identified in step 3 and ecosystem services identified in step 1 is reported in the relationship matrix A in chapter 3.2.3.

In step 4 the functional groups of reef fish and coral were identified based on their functional roles in the key ecosystem processes in coral reef habitats, as identified in step 3. In addition, other indicators or keystone species other then reef fish and coral were included if considered an important indicator for key ecological processes, for example sea urchins and their functional role in grazing of algae.

(B) The relationship between functional groups selected in step 4 and ecological functions identified in step 3 is presented in relationship matrix B in chapter 3.3.3.

In step 5 of the ecological analysis functional value of habitats and locations is assigned similar to the approach in the third theoretical concept of Harborne et al. (2006). Functional value is defined as the importance of each habitat to each ecological function (Harborne et al., 2006). The importance is measured as the representation of fish and coral functional groups in each habitat at an ordinal scale (3=high, 2=medium, 1=low, 0=none), based on fish densities and benthic cover. Selected coral reef habitats were the shallow zone and the reef zone, as explained in chapter 2.2.5. These two habitats were surveyed at 116 locations on Bonaire and Klein Bonaire, for which site selection is referred to chapter 2.3.2.

(C) The representation of functional groups in the shallow zone and reef zone at 116 survey locations is reported in matrices C.1 and C.2 in chapter 4 for fish and corals respectively. These matrices show for each functional group the functional value at 232 sites, which number of sites results from coupling habitats and locations.

(D) The ordinal scale values of functional groups from matrix C enabled a semi-quantitative analysis of the habitat functional value at 232 sites to support ecosystem services. For each ecosystem service the functional groups with a functional role in the delivery of that ecosystem service were selected using the established relationships between services and functions of matrix A and functions and functional groups of matrix B. Ordinal scales of selected functional groups were summed, including a weighting factor according to the level of importance, essential or supporting, for service delivery. The resulting matrix D was used to produce functional value maps in chapter 5, which were analysed to find out which parts of the island are ecologically important for which ecosystem services.

2.2.4 Step 6 and 7: Value map and Threat analysis

Step 6 is the economic value map, a project deliverable of "What's Bonaire Nature worth?" to visualize and assign value to the most precious areas for conservation like biodiversity hotspots (Wolfs, 2011). This value map is designed by IVM through mapping the economic value of ecosystem services. Economic valuation estimates direct use, indirect use and non-use value. As mentioned before direct use values are easy to estimate (Van Beukering et al., 2007) and easy to map, because the location of use is usually known. Indirect use values are more difficult to estimate because of the complexity to estimate the level of use in relation to the ecosystem (Van Beukering et al., 2007) and also more difficult to map as the underlying ecosystem function and not the location of use needs to be mapped. Therefore it is important to include in the value map not only the economic value, but also the functional value of habitat locations to ecosystem functions, because the underlying ecological processes and structures need to be conserved to sustain the future delivery of ecosystem services.
Such a functional value map highlights hotspots of functional value to ecosystem functions that have the capacity to deliver the ecosystem services. These hotspots of functional value can then be considered for conservation (Harborne et al., 2006). Such a map also reveals areas of higher sensitivity, resistance or resilience to environmental pressures. As part of this research, several maps were produced. In chapter 4 maps of functional group representation at the survey sites are reported for each functional group. Functional value maps for each ecosystem service, showing the functional value of survey sites to support ecosystem services, are reported in chapter 5.

Step 7 is a threat analysis, which refers to the project deliverable of "What's Bonaire Nature worth?" to produce an overview of direct and indirect drivers of change(Wolfs, 2011). The functional value map is made more informative if a threat map is added, showing susceptibility to impacts that are likely to reduce functional values (Harborne et al., 2006). For this a threat analysis is required of direct and indirect, natural and anthropogenic drivers of change and their impact on functional values, which fell outside the scope of this research. However, in the analysis of functional values maps an attempt was made to link the outcome with the absence or presence of identified threats such as coastal development, cruise tourism (Wolfs, 2011), pollution from solid waste and sewage, run-off, climate change, disease, invasive species and overfishing (Meesters et al., 2010). Furthermore many drivers of change will have a direct impact on either habitats or functional groups: overfishing might cause depletion of certain fish stock that are critical within their functional group; nutrient loading and pollution may alter key ecosystem processes from one state to an alternative state; habitat destruction reduces the size of the habitat and thereby the availability of structure. This research facilitates an analysis of potential drivers of change and their impacts by providing a framework of critical functional group and key ecosystem processes that are required for a healthy ecosystem that delivers ecosystem services in a sustainable manner.

2.2.5 Habitats

This research did not adopt all ten habitats that have been used in the third theoretical concept of Harborne et al. (2006), which classification is based on coastal geomorphology and benthic cover (Mumby and Harborne, 1999). Instead only two coral reef habitats were identified for the snorkel survey for the following reasons. First, habitats deeper than approximately 10 meter could not be included in the snorkel survey due to depth limits in a visual census from the surface. Second, not all habitats are present in the geomorphology on the leeward coast of Bonaire, such as mangroves and seagrass lagoons which are part of the ten habitat types of Harborne et al. (2006).

The two types of coral reef habitat distinguished in the snorkel survey were: shallow reef flat (approximately 0-5m) and deeper fore reef (5-10m). These two habitat types are referred to as 'Shallow zone' and 'Reef zone'. Shallow is the part of the reef from shore to reef crest, including the reef crest and the shoreward reef flat with rubble, sand and some coral patches. Reef is the part of the reef seaward from the reef crest to the upper forereef with coral-dominated benthic cover (approximately 5-10m). This classification was based on a simple coral reef zonation into back reef, reef crest and fore reef. Each of these zones includes multiple habitats.

- Back reefs, also known as lagoons, have seagrass beds, mangrove forests, sand plains and patch reef [5]. A characteristics of fringing reefs is that the reef grows at the edge of the coast without intervening lagoon (Pinet, 1998) which is applicable for Bonaire where such lagoons are absent on the surveyed leeward coast.
- Reef crests are the edge of the reef slope and include algal ridges and reef flat habitats. Algal ridges hardly occur in the Caribbean, instead windward reef crests are dominated by the branching coral species *Acropora palmata*. Reef flats are habitats composed of dead coral rubble and carbonate sand at the shoreward side of the reef crest, occasionally used to denote the entire back reef zone [5]. Because the back reef on the leeward shore of Bonaire is virtually non-existing, the 'Shallow zone' habitat type is the reef crest, including the reef flat with rubble, sand and some patches of coral.
- Fore reefs are characterized by a reef sloping from the reef crest to the seafloor with a <45° slope (Mumby and Harborne, 1999). In this research only the upper fore reef is included, which typically extends seaward from the reef crest to 15 meter depth [5].

2.3 Data collection

The chart in figure 5 gives an overview how of required data, collection methods and data analysis outputs.

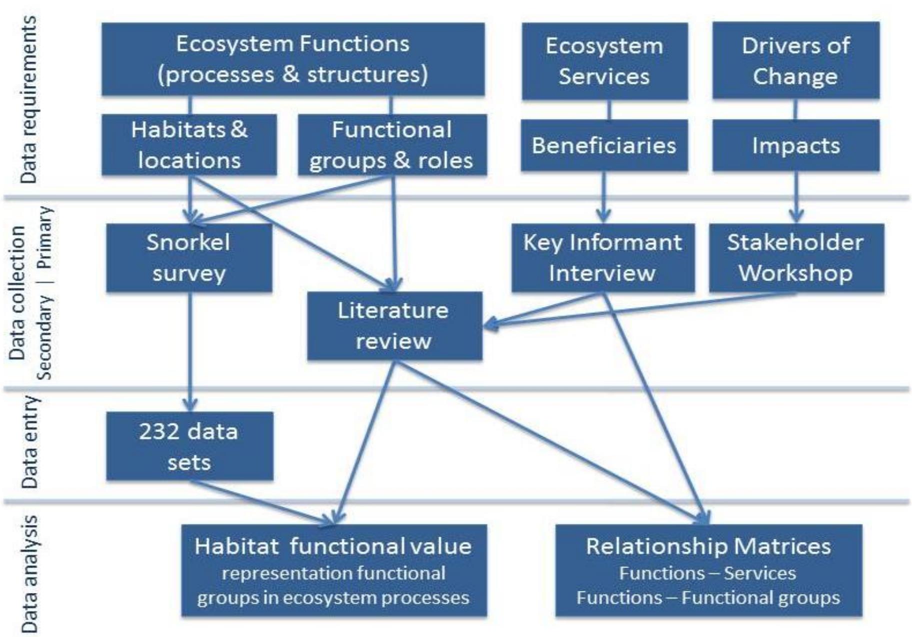


Figure 5. Data requirements, methods for data collection and outputs of data analyses

Data collection was done through a combination of primary data collection on Bonaire and secondary data collection in the Netherlands through an extensive literature review. Primary data collection included a snorkel survey, an interdisciplinary stakeholder workshop and key informant interviews. The latter helped to collect additional secondary data from grey literature.

2.3.1 Literature review

The literature review was done as preparation to design the research approach including theoretical framework, conceptual model and methods to collect and analyse data. The literature review was also used to identify ecosystem functions of coral reefs, underlying key ecological processes and biophysical structures and crucial functional groups and their functional role in these processes and structures, in order to answer the first, second and third research question. Reviewed literature included mainly peer-reviewed papers, some reference books as well as grey literature reports produced and published by governmental agencies, non-governmental organizations and scientific institutions.

2.3.2 Primary data collection: Snorkel survey

The snorkel survey aimed to answer the fourth research question by collecting primary data on presence of fish and coral functional groups on as many locations as feasible within a period of two weeks and given the weather and wave conditions. Due to the usual high waves and difficult access on the windward coast, reefs included in the survey were on the leeward western coast of Bonaire and the entire coast of Klein Bonaire. These leeward fringing reefs typically have a terrace of 20-250 meter width that gently slopes to a drop-off at 5-15 meter depth (Van Duyl, 1985).

The design of the survey was a visual census method using snorkel instead of the more frequently used scuba. Snorkel surveys are mentioned in several fish, macro-invertebrate and benthic community census methods (Hill and Wilkinson, 2004) and it was selected for this research to increase the number of locations and cover a larger area, namely the entire leeward coast. A survey covering this large an area has according to our knowledge not been done since the mapping of the reefs of Bonaire by Van Duyl (1985). A survey with scuba transects has limitations in maximum dive time and minimum surface intervals between dives, while a snorkel transect took less the 30 minutes including transportation to the next transect, meaning 10-14 transects per day were feasible. Other advantages using snorkel are that fish are less disturbed by a snorkeler compared to a diver (Hill and Wilkinson, 2004) and that counting individuals from the substratum to the water surface (Green and Bellwood, 2008) is easier while looking down from the surface. The disadvantages using snorkel are limited depth ranges that can be surveyed (i.e. not below the drop-off) and reduced accuracy to observe small or cryptic species at greater depth. To prevent observer bias in the observations one observer collected fish and another observer collected coral data, to at least make observer bias consistent and increase precision. Furthermore transects were video-recorded to make detailed analysis of the benthos possible.

Site selection: Transects were selected in Google Earth by marking a transect site every 500 meter. Sites were given a transect identification (ID): B00 – B96 for sites on the leeward coast of Bonaire and KB00-KB20 for sites along the 11 km coastline of Klein Bonaire. Even ID numbers (B00, B02, etc.) marking each kilometer were entered in Google Earth, as shown on the large map in figure 6. If possible sites were accessed from shore, for example the sites marked by the yellow GPS track line on the small map in figure 6. Sites not accessible from shore were surveyed by boat, for example the sites with the blue GPS track line. Two sites (B23 and B68) had to be skipped due to access problems, i.e. at the oil storage terminal a large oil tanker of 330 meter blocked access to one of our transects. Longitude and latitude coordinates of selected transect sites were stored in a portable GPS receiver. This GPS was used to search each site during the survey, and a GPS waypoint of the actual site was made at the start of each transect. An additional portable GPS receiver was sealed in a waterproof case and carried on the water surface during snorkel observations to measure distance and direction of transects. Receiving GPS signals worked well through the case and at the surface.

Figure 6. Large map: planned survey sites on Bonaire (transect ID B00-B96) and Klein Bonaire (transect ID KB00-KB20), whereby even numbers were entered being one kilometre apart from each other. Small map: close-up of actual survey sites accessed from shore (yellow GPS track) and by boat (blue GPS track), whereby the short tracks perpendicular to the coast depict transects surveyed and the connecting lines show the route travelled by car or by boat to access the site.

Transect description: Transects were perpendicular to the coast, swimming from the shore to the drop-off and back and the other way around when accessing the site by boat instead of by car. This meant each transect was covered twice. For coral one track was video recorded, and the other track was used to register benthic functional groups. For fish one track was used to register abundance of functional groups and the other track to register fish biodiversity of other species. Observer swimming speed was on average 8 meter per minute. Recommended speed is 10 meter per minute for video transects and 6 meter per minute for cryptic Serranidae (groupers) while for fish in general a constant speed is more important as more fish is seen when swimming slowly (Hill and Wilkinson, 2004). Transects were conducted between 8.30 and 16.00 hours, which is within to the recommended time for fish transects and close to the recommended time for video transects from 8.30 till 15.30 hours (Hill and Wilkinson, 2004).

Fish observation: Fish minimum size for inclusion was 10 cm or 5 cm for smaller species such as Pomacentridae (chromis and damsels). Fish transect dimension was 2.5 meter on either side of an imaginary transect line. This transect width of 5 meter and the variable transect length measured by GPS were used to standardize fish counts per transect to fish abundance per 100 m^2, a unit commonly used in fish surveys including in the secondary data collected. Aim of the research was to get abundance of functional groups per location measured at a semi-quantitative scale (3=high, 2=medium, 1=low), but this was based on more detailed, quantitative data collection. This involved more data to collect, but nevertheless was used to avoid interpretation of scales during observation and to facilitate that observations during the entire track were included as objective as possible. In total 89 species were included in the survey as listed in appendix B: 49 species from 7 families (Scaridae; Acanthuridae; Pomacentridae; Haemulidae; Lutjanidae; Serranidae and Carangidae) plus 8 predatory species from another 7 families were distinguished to assess functional groups; another 32 species from 17 families were included for the biodiversity assessment. In addition fish maximum size was recorded for Serranidae and large species of Lutjanidae and Carangidae (80 cm or above).

Coral observation: For the benthic composition the percentage cover of massive, branching and soft corals, macro-algae, cyanobacteria mats, sponges, coral rubble, sand and rock was recorded based on visual appraisal of the survey area. In addition threats or impacts from threats to stony corals were recorded, such as coral mortality, diseases, bleaching, parrotfish (*Scaridae spp.)* bite marks and presence of nuisance species, such as tunicate mats (*Trididemnum solidum*). Other parameters recorded were coral diversity, coral maximum size, sea urchins (*Diadema antillarum)* and reef topography on a scale from 0 to 4 whereby 0 = no vertical relief, 1 = low and sparse relief, 2 = low but widespread relief, 3 = moderately complex, 4 = very complex with numerous caves and overhangs.

Equipment: Data were registered on fish and coral datasheets of waterproof paper, for which is referred to the examples in appendix C. Materials used were waterproof paper, underwater slate and a pencil on a string. As mentioned earlier the observer recording coral also used a Sanyo video camera type vpc-hd2000, two GPS, a Qstarz lap timer to record tracks and a Garmin eTrex H to search transect sites and make weigh points, and a Otterbox waterproof case for the GPS carried at the water surface. In addition STINAPA boats, the chief marine park ranger and a boat driver volunteer were available during six survey days to access sites that were not accessible by car from shore.

Training and testing: Prior to the survey there was ample time for me, the observer collecting fish data, to refresh and practise fish identification skills, using laminated waterproof fish identification cards. These cards, for which is referred to appendix D, show species by functional group with their scientific and common name, as well as their maximum and average total length, based on information and pictures from FishBase [6]. A pilot of nine transect was done a few weeks prior to start of the survey, to improve the design of the data entry sheets, to give input into the ordinal scaling (of high, medium, low levels) and to make a realistic planning. Of the planned sites in eleven days plus two spare days, actual data collection was completed according to plan in eleven days.

2.3.3 Primary data collection: Stakeholder workshop session

The stakeholder workshop held on Bonaire from 12-14 May 2011 was the kick-off of the project “What’s Bonaire nature worth?”. The workshop was lead by an environmental economist of IVM and attended by local and international stakeholders from the fields of coral reef ecology, marine biology and nature conservation from STINAPA, the organisation managing the marine and terrestrial parks, the Sea Turtle Conservation Bonaire (STCB) and research institutes Carmabi on Curacao and CIEE on Bonaire, as well as by representatives of the government, cultural and tourism sectors. In this workshop a session on the ecological component of the project was presented by Erik Meesters of IMARES and myself. The objective of this session was twofold. First, this research approach and the snorkel survey were presented. Second, in four interdisciplinary working groups stakeholders were asked to identify impacts of a given threat on habitats and ecosystem processes and to determine the relationship between threat and ecosystem service delivery. The four main threats for Bonaire, selected during the workshop by the stakeholders, were invasive species, coastal development, cruise tourism and solid waste.

2.3.4 Secondary data collection

Secondary data refers to recent coral reef studies specifically on Bonaire, such as grey literature reports on the status and trends of Bonaire's coral reefs by CIEE (Steneck and Arnold, 2009) and coral reef resilience assessments (Bruckner et al., 2010; IUCN, 2011) as well as published studies on the coral and fish communities of Bonaire (Sandin et al., 2008; Sommer et al., 2011). These data were collected through participation in the stakeholder workshop and a key informant interview with the Bonaire National Marine Park manager to get access to underlying data of the reports.

2.4 Data entry and quality control

Data were entered from the waterproof paper in an Excel datasheet daily during the fieldwork, immediately after finishing the survey. Advantage was that unclear data were entered correct in Excel by checking the video, memorizing the survey sites of the day or consulting the data or memory of the other observer. Daily quality control on typing errors in Excel was done the next morning prior to starting the survey and erasing the data to use the waterproof paper again.

After the fieldwork was finished, quality control of Excel datasheets was done to check on completeness and correctness, to standardize data entries and to prepare data sets for statistical analysis in software application R. Data were completed with coordinates of weigh points and transect lengths measured from the GPS survey tracks that were downloaded into Google Earth. Few missing data such as end time and fish maximum size were completed from respectively the datasheet of the other observer, and by calculating the average maximum size. Data were corrected for minor inconsistencies in data registration at the first day of the survey, when occurrence instead of abundance was recorded for those species that were included to measure biodiversity. The preparation for data analysis included filling empty cells in the data sheet with value zero and transposing data to get data per survey in a row and data per parameter in a column as preferred by statistical applications such as R. In the fish datasheet the following calculations were added, because collected data were counts of individuals at species level: subtotals per fish family (∑ individuals of species of each family); fish abundance (∑ individuals of all species); fish biodiversity (count of species); and transect size in m^2 (length x width). Finally, standardization of data was done to enable comparison with quantitative secondary data from other surveys and to apply ordinal scales in the data analysis that were based on the standard unit used in literature. Fish abundance was standardized from number of fish per transect into the unit fish per 100 m^2 (fish/ transect size in m^2 x 100 m^2). Benthic composition expressed as a percentage was standardized to add up to 100 percent. Fish biodiversity was not standardized to 100 m^2, because measurement was based on species seen, irrespectively of the number of fish per species recorded.

2.5 Data analysis

Data analysis was twofold. First, the literature review was used to analyze the relationships between functional groups and ecosystem functions as well as ecosystem functions and ecosystem services. Second, primary data were analyzed to determine the functional value of habitats and locations, using secondary data from grey literature to determine appropriate ordinal scales.

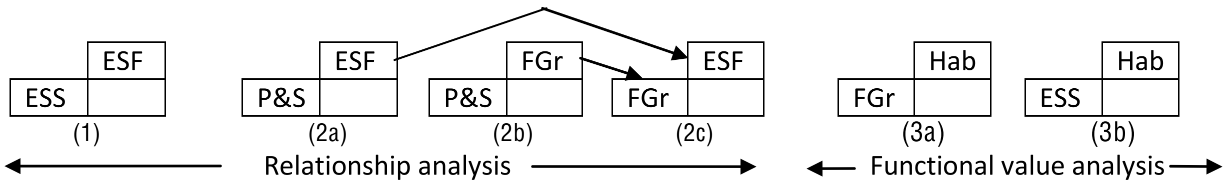


Figure 7. Steps in the data analysis

(1) Relationship Ecosystem Functions (ESF) – Ecosystem Services (ESS)
(2) Relationship Ecosystem Functions (ESF) – Functional Groups (FGr) in 3 steps
(2a) Ecological Processes and Biophysical Structures (P&S) underlying Ecosystem Functions (ESF)
(2b) Functional Groups (FGr) based on their functional role in Processes and Structures (P&S)
(2c) Functional Groups (FGr) and their functional role in Ecosystem Functions (ESF)
(3) Functional Value of Habitats and Locations (Hab) – Ecosystem Services (ESS) in 2 steps
(3a) Functional Groups (FGr) representation in Habitats and Locations (Hab)
(3b) Importance of Habitats and Locations (Hab) to support Ecosystem Services (ESS)

2.5.1 Relationship analysis

Two relationships were analyzed in the literature study: (1) functional groups versus ecosystem functions and (2) ecosystem functions versus ecosystem services. The outcome of this analysis is presented in tables or matrices listing e.g. columns with all functions and rows with all services and the presence or absence of a relationship between each function and each service. The resulting matrices from this relationship analysis are illustrated in figure 7 and explained for each step below:
(1) The relationship ecosystem functions versus ecosystem services was determined, starting with the identification of ecosystem services and ecosystem functions applicable for coral reefs on Bonaire. Ecosystem services were identified using the TEEB classification of 22 services as mentioned in chapter 2.1.2 and listed in appendix A. This list was specified for services provided by coral reef ecosystems, based on literature. The final shortlist only included services relevant for Bonaire, based on observations of the researcher and input from the project coordinator. Ecosystem functions were identified from different sources of literature, which are specified in the matrices in chapter 3.
(2) The relationship ecosystem function versus functional groups was established (2c), by specifying the ecological processes and biophysical structures needed for each identified ecosystem function (2a). Then a selection of functional groups was made based on their functional role in each ecological process and/or structure (2b). Criteria for functional group selection were also feasibility for data collection in a visual census survey using snorkel.

2.5.2 Functional value analysis

The functional value analysis to determine the functional value of habitats and locations to support the delivery of ecosystem services consisted of two steps:
(3a) Analysis of the representation of functional groups in habitats based on two main variables from the primary data, abundance of species within functional groups and occurrence of species to measure biodiversity. Occurrence is defined as a record of a species, whether one or more fish or coral colonies. Abundance is defined as the number of fish or percentage coral cover recorded in that occurrence.
The functional value analysis started with comparing the standardized dataset of functional groups in all 232 habitat locations with the ordinal scale to determine if the level of importance was high, medium, low or not important. These semi-quantitative ordinal scale levels had been defined prior to the fieldwork for each functional group, in order to know how to scale the quantitative data collected (e.g. # fish/100m^2, % coral cover). The method used to set ranges for each level was based on quantitative data from recent studies on the fish and coral community status on Bonaire. For setting levels of coral functional groups quantitative data of two resilience studies by IUCN (2011) and Bruckner et al. (2010)

and the research of Sommer et al. (2011) were used, although underlying data of the latter two were not available. For setting levels of fish functional groups quantitative data of the study of Steneck and Arnold (2009), Harborne et al. (2006) and data of the pilot were used. In order to calculate with the results in the functional value analysis in step 3b, the ordinal scale was adapted to a numerical scale from 3 (=high), 2 (=medium), 1(=low) and 0 (=no representation).

After scaling the 232 data sets to determine the functional value a check was done if ordinal scale levels were realistically set, by checking the percentage occurance of high, medium and low levels for each functional group. For those with unrealistic outcomes, for example damselfish had a high functional value in 50% of the locations, the ordinal scale ranges were adjusted. First, the distribution of collected data (number of fish per location) was tested for normality using the Shapiro-Wilk normality test. Then the distribution was square root transformed to approach a normal distribution and the ordinal scale levels were adjusted such that the power of the square root mean $(\sqrt{\text{mean}})^2$ was within the range of the medium level.

(3b) Analysis of the importance of habitats to support the delivery of ecosystem services started with the selection of functional groups with a functional role in the delivery of each ecosystem service, using matrix A and matrix B as described in the conceptual model. Then for each habitat and location a numerical functional value was calculated based on the sum of functional values of selected functional groups from matrix C.1 and C.2, including a weighting factor to express the level of importance for service delivery. The resulting matrix D with a broad range of numerical functional values (0 to 71) was transformed into the same semi-quantitative ordinal scale from 0 to 3, to enable mapping of habitats at the level of high, medium, low or no importance.

3 RESULTS RELATIONSHIP ANALYSIS

In this chapter the relationships between ecosystem services, functions, processes and structures are explored. Chapter 3.1 starts with an overview of definitions and differences between these terms. The following chapters elaborate on the identification of coral reef ecosystem services, functions, processes and structures.

The identification of services emphasizes how services are beneficial in the socio-economic context of Bonaire. This answers the first research question 'Which ecosystem services are provided by coral reefs on Bonaire?' in chapter 3.2.1. The identification of functions, processes and structures has an ecological approach and emphasizes on how a coral reef ecosystem functions. The second research question 'What are key ecological processes and structures that determine ecosystem functions?' is answered by linking the functions identified in chapter 3.2.2 with the underlying processes and structures in chapter 3.3.1. In chapter 3.3.2 the third research question 'What are crucial functional groups and their functional roles to support these key processes and structures?' is answered by examining the link between functional groups as an indicator or proxy of processes and structures.

Following the conceptual model of this research, two relationships between components of the model are established in this chapter: (A) The relationship between functions and services they deliver in Matrix A in chapter 3.2.3 and (B) the relationship between functional groups and the functions they support in Matrix B in chapter 3.3.3. The latter is used in chapter 5 to translate the representation of functional groups at 232 sites coupling habitats and locations to a functional value of habitat locations to support ecosystem functions that are necessary to provide ecosystem services of coral reefs on Bonaire.

3.1 Ecosystem function, service or process?

The terms 'function' and 'service' are used interchangeably in scientific literature (Cesar, 2000), as well as the terms 'function' and 'process'. In this research the definitions of TEEB are followed, which were already introduced in the theoretical framework in chapter 2 and summarized here.

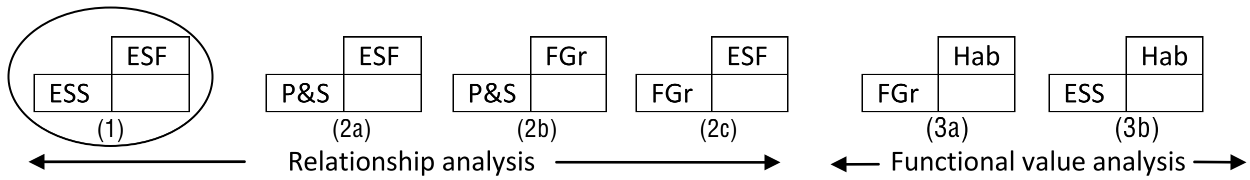
Ecosystem services are the direct and indirect benefits people obtain from ecosystems (MEA, 2005; TEEB, 2010b). Direct benefits can be extractive if goods are harvested from the ecosystem or non-extractive if the ecosystem provides the scenery or information required for social and cultural services. Indirect benefits are largely invisible, such as the benefits for human health, safety and well-being of most regulating services.

Ecosystem functions are a subset of interactions between ecosystem structures and processes that determine the capacity of an ecosystem to provide ecosystem services (TEEB, 2010b). Functions refer to the functioning of ecosystems and the potential to provide services, regardless of the use of the services. The use depends on whether there are beneficiaries to enjoy the benefit which is determined by the socio-economic context rather than the ecosystem itself.

Ecosystem processes are physical, chemical or biological changes or reactions in an ecosystem (TEEB, 2010b). Core ecosystem processes include production, decomposition, erosion, nutrient cycling and fluxes of nutrients and energy (MEA, 2005; TEEB, 2010b). **Ecosystem structures** are the biological and physical architecture of an ecosystem. The composition of species making up the architecture may vary (TEEB, 2010b) and can be stony coral species that provide physical structures and fish species that are part of the biological composition of an ecosystem.

3.2 Linking ecosystem functions and ecosystem services

The relationship between ecosystem functions and ecosystem services was examined as part of the encircled first step in the data analysis as illustrated below, which was explained in further detail in figure 7 of chapter 2.5.



3.2.1 Identification of ecosystem services

The ecosystem services which are valued in the project "What's Bonaire nature worth?" are: fisheries; materials; coastal protection; tourism; recreation; amenity services; knowledge and education (Wolfs, pers. comm., 15/8/2011). For the purpose of this research, to determine the relationship between ecosystem services and ecosystem functions, all ecosystem services provided by coral reefs in Bonaire were identified. Because in scientific literature the terms functions and services are used interchangeably (Cesar, 2000), it was important to make a clear distinction what in the context of this research were considered services and what functions.

Table 2. Ecosystem services provided by coral reefs on Bonaire.
TEEB numbers refer to which 22 services of their classification are applicable for coral reef ecosystems.

	ECOSYSTEM SERVICES	TEEB ref #
	Provisioning services	
1	Seafood products[1]	1
2	Raw material for production of lime and cement[2wordt1]	3
3	Raw material for medicines[2]	5
	Regulating services	
4	Shoreline protection[1]	9
5	Waste assimilation	11
6	Biological maintenance of resilience	15
	Habitat services	
7	Maintenance of habitats	16
8	Maintenance of biodiversity and genetic diversity	17
	Cultural services	
9	Aesthetic values and artistic inspiration[1 eruit]	18
10	Support of tourism and recreation[1]	19
11	Support of cultural identity[1eruit]	20
12	Educational and scientific information services[1]	22

[1] Services included for economic valuation in the project
[2] Goods extracted on Bonaire in the past, but without actual use value currently.

Identified services as shown in table 2 were categorized into provisioning, regulating, habitat and cultural services and numbered according to the 22 services of the TEEB classification (De Groot et al., 2010), for which is referred to appendix A. All 22 services identified by TEEB were evaluated in this research, but not all are applicable for coral reef ecosystems. For example climate regulation through carbon sequestration of atmospheric carbon dioxide (CO_2) is a service of oceans (Ware et al., 1991; Nellemann et al., 2009), but not a service of coral reef ecosystems as reefs actually contribute to the global carbon cycle (Ware et al., 1991). Oceans are the largest long-term carbon sink, because 55% of atmospheric CO_2 is captured by marine organisms, whereby mangroves and seagrass account for most

of the carbon storage in ocean sediments (Nellemann et al., 2009). Because corals transform CO_2 into calcium carbonate ($CaCO_3$) reefs are often thought of as carbon sinks as well. However, the precipitation of calcium carbonate is accompanied by a shift in the pH of the seawater that results in a release of CO_2. This is part of the natural CO_2 cycle (Ware et al., 1991) and coral reef ecosystems cover only 0.17 percent of the global marine area (Costanza et al., 1997), so the global impact of coral reefs as carbon source is negligible (Ware et al., 1991).
Moberg and Folke (1999) identified goods and services specifically provided by coral reefs, which formed the basis for the identification of services in this research. Some services are not applicable in Bonaire, for example extraction of fish and shells for use as ornamentals and extraction of coral blocks, rubble and sand from the reef for use as building materials, because all resource extraction except fishing is prohibited in the Bonaire National Marine Park [7]. Some other services identified by Moberg and Folke (1999) were within the context of this research considered functions or processes, following the definitions of TEEB (De Groot et al., 2010). For example nitrogen (N_2) fixation, the conversion of dissolved atmospheric N_2 into organic nitrogen compounds (Castro and Huber, 2008). This is considered a supporting service, because it is an underlying process that supports productivity in nutrient poor environments such as coral reefs. Supporting services are omitted by TEEB as ecosystem service (De Groot et al., 2010) and therefore not included as ecosystem service in this research.

The twelve identified ecosystem services of coral reefs on Bonaire as listed in table 2 are briefly introduced below, including their relevance for Bonaire.

Provisioning services

Provisioning services are the products obtained from ecosystems (MEA, 2005; TEEB, 2010b), including food, raw materials and medical resources.

1) Seafood products from reef-related fisheries constitute 9-12% of the world's total fisheries (Moberg and Folke, 1999). Coral reef fisheries are small-scale and are not part of the global FAO database which covers mainly industrial fisheries, so there is no consensus on the world's coral reef catch (Pauly, 2008). Pauly (2008) distinguishes three types of coral reef fisheries: (1) recreational fisheries in high income areas, (2) traditional reef fisheries under traditional rules in low income areas and (3) small-scale fisheries, such as traditional reef fishers and fish suppliers of tourist resorts and the life-fish exporters. Coral reef fisheries in Bonaire falls within the latter type, which is limited to small-scale local fisheries using traditional fishing methods [7].

2) Raw material for production of lime and cement involves mining of coral reef blocks, coral rubble and sand, to be used as construction material or pH regulator (Moberg and Folke, 1999). As mentioned above such resource exploitation is not allowed in the Bonaire National Marine Park. However, dead corals have been and are still extracted from the limestone plateaux at the northern coast of Bonaire by scraping off the top layer of limestone. The raw material is crushed to produce lime, which is used for house construction. Limestone mining is officially prohibited since 2006, but the law provides for conditional agreements with mining companies to allow them to continue their activities (Bonaire, 2005). Although this form of coral mining does not involve extraction of corals from the marine environment, but from ancient reefs that over geological times became part of the island, this is a service that originates from coral reef structures.

3) Raw material for medicines have been discovered in seaweeds, sponges, molluscs, corals, gorgonians and sea anemones (Moberg and Folke, 1999) as well as in the marine microbial communities inhabiting tunicates (Fouke, pers. comm., 8/9/2011). A large number of compounds are found in blue-green algae of which most are useful as biochemical research tool, but a few have the potential to be developed into commercial products (Moore, 1996). Identifying natural products and their anticancer, antimicrobial, anti-inflammatory or anti-coagulating properties as well as their biosynthetic pathways is challenging (Bumpus et al., 2009). Nevertheless more than half of the 1000 antibacterial and anticancer medicines introduced from 1981 to 2006 are natural products or synthetic derivatives thereof (Bumpus et al., 2009). In the 1970s one such natural product was discovered and extracted from the coral reef on Bonaire, a cyanobacterial symbiont (*Prochloron didemni*) that inhabits host ascidian invertebrates (tunicates). This cyanobacterium was synthesized and the derivative is being used as ingredient in Neosporin, the brand name for an oral antibiotic (Fouke, pers. comm., 8/9/2011).

Regulating services

Regulating services are the benefits obtained from the regulation of ecosystem processes (MEA, 2005; TEEB, 2010b), including moderation of extreme weather events, waste assimilation and pest regulation.

4) Shoreline protection is the protection of the coast against currents, waves, tropical storms and hurricanes by physical barriers provided by coral reefs to prevent erosion and damage to coastal development and protect or create lagoons and sedimentary environments (Moberg and Folke, 1999; Moberg and Rönnbäck, 2003). Bonaire lies on the southern edge of the hurricane belt, and roughly once every 100 years experiences considerable damage (MDNAA, 2010). In the last decades hurricane activity in the western Atlantic has increased due to increased water temperature in the North Atlantic and decrease in vertical wind shear. These changes show a multi-decadal time scale, reason why the higher hurricane activity is expected to continue for another 10 to 40 years (Goldenberg et al., 2001). Most significant tropical storms in the past decades were Joan in 1988, Bret in 1993, Cesar in 1996, Ivan in 2004, Emily in 2005, Felix in 2007 and Omar in 2008. Ivan, Emily and Felix were classified as a hurricane with wind speeds higher than 118 km/h. Also hurricane Lenny in 1999, with its centre passing the lesser Antilles island of Sint Maarten, caused damage in Bonaire (MDNAA, 2010). Damage varied, ranging from heavy rain and rough sea to large waves on the leeward coast causing beach erosion and damaging vessels and coastal facilities (MDNAA, 2010). Normally Bonaire experiences high waves on the windward shore (IUCN, 2011) from easterly trade winds blowing east to west with occasional wind reversals (IUCN, 2011). Most residential and industrial development is at the western shore and the eastern shore has a large lagoon with mangrove forests and seagrass beds, protected by a barrier reef.

5) Waste assimilation is the ability of coral reefs to transform, detoxify and sequester nutrients and wastes released by people, such as oil and persistent pollutants (Moberg and Folke, 1999). Nutrient enrichment occurs by nitrogenous nutrients from acid rain and inorganic nutrients such as nitrogen and phosphorous from fertilizers, sewage and waste water discharge. Excess nutrients are removed from the water through uptake by plants and algae (Peterson and Lubchenco, 1997). This increases the supply of organic matter, a process called eutrophication (Nixon, 1995). Excess eutrophication reduces ecosystem services as a consequence of oxygen depletion and nuisance algal blooms (Peterson and Lubchenco, 1997). Water quality monitoring on Bonaire takes place since 2006 to access nutrient enrichment from coastal development and these measurements indicate threats of eutrophication and macro-algal overgrowth (Bouchon et al., 2008). Since Bonaire became a special municipality of Caribbean Netherlands in 2010 sewage and solid waste treatment facilities on the island are under development (personal observation). Bonaire has an oil storage terminal where transportation takes place with oil tankers [1] and in the past accidents such as fire and oil tanker damage to the nearby reef have occurred (personal observation). BOPEC oil terminal recently received a permit within the framework of the new BES Maritime Management Law that entered into force in October 2011. The permit includes guidelines to prevent incidents concerning fire safety, nautical safety, containment of oil spills and protection of the fragile maritime environment [8].

6) Biological maintenance of resilience is the ability of species or groups of species to regulate ecosystem processes and functions (Moberg and Folke, 1999) in order to maintain resilient coral reefs and avoid a shift from a favourable coral-dominated state to an algal-dominated state (Done, 1992; Hughes, 1994). Ecological or ecosystem resilience is defined as the capacity to absorb disturbances, to resist change and adapt to change in order to keep the same function, structure and feedbacks (Walker et al., 2004; Nystrom et al., 2008). Feedback mechanisms can refer to positive or negative feedback loops (Mumby and Steneck, 2008). Feedbacks that stabilize ecosystem states involve both biological, physical and chemical mechanisms (Scheffer et al., 2001). A positive biological feedback mechanism is high grazing intensity to decrease algal cover which enables coral recruitment and prevents coral overgrowth, both increasing coral cover and the structural complexity of the reef. This enables fish recruitment which increases grazing intensity. A negative feedback loop involves the same processes in reversed direction (Mumby and Steneck, 2008). This biological feedback mechanism on macro-algae by herbivores is an example of biological control of pest species through predator-prey relationships, which is considered an ecosystem service by TEEB (Elmqvist et al., 2010) and MEA (MEA, 2005). Such biological control is important for the maintenance of coral reef resilience, as loss of resilience affects the quality and quantity of the delivery of ecosystem services (Moberg and Folke, 1999). Hence, maintenance of coral reef resilience is a regulating service that indirectly is beneficial for people.
Principle grazers include parrotfish and sea urchins. A recent modelling study of Edwards et al. (2010) on the impact of two major sources of disturbances on Caribbean coral reefs, coral bleaching and hurricanes, in a situation with and without parrotfish and sea urchins, included Bonaire as a case study.
The study predicted that under realistic regimes of disturbances, Bonaire is amongst other case study locations best able to maintain a stable percentage coral cover, for another 50 years if sea urchins are present and parrotfish unexploited. This expectation is also due to the fact that Bonaire experiences less intense hurricane disturbance (Edwards et al., 2010). The model is supported empirically, because Bonaire is amongst the healthiest reefs in the Caribbean currently (Kramer, 2003).
On Bonaire parrotfish are not specifically targeted in conservation management, but there are fish reserves and parrotfish is generally considered not tasteful as food (personal observation). However, it is suggested that maintenance of resilience by grazing herbivores is threatened by invasive lionfish. Lionfish consume the herbivores, which may contribute to regime shifts on Caribbean coral reefs (Barbour et al., 2011). On Bonaire eradication of lionfish is taking place through fishing for conservation purposes, by giving recreational divers a licence to spear fish and kill lionfish. Since lionfish are considered tasty and hunting is considered a challenge by numerous people, spear fishing for lionfish and lionfish barbeque parties are now a popular recreational and social event on Bonaire (personal observation).

Habitat services

Habitat services are the important roles of ecosystems to provide living space for resident and migratory species, thereby maintaining the nursery service and gene pool (TEEB, 2010b).

7) Maintenance of habitats refers to the complex three-dimensional coral reef structures that provide spawning, nursery, breeding and feeding areas for many different species (Moberg and Folke, 1999), thereby providing a living space for the highest diversity of species of all explored marine habitats (Moberg and Rönnbäck, 2003). This diversity and abundance of habitats, corals and fish is one of the reasons why coral reefs, and particular those in Bonaire as the more healthy reefs in the Caribbean, are so attractive for diving and snorkelling.

8) Maintenance of biodiversity and genetic diversity refers to the biological diversity of coral reefs as the most species-rich habitats of the world (Moberg and Folke, 1999). Biodiversity is important for maintenance of genetic biodiversity, within and between populations, to enable evolution and adaptive radiation to habitats through natural selection within species (Elmqvist et al., 2010). Biodiversity is also considered important for the ecological integrity of the ecosystem (Elmqvist et al., 2010) and integrity reflects the capacity of the ecosystem to support services for people (De Leo and Levin, 1997). The integrity of a system is retained if its components and the functional relationships between components are preserved, whereby components in ecosystems refer to the species composition and diversity in the community (De Leo and Levin, 1997). Also on Bonaire the sustainable use of ecosystem services and the current and future economic benefits depend on the integrity of the ecosystem.

Cultural services

Cultural services are the non-material benefits people obtain from ecosystems through aesthetic experience, spiritual enrichment, recreation, reflection and cognitive development (MEA, 2005; TEEB, 2010b).

9) Aesthetic values and artistic inspiration are the pleasure and inspiration for culture, art and design coral reefs provide to people (Moberg and Folke, 1999; Elmqvist et al., 2010), derived from scenic views of coral reef seascapes and proximity to open space [9]. Most residential and recreational areas on Bonaire are along the coast with scenic views of the tropical clear blue water and the island of Klein Bonaire. The more expensive properties and tourist resorts typically have direct and open access to the sea. There are a number of art galleries on Bonaire that sell local art and handicrafts inspired by the coral reefs and reef fish (personal observation).

10) Support of tourism and recreation by coral reefs (Moberg and Folke, 1999) includes biodiversity-based tourism and recreation such as diving, snorkelling and fishing and other water-based activities include kayaking, kite surfing, windsurfing, and swimming off beaches (Debrot et al., 2010). This service is evident in Bonaire, where the private sector is successfully marketing the island as tourist destination (Dixon et al., 1993), the island is known as 'Divers Paradise' [1] and is recognized as such by multiple awards from divers and diving magazines [10]. Dive tourism began in 1963 and grew to between 32.000 and 42.000 visiting divers in 2000 and 2008 respectively, which is on average 60% of total tourism on Bonaire (TCB, 2009). Surfing is also popular for tourism and recreation, due to the prevailing easterly trade winds combined with the calm and shallow water in Lac Bay. Although Lac Bay is located on the rough windward coast, the barrier reef in front of Lac provides protection from the high waves.

11) Support of cultural identity refers to less tangible and often forgotten cultural values that people derive from coral reefs (Moberg and Folke, 1999) such as *social relations* that are influenced by the presence of a fishing society, a *sense of place* of the community which is associated with recognized features of their marine environment such as water clarity and perceived cleanliness and *cultural heritage* of historically or culturally significant seascapes or species (MEA, 2005) such as the conch monument at the shore of Lac Bay.

12) Educational and scientific information services refer to the use of reef organisms in monitoring and pollution records (Moberg and Folke, 1999). Coral reefs provide opportunities for formal and informal education, cognitive development and knowledge exchange through awareness campaigns, educational programs and scientific research (MEA, 2005). On Bonaire these services are carried out by STCB, CIEE, BNMP and independent, visiting researchers.

3.2.2 Identification of ecosystem functions

Ecosystem functions that underpin the identified ecosystem services were identified and categorized following the TEEB classification into production, regulation, habitat and information functions (De Groot et al., 2010) as shown in table 3.

Table 3. Coral reef ecosystem functions that provide ecosystem services.

ECOSYSTEM FUNCTIONS	
	Production functions
1	Primary production
2	Secondary production
3	Tertiary and higher production
4	Construction of reef framework
5	Generation of coral sand and sediment
	Regulation functions
6	Modification of wave and current patterns
7	Removal or breakdown of excess or xenic nutrients and compounds
8	Nutrient cycling
9	Trophic-dynamic regulation of species diversity
	Habitat functions
10	Provision of refuge, nursery and reproduction habitats
11	Physical and biological support through 'mobile links'
	Information functions
12	Seascape
13	Biodiversity

The main literature used to identify functions were Done et al. (1996), Costanza (1997), De Groot et al. (2002) and Harborne et al. (2006). The focus was on functions that are essential for the delivery of identified services. Service delivery is dependent on a variety of complex and dynamic interactions between species within a coral reef ecosystem and between interconnected ecosystems (Moberg and Folke, 1999). This ecological complexity of structures and processes can be translated into a more limited number of ecosystem functions (de Groot et al., 2002). Given this ecological complexity it was impossible within the context and timeframe of this research to include all functions, so the focus was on functions that have underlying processes and structures with measurable indicators.

The thirteen identified functions of coral reefs ecosystems as listed in table 3 are described below. Included in the description are key ecological processes and biophysical structures that determine these ecosystem functions.

Production functions

At the basis of the production function is carbon fixation through photosynthesis, which produces compounds that follow either a bioconstructional or a trophic pathway as described by Done et al. (1996). The bioconstructional pathway refers to the accumulation of calcium carbonate building blocks, the cements which bind them into a reef framework, the sediments from physical and biological erosion of the coral reef and the sand-sized skeletal elements of non-framework building plants and animals. The trophic pathway refers to the food web, including the accumulation of protein resources through plant-herbivore-predator links and the loss of these resources through detritus (Done et al., 1996). The net accumulation of the reef framework in the bioconstructional pathway is essential for the long-term structural integrity of a reef (Done et al., 1996). The main components of both pathways are described below.

1) Primary production is at the basis of the food chain and is important for the production of fish biomass and the formation of coral reefs. It requires autotrophs that through photosynthesis convert energy, inorganic carbon, water and nutrients into organic compounds (de Groot et al., 2002). Macro-algae and turf algae are important autotrophs on coral reefs as they are an important food source for grazers. For reef building corals a particular group of unicellular algae, the symbiotic zooxanthellae, is essential to enhance the production of their calcium carbonate. Other primary producers are cyanobacteria and coralline algae. Cyanobacteria are blue-green algae that are important fixers of nitrogen to make nitrogen compounds available as essential nutrient for primary production. All coralline algae contribute calcium carbonate to reef sediments, which is important for reef construction and sand production (Castro and Huber, 2008) and is discussed as part of ecosystem function 4 and 5.

2) Secondary production by herbivorous fish and herbivorous invertebrates such as sea urchins through grazing of algae supports energy transfer to higher trophic levels in the food chain which generate a larger variety of living biomass (de Groot et al., 2002). Secondary producers have multiple other functions, for which the functional group of herbivores is split in different sub-groups of bioeroders, scrapers and grazers (Bellwood et al., 2004) although slightly different categorization of grazing has been applied by others which is discussed as part of the identification of functional group in chapter 4.2 (Steneck, 2001; Green and Bellwood, 2008; Steneck and Arnold, 2009; IUCN, 2011). These sub-groups reflect their complementary functional roles, besides energy transfer, to support the processes of bioerosion and grazing. These processes are further discussed as part of ecosystem function 5 and 9 respectively. The distinction between sub-groups is also relevant for the process of competition for resources (Hughes et al., 2005). Competition can be considered as an increase of the functional redundancy, whereby one species of herbivores compensates for the loss of another species (Bellwood et al., 2004). However, because one herbivorous species may have a different complementary functional role, loss of a major species or sub-group may result in loss of their functional role or an unsustainable increase of another sub-group with a undesirable effect on their functional role. An example of this is also discussed as part of ecosystem function 5.

3) Tertiary and higher production refers to predation on secondary producers and higher trophic levels by planktivorous, omnivorous and piscivorous fish and invertebrates which also supports energy transfer in the food chain (Bellwood et al., 2004). Predators often feed on prey from different trophic levels, so tertiary and higher producers are categorized based on diet composition whereby apex or top predators are piscivores with trophic level 4.5 or higher, carnivores and omnivores have trophic levels between 2.1 and 4.5 and planktivores have trophic level 3.0 (Newman et al., 2006). Another function of tertiary and higher producers is predation and their functional role in predator-prey relationships in a food web (Hughes et al., 2005), which is further discussed as part of the trophic-dynamic regulation of species diversity in ecosystem function 9.

4) Construction of reef framework takes place through the process of calcification (P), whereby calcifying organisms bind carbon dioxide and calcium and transform this into calcium carbonate which is accumulated into skeletons of aragonite and calcite. These calcifying organisms are either framework builders or non-framework builders (Done et al., 1996). Primary framework builders are massive, branching or platy stony corals and various encrusting coralline algae that cement the building blocks of stony corals into a reef framework (Done et al., 1996; Castro and Huber, 2008). Secondary framework builders are smaller stony corals and species such as bivalve molluscs that add small-scale topographic complexity to the framework (Done et al., 1996). Non-framework builders such as foraminifera, erect coralline algae and most molluscs are species that contribute with their shells and skeletal fragments to the reef sediment and to the framework itself when reef sediment is trapped inside the framework (Done et al., 1996). Soft corals and sea fans do not contribute substantially to reef building (Sheppard et al., 2009).

5) Generation of coral sand and sediment is the production of reef sediments including coral rubble, sand, silt and clay through physical and biological processes (Moberg and Folke, 1999) which facilitates communities living in the sediment (Hutchings, 1986). The calcifying organisms that were classified above as non-framework builders contribute to the reef sediment through physical erosion of their calcium carbonate shells and skeletal fragments (Done et al., 1996). Biological erosion of coral reef structures takes place through the processes of grazing, etching and boring by fish, invertebrates and bacteria (S). This involves both mechanical abrasion and chemical dissolution. Grazers scrape live or dead coral and rubble from the surface when they remove algae from coral reef structures. Thereby they recycle existing sediment and produce new sediment that erodes the reef. Principal grazers are echinoids (sea urchins) and a variety of fish, less important grazers are gastropods (snails). Some fish accidentally ingest existing sediment while foraging, for example goatfish, other fish such as Acanthurids (surgeonfish) and Scarids (parrotfish) scrape the surface with their teeth and have an alimentary tract adjusted to ingest carbonate and grind it into smaller particles thereby producing new sediment. Echinoids, such as *Diadema antillarum,* graze and erode the reef by scraping the substrate to form a shallow depression, but they excrete similar sized particles as they ingest. Sediment production and calcium carbonate dissolution also occurs from boring invertebrates, such as excavating sponges, bivalve molluscs (shellfish), sipuculans (peanot worm) and polychaetes (worms) such as the Christmas tree worm (Hutchings, 1986). Echinoids are more destructive bioeroders then fish, because they burrow into the reef matrix, while fish mainly feed on dead corals and from convex surfaces, avoiding flat and concave surfaces (Bellwood et al., 2004). Therefore competition between these two sub-groups of grazers is important. Reduced levels of competition from herbivorous fish due to overfishing, resulted in unsustainable high populations of grazing sea urchins in the Caribbean. This in turn resulted in more destructive bioerosion, followed by mass mortality of sea urchins after a species-specific disease outbreak in the Caribbean in the 1980s, which induced coral overgrowth by algae due to reduced grazing levels and large scale degradation of Caribbean coral reefs (Hughes, 1994; Hughes et al., 2005).
Biological erosion has other functions besides the generation of coral sand and sediment. It facilitates cementation that is necessary for construction of the coral reef framework (Hutchings, 1986). It also increases the surface complexity and creates newly available substrate for many sedentary species including corals, which is important to maintain species diversity (Connell, 1978).

Regulation functions

Regulation functions refers to the regulation and maintenance of ecological processes such as modification of wave and current patterns, regulation of predatory control mechanisms, storage and recycling of nutrients and removal and breakdown of excess nutrients and xenic compounds.

6) Modification of wave and current patterns occurs because coral reef structures act as physical barriers and modify waves and currents through wave refraction and wave energy dissipation (Harborne et al., 2006). This is most obvious in lagoons to the leeward side of coral reefs with calm conditions for seagrass beds and mangroves (Moberg and Rönnbäck, 2003). Data collected from several Caribbean casestudies by Harborne et al. (2006) showed reductions in wave heights of 20-26% to 50%, wave energy reduction of 35-45% to 72-97%, tidal current speeds reductions of 30% up to 60-70% as tidal currents are transformed by frictional effects from strong rectilinear to weak variable currents. The extent of the modification depends on the coral reef structure and its topographic complexity, presences of coral spurs and sediment grooves and water depth as well as on the tidal range. Water movement is altered significantly as it flows across the fore reef, but the reef crest also has a vital role with greatest wave breaking on the reef crest at low tide. This function of reef crest zones has been significantly reduced as a result of the reduction in branching *Acropora* coral species (Harborne et al., 2006). *Acropora* coral species have been severely damaged by white-band disease in the Caribbean in the 1980s (Gladfelter, 1982) and are due to their growth form more susceptible to hurricane damage (Gardner et al., 2005). Under normal conditions the natural breakwaters formed by a healthy reef renew at a rate that slightly exceeds the rate of bioerosion and wave erosion (Sheppard et al., 2009). However, hurricanes cause considerable damage to corals and contribute to coral cover decline. Recovery to a pre-storm state takes at least eight year (Gardner et al., 2005). The loss of *Acropora* coral species also had an impact on the habitat function, which is further discussed as part of ecosystem function 10.

7) Removal or breakdown of excess or xenic nutrients and compounds is the function of marine ecosystems to assimilate waste (Costanza et al., 1997). Excess algal production induced eutrophication can be reduced through biological filtering of suspended material by filter feeding organisms such as bivalve molluscs. This not only improves the water quality, but also transfers production from the pelagic to the benthic foodweb (Peterson and Lubchenco, 1997). Oil is detoxified by microbes in the marine environment by turning hydrocarbons into carbon dioxide and water (Peterson and Lubchenco, 1997). More persistent non-biodegradable pollutants can accumulate in organisms and sediments, thereby only temporarily immobilising and sequestering these pollutants. They often re-enter the environment at some point, which moves the problem in time and space (De Groot, 1992).

8) Nutrient cycling refers to the acquisition, internal cycling and storage of nutrients such as the carbon, nitrogen, phosphorus cycles of these essential elements (Costanza et al., 1997). Phosphate (PO_4^{3-}) and nitrate (NO_3^-) are required by plants to synthesize organic material through photosynthesis and tend to be in short supply in surface waters. In all cycles there is a major reservoir of the element, such as phosphate rock on land, nitrogen gas (N_2) in the atmosphere and carbon dioxide (CO_2) in the carbonate system (H_2CO_3—HCO_3^-—CO_3^{2-}) in water. Carbon is fixed into organic compounds by photosynthetic organisms. Phosphate enters the water through erosion. Atmospheric N_2 must first be converted into a nitrogen compound before it can enter the cycle. This is done through a process called nitrogen fixation by bacteria, whereby cyanobacteria account for over half of the of atmospheric N_2 fixation. Once in the cycle, the elements circulate through animals and plants by excretion and decay, but micro-organisms dominate the cycles by making the elements available again (Castro and Huber, 2008).

9) Trophic-dynamic regulation of species diversity is the biological control mechanisms through predation by keystone predators on prey species and by top predators on herbivores (Costanza et al., 1997). A keystone predator is a predatory species whose effect on community structure and species diversity is large relative to its abundance (Castro and Huber, 2008). Davic (2003) suggests to identify keystone species within functional groups whose top-down effect on species diversity and competition is large relative to its biomass dominance within a functional group. Biological control includes removal of algae by major herbivorous fish such as *Scaridae* (parrotfish) and by *Diadema antillarum* prior to the major die-off of this species of sea urchin in the Caribbean (Hughes, 1994). Biological control of nuisance species such as the invasive lionfish species in the Caribbean, *Pterois volitans* and *Pterois miles,* could also be a function of coral reef ecosystems. However, predation on lionfish is considered rare and limited to incidental predation by *Sirranidae* (groupers) and *Gymnotorax funebris* (green moray eels)

(Barbour et al., 2011). The disadvantage of the anthropogenic control of this pest species through spear fishing, compared to biological control, is that it is not considered to be the solution to complete eradication and substantial reduction of the adult population will only be feasible in small, localized areas where spear fishing is intense over multiple consecutive years (Barbour et al., 2011).

Habitat functions

Habitat functions are related to the provision of habitat and the connectivity with adjacent habitats and interdependencies between different habitats.

10) Provision of refuge, nursery and reproduction habitats is an important function of coral reef ecosystems, because the topographic complexity of coral reefs provides a variety of macro- and micro-habitats. Reef-building corals for example form a primary micro-habitat for symbiotic zooxanthellae. Topographic complexity is expressed by the surface rugosity of the contours and crevices of the reef, which is a multitude of the linear distance of that surface area due to the vertical relief or height, holes, overhangs and the variety of growth forms at coral reefs (Luckhurst and Luckhurst, 1978). This three-dimensional structure provides substrate and resources to facilitate larval settlement and recruitment of benthic invertebrates into the adult population (Idjadi and Edmunds, 2006) and it provides refuge from post-settlement predation for reef fish (Steele, 1999). Topographic complexity is positively correlated with primary productivity, biomass production, species diversity and abundance (Luckhurst and Luckhurst, 1978; Gratwicke and Speight, 2005; Gratwicke and Speight, 2005). Topographic complexity is also an important factor in ecological processes, such as water flow around, over and through the reef, wave energy dissipation, and thereby nutrient uptake (Zawada et al., 2010).

11) Physical and biological support through mobile links is the function to support adjacent ecosystems of coral reefs such as seagrass beds, mangrove forests and the open ocean (Moberg and Folke, 1999). The physical barrier of coral reefs helps to create lagoons for growth of seagrass and mangroves (Moberg and Folke, 1999; Harborne et al., 2006). The biological support is through mobile links of species that use the adjacent habitats as nursery or feeding grounds and in the process transfer energy in the food web of these habitats and influence the nutrient cycle through excretory and fecal products (Ogden and Gladfelter, 1983). Another mobile link is through connectivity, which is the extent to which a reef is supplied with pelagic propagules which replenish its adult population with fish, coral and other benthic invertebrate larvae. Pelagic larvae may transfer energy in the food web as well, if they function as food source or else they may settle and recruit into the population. But even then settlement of coral larvae may be sporadic and of the wrong type, for example non-framework building coral larvae in a reef framework zone (Done, 1995). A key element in coral reef resilience is successful larval colonization by the full range of coral functional groups characteristic for the area (Bellwood et al., 2004). Coral reefs also export organic material such as mucus, plankton and dissolved organic matter back to the pelagic food web (Hatcher, 1997).

Information functions

According to the theoretical framework of TEEB as presented in figure 3 the information function refers to the landscape and the information it provides in the broadest sense. For coral reef ecosystems this is translated into the seascape and the biodiversity within this seascape.

12) Seascape is defined in seascape ecology literature as wholly or partially submerged marine landscapes (Pittman et al., 2011). The tropical coastal seascape often includes interconnected ecosystems of coral reefs, seagrass beds and mangrove forests that produce a variety of ecosystem services (Moberg and Rönnbäck, 2003). Seascapes have the scenic views and open space which determine the aesthetic, recreational and cultural value and provide artistic inspiration.

13) Biodiversity within the seascape may not be the typical identifier of the cultural services provided by ecosystems, but nevertheless underlies the character of the seascape as perceived by people (Elmqvist et al., 2010) . Although biodiversity varies greatly among these services, biodiversity plays an important role in promoting a sense of place in most societies and has considerable intrinsic cultural value. The link between biodiversity and recreational and educational services is particularly important (De Groot et al., 2010; Elmqvist et al., 2010) such as biodiversity-based research and education on coral reef ecology and tourism and recreation such as diving, snorkelling and fishing.

3.2.3 Relationship between ecosystem functions and ecosystem services

The relationship between ecosystems and the benefits they provide is often non-linear and complex (Reyers et al., 2010). Ecosystem functions and services do not show a one on one relationship, because a single service can be the product of two or more functions and a single function can contribute to two or more services (Costanza et al., 1997). Matrix A in table 4 visualises these complex relationships.

Table 4. Relationship Matrix A: ecosystem functions – ecosystem services. A refers to relationship A in the conceptual model of this research as elaborated in chapter 2.2

RELATIONSHIP 1

Relationships
- ■ = essential function for service delivery
- ▒ = supporting function to service delivery
- (blank) = no relationship

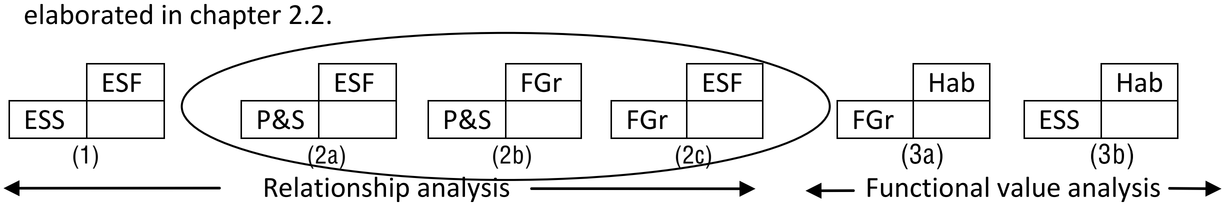
References
[1] Moberg and Folke (1999)
[2] De Groot et al. (2002)
[3] Bellwood et al. (2004)
[4] Done et al. (1996)
[5] Costanza et al. (1997)
[6] Harborne et al. (2006)
[7] TEEB (2010)

ECOSYSTEM SERVICES	**Production functions**	1. Primary production[2,6]	2. Secondary production[2,3,6]	3. Tertiary and higher production[3,6]	4. Construction of reef framework[4]	5. Generation of coral sand[1] and sediment[1,4]	**Regulation functions**	6. Modification of wave and current patterns[5,6]	7. Removal or breakdown of xenic nutrients and compounds[2,5]	8. Nutrient cycling[2,5]	9. Trophic-dynamic regulation of species diversity[2,5]	**Habitat functions**	10. Provision of refuge, nursery and reproduction habitats[2,3]	11. Physical and biological support through 'mobile links'[1]	**Information functions**	12. Seascape[7]	13. Biodiversity[7]
Provisioning services																	
1. Seafood products[1]		▒	■	■									▒	▒			
1. Raw material for production of lime and cement[1]					■												
1. Raw material for medicines[1]		■															■
Regulating services																	
4. Shoreline protection[1]		▒			▒			■					▒	▒			
5. Waste assimilation[1]		■							■	▒							
6. Biological maintenance of resilience[1]		▒	■	■									▒	▒			
Habitat services																	
7. Maintenance of habitats[1]		■			■	■		▒					■				
8. Maintenance of biodiversity and genetic diversity[1]		■	■	■	■					▒	▒		▒	▒			■
Cultural services																	
9. Aesthetic values and artistic inspiration[1]		▒	■	■	■	■		▒								■	▒
10. Support of tourism and recreation[1]		▒	■	■	■	■		▒	▒				▒	▒		■	■
11. Support of cultural identity [1]			▒	▒		▒										■	▒
12. Educational and scientific information services[1]		■	■	■	■	■		■	■	■	■		■	■			■

Table 4 presents the relationship between identified ecosystem functions and ecosystem services. The relationship is expressed as the importance of the function to deliver the service. The shading of the cells expresses the importance, whereby dark grey = essential function, light grey = supporting function and no shading = no relationship between the function to deliver the service. Supporting function in this context was defined as direct support to an essential function, for example primary production that supports harvestable fish biomass production and provision of refuge, nursery and reproduction habitats that support fish biomass production. Indirect support (support to a supporting function) is not considered a supporting function, for example calcification supports habitat provision which makes it an indirect support of fish biomass production.

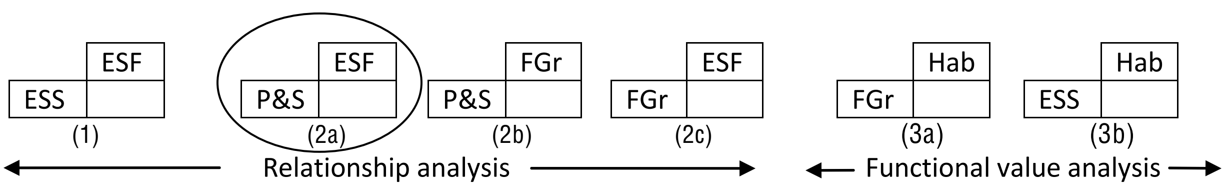
3.3 Linking functional groups and ecosystem functions

The relationship between functions and functional groups was examined in three steps as encircled in below illustration of the data analysis, for which is referred to figure 7 in chapter 2.5 for a detailed explanation. First ecological processes and biophysical structures were linked to ecosystem functions in step 2a (Matrix B.1). Then functional groups were linked to these processes and structures in step 2b (Matrix B.2). In step 2c the above two relationships were combined in Matrix B, linking functional groups and ecosystem functions. B refers to relationship B in the conceptual model of this research as elaborated in chapter 2.2.



3.3.1 Identification of ecological processes and biophysical structures

For all ecosystem functions eight key underlying processes and structures were identified and their functional relationships examined as part of step 2a in the relationship analysis.



Also processes, structures and functions do not show one on one relationship, so one process or structure can contribute to multiple functions and one function can be determined by multiple processes or structures. The established functional relationships are shown in table 6. Table 6 lists the eight processes and the multiple biophysical structures that perform each process, whereby the number of the process corresponds to the number of the structures, as shown in the example in table 5.

Table 5.Example of a key ecological process and corresponding (numbering of) biophysical structures.

ECOLOGICAL PROCESSES AND BIOPHYSICAL STRUCTURES			
	Processes		**Structures**
5	Calcification and accretion of calcium carbonate	5.1	Primary framework builders
		5.2	Secondary framework builders
		5.3	Non-framework builders

Table 6. Relationship Matrix B.1: Ecosystem functions – Ecological processes and structures.

RELATIONSHIP 2a

Relationships

■ = underlying process or structure determining the function

□ = no relationship

References

[1] Moberg and Folke (1999)

[2] De Groot et al. (2002)

[3] Bellwood et al. (2004)

[4] Done et al. (1996)

[5] Costanza et al. (1997)

[6] Harborne et al. (2006)

[7] TEEB (2010)

ECOLOGICAL PROCESSES AND BIOPHYSICAL STRUCTURES	**Production functions**	1. Primary production [2,6]	2. Secondary production [2,3,6]	3. Tertiary and higher production [3,6]	4. Construction of reef framework [4]	5. Generation of coral sand [1] and sediment [1,4]	**Regulation functions**	6. Modification of wave and current patterns [5,6]	7. Removal or breakdown of xenic nutrients and compounds [2,5]	8. Nutrient cycling [2,5]	9. Trophic-dynamic regulation of species diversity [2,5]	**Habitat functions**	10. Provision of refuge, nursery and reproduction habitats [2,3]	11. Physical and biological support through 'mobile links' [1]	**Information functions**	12. Seascape[7]	13. Biodiversity[7]
Processes																	
1. Photosynthesis [6]		■			■					■			■				
2. Grazing[6]			■								■		■	■			
3. Predation on secondary and higher producers[6]				■							■			■			
4. Coral recruitment[6]					■									■			
5. Calcification[6] and accretion of calcium carbonate[4]					■								■			■	
6. Biological erosion [4,6]						■							■			■	
7. Wave energy dissipation and current reduction and diversion [6]						■		■						■		■	
8. Nitrogen fixation [6]										■							
Structures																	
1.1. Calcification enhancers: zooxanthellae		■			■												
2. Nitrogen fixers: Cyanobacteria		■								■							
3. Calcareous algae		■															
4. Macro algae		■											■				
5. Turf algae		■															
2.1. Scraping, excavating, denuding and browsing herbivorous fish[6]			■								■			■			
2. Herbivorous invertebrates			■								■						
3.1 Planktivorous, omnivorous and piscivorous fish[6]				■							■			■			
2. Fish species diversity [6]																	■
4.1. Coral species diversity [6]																	■
5.1. Primary framework builders: stony corals, encrusting coralline algae[4]					■			■					■				
2. Secondary framework builders: small stony corals, bivalve molluscs[4]					■			■					■				
3. Non-framework builders: erect coralline algae, molluscs spp.[4]						■											
6.1. Boring bioeroders: micro and macro invertebrates[4]						■							■				
2. Grazing bioeroders: sea urchins and parrotfish						■							■				
7.1. Topographic structure of habitat (structural complexity)								■					■				■
8.1. Microbes[1]										■							

Each of the eight processes (P) and corresponding biophysical structures (S) are briefly described below, including their functional relationship with the thirteen ecosystem functions and some examples of the consequences if these processes and structures are disturbed.

1) Photosynthesis (P) by autotrophs (S)

Photosynthesis is the key process of conversion of energy, inorganic carbon, water and nutrients into organic compounds, which results in primary production as the basis of the food web. The biological structures carrying out this process are various types of autotrophs, from bacteria to algae, as listed in table 5. Zooxanthellae, endoysymbiotic dinoglagellate algae, are a special type of autotroph, because they require stony corals or another invertebrate host as primary habitat and because they significantly enhance calcification (Sheppard et al., 2009). Corals fix four times as much carbon and zooxanthellae provide their host with up to 95% of the organic carbon they produce (Muscatine et al., 1984) and up to 30% of their host nitrogen requirements from dissolved nitrogen uptake (Bythell, 1990; Wild et al., 2011) which both facilitate accelerated coral growth, reproduction and maintenance . Bleached corals, caused by the expulsion of photo-pigment rich zooxanthellae due to thermal stress of raised seawater temperatures, show reduced calcification up to 22-37% of normal growth rates (Leder et al., 1991; Wild et al., 2011) and lower coral tissue regeneration rates of damaged corals (Meesters and Bak, 1993). This illustrates the importance of zooxanthellae in the calcification process and in the nutrient cycle. Macro-algae patches also provide refuge and nursery habitat.

2) Grazing (P) by herbivorous fish and invertebrates (S)

Grazing is the key process of excavating, scraping, cropping, denuding and browsing of turf and macro-algae which has critical functions in coral reef ecosystems such as the conversion of primary production to fish-based trophic pathways, the provision of suitable substrate for settlement of coral larvae and coral recruitment and the mediation of competition between macro-algae and corals by reducing coral overgrowth and light reduction by macro-algae (Mumby et al., 2006). The biological structures carrying out this process are herbivorous fish and herbivorous invertebrates. The loss of principal herbivorous fish, such as parrotfish and surgeonfish, due to overfishing and of principal herbivorous invertebrates, such as sea urchins, due to disease caused widespread algal blooms and phase shifts from coral-dominated to algal-dominated ecosystems (Bellwood and Hughes, 2001).

3) Predation (P) by a diversity of fish species including piscivores, omnivores and planktivores (S)

Predation is a key process to transfer energy to higher levels in the trophic pathway for secondary and higher production (Done et al., 1996). Keystone and apex predators also have a functional role in predator-prey relationships in a food web (Costanza et al., 1997; Hughes et al., 2005). Overexploitation of reef fisheries first depletes large predators, such as groupers, and there is evidence that this results in top-down alterations of the food web. This is especially true in less species diverse bioregions such as the Caribbean, where lower functional redundancy and response diversity may result in greater impact from loss of predators (Bellwood et al., 2004). For example the high densities of sea urchins on overfished reefs prior to their major die-off caused by a pathogen, was almost certainly due to loss of predators on sea urchins combined with reduced competition for resources from loss of herbivorous fish (Hughes, 1994).

4) Coral recruitment (P) by a diversity of coral species (S)

Coral recruitment is the key process of larval colonization into the adult population by the full range of coral species and functional groups characteristic for the bioregion. This is important to maintain a healthy, diverse coral reef and to resist phase shifts to less desirable, degraded states (Bellwood et al., 2004). Successful recruitment depends on four major factors: phototactic behaviour of the larvae, reproductive seasonality, substrate availability, and survival under pressures of predation and competition (Harborne et al., 2006). But even then settlement of coral larvae may be sporadic and of the wrong type, for example non-framework building coral larvae that settle in a reef framework zone (Done, 1995). Successful recruitment is an example of connectivity and an important ‘mobile link’.

5) Calcification and accretion of calcium carbonate (P) by framework and non-framework builders (S)

Calcification is the key process of accretion of calcium carbonate by framework and non-framework builders to convert primary production into the bioconstructional pathway. The net accumulation of the reef framework in the biocontructional pathway is essential for the structural integrity of a coral reef

(Done et al., 1996). Net accumulation is the sum of gross accretion of calcium carbonate minus bioerosion of calcium carbonate structures, which is discussed as part of the next key process. Primary framework builders are massive, branching and platy stony corals and encrusting coralline algae that cement the stony corals into a framework and create structural complexity. Secondary framework builders are smaller stony corals and species such as bivalve molluscs that add small-scale structural complexity (Done et al., 1996). Structural complexity is important for the provision of habitats and for wave energy dissipation (Zawada et al., 2010). Non-framework builders are erect coralline algae and other calcifying organisms that have a minor contribution to the framework, when reef sediment composed of their shells and skeletal fragments is trapped inside the framework (Done et al., 1996). Their role into generation of reef sediment is more important. Calcification is also an important process to create the typical coral reef seascape with clear blue water above sandy substrates combined with dark blue patches above coral substrate.

6) Biological erosion of calcium carbonate structures (P) by boring and grazing bioeroders (S)
Bioerosion is the key process of biological erosion of coral reef structures(P) by excavating and scraping herbivorous fish and micro- and macro-invertebrates (S) such as echinoids, bivalve molluscs, polychaete worms, encrusting or boring sponges and filamentous algae that bore into the reef or graze the algae by scraping the surface (Hutchings, 1986). Grazers such as excavating and scraping parrotfish and scraping and boring sea urchins are key bioeroders. As long as sea urchin abundance is low it can add to topographic complexity, but it can erode the reef to rubble and sand at too high abundance (Done et al., 1996). The function of bioerosion is generation of coral sand and reef sediment, which provides habitat and gives the tropical clear blue water colour to the coral reef seascape.

7) Wave energy dissipation (P) by topographic complex structures (S)
The key processes of wave refraction and wave energy dissipation and current reduction and diversion are important to modify wave and current patterns. The reef framework is the physical structure that provides this natural breakwater and barrier to support creation and protection of adjacent habitats. The extent of modification depends amongst others on topographic complexity of the reef framework. In the Caribbean two major shallow-water habitats have largely disappeared, the elkhorn coral '*palmata* zone' and the staghorn coral '*cervicornis* zone', both branching corals. Especially elkhorn coral is structurally complex and has many large branches, which has a critical function in habitat provision and wave energy dissipation (Bellwood et al., 2004). Sediment deposition is another function of wave energy dissipation (Harborne, 2006).

8) Nitrogen fixation (P) by microbes and cyanobacteria (S)
Nitrogen fixation is a key process to convert atmospheric N_2 from the nitrogen reservoir into a nitrogen compound so it can enter the nitrogen cycle. Other reservoirs of essential elements for primary production, such as carbon and phosphorus, are either available in seawater or enter the water through erosion. The most important biophysical structures for nitrogen fixation are cyanobacteria.

3.3.2 Identification of functional groups
For all ecological processes and structures crucial functional groups were identified and their functional roles to support these processes and structures examined as part of step 2b in the relationship analysis.

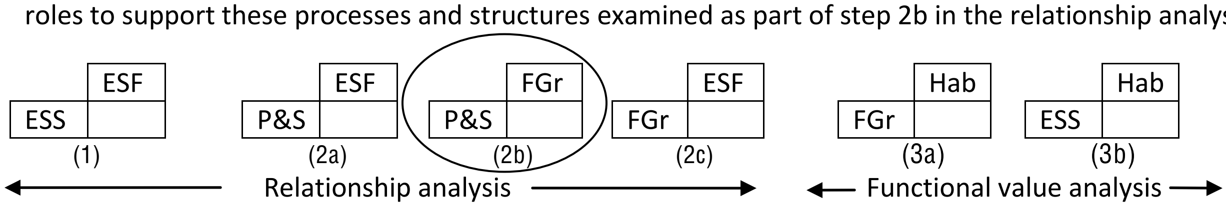


Table 7 shows the functional groups and other indicators identified for their functional role in the eight key ecological processes and biophysical structures.

Table 7. Relationship Matrix B.2: Ecological processes and structures – Functional groups.

RELATIONSHIP 2b — **FUNCTIONAL GROUPS AND INDICATORS for functional value of habitats to support ESP, ESF and ESS**

Relationships
■ = functional group as indicator for process or structure
□ = no relationship

References
[1] Moberg and Folke (1999)
[2] De Groot et al. (2002)
[3] Bellwood et al. (2004)
[4] Done et al. (1996)
[5] Costanza et al. (1997)
[6] Harborne et al. (2006)
[7] TEEB (2010)

ECOLOGICAL PROCESSES AND BIOPHYSICAL STRUCTURES	1.1 Density herbivorous fish [6] - scrapers, excavators (proxy)	1.2 Density herbivorous fish [6] - denuders (proxy)	1.3 Density herbivorous fish [6] - browsers (proxy)	2. Density planktivorous fish [6] (proxy)	3. Density omnivorous fish [6] (proxy)	4. Density predatory fish [6] (proxy)	5. Fish biodiversity	6. Fish abundance	7. Fish maximum size	8. Branching coral cover [4,6]	9. Massive coral cover [6]	10. Coral Cover	11. Algal cover (Macro/turf/calcareous algae) [4]	12. Gorgonian, soft coral cover	13. Sponge cover	14. Sand, rubble and rock cover	15. Coral biodiversity [6]	16. Coral maximum size	17. Structural complexity	18. Coral mortality, disease and bleaching	19. Coral bite marks	20. Cyanobacteria[6]	21. *Trididemnum solidum* (tunicate)	22. *Diadema antillarum* (sea urchin) [6]
Processes																								
1. Photosynthesis [6]													■									■		
2. Grazing[6]	■	■	■																		■			■
3. Predation on secondary and higher producers[6]				■	■	■			■															
4. Coral recruitment[6]																								
5. Calcification[6] and accretion of calcium carbonate[4]										■	■	■												
6. Biological erosion [4,6]	■															■					■			■
7. Wave energy dissipation and current reduction and diversion [6]										■	■	■		■				■						
8. Nitrogen fixation [6]																						■		
Structures																								
1.1. Calcification enhancers: zooxanthellae																				■				
2. Nitrogen fixers: Cyanobacteria																						■		
3. Calcareous algae																								
4. Macro algae													■											
5. Turf algae																								
2.1. Scraping, excavating, denuding and browsing herbivorous fish[6]	■	■	■																					
2. Herbivorous invertebrates																								■
3.1 Planktivorous, omnivorous and piscivorous fish[6]				■	■	■			■															
2. Fish species diversity [6]							■	■																
4.1. Coral species diversity [6]																	■							
5.1. Primary framework builders: stony corals, encrusting coralline algae[4]										■	■	■												
2. Secondary framework builders: small stony corals, bivalve molluscs[4]																								
3. Non-framework builders: erect coralline algae, molluscs spp.[4]																								
6.1. Boring bioeroders: micro and macro invertebrates[4]																								
2. Grazing bioeroders: sea urchins and parrotfish	■																							■
7.1. Topographic structure of habitat (structural complexity)																			■					
8.1. Microbes[1]																								

Functional groups can have different and complementary roles (Bellwood et al., 2004), so one functional group could be used as indicator for multiple processes. For example excavating and scraping herbivorous fish not only have a functional role in grazing algae, but also in bioerosion of the reef framework and in habitat provision by exposing the reef for larval settlement (Bellwood et al., 2004). One process can also have multiple indicators, for example bioerosion can be estimated based on the presence of principle bioeroders, such as sea urchins and parrotfish, or presence of carbonate sediment, sand and rubble. Direct measurements of processes are not always possible, but functional groups can provide useful proxies (Harborne et al., 2006). For example, quantification of grazing rate requires measurements of bites per minute multiplied by the size of bites per individual fish per fish species multiplied by the abundance per fish species (Fox and Bellwood, 2007). Because these parameters were not available, herbivorous fish density was used as a proxy for grazing.

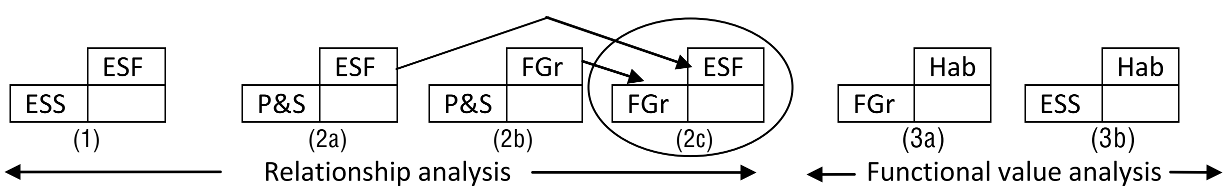
For some processes and structures no indicators were identified, because of the choice of visual census technique. For example sampling of coral recruits is normally done using 1 m^2 quadrants and scuba to be close to the substrate. Hence coral recruitment was not measured, nor were several structures such as small or cryptic species: microbes, encrusting and erect coralline algae, turf algae, filamentous algae, micro- and most macro-invertebrates including molluscs, polychaete worms, boring or encrusting sponges. For nitrogen fixation only a weak indicator was identified, namely visible cyanobacteria mats.

For some functional groups there was an obvious relationship with one or more identified structures, because the structures already included groups of species based on their functional role. For example, fish functional groups were identified based on their functional role to transfer energy in the trophic pathway, and categorized according to their trophic guild in herbivores, planktivores, omnivores and piscivores. Herbivores were, based on their functional role in other ecosystem processes, categorized in the functional groups of excavating and scraping herbivores, denuding herbivores and farming herbivores. How precisely this classification is build up is explained in more detail in chapter 4.2.

For other functional groups and indicators there was not a clear relationship with one or more of the identified processes, structures or functions. They were included in the snorkel survey, because they are common parameters to include in a coral reef survey. For example fish maximum size of large piscivores (groupers, snappers and jacks) is an indicator of coral reef ecosystem health as large fish are more productive, so the best was to link this indicator with tertiary and higher production and with trophic-dynamic regulation by these apex predators. Rubble, sand and rock cover is an indicator of coral reef health as well, and it was used as a proxy for the process of bioerosion for generation of sand and sediment and could be negatively linked to the provision of habitat and modification of waves and currents. Coral mortality, disease and bleaching were also included as indicators of coral reef health, but the weak link with future bioerosion was not included, nor was the negative link with the processes of calcification and photosynthesis due to a lack of zooxanthellae. Sponge cover is a common species to include in benthic surveys, but their functional role in removal of excess nutrients and nutrient cycling was not examined in this research. Gorgonian cover was included as another common species, but their functional role was also not further examined. *Trididemnum solidum*, a tunicate, is a nuisance species and was included as indicator for the threat of invasive species, so their functional role was irrelevant. Lionfish was also included as indicator for invasive species threat.

3.3.3 Relationship between functional groups and ecosystem functions

All functional groups were linked to ecosystem functions based on their functional roles to support ecosystem functions as part of step 2c in the relationship analysis.



Relationships were established by consolidating the results from table 6 (relationship 2a) and table 7 (relationship 2b) into one matrix, whereby processes and structures were used as intermediate step to find the link between functional groups and the functions they support. For example, the functional group excavating herbivorous fish was identified as an indicator for processes grazing and bioerosion in table 7. Looking at table 6 the grazing process determines the functions 2) secondary production 9) trophic dynamic regulation and 11) mobile links. The bioerosion process determines the functions 5) generation of coral sand and sediment, 10) provision of habitat and 12) seascape. This analysis was done for each identified functional group and resulted in Matrix B as presented in table 8.

Table 8. Relationship Matrix B: Functional groups – Ecosystem functions. B refers to relationship B in the conceptual model of this research as elaborated in chapter 2.

RELATIONSHIP 2c

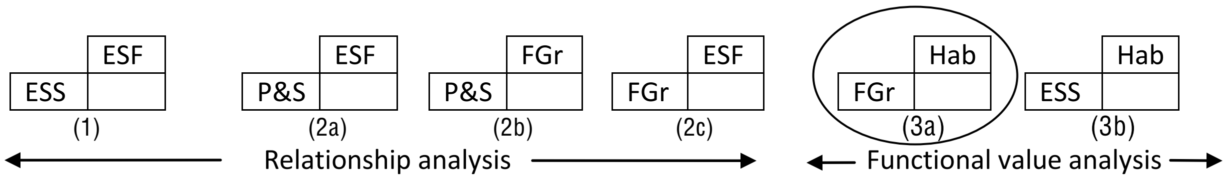
Relationships
- ■ = functional group as indicator for quality of ecosystem functions
- □ = no relationship

References
- [1] Moberg and Folke (1999)
- [2] De Groot et al. (2002)
- [3] Bellwood et al. (2004)
- [4] Done et al. (1996)
- [5] Costanza et al. (1997)
- [6] Harborne et al. (2006)
- [7] TEEB (2010)

FUNCTIONAL GROUPS AND OTHER INDICATORS	**Production functions**	1. Primary production [2,6]	2. Secondary production [2,3,6]	3. Tertiary and higher production [3,6]	4. Construction of reef framework [4]	5. Generation of coral sand [1] and sediment [1,4]	**Regulation functions**	6. Modification of wave and current patterns [5,6]	7. Removal or breakdown of xenic nutrients and compounds [2,5]	8. Nutrient cycling [2,5]	9. Trophic-dynamic regulation of species diversity [2,5]	**Habitat functions**	10. Provision of refuge, nursery and reproduction habitats [2,3]	11. Physical and biological support through 'mobile links' [1]	**Information functions**	12. Seascape [7]	13. Biodiversity [7]
1.1 Density herbivorous fish[6] - scrapers, excavators (proxy)			■			■					■		■	■		■	
1.2 Density herbivorous fish[6] - denuders (proxy)			■								■			■			
1.3 Density herbivorous fish[6] - browsers (proxy)			■								■			■			
2. Density planktivorous fish[6] (proxy)				■							■			■			
3. Density omnivorous fish[6] (proxy)				■							■			■			
4. Density predatory fish[6] (proxy)				■							■			■			
5. Fish biodiversity																	■
6. Fish abundance																	■
7. Fish maximum size				■							■						
8. Branching coral cover[4,6]					■			■					■			■	
9. Massive coral cover[6]					■			■					■			■	
10. Coral Cover					■			■					■			■	
11. Algal cover (Macro/turf/calcareous algae)[4]		■			■	■							■				
12. Gorgonian, soft coral cover								■									
13. Sponge cover																	
14. Sand, rubble and rock cover						■											
15. Coral biodiversity[6]																	■
16.Coral maximum size								■									
17. Structural complexity								■					■				■
18. Coral mortality, disease and bleaching																	
19. Coral bite marks						■							■				
20. Cyanobacteria[6]		■								■							
21. *Trididemnum solidum* (tunicate)																	
22. *Diadema antillarum* (sea urchin) [6]			■			■					■		■				

4 RESULTS SNORKEL SURVEY

In this chapter the results from the analysis of primary data collected with the snorkel survey are reported to answer the fourth research question 'What is the level of representation of functional groups in coral reef habitats and locations on Bonaire?'. This analysis was part of step 3a in the functional value analysis as illustrated below and explained in figure 7 in chapter 2.5. Chapter 4.1 explains how marine and coastal resource user groups were identified to cluster data and examine correlations between functional groups and resource use. Chapter 4.2 elaborates on the analysis of fish functional groups and chapter 4.3 on the analysis of coral functional groups.



4.1 Marine and coastal resource use at survey locations

As explained in chapter 2.3.2 two coral reef habitats were selected: the shallow zone and the reef zone. These two habitats were surveyed at 116 locations on Bonaire and Klein Bonaire, with ID numbers B00-B96 and KB00-KB20 respectively. Coupling the two habitats and 116 locations resulted in 232 datasets. Because multivariate statistical analysis to cluster locations according to *similarities* in representation of functional groups did not result in significant clusters, locations were compared according to *differences* in representation of functional groups based on predefined groups in Kruskal Wallis non-parametric tests. For example, data collected from transects in residential areas were compared to those in marine reserves, to analyze whether statistical significant differences between groups were observed. Locations were divided in 7 groups as presented in table 9, based on different coastal and marine resource use.

Table 9. Group division of snorkel sites into marine and coastal resource use groups. Coastal resource use includes coastal development for residential and industrial use. Marine resource use includes the restricted use areas of the Marine and Fish reserve, the frequently used, easy access areas by dive tourism and the least used areas like the uninhabited island of Klein Bonaire and remote, difficult to access areas.

Resource use	Specification	Transect ID
1. Residential	Belnem (including Donkey beach B30-B32)	B26 – B32
	Kralendijk (excluding overlapping Fish Reserve B34-B35)	B36 – B39
	Hato (excluding overlapping Fish Reserve B43-B44)	B45 – B45
	Sabadeco	B46 – B50
2. Industrial	Bopec oil storage terminal	B66 – B69
	Cargill corporation salt production	B16 – B19
3. Dive tourism	Dive sites north	B51 – B61
	Dive sites south (including Pink beach B14)	B04 – B15, B20 – B25
4. Marine Reserves	Karpata – Gotomeer	B62 – B65
	Boka Slagbaai – Playa Frans	B79 – B83
5. Fish Reserves	Playa Chachacha – Plaza Resort	B33 – B35
	Punt'i Waya (Hato Gate) – Harbour Village Beach Resort	B40 – B44
6. Remote	South	B00 – B03
	North (including Playa Frans B78, Boka Slagbaai B84-B85, Playa Funchi B88, Playa Benge B90, Boka Bartol B94)	B70 – B78, B84 – B96
7. Island	Klein Bonaire	KB00 – KB20

Coastal resource use groups were divided in intensively used coastal areas with residential and industrial development and uninhabited coasts of Klein Bonaire and remote areas. On Klein Bonaire coastal and marine resources use is limited to some tourism and recreation through boat diving trips and beach day-trips. Remoteness was defined as difficult access from shore, either due to high waves in the south and cliffs in the north, and long boat driving distance from Kralendijk. Marine resource use groups were divided according to the zonation of the MPA in Marine and Fish reserves. Marine reserves, established from the start of the establishment of the MPA in 1979 (STINAPA, 2006), do not allow any resource use, including diving, snorkelling, surfing, fishing, anchoring and mooring, with the exception of fisheries with traditional fishing gear (Bonaire, 2010a). Fish reserves, established in 2008 (Bonaire, 2007), do not allow any fishing, except on invasive lionfish species *Pterois spp.* (Bonaire, 2010a; Bonaire, 2010b). Other identified marine resource use groups were tourism and recreation. The group tourism included only easy access dive sites, although diving is possible everywhere except in the marine reserve. Recreation was not included as separate group, even though recreation at the public beaches Pink beach, Donkey beach, Playa Frans, Boka Slagbaai, Playa Funchi, Playa Benge and Boka Bartol is an important resource use. Reason was that these beaches are scattered along the leeward coast of Bonaire and therefore not likely to form a uniform group. In addition, survey sites were not always exactly in front of a beach smaller in size and therefore not an accurate measurement.

4.2 Functional value analysis of fish functional groups

As explained in chapter 2.2.3 functional value is defined as the importance of a habitat to an ecological function. The importance is measured as the representation of fish and coral functional groups in each habitat location at an ordinal scale, based on fish abundance and occurrence and benthic cover. Fish functional groups included in the survey and their functional roles are elaborated in chapter 4.2.1. Levels set for the ordinal scaling are explained in chapter 4.2.2, as well as the resulting matrix C showing for each functional group the functional value at each habitat location and the resulting maps of functional values on a spatial scale. In chapter 4.2.3 the results of the non-parametric Kruskal Wallis tests on group differences between resource use groups in the representation of fish functional groups are presented.

4.2.1 Fish functional groups and functional roles

The 89 fish species included in the survey were selected based on the functional groups identified in chapter 3.3.2 and based on species occurrence on Bonaire. Species occurrence was determined by taking species included in other surveys on Bonaire, such as by Steneck and Arnold (2009) and IUCN (2011). For an overview of fish species included in the survey is referred to appendix B. A summary of the families included in the fish functional groups is given in table 10.

Table 10. Fish families included in fish functional groups and other indicators of ecosystem functioning.

FISH FUNCTIONAL GROUPS AND OTHER INDICATORS	
1.1	Escavating and scraping herbivores: *Scaridae* (parrotfish)
1.2	Denuding herbivores: *Acanthuridae* (surgeonfish)
1.3	Farming herbivores: *Pomacentridae* (damselfish)
2.	Planktivores: *Pomacentridae* (chromis)
3.1 3.2	Omnivores: *Haemulidae* (grunts) and *Lutjanidae* (snappers)
4.1 4.2 4.3	Piscivores: *Serranidae* (groupers) *Carangidae* (jacks) and 8 predators from 7 families
5.	Fish biodiversity: above 57 species plus 32 other species from 17 families
6.	Fish abundance: all 89 species from 31 families
7.	Fish maximum size: Serranidae and large Lutjanidae and Carangidae (>80cm)

The functional role of the above functional groups to support key ecosystem functions and sustain ecosystem services has been elaborated in chapter 3 and is not further discussed here. The classification of herbivores in functional groups of excavating and scraping herbivores, denuding herbivores and farming herbivores was mentioned in chapter 3, but is explained in more detail here.
Herbivores were based on their functional role in other ecosystem processes, not just categorized based on their trophic guild, but also based on their feeding range, feeding method and diet. Herbivorous fish functional groups were first classified based on feeding range in:

- Farming herbivores
- Roving herbivores, which was further classified based on their diet in:
    - Browsing herbivores
    - Grazing herbivores, which was further classified based on their feeding method in:
        - Scraping herbivores
        - Excavating herbivores
        - Denuding herbivores

Roving herbivores are foragers that feed over large distances of substratum, such as parrotfish, surgeonfish (Ceccarelli et al., 2011) and chubs (Ferreira and Goncalves, 2006). Farming herbivores are territorial herbivores, primarily damselfish, which defend feeding territories from foragers (Ceccarelli et al., 2011). Roving herbivores can be further classified in two functional groups based on the algae they eat: grazers and browsers (Hoey and Bellwood, 2010). Browsers consistently feed on erect macro-algae (Green and Bellwood, 2008; Hoey and Bellwood, 2010). They remove only the algae and associated epiphytic material. They have an important functional role in reducing coral overgrowth and shading by macro-algae (Green and Bellwood, 2008). Grazers feed primarily on the epilithic algal matrix, or turf algae (Hoey and Bellwood, 2010), and can be further classified in three functional groups based on the way they eat: scrapers, excavators and denuders (Steneck, 2001; Green and Bellwood, 2008). Scrapers take non-excavating bites and remove turf algae, sediment and other loose material by cropping and scraping the coral surface. Their functional role is limiting the establishment and growth of macro-algae by removing turf algae and cleaning the substratum for coral larvae settlement and coral recruitment. They have a minor role in bioerosion and process only existing and not new sediment. Excavators take deeper bites from the coral surface and also remove dead coral. Their functional role is similar to scrapers, but in addition they have a major role in bioerosion (Green and Bellwood, 2008). Denuders do not bite into coral structures and just remove turf algae, so they do not have a functional role in bioerosion and in coral recruitment by cleaning the substratum (Steneck, 2001), but they do reduce coral overgrowth and shading by macro-algae (Green and Bellwood, 2008).

4.2.2 Ordinal scaling and mapping of fish functional values in survey locations

Ordinal scaling of the standardized dataset of numbers of fish per 100 m^2 for each functional group was done to assign semi-quantitative ordinal scale levels to each functional group at each survey location.

The ordinal scale for fish functional groups contained four levels: 3=high, 2=medium, 1=low and 0=no representation. To set appropriate levels, secondary quantitative data were reviewed. The studies of Steneck and Arnold (2009) and IUCN (2011) provided the most relevant data, as those studies took place on Bonaire and included most species that were included in the snorkel survey. Quantitative data from the meta-analysis of Harborne et al. (2006) provided also a good reference, for those species that were not included in studies on Bonaire. For a specification of which references were used for the ordinal scaling of which species is referred to appendix B. After the ordinal scaling of the dataset from numbers of fish per 100m^2 to level 0 to 3, a check was done if ordinal scale levels were realistically set based on more or less equal percentage occurrence per level. Adjustments were made as described in chapter 2.5.2, resulting in the final ordinal scale levels as shown in table 11.

Table 11. Ordinal scale levels of fish abundance in numbers of fish/100m^{2}.
Fish maxium size is in cm and fish biodiversity in numbers of fish.

FUNCTIONAL GROUPS	Low	Medium	High
PARROTFISH - *SCARIDAE*	2	2-6	6
SURGEONFISH - *ACANTHURIDAE*	4	4-14	14
DAMSELFISH - *POMACENTRIDAE*	1	1-10	10
CHROMIS - *POMACENTRIDAE*	5	5-20	20
GRUNTS - *HAEMULIDAE*	1	1-10	10
SNAPPERS - *LUTJANIDAE*	1	1-6	6
GROUPERS - *SERRANIDAE*	1	1-3	3
JACKS - *CARANGIDAE*	1	1-2	2
OTHER SPECIES	1	1-2	2
FISH MAXIMUM SIZE	20	20-50	50
FISH ABUNDANCE	20	20-50	50
FISH BIODIVERSITY	17	17-21	21

The result of the ordinal scaling of the fish dataset is presented in Matrix C.1 in appendix E and shows fish functional group representation per habitat and location. This matrix was used as input to visualize the representation of each functional group on the map of Bonaire and resulted in 24 maps. The fish biodiversity and parrotfish abundance maps are shown in figure 8 and 9 and discussed here as an example what information these maps provide. For a complete overview of all maps is referred to appendix F, because the maps have not been analyzed on an individual basis in detail as they were an intermediate step in the functional value analysis of the importance of habitats for ecosystem services.

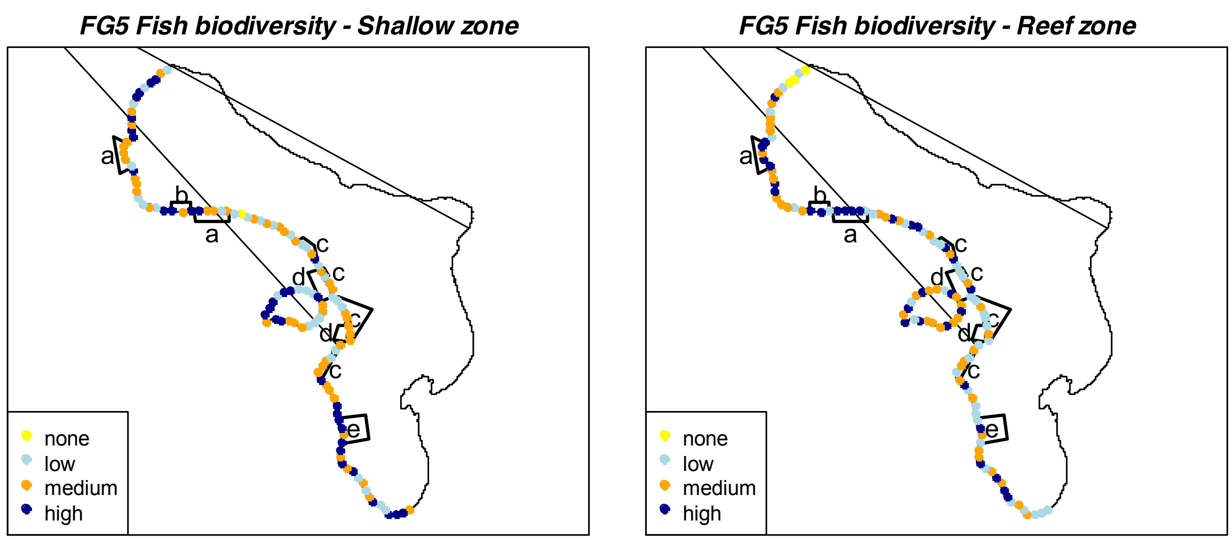


Figure 8. Functional value maps of shallow and reef habitats measured by the level of representation of biodiversity of fish species (FG5 refers to Functional Group indicator number 5 as listed in table 10). Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area of Sabadeco, Hato, Kralendijk and Belnem, d=fish reserves and e=Cargill salt production.

Figure 8 shows that certain habitats and locations provide higher levels of biodiversity of fish species than others. In the shallow zone the remote north and south and the parts of Klein Bonaire furthest away from the mainland have higher biodiversity, in the reef zone the marine reserves (label a) have a remarkably higher biodiversity. The residential area (label c) still have medium to low biodiversity which could be explained by the presence of piers and the shelter this provides for large schools of fish. The fish reserves (label d) do not seem to be very different from the adjacent locations.

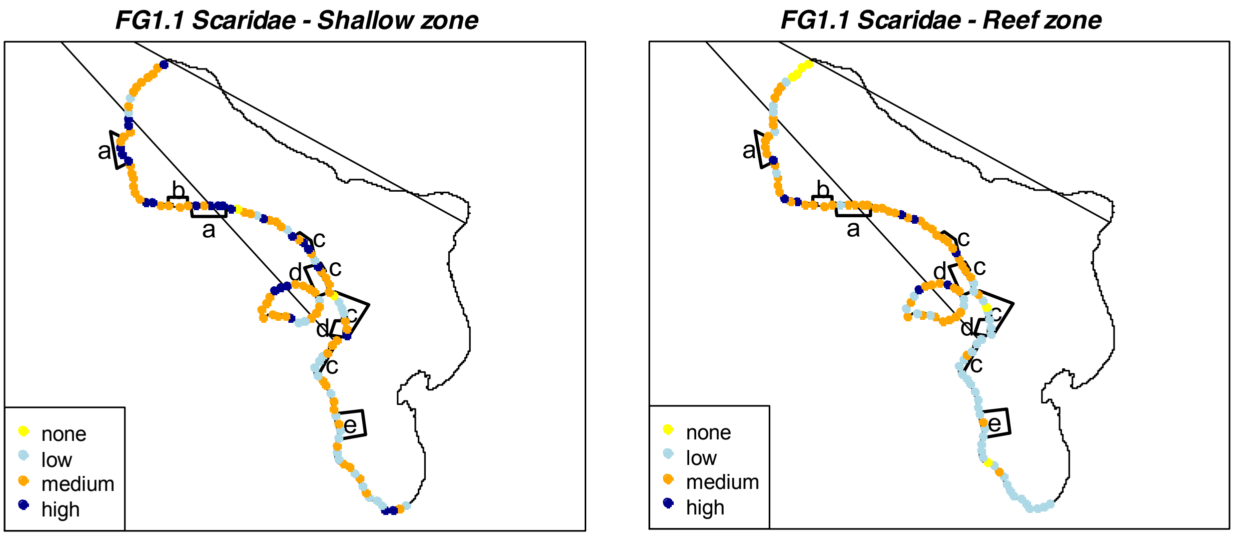


Figure 9. Functional value maps of shallow and reef habitats measured by the level of representation of parrotfish, the functional group of escavating and scraping herbivores (FG1.1 refers to Functional Group indicator number 1.1 as listed in table 10). Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area of Sabadeco, Hato, Kralendijk and Belnem, d=fish reserves and e=Cargill salt production.

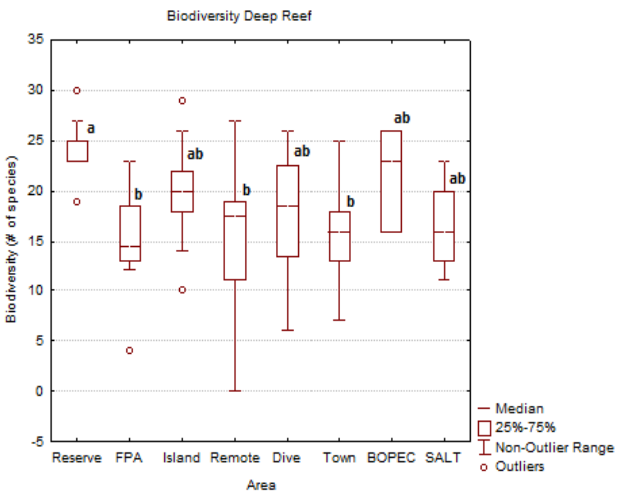
Figure 9 shows that in the shallow zone the abundance of parrotfish is highest in or near the marine reserves (label a) and in front of Sabadeco (label c). In the reef zone there are remarkably low values all along the south-western coast.

4.2.3 Differences in fish functional values between resource use groups

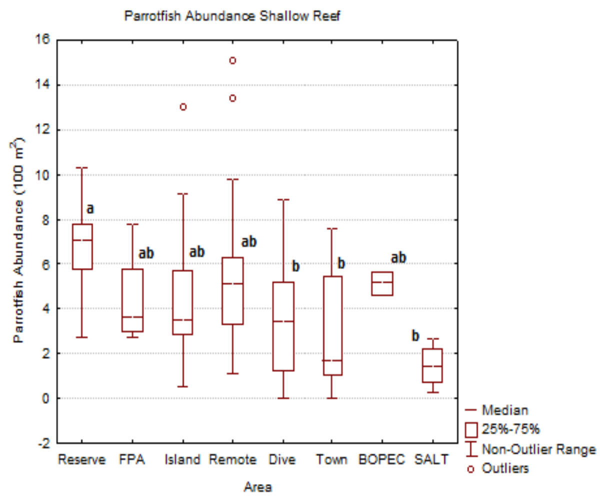
The fish functional value maps show many different patterns of high, medium and low functional values for each functional group. The labels on the map help to visualize where the different marine and coastal resource use groups are located that can explain some of these different patterns. In addition, statistical analyses were performed to examine similarities and differences between locations. The multivariate analyses used were cluster dendrograms and multi dimensional scaling, but both did not result in clusters of locations with similar functional values for all functional groups combined. Therefore a group difference analysis was carried to examine if the predefined resource use groups as identified in chapter 4.1 explained the differences between locations. The statistical tests used were the non-parametric Kruskal Wallis test combined with multiple comparisons test.

In figure 10 two of these tests are shown as example, while for the complete set of tests is referred to appendix G for group differences in the shallow zone and to appendix H for group differences in the reef zone. Figure 10 A and B present significant differences between resource use groups related to fish biodiversity in the reef zone and figure 10 C and D present significant differences related to parrotfish abundance in the shallow zone. These two examples were chosen, because they show significant differences and because these statistical tests underpin the visual assessment of differences in the functional value maps for fish biodiversity (figure 8) and parrotfish (figure 9).

(A) Fish Biodiversity (# spp.): KW-H(7;116)=26,6393; p=0,0004



(C) Parrotfish Abundance (100 m^2): KW-H(7;116)=23,986; p=0,0011



(B) Fish Biodiversity multiple comparisons test

Multiple Comparisons p values (2-tailed); Biodiversity (# of species) (DefinitiefFi
Independent (grouping) variable: Area
Kruskal-Wallis test: H (7, N= 116) =26,63930 p =,0004

Depend.: Biodiversity (# of species	Reserve R:98,333	FPA R:41,375	Island R:72,381	Remote R:45,962	Dive R:59,339	Town R:44,794	BOPEC R:81,000	SALT R:47,250
Reserve		0,01375	1,00000	0,00158	0,06939	0,00315	1,00000	0,32146
FPA	0,01375		0,74151	1,00000	1,00000	1,00000	1,00000	1,00000
Island	1,00000	0,74151		0,20764	1,00000	0,33397	1,00000	1,00000
Remote	0,00158	1,00000	0,20764		1,00000	1,00000	1,00000	1,00000
Dive	0,06939	1,00000	1,00000	1,00000		1,00000	1,00000	1,00000
Town	0,00315	1,00000	0,33397	1,00000	1,00000		1,00000	1,00000
BOPEC	1,00000	1,00000	1,00000	1,00000	1,00000	1,00000		1,00000
SALT	0,32146	1,00000	1,00000	1,00000	1,00000	1,00000	1,00000	

(D) Parrotfish abundance multiple comparisons test

Multiple Comparisons p values (2-tailed); Parrotfish Abundance (100 m²) (DefinitiefF
Independent (grouping) variable: Area
Kruskal-Wallis test: H (7, N= 116) =23,98603 p =,0011

Depend.: Parrotfish Abundance (100 m²)	Reserve R:89,056	FPA R:61,313	Island R:60,810	Remote R:71,135	Dive R:48,250	Town R:41,853	BOPEC R:75,000	SALT R:20,000
Reserve		1,00000	0,98056	1,00000	0,04319	0,01853	1,00000	0,01772
FPA	1,00000		1,00000	1,00000	1,00000	1,00000	1,00000	1,00000
Island	0,98056	1,00000		1,00000	1,00000	1,00000	1,00000	0,73152
Remote	1,00000	1,00000	1,00000		0,34920	0,14688	1,00000	0,12992
Dive	0,04319	1,00000	1,00000	0,34920		1,00000	1,00000	1,00000
Town	0,01853	1,00000	1,00000	0,14688	1,00000		1,00000	1,00000
BOPEC	1,00000	1,00000	1,00000	1,00000	1,00000	1,00000		0,90304
SALT	0,01772	1,00000	0,73152	0,12992	1,00000	1,00000	0,90304	

Figure 10. Group difference analysis of functional groups Fish Biodiversity (FG5) in the reef zone habitats and Parrotfish Abundance (FG1.1) in the shallow zone habitats.
Graph (A) shows a boxplot with median values of the eight predefined resource use groups. The Kruskal Wallis test shows there is a significant difference (p=0.0004) between groups, with sample size N=116 and df=7. Table (B) shows the corresponding Multiple Comparisons test with highlighted in red significant differences between Marine reserves compared to Fish reserves (FPA), Remote area and Residential area (Town).
Graph (C) shows a boxplot with median values of the eight predefined resource use groups. The Kruskal Wallis test shows there is a significant difference (p=0.0011) between groups, with sample size N=116 and df=7. Table (D) shows the corresponding Multiple Comparisons test with highlighted in red the significant differences between Marine reserves compared to Dive tourism area (Dive), Residential area (Town) and Industrial salt production area (Salt).

Unfortunately most of the other group difference tests in appendix G and H did not result in significant differences, only surgeonfish and damselfish in both the shallow and the deep zone did. Appendix G shows a significant difference in surgeonfish abundance in the shallow zone of Klein Bonaire and remote area and in damselfish abundance in the shallow zone of Klein Bonaire compared to dive tourism area, residential area and industrial salt production area. Appendix H shows a significant difference in surgeonfish abundance in the reef zone of the marine reserves and dive tourism area and in damselfish abundance in the reef zone of Klein Bonaire compared to remote area.

4.3 Functional value analysis of coral and other benthic functional groups

Similar as for fish, functional groups of corals and other benthos included in the survey are elaborated in chapter 4.3.1. Levels set for the ordinal scaling are explained in chapter 4.2.2, as well as the resulting matrix D showing for each functional group the functional value at each habitat location and the resulting maps of functional values on a spatial scale.

4.3.1 Coral and other benthic functional groups and functional roles

The benthic composition including coral species and other substrate cover, were selected based on their functional role as identified in chapter 3.3.2. An overview of the species within functional groups and other indicators is given in table 12.

Table 12. Benthic species included in benthic functional groups and other indicators of ecosystem functioning.

CORAL FUNCTIONAL GROUPS AND OTHER INDICATORS	
8.1 8.2	Branching coral cover: *Acropora palmata (elkhorn) , Acropora cervicornis (staghorn)*
9.1 9.2	Massive coral cover: *Montastrea annularis, Montastrea faveolata*
10.	Coral Cover
11.	Macro algal cover
12.	Gorgonian and other soft coral cover
13.	Sponge cover
14.1 14.2 14.3	Sand, coral rubble and rock cover
15.	Coral biodiversity
16.	Coral maximum size
17.	Structural complexity
18.1 18.2	Coral mortality and bleaching
19.	Coral bite marks from parrotfish
20.	Cyanobacteria
21.	*Trididemnum solidum* (tunicate)
22.	*Diadema antillarum* (sea urchin)

Functional group 21 and 22 were omitted from the analysis, because nuisance tunicate species *Trididemnum solidum* and grazing and bioeroding sea urchin species *Diadema antillarum* were only present at very few locations.

4.3.2 Ordinal scaling and mapping of benthic functional values in survey locations

Ordinal scaling of percentage cover of benthic functional groups was done to assign semi-quantitative ordinal scale levels to each functional group at each survey location. The ordinal scale for benthic functional groups contained five levels: 4=high, 3=medium, 2=low, 1=present and 0=no representation.

This was one level more than for fish, to enable assigning level 1 or 'present' to very low cover of less than one percent.

The result after ordinal scaling of the benthic dataset is presented in Matrix C.2 in appendix E and shows benthic functional group representation per habitat and location. This matrix was used as input to visualize the representation of each functional group on the map of Bonaire and resulted in 36 maps for which is referred to appendix I. Some maps of crucial functional groups for coastal protection, habitat provisioning and the long-term structural integrity of the coral reef are discussed here and presented in figure 11, 12 and 13.

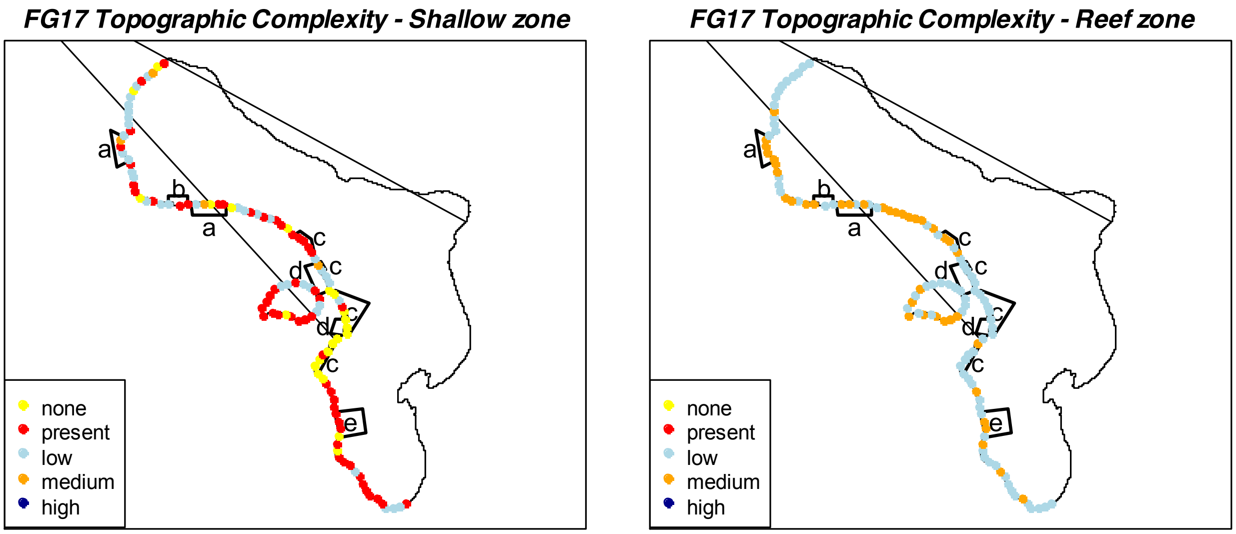


Figure 11. Functional value maps of shallow and reef habitats measured by the level of structural complexity of the substrate (FG17 refers to Functional Group indicator number 17 in table 12). Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area of Sabadeco, Hato, Kralendijk and Belnem, d=fish reserves and e=Cargill salt production.

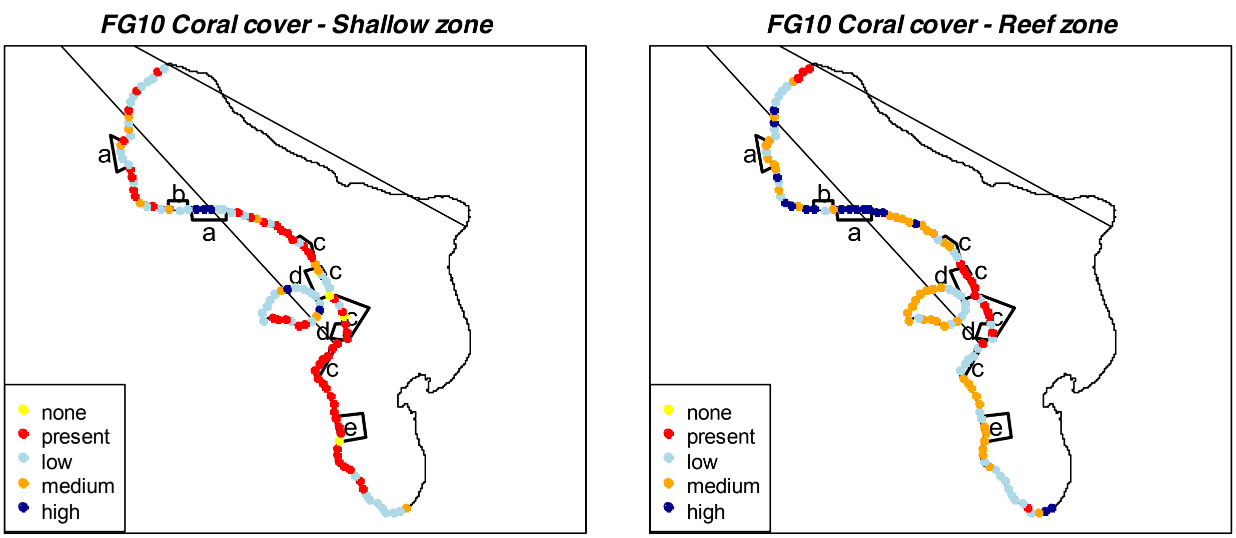


Figure 12. Functional value maps of shallow and reef habitats measured by the level of coral cover (FG10 refers to Functional Group indicator number 10 in table 12). Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area of Sabadeco, Hato, Kralendijk and Belnem, d=fish reserves and e=Cargill salt production.

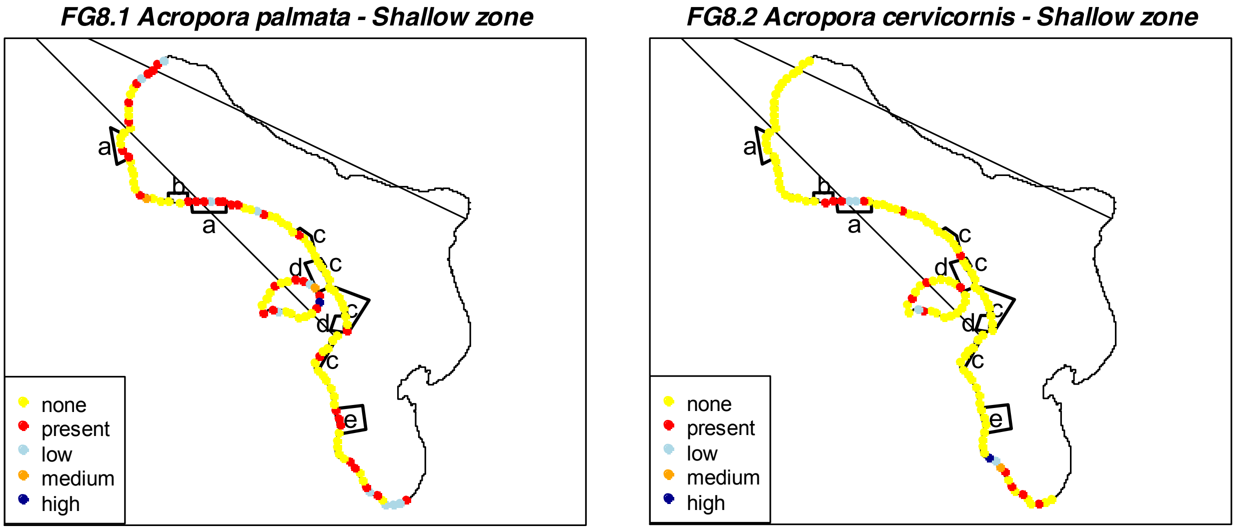
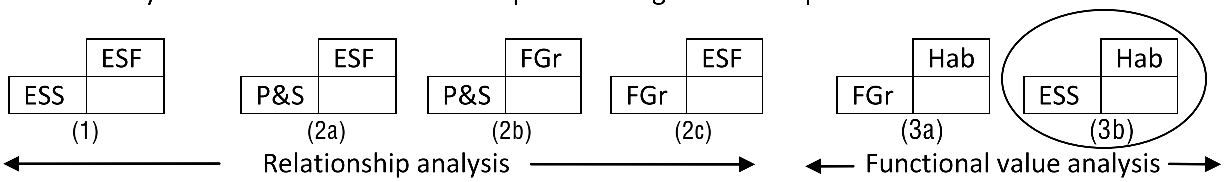


Figure 13. Functional value maps of shallow habitats measured by the level of branching Acropora spp. (FG8.1 and FG8.2 refers to Functional Group indicator numbers 8.1 and 8.2 in table 12). Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area of Sabadeco, Hato, Kralendijk and Belnem, d=fish reserves and e=Cargill salt production.

The topographic complexity as presented in figure 11 is very low to non-existing in the shallow zone habitats in the south-western coast of Bonaire and Klein Bonaire and slightly higher at the marine reserves and one of the fish reserves. This corresponds with figure 12, showing a high coral cover in the shallow zone in the marine reserves and the very low to non-existing coral cover in the shallow zone in the south-western coastline. These shallow zones are characterized by high sand cover (see FG14.1 in appendix I). As figure 13 shows, the high coral cover in the shallow zone in one of the marine reserves and parts of Klein Bonaire is partially explained by the presence of *Acropora spp.* as well as *Montastrea annularis* (see FG9.1 in appendix I). Figure 13 also shows that *Acropora palmata* and to a lesser extent also *Acropora cervicornis* show some recovery in the far south and far north. *Acropora spp.* cover in the reef zone is virtually non-existent as it is a typical shallow-water species and therefore not shown here.

5 RESULTS FUNCTIONAL VALUE ANALYSIS

In this chapter the results from the snorkel survey as presented in Matrices C.1 and C.2 are combined with relationship Matrices A and B from chapter 3 to answer the main research question 'What is the functional value of coral reefs on Bonaire to ecosystem services, measured as the representation of crucial functional groups that support key ecological processes and biophysical structures that provide ecosystem services (and ultimately support coral reef resilience)?'. This is the last step in the functional value analysis as illustrated below and explained in figure 7 in chapter 2.5.



5.1 Functional value of habitats and locations to deliver ecosystem services

In the last step of the functional value analysis each ecosystem service was linked to one or more functional groups that underpin the provision of that service. Then for each habitat and location a functional value was calculated based on the sum of functional values of selected functional groups. After numerical functional values were transformed into a semi-quantitative ordinal scale, these semi-quantitative functional values of 116 locations in two coral reef habitats were mapped to visualise how each location supports the delivery of the twelve ecosystem services.

5.1.1 Assigning functional values to habitats and locations

For each ecosystem service the functional groups that underpin the provision of that service were selected. This was done in a similar manner as in chapter 3.3.3 by consolidating the results from matrix A (relationship services – functions) and matrix B (relationship functional groups – services) to find the functional groups that underpin each service. For example, for the service shoreline protection an essential function is modification of wave and current patterns (matrix A). Structural complexity is an important factor determining wave energy dissipation and branching *Acropora palmata* and massive *Montastrea spp.* are important coral functional groups. Larger coral colonies and higher coral cover also increase wave energy dissipation (matrix B).

A weighting factor was assigned to each functional group to account for the importance of functional groups. Using the above example, structural complexity, Acropora palmata cover and Montastrea spp. cover were given the highest weighting factor 2. Stony coral cover was given a weighting factor 1, because coral cover is implicitly included in the functional value of structural complexity, branching and massive coral cover. Soft coral cover was also given a weighting factor 1, because they are less able to dissipate wave energy. Coral maximum size was given a weighting factor 1, because this indicator was measured for Montastrea colonies and is therefore also implicitly included in the functional value of Montastrea coral cover.

This analysis of Matrix A and B was done for each ecosystem service and resulted in table 13. Table 13 shows which functional groups are considered essential indicators for ecosystem service delivery, marked with an 'x' and given the highest weight, and which functional groups were given a lower weight, marked with an 'o'. Weighting factors chosen were 1 and 2, but the calculation spreadsheet was designed such that it provides for other values to be entered. The spreadsheet also provides for negative values, because for example high sand cover has a negative functional relationship with shoreline protection.

Table 13. Functional groups and other indicators that underpin delivery of ecosystem services.

x = essential functional relationship (high weigth)
o = supporting functional relationship (low weight)
-x = negative functional relationship

ECOSYSTEM SERVICES	FUNCTIONAL GROUPS AND OTHER INDICATORS: 1.1 Scaridae	1.2 Acanthuridae	1.3 Pomacentridae (damsel)	2 Pomacentridae (chromis)	3.1 Haemulidae	3.2 Lutjanidae	4.1 Serranidae	4.2 Carangidae	4.3 Predators other	5 Fish biodiversity	6 Fish abundance	7 Fish maximum size	8.1 Acropora palmata	8.2 Acropora cervicornis	9.1 Montastrea annularis	9.2 Montastrea faveolata	10 Coral Cover	11 Macro algae cover	12 Gorgonian cover	13 Sponge	14.1 Sand cover	14.2 Rubble cover	14.3 Rock cover	15 Coral biodiversity	16 Coral maximum size	17 Structural complexity	18.1 Coral mortality	18.2 Coral bleaching	19 Coral bite marks	20 Cyanobacteria
1. Seafood products	o	o	o	o	x	x	x	x				x																		
2. Raw material for production lime and cement																	x								o					
3. Raw material for medecines																	o	o	o	o				x						o
4. Shoreline protection													x		x	x	o								o	x				
5. Waste assimilation																														x
6. Biological maintenance of resilience	x	x					o	o	o																					
7. Maintenance of habitats													o	o	o	o	o	o								x			o	
8. Maintenance of biodiversity and genetic diversity										x	o						o							x						
9. Aesthetic values and artistic inspiration																	x				x									
10. Support of tourism and recreation										x	x	x					x							x	x					
11. Support of cultural identity	o	o	o	o	x	x	x	x				x									x									
12. Educational and scientific information services	o	o	o	o	o	o	o	o	o	x	x	o	o	o	o	o	x	x	o	o				x	o	x	o	x	o	o

Table 13 was used to calculate the functional value of each habitat location to deliver each ecosystem service. Using the same example again, the functional value to provide coastal protection is the sum of all functional values of selected functional groups multiplied by their weighting factor. For example: functional value structural complexity (0-4) x 2 + functional value coral cover (0-4) x 1 + etc.
The resulting numerical functional value of each habitat location to deliver each service was scaled into a semi-quantitative ordinal scale with levels high, medium, low and none, using the ordinal scale levels for each service as shown in table 14.

Table 14. Ordinal scale levels of functional values per ecosystem service.

ECOSYSTEM SERVICES	Low	Medium	High
1. Seafood products	> = 14	15-20	= > 21
2. Raw material for production lime and cement	> = 6	7-9	= > 10
3. Raw material for medecines	> = 10	11-17	= > 18
4. Shoreline protection	> = 16	17-26	= > 27
5. Waste assimilation	> = 4	5-6	= > 7
6. Biological maintenance of resilience	> = 7	8-14	= > 15
7. Maintenance of habitats	> = 10	11-19	= > 20
8. Maintenance of biodiversity and genetic diversity	> = 9	10-15	= > 16
9. Aesthetic values and artistic inspiration	> = 8	9-12	= > 13
10. Support of tourism and recreation	> = 18	19-30	= > 31
11. Support of cultural identity	> = 18	19-26	= > 27
12. Educational and scientific information services	> = 37	38-72	= > 73

The ordinal scale levels were set based on the following principles: 0 (= no functional value) was assigned if the total numerical functional value was zero or if the sum of the essential functional group values was zero; 1 (= low functional value) was assigned if the total numerical functional value was equal to or lower than the sum of all functional groups having value 1 multiplied by their weighting factor; 2 (=

medium functional value) was assigned if the total numerical functional value was equal to or lower than the sum of all functional groups having value 2 multiplied by their weighting factor; 3 (= high functional value) was assigned for numerical functional values with a higher sum than the upper bound of the medium functional value.
The resulting matrix D in appendix E shows the functional values of all 232 sites to all ecosystem services on a scale from 0 to 3. This was used to produce functional value maps.

5.1.2 Functional value maps of habitats to support ecosystem services

The 24 functional value maps show for the two coral reef habitats, the shallow zone and the reef zone, what are the functional values on a spatial scale. Each survey location has a high, medium, low or no importance in the delivery of the 12 ecosystem services. This shows which parts of the island are ecologically important for which ecosystem service. The maps were analyzed by comparing the outcome with the resource use groups as identified in chapter 4.1, whereby labels a-e in the maps refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area of Sabadeco, Hato, Kralendijk and Belnem, d=fish reserves and e=Cargill salt production. The fish and benthic functional value maps of appendix F and I were also used to explain the final maps as presented in figure 14 to figure 24 and discussed for each ecosystem service below:

<u>Ecosystem Service 1: Seafood</u>

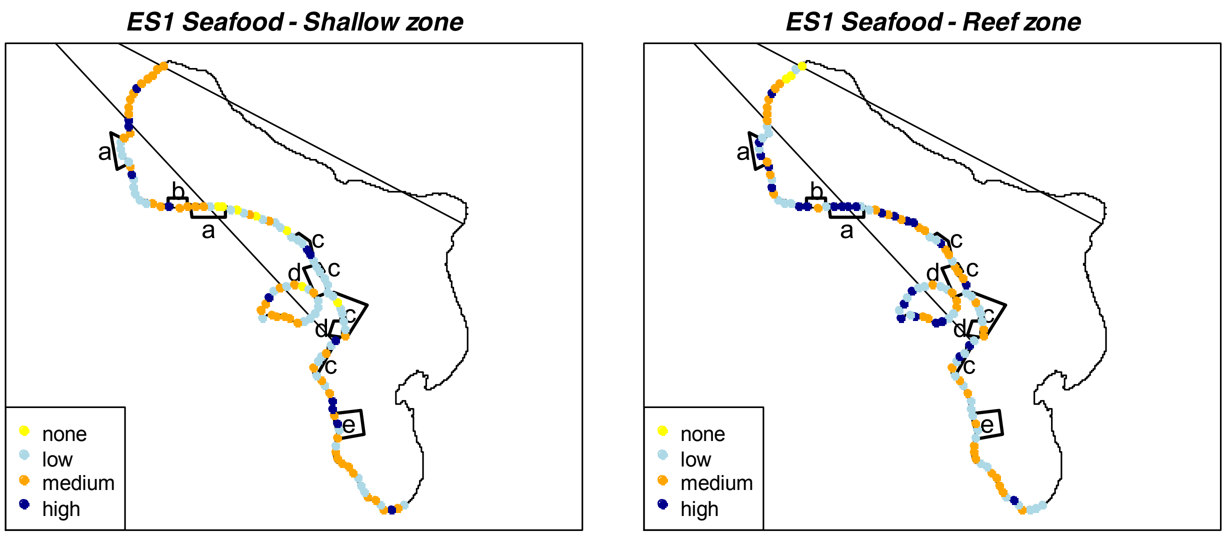


Figure 14. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Seafood.

The remote area on Bonaire and Klein Bonaire and the area between Bopec (b) and the adjacent marine reserve (a) have a higher functional value to support fisheries than the residential area. This is especially true for the shallow zone and to a lesser extent for the reef zone, which also has medium to high functional value at Sabadeco and Hato residential area. The shallow zone in the fish reserves does not distinguish itself from adjacent residential area, but the reef zone in the fish reserves does have a slightly higher value. The area with the highest functional value can be observed in the reef zone on either side of Bopec, with the marine reserve where no activity is allowed to the right and a small area to the left where activity is probably also limited due to the proximity to the large oil tankers. The yellow area in the reef zone in the far north can be explained by the very gradual slope of the shallow zone and a reef zone that was too far and too deep, hence no fish were recorded in the reef zone. The yellow dots in the shallow zone can be explained by the complete absence of grunts, snappers, groupers and jacks.

Ecosystem Service 2: Raw material for production of lime and cement

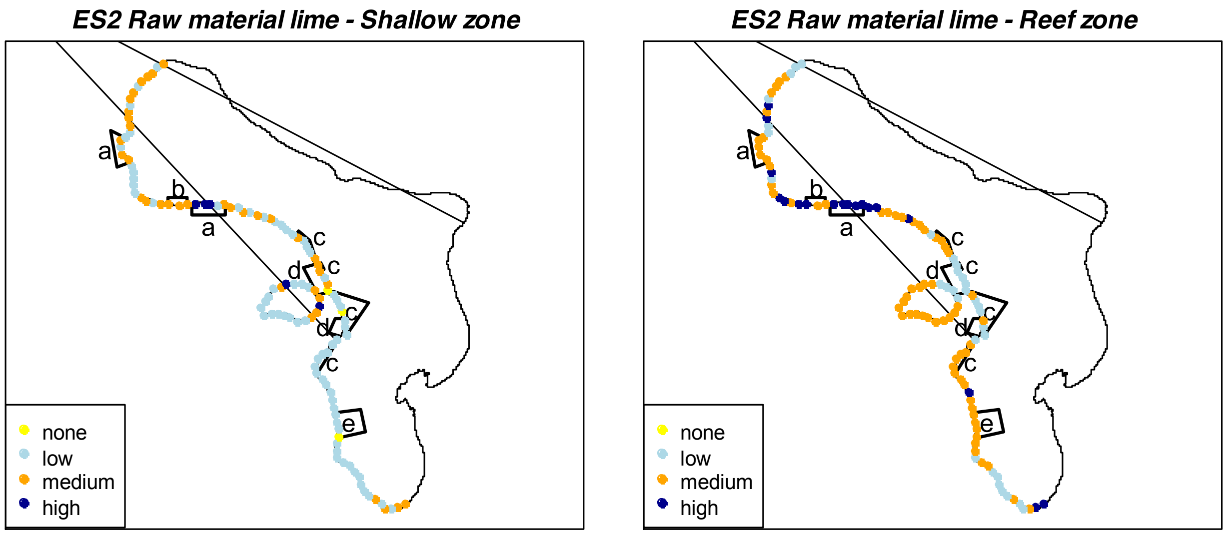


Figure 15. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Raw material for production of lime and cement.

This ecosystem service, extraction of lime, is prohibited from the coral reef and restricted from ancient reefs on land. Furthermore formation of limestone on land takes place over geological times, so it is difficult to link the current coral reef ecosystem to a service delivered in the very far future. However, the assumption is that areas with highest coral cover and largest coral colony size have the highest functional value for future delivery of raw material. As the maps show the shallow zone obviously has a lower functional value, and highest value in the reef zone can be observed near the marine reserve and in the far south. This area where occasional limestone mining takes place is in the northeast, which area was not included in the survey of this research.

Ecosystem Service 3: Raw material for medecines

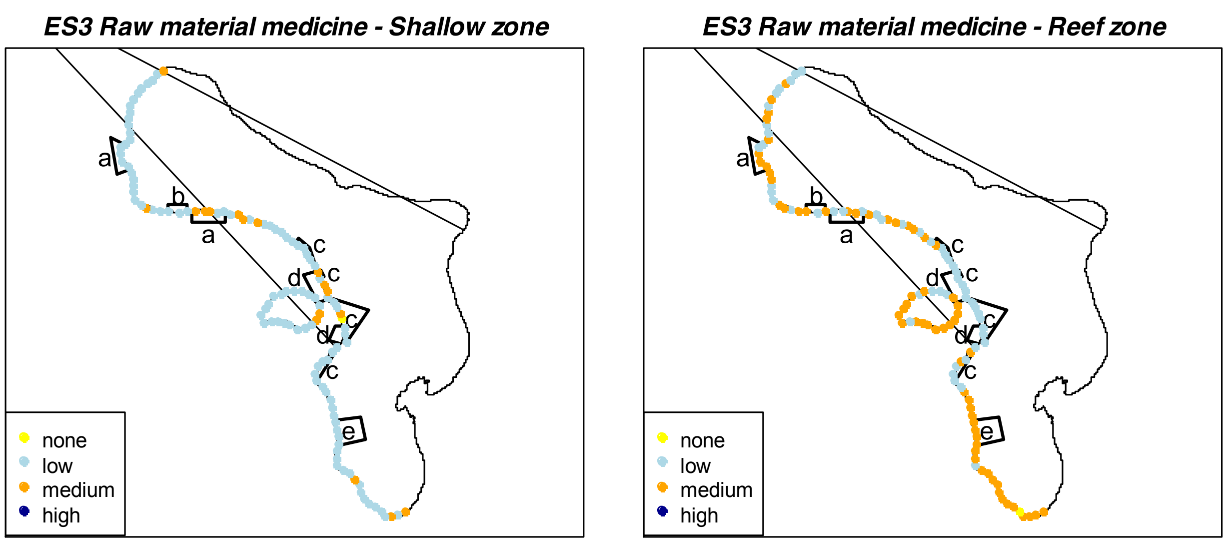


Figure 16. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Raw material for production of lime and cement.

This ecosystem service, extraction of compounds for the production of medicines, is another service that is currently not taking place in Bonaire. Besides, a wide range of benthos can be used for bioprospecting, ranging from cyanobacteria to seaweeds, sponges, molluscs, corals, gorgonians and sea anemones. Therefore it is difficult to link a specific benthic functional group or indicator to this ecosystem service. The most realistic choice would be biodiversity, as a higher diversity of species increases the availability of a wide range of potential compounds for next generations. However, the biodiversity indicator only includes coral biodiversity. Therefore also macro algae, cyanobacteria, soft coral and sponge cover have been included as their abundance also supports the availability of potential compounds for future generations. The resulting functional value maps are largely influenced by coral biodiversity, hard and soft coral cover, as the macro algae, cyanobacteria and sponge cover generally had value 0 to 1 (sea FG11, FG13 and FG20 in appendix I).

Ecosystem Service 4: Shoreline protection

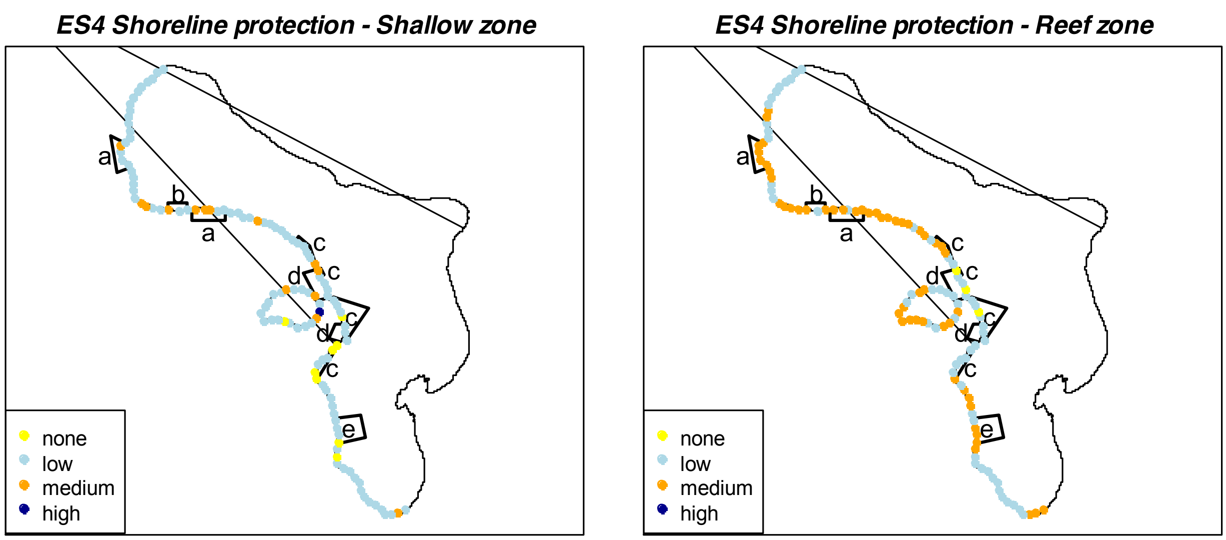


Figure 17. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Shoreline protection.

As mentioned in the previous chapter, shoreline protection is largely determined by *Acropora palmata* in the shallow zone and *Montastrea spp.* in the reef zone. These are isolated locations in the shallow zone, with one high functional value location on Klein Bonaire due to high representation of *Acropora palmata* (FG8.1 in appendix I). In the reef zone, there are large area of medium functional value due to medium to high representation of *Montastrea annularis* (FG9.1 in appendix I) and a medium level topographic complexity (FG17 in appendix I). The shoreline in the far north and far south and in the residential area are least protected.

Ecosystem Service 5: Waste assimilation

Waste assimilation is a difficult ecosystem service to measure, as the essential function to remove and breakdown excess nutrients and xenic compounds is mainly related to biological filtering of filter feeders and microbial processes. Since species with this functional role were merely not included in the survey, only cyanobacteria mats were selected as indicator of enhanced waste assimilation of excess nutrients. The resulting map shows hardly any medium to high representation of these cyanobacteria mats, and low representation is scattered around oil terminal Bopec, Boca Slagbaai, the beach north of the most northern marine reserve and dive sites east of the other marine reserve and at the southern part of Klein Bonaire.

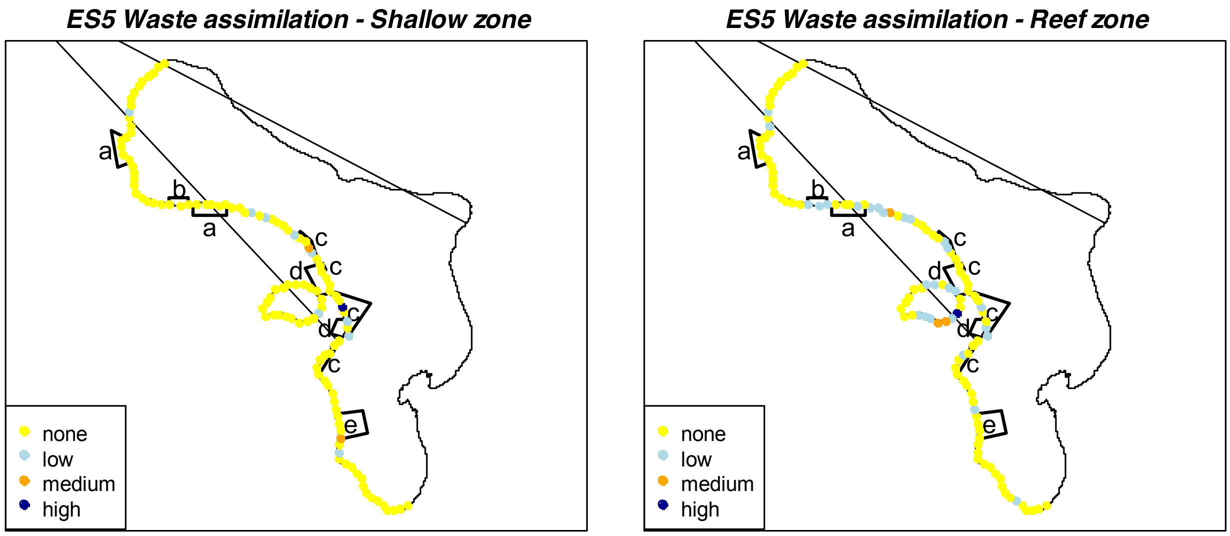


Figure 18. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Biological maintenance of resilience.

Ecosystem Service 6: Biological maintenance of resilience

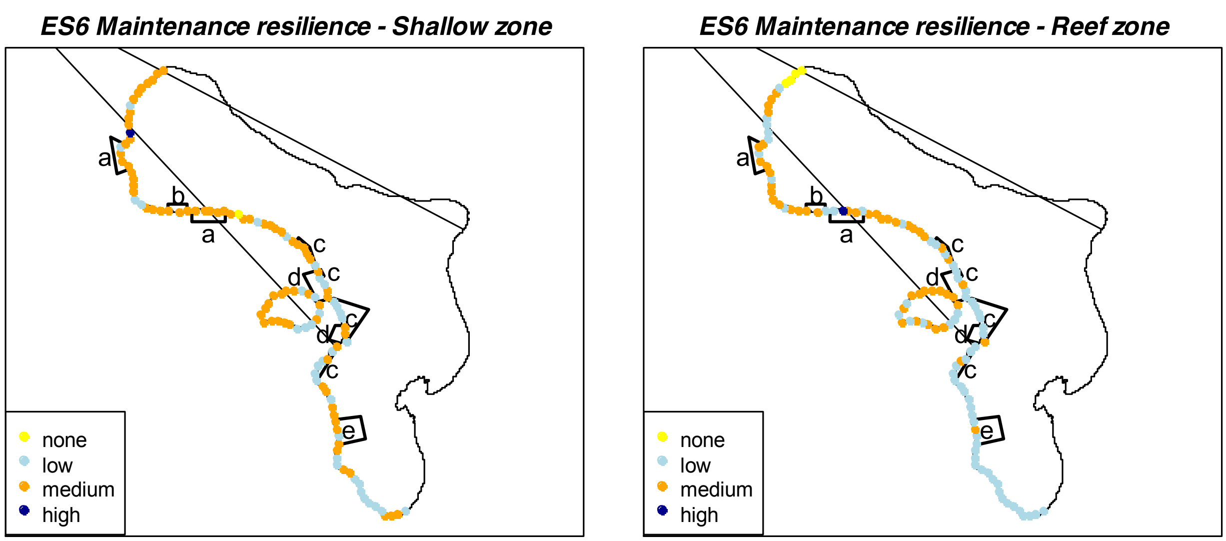


Figure 19. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Biological maintenance of resilience.

Resilience is defined as the capacity of an ecosystem to cope with disturbances without shifting from a coral-dominated state into an algae- or even rubble-dominated state. This is related to the maintenance of important ecosystem processes such as grazing by herbivores and abundant coral recruitment. Because the latter was not included in the survey, resilience is related to the representation of excavating, scraping and denuding herbivorous *Scaridae* and *Acanthuridae* species. The maps show resilience is highest north from the residential area and lowest in the south. This can be related to the higher sand cover and lower food availability of algal turf.

Ecosystem Service 7: Maintenance of habitats

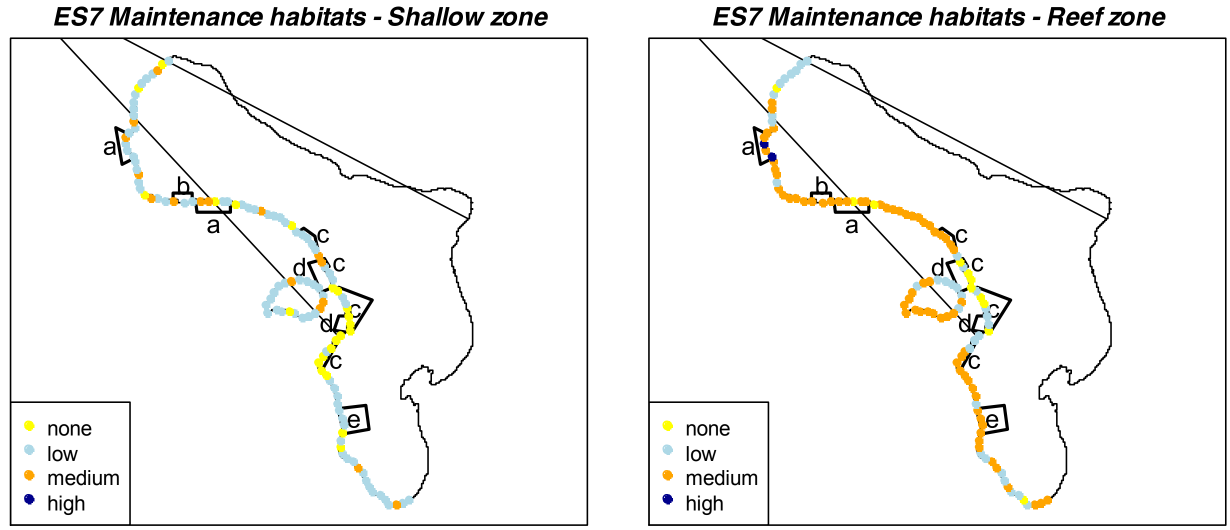


Figure 20. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Maintenance of habitats.

Most important indicator for the provision of micro- and macro-habitats is the topographic complexity. This topographic complexity is supported by the presence of *Acropora spp.* and *Montastrea spp.*, but also macro algae provide habitat and coral bite marks from parrot fish support the provision of bare substrate to enable coral larvae settlement. The maps clearly show that both the shallow and reef zone near residential area have no to low importance in habitat provision. The reef zone in the far north also has a low value, but this can be explained by the very gradual slope of the shallow zone and a reef zone that was too far and deep to properly include topographic complexity in the survey at these locations.

Ecosystem Service 8: Maintenance of biodiversity and genetic diversity

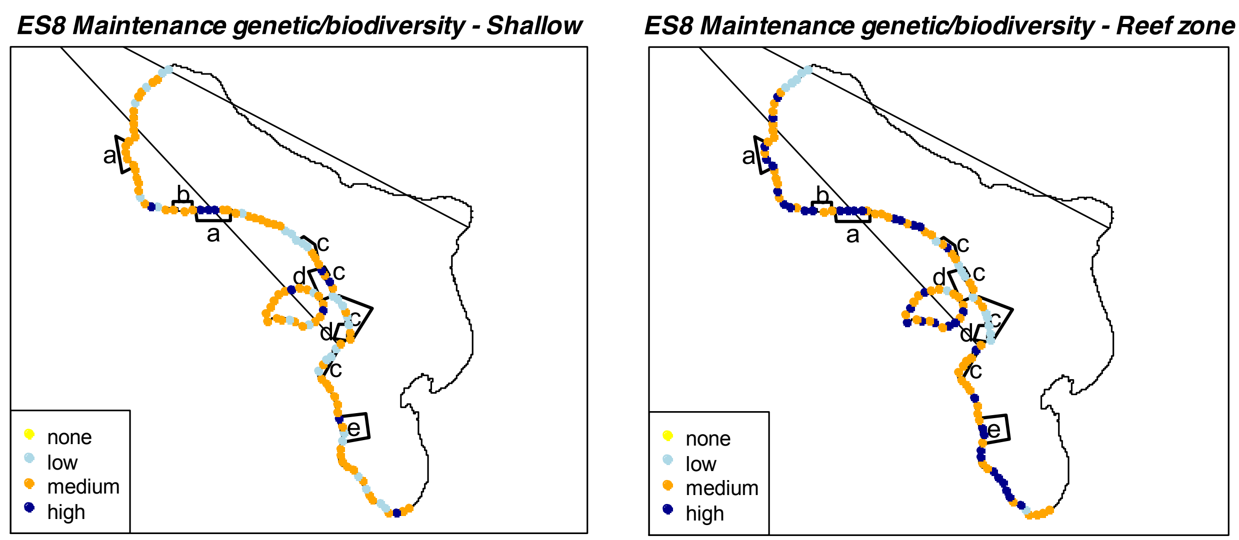


Figure 21. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Maintenance of biodiversity and genetic diversity.

For the maintenance of biological and genetic diversity this research focused on species diversity, which does not cover all scales of biodiversity, ranging from genes to the entire ecosystem. Species diversity incorporates the number of species and the relative abundance. Essential indicators for species diversity are fish and coral biodiversity, while total fish and coral abundance were selected as indicator to support relative abundance. Relative abundance refers to how common or rare a species is in relation to other species and says something about species evenness, which is not captured in total abundance, but it is assumed that total abundance is likely to have a positive relationship with relative abundance. The maps show that biodiversity is high in the marine reserves and in the reef zone in the remote south.

Ecosystem Service 9: Aesthetic values and artistic inspiration

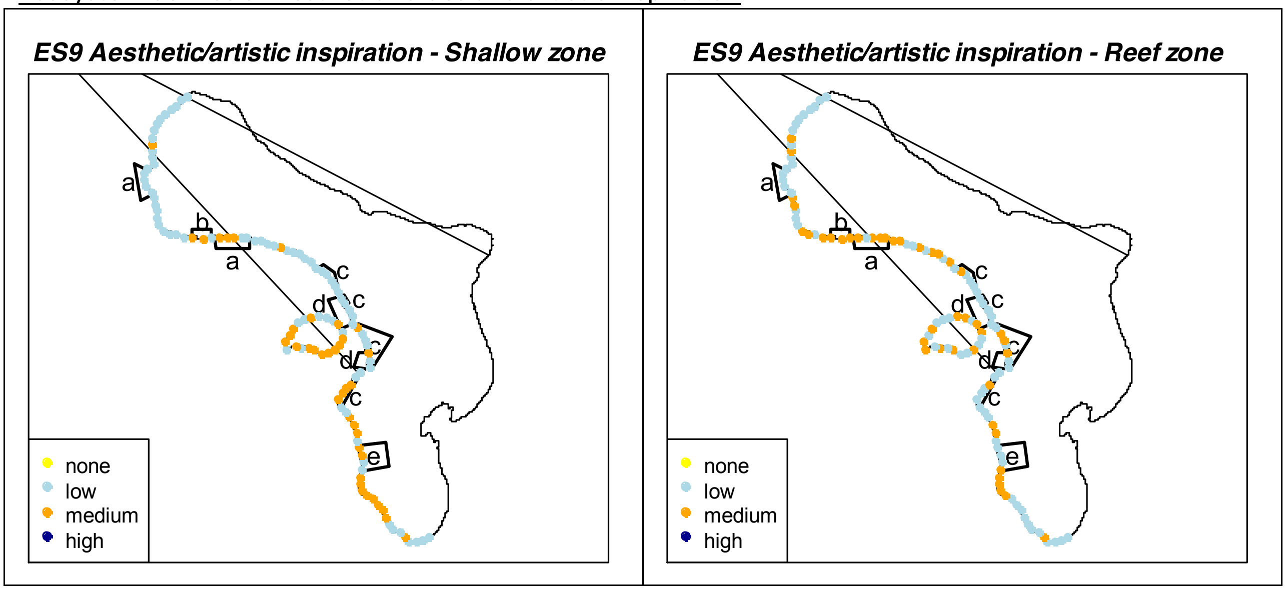


Figure 22. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Aesthetic values and artistic inspiration.

To appreciate aesthetic values of coral reefs, scenic views of this tropical coastal seascape and proximity to open space are essential. The functional groups of sand and coral cover are essentially providing the typical seascape in shades of blue. In the shallow zone this typical seascape is most prominent in the south-west due to the presence of a large shallow zone with beaches and sandy substrate. The other more isolated locations offering a medium amenity value are also near beaches like Boca Slagbaai and the beach at dive site 1000 steps. In the reef zone the area between Bopec and Sabadeco residential area has a medium amenity value, which is due to the higher coral cover that happens to be more near shore and in combination with the rocky coastline and cliffs offers scenic views.

Ecosystem Service 10: Support of tourism and recreation

The support of tourism and recreation on Bonaire focuses on biodiversity-based activities like diving, snorkelling and small-scale recreational fishing. For these activities essential functional groups that are appreciated by tourists are the more general indicators like fish and coral biodiversity, fish and coral abundance and large fish and coral colonies. The resulting maps show support of these activities is higher in the reef zone than in the shallow zone. Reefs north and south of the residential area and on Klein Bonaire have the highest (medium to high) functional value, with the largest area of high value in the marine reserves and on the other side of Bopec. These are non-use zones for tourists, so although value is highest these area cannot be appreciated by and as such do not support dive tourism.

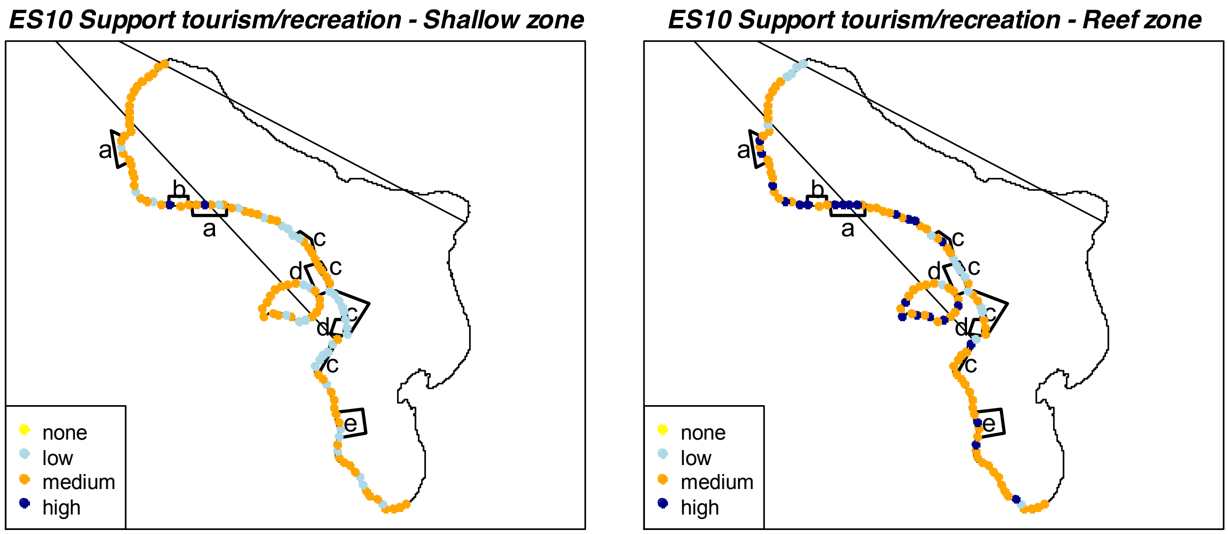


Figure 23. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Support of tourism and recreation.

<u>Ecosystem Service 11: Support of cultural identity</u>

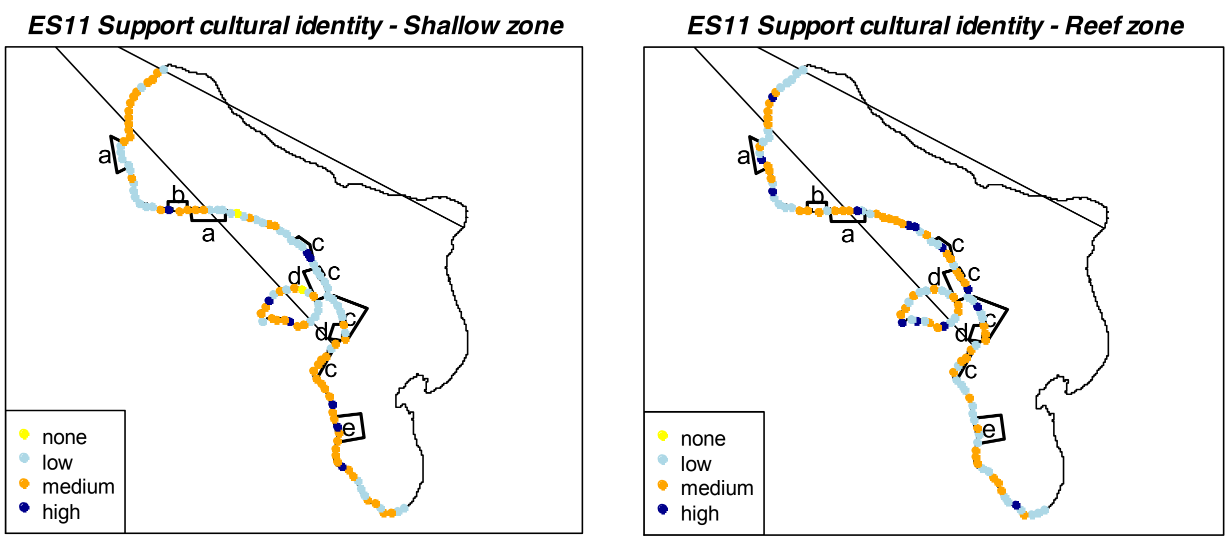


Figure 24. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Support of cultural identity.

Cultural identity on Bonaire is related in this research to social relations derived from the (recreational) fishing community and to a sense of place related to beach where cultural celebrations take place. Especially the shallow zone shows medium to high functional values near beaches and recreational fishing area. The reef zone resembles the reef zone map in figure 14, because the presence of seafood is essential in the support of cultural identity.

<u>Ecosystem Service 12: Educational and scientific information services</u>

One can argue that the entire coral reef provides information that is essential for education and scientific research. Functional groups selected as most essential for scientific research were coral cover, algal cover, coral bleaching, structural complexity, fish abundance and fish and coral biodiversity. Most other functional groups are supporting educational and scientific information services as well. Therefore the interpretation of the maps is ambiguous, as it is very generalist in represents almost all functional groups.

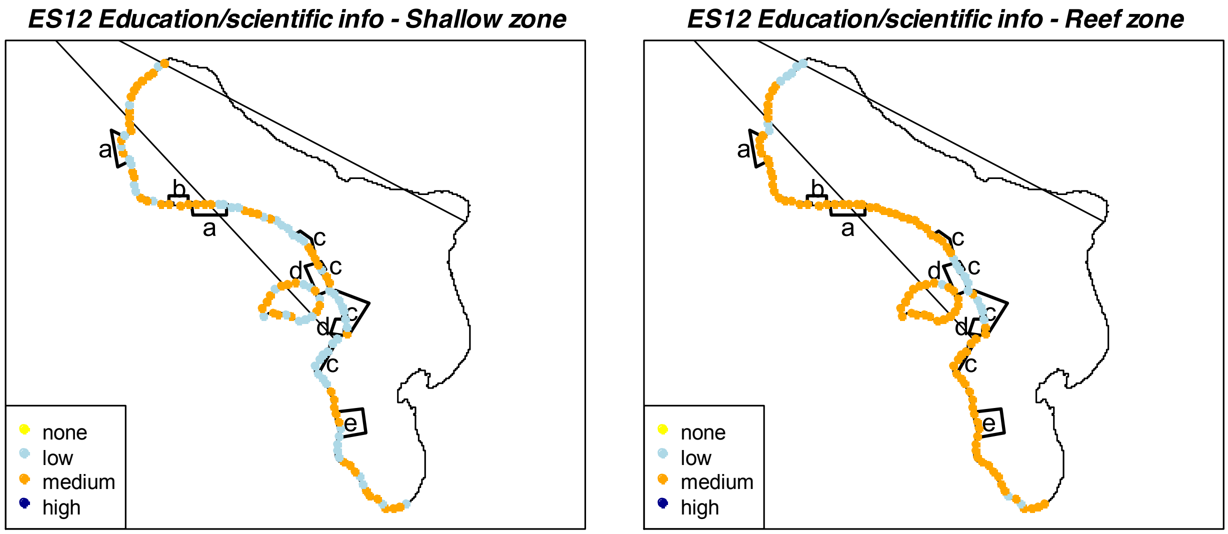


Figure 25. Functional value maps of shallow and reef habitats to support the delivery of ecosystem service Educational and scientific information services.

6 DISCUSSION AND RECOMMENDATIONS

6.1 Context of this research and other studies

This section summarizes the findings of this research and puts them in the context of other studies. As mentioned in the method overview this research was a combination of a literature review and empirical data collection. The strength of the empirical data collection is that observations of the coral reefs of Bonaire were covering half of the island from shore to reef crest (0-10m) with regular, short intervals between survey sites. A survey covering such a large area, 60 kilometer of coastline with transects every 500m, has according to our knowledge not been done since the mapping of the reefs of Bonaire by Van Duyl (1985). It complements data collected by other studies on Bonaire, which have a smaller spatial scale, but methodological advantages due to either regular time intervals or precision of measurement techniques. These studies include the bi-annual time series survey of Steneck et al. (2009) which was done in 2007, 2005 and 2003 as well on 8 study sites at 10m depth and several incidental surveys, conducted by IUCN on 21 sites at 10m depth (2011), Bruckner et al. on 25 sites at three depth ranges (2010) and Sommer et al. on 14 sites at three depths (2011). The advantage of this research is that it provides a more complete overview of the status of the coral reefs on Bonaire, while the disadvantage is that is provides less accurate measurements due to the choice of observation method using snorkel instead of scuba. The type of measurements with the snorkel survey did not differ substantially from the scuba surveys, measuring fish abundance and coral cover. The novelty of our snorkel survey was the visual assessment of topographic or structural complexity. Techniques frequently used to access topographic habitat structure are linear versus contour rugosity, reef height and size distribution of reef holes (Wilson et al., 2007). Wilson et al. (2007) found in their comparative study between these techniques and visual assessment that the latter effectively assessed topographic complexity except at detailed spatial scale of holes <10 cm diameter. Visual appraisal of percentage cover of massive, branching and soft coral, macro-algae, rubble and rock was also a good measure of benthic composition compared to a line intercept transect. Although visual techniques are prone to observer bias, after training they can be used to quickly provide a reliable and effective means of assessing habitat complexity and benthos on coral reefs (Wilson et al., 2007).

This research is innovative in its attempt to link the economic value of ecosystem services with an ecological value of habitats to support these ecosystem services. Mumby et al. (2008) also established a relationship between habitats and ecosystem services, based on the same study of Harborne et al. (2006) as this research built upon. The method for quantification of ecosystem services by habitat was done through a multidisciplinary working group assigning value on a scale from 0-3. The difference is that this research used primary data of ecological functioning instead of expert opinion to assign functional values. The relationships between ecosystem services, functions, processes and structures as defined in this research followed the theoretical framework of The Economics of Ecosystems and Biodiversity (TEEB). The TEEB platform is in need of (published) case studies which implement their methodology (Patrick ten Brink, pers. comm., 26/9/2011). At the same time TEEB acknowledges that the relationship between ecosystems and the benefits that they provide is often non-linear and complex (Reyers et al., 2010), resulting in an inevitable simplification of this complexity. Nevertheless this research is considered a useful and first step to come to a method to capture these relationships.

6.2 Methodological flaws, assumptions and gaps

The simplification of non-linearity and complexity in established functional relationships due to natural variability and knowledge gaps about ecosystem functioning is the main flaw of this research. Relationships between ecosystem functioning and how processes and structures affect the provision of services they provide are often non-linear and complex (Brondízio et al., 2010; Reyers et al., 2010). and Functions and services also do not show one on one relationships (Costanza et al., 1997). Although this simplification is considered a limitation of this research, it is also considered inevitable for this research and not an excuse to not try to come to relationships. Besides this simplification, the relationship matrices do not account for inter-linkages between different ecosystem services, whereby one service has an impact on another service, for example how a provisioning service (fisheries) relates to a regulating service (maintenance of biodiversity and biological maintenance of resilience). It is recognized in environmental economics literature that it is a challenge and difficult to account for these inter-linkages between services (Brondízio et al., 2010).

A methodological flaw in the primary data collection is the choice of the survey method. A snorkel survey has its limitations as visual census technique, because reefs deeper than approximately 10 meter could not be included in the survey. For this reason only two habitat types could be distinguished, the shallow zone and the reef zone, while the deeper fore reef habitats were excluded. Also accuracy to observe small or cryptic species reduced at greater depth. As mentioned in the methodology chapter observer bias was reduced and precision increased by having one observer collecting fish and another observer collecting coral data and by video-recording transects to make detailed analysis of the benthos possible. Receiving GPS signals worked well through the waterproof case carried at the surface, but the last four tracks were not record by the GPS, possibly because the GPS was entangled and slightly submerged.

In chapter 4 differences between resource use groups were analyzed using a non-parametric Kruskal Wallis test for more than two groups of not-normal distributed data. The flaw in using this test is that the minimal sample size required is five measurements (Zijp, 1974), while the industrial use groups were three and four sites respectively for Bopec oil storage terminal and Cargill salt production. Hence, p-values for significant differences between groups are not reliable for those two industrial use groups. Public beaches were not considered as a separate resource use group, even though beaches are important and frequently used for recreation. The assumption was that beaches are not likely to form a uniform group, because they are scattered along the leeward coast of Bonaire. Therefore beaches were grouped in the overlapping resource use group, for example Boka Slagbaai beach was included as remote area and Pink beach as dive tourism area. As a result, potential impacts from beach recreation could not be analyzed.

In the ordinal scaling no distinction was made in levels between the two habitat types. This is debatable, because not all species inhabit both the shallow and the reef zone equally. For example, chromis are plankton feeders and typically found in the water column above the reef slope, presumably resulting in higher abundance in the reef zone than in the shallow zone. The uniform ordinal scale levels do not provide information on what are high, medium or low levels in the reef zone or the shallow zone. However, the purpose of the research was to determine levels of representation of fish and corals in one habitat, relative to representation in another habitat and not relative to representation in other locations within one habitat type. In the example of chromis, none to low representation in the shallow zone and medium to high representation in the reef zone is an expected outcome, with a large difference between habitats and some variation between locations.

6.3 Project management implications

The functional value maps are meant to be used as part of one of the project deliverables of "What's Bonaire Nature Worth?": the value map. The economic value could be compared to the functional value in an GIS overlay to match if areas of high economic value match areas with high functional value. The functional value map could also be used in the scenario analysis and policy brief to allocate areas of conservation potential, because of their high functional value. Given the simplifications in the relationship analysis as discussed in the previous section, it is questioned here how useful and usable the functional value maps are to be used for this purpose.

6.4 Next steps and suggestions for further research

Outside the scope of this ecological research was an analysis of drivers of change and threats to the coral reef ecosystem functions on Bonaire. Also a comparison between the results of the snorkel survey and the results of the various scuba surveys as mentioned in chapter 6.1 was not incorporated in this research due to time constraints. Some more suggestions for further research in a threat analysis and comparative analysis are made in this chapter. The comprehensive data set from the snorkel survey could also be used to analyze correlations between fish and coral functional groups, for example the correlation between topographical complexity and fish abundance and diversity, as well as coral cover and diversity.

With regards to the comparative analysis between the primary data of this research and the secondary data of other studies on Bonaire, a distinction can be made in two types of analysis: comparative and complementary. A complementary analysis refers to the use of secondary data to complement and fill the gaps of the primary data collected. For example, coral recruitment was not included, because these are small species or colonies that could not be observed doing visual assessment using snorkel. Another example is to use secondary data from surveys at deeper fore reefs, to complement the limited types of habitats covered in the snorkel survey. Other habitats not covered in the snorkel survey were mangrove forests and seagrass beds. A potential secondary data source are semi-quantitative data of the presence of fish functional groups in mangroves and seagrass in a literature review of Nagelkerken (2007). These semi-quantitative data have an ordinal scale from absent to low density to high density. A comparative analysis refers to the comparison of similar sites or similar parameters. For example the IUCN resilience study classified survey sites as high, medium and low resilience, which can be compared to the outcome of the functional value of the fourth ecosystem service 'Maintenance of biological resilience'.

With regards to the treat analysis, many drivers of change will have a direct impact on either habitats or functional groups: overfishing might cause depletion of certain fish stock that are critical within their functional group; nutrient loading and pollution may alter key ecosystem processes from one state to an alternative state; habitat destruction reduces the size of the habitat and thereby the availability of structure. This research facilitates an analysis of potential drivers of change and their impacts by providing a framework of critical functional groups required for a healthy ecosystem delivering ecosystem services in a sustainable manner. A suggestion is to map threats by linking each threat with a functional group as indicator measuring the impact from that threat. The relevant maps of functional group representation can be used as map to visualize impacts from that threat. For example, increased algal cover and herbivorous fish can be used as indicator of the impacts from nutrient loading. Another suggestion is to link each threat with a resource use group and compare for functional groups that were identified as indicator, the differences between user groups where the threat is absent or present. For example coral cover and coral diversity can be used as indicators of the impact from sedimentation from coastal development. Residential area and industrial area can be compared with the other resource use groups where coastal development is absent.

7 Conclusions

This research established the relationship and functional value of coral reefs on Bonaire to support ecosystem services delivered by these coral reefs. Relationships were established based on an extensive literature study and included the link between economics and ecosystem functioning and biodiversity, which is often the missing link in economic valuation studies. The relationship analysis showed the complexity of ecosystem functioning, because there were few one-on-one relationships between ecosystem services and functions, or between functions and processes and structures or between functional groups and functions. Nevertheless the essential functions, processes and structures of coral reefs have been summarized and justified in a concise manner in relationship matrices. The functional group approach was a useful concept to link species and their ecological roles in ecosystem processes, and can also be used to link theory and practice in coral reef resilience assessments (Nystrom et al., 2008).

The snorkel survey resulted in 60 maps showing for 30 functional groups in two habitats their level of representation at each survey location. These 60 variables were analyzed in a multivariate analysis, which did not result in clusters of locations with similar functional values for all functional groups combined. Predefined clusters of locations, based on resource use groups, were then analyzed for resource use group differences in functional values for each functional group separately. This resulted in some statistically significant differences between resource use groups, but this was not sufficient to justify that differences between functional values are explained by these predefined resource use groups. The maps do provide a visual appraisal of the level of representation of crucial functional groups along the entire leeward coast of Bonaire, which has not been done at such a large scale since the mapping of coral reefs on Bonaire in 1985 (Van Duyl, 1985). Furthermore these data were used as input for the functional value analysis.

The functional valuation of habitats and locations to support coral reef ecosystem services did highlight area of importance to ecosystem services, such as the marine reserves supporting fish and coral biodiversity, calcium carbonate production for reef framework building and fish abundance of higher trophic levels which are preferred seafood. Residential area were showing no to low importance in the support of ecosystem services, especially with regards to services dependant on structural complexity and coral cover, such as shoreline protection and habitat provision. Surprisingly fish biodiversity and abundance had a low to medium functional value, thereby supporting the fisheries and tourism. The fish reserves which are located in the residential area may contribute to this. Also it is clear that the more remote the residential area are, such as Belnem south and Sabadeco north of Kralendijk, the more services they support.

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APPENDICES

Appendix A – Classification of ecosystem services by TEEB and MEA
Appendix B – Fish species surveyed and references used for ordinal scaling
Appendix C – Fish and benthos data registration sheets
Appendix D – Fish identification sheets
Appendix E – Matrix C: Fish and Benthos functional group representation per habitat and location and Matrix D: Functional values to support ecosystem services per habitat and location
Appendix F – Functional value maps of habitats based on representation fish functional groups
Appendix G– Statistical analysis of group differences between resource use groups for fish functional values in shallow zones
Appendix H – Statistical analysis of group differences between resource use groups for fish functional values in reef zones
Appendix I – Functional value maps of habitats based on representation benthic functional groups

Appendix A – Classification of ecosystem services by TEEB and MEA

TEEB ref #	TEEB ecosystem services (De Groot, 2010)	MEA ecosystem services (MEA, 2005)
	Provisioning	**Provisioning**
1	Food	Food
2	Water	Fresh water
3	Raw material	Fiber
		Fuel
4	Genetic resources	Genetic resources
5	Medical resources	Biochemicals, natural medicines and pharmaceuticals
6	Ornamental resources	Ornamental resources
	Regulating	**Regulating**
7	Air quality regulation	Air quality regulation
8	Climate regulation	Climate regulation
9	Moderation of extreme events	Natural hazard regulation
10	Regulation of water flows	Water regulation
11	Waste treatment	Water purification and waste treatment
12	Erosion prevention	Erosion regulation
13	Maintenance of soil fertility	
14	Pollination	Pollination
15	Biological control (split in 2 in MEA)	Disease regulation
		Pest regulation
	Habitat	na
16	Maintenance of life cycles of migratory species	
17	Maintenance of genetic diversity (and gene pool protection)	
	Cultural	**Cultural**
18	Aesthetic information	Aesthetic values
19	Opportunities for recreation and tourism	Recreation and ecotourism
20	Inspiration for culture, art & design (split in 5 in MEA)	Cultural heritage values
		Cultural diversity
		Social relations
		Sense of place
		Inspiration
21	Spiritual experience	Spiritual and religious values
22	Information for cognitive development (split in 2 in MEA)	Knowledge systems
		Educational values
	na	**Supporting**
		Soil formation
		Photosynthesis
		Primary production
		Nutrient cycling
		Water cycling

Appendix B – Fish species surveyed and references used for ordinal scaling

No.	Code	Description common name - scientific name	Secondary data sources IUCN (2011)	Steneck (2009)	Harborne (2006)
	S_TOT	**PARROTFISH - *SCARIDAE***			
1	S_STOP	Stoplight Parrotfish - *Saprisoma viride*	x	x	x
2	S_QUEE	Queen Parrotfish - *Scarus vetula*	x	x	
3	S_PRIN	Princess Parrotfish - *Scarus taeniopterus*	x	x	
4	S_STRIP	Striped Parrotfish - *Scarus iserti*	x	x	
5	S_RAIN	Rainbow Parrotfish - *Scarus guacamaia*	x		
6	S_REDB	Redband Parrotfish - *Sparisoma aurofrenatum*	x	x	
7	S_REDT	Redtail Parrotfish - *Sparisoma chrysopterum*	x	x	
8	S_REDF	Redfin Parrotfish - *Sparisoma rubripinne*	x	x	
9	S_MIDN	Midnight Parrotfish - *Scarus coelestinus*	Added for biodiversity record		
	A_TOT	**SURGEONFISH - *ACANTHURIDAE***			
10	A_OCEA	Ocean Surgeonfish - *Acanthurus bahianus*	x	x	x
11	A_DOCT	Doctorfish - *Acanthurus chirurgus*	x	x	x
12	A_BLUE	Blue Tang - *Acanthurus coeruleus*	x	x	x
	D_TOT	**DAMSELFISH - *POMACENTRIDAE***			
13	D_SPOT	Three spot Damselfish - *Stegaste planifrons*	x	x	x
14	D_BEAU	Beaugregory - *Stegastes leucostictus*	x	x	
15	D_LONG	Longfin Damselfish - *Stegastes diencaeus*	x	x	
16	D_DUSK	Dusky Damselfish - *Stegastes adustus*	Added in functional group		
17	D_BICO	Bicolor Damselfish - *Stegastes partitus*	Added in functional group		
18	D_YELL	Yellowtail Damselfish - *Microspathodon chrysurus*	x	x	
	C_TOT	**CHROMIS - *POMACENTRIDAE***			
19	C_BLUE	Blue Chromis - *Chromis cyanea*			x
20	C_BROW	Brown Chromis - *Chromis multilineata*			x
	H_TOT	**GRUNTS - *HAEMULIDAE***			
21	H_CAES	Caesar Grunt - *Haemulon carbonarium*	x	x	
22	H_SMAL	Smallmouth Grunt - *Haemulon chrysargyreum*	x	x	
23	H_FREN	French Grunt - *Haemulon flavolineatum*	x	x	x
24	H_WHIT	White Grunt - *Haemulon plumieri*		x	
25	H_BLUE	Bluestriped Grunt - *Haemulon sciurus*	x	x	
26	H_SAIL	Sailors Choice - *Haemulon parra*	Added for biodiversity record		
27	H_MARG	Black Margate - *Anisotremus surinamensis*	x	x	
	L_TOT	**SNAPPERS - *LUTJANIDAE***			
28	L_SCHO	Schoolmaster Snapper - *Lutjanus apodus*	x	x	
29	L_CUBE	Cubera Snapper -*Lutjanus cyanopterus*	x	x	
30	L_GREY	Grey Snapper - *Lutjanus griseus*		x	
31	L_MAHO	Mahogany Snapper - *Lutjanus mahogoni*	x	x	
32	L_DOGS	Dog Snapper - *Lutjanus jocu*	Added for biodiversity record		
33	L_MUTT	Mutton Snapper - *Lutjanus synagris*	Added for biodiversity record		
34	L_YELL	Yellow-tail Snapper - *Ocyurus chrysurus*	x	x	
	G_TOT	**GROUPERS - *SERRANIDAE***			
35	G_NASS	Nassua Grouper - *Epinephelus striatus*			x
36	G_BLAC	Black Grouper - *Mycteroperca bonaci*		x	
37	G_TIGE	Tiger Grouper - *Mycteroperca tigris*	x	x	
38	G_YELL	Yellowfin Grouper - *Mycteroperca venenosa*		x	
39	G_GRAY	Graysby - *Epinephelus/Cephalopholis cruentata*	x	x	
40	G_CONE	Coney - *Epinephelus fulvus/Cephalopholis fulva*	x	x	
41	G_REDH	Red Hind - *Epinephelus guttatus*	x	x	
42	G_ROCK	Rock Hind - *Epinephelus adscensionis*	x	x	
43	G_HARL	Harlequin Gass - *Serranus tigrinus*	x	x	
44	G_HAML	Hamlets - *Hypoplectrus spp.*	x	x	

			Secondary data sources		
No.	Code	Description common name - scientific name	IUCN (2011)	Steneck (2009)	Harborne (2006)
	J_TOT	**JACKS - *CARANGIDAE***			
45	J_HORS	Horse eye Jack - *Caranx latus*	x	x	
46	J_BARJ	Bar Jack - *Caranx ruber*	x	x	
47	J_PALO	Palometa - *Trachinotus goodei*	Added for biodiversity record		
48	J_BLAC	Black Jack - *Caranx lugubris /* Crevalle - *Caranx hippos*	Added for biodiversity record		
49	J_PERM	Permit - *Trachinotus falcatus /* African Pompano - *Alectis ciliaris*	Added for biodiversity record		
	P_TOT	**OTHER PREDATORS**			
50	P_TRUM	Trumpetfish - *Aulostomus maculatus*	x	x	
51	P_HOGF	Spanish Hogfish - *Bodianus rufus*	x	x	
52	P_FLOU	Peacock Flounder - *Bothus lunatus*	x	x	
53	P_MORA	Morays - *Gymnothorax spp.*	x	x	
54	P_SCOR	Spotted Scorpionfish - *Scorpaena plumieri*	x	x	
55	P_LION	Lionfish - *Pterois volitans*	Added for invasive species		
56	P_BARR	Great Barracuda - *Sphyraena barracuda*	x	x	
57	P_LIZA	Sand Diver / Lizardfish - *Synodus intermedius*	x	x	
		OTHER SPECIES			
58	O_SERG	Sergeant Major - *Abudefduf saxatilis*	Added for biodiversity record		
59	O_GOAT_YELL	Yellow Goatfish - *Mulloidichthys martinicus*	Added for biodiversity record		
60	O_GOAT_SPOT	Spotted Goatfish - *Pseudupeneus maculatus*	Added for biodiversity record		
61	O_ANGE_ROCK	Rock Beauty - *Holacanthus tricolor*	x		
62	O_ANGE_FREN	French Angelfish - *Pomacanthus paru*	x		
63	O_ANGE_QUEE	Queen Angelfish - *Holacanthus ciliaris*	Added for biodiversity record		
64	O_FILE	Filefish - *Monacanthidae spp.*	Added for biodiversity record		
65	O_BALL_TRUN	Trunkfish - *Lactophrys spp.*	Added for biodiversity record		
66	O_BALL_COWF	Cowfish - *Acanthostracion spp.*	Added for biodiversity record		
67	O_BALL_BURR	Burrfish - *Chilomycterus spp.*	Added for biodiversity record		
68	O_BALL_PORC	Porcupine - *Diodon spp.*	Added for biodiversity record		
69	O_SOLD_SPP.	Squirrelfish - *holocentridae spp.*	Added for biodiversity record		
70	O_BUTT_BAND	Banded Butterflyfish - *Chaetodon striatus*	x		
71	O_BUTT_4EYE	Four eye Butterflyfish - *Chaetodon capistratus*	x		
72	O_BUTT_REEF	Reef Butterflyfish - *Chaetodon sedentarius*	x		
73	O_WRAS_BLUE	Bluehead Wrasse - *Thalassoma bifasciatum*	Added for biodiversity record		
74	O_WRAS_YELL	Yellowhead Wrasse - *Halichoeres garnoti*	Added for biodiversity record		
75	O_WRAS_PUDD	Puddingwife - *Halichoeres radiatus*	Added for biodiversity record		
76	O_WRAS_CREO	Creole Wrasse - *Clepticus parrae*	Added for biodiversity record		
77	O_TRIG_BLAC	Black Durgon - *Melichthys niger*	Added for biodiversity record		
78	O_TRIG_OCEA	Ocean Triggerfish- *Canthidermis sufflamen*	Added for biodiversity record		
79	O_TRIG_QUEE	Queen Triggerfish - *Balistes vetula*	Added for biodiversity record		
80	O_CHUB_SPP	Bermuda Chub - *Kyphosus sectatrix*	x		
81	O_CREO	Atlantic Creolefish - *Paranthias furcifer*	Added for biodiversity record		
82	O_SOAP	Greater Soapfish - *Rypticus saponaceus*	Added for biodiversity record		
83	O_MAJO	Yellowfin Mojarra - *Gerres cinereus*	Added for biodiversity record		
84	O_BONE	Bonefish - *Albula vulpes*	Added for biodiversity record		
85	O_WAHO	Wahoo - Acanthocybium solandri / Cero - *Scomberomorus regalis*	Added for biodiversity record		
86	O_TARP	Tarpon - *Megalops atlanticus*	Added for biodiversity record		
87	O_TURT	Turtle	Added for biodiversity record		
88	O_SQUI	Squid	Added for biodiversity record		
89	O_RAY	Southern Stingray - *Dasyatis americana*	Added for biodiversity record		

Appendix C – Fish and benthos data registration sheets

	FISH DATA ENTRY SHEET		Date:	…….	May / June 2011											
			Site # ...		Site # ...		Site # ...		Site # ...		Site # ...		Site # ...		Site # ...	
	Fish diversity & abundance	Code	sand	reef	sand	reef	sand	reef	sand	reef	sand	reef	sand	reef	sand	reef
	GPS Weigh point	Wpt														
	Time in	In														
	Time out	Out														
	Max size fish (groupers in cm)	FMS														
PARROTFIS	Stoplight - *Saprisoma viride*	Pstop														
	Queen - *Scarus vetula*	Pquee														
	Princess - *Scarus taeniopterus*	Pprin														
	Striped - *Scarus iserti*	Pstri														
	Rainbow - *Scarus guacamaia*	Prain														
	Redband - *Sparisoma aurofrenatum*	Predb														
	Redtail - *Sparisoma chrysopterum*	Predt														
	Redfin - *Sparisoma rubripinne*	Predf														
SUR	Ocean surgeonfish - *Acanthurus bahianus*	Socea														
	Doctorfish - *Acanthurus chirurgus*	Sdoct														
	Blue Tang - *Acanthurus coeruleus*	Sblue														
DAMSEL	Three spot - *Stegaste planifrons*	Dspot														
	Beaugregory - *Stegastes leucostictus*	Dbeau														
	Longfin - *Stegastes diencaeus*	Dlong														
	Dusky - *Stegastes adustus*	Ddusk														
	Bicolor - *Stegastes partitus*	Dbico														
	Yellowtail - *Microspathodon chrysurus*	Dyell														
CH	Blue Chromis - *Chromis cyanea*	Cblue														
	Brown Chromis - *Chromis multilineata*	Cbrow														
GRUNT	Caesar grunt - *Haemulon carbonarium*	Hcaes														
	Smallmouth grunt - *Haemulon*	Hsmal														
	French grunt - *Haemulon flavolineatum*	Hfren														
	White grunt - *Haemulon plumieri*	Hwhit														
	Bluestriped Grunt - *Haemulon sciurus*	Hblue														
	Black margate - *Anisotremus surinamensis*	Hmarg														
SNAPPER	Schoolmaster - *Lutjanus apodus*	Sscho														
	Cubera snapper -*Lutjanus cyanopterus*	Scube														
	Grey snapper - *Lutjanus griseus*	Sgrey														
	Mahogany snapper - *Lutjanus mahogoni*	Smaho														
	Lane snapper - *Lutjanus synagris*	Slane														
	Yellow-tail snapper - *Ocyurus chrysurus*	Syell														
SERRANIDAE	Nassua grouper - *Epinephelus striatus*	Gnass														
	Black grouper - *Mycteroperca bonaci*	Gblac														
	Tiger grouper - *Mycteroperca tigris*	Gtige														
	Yellowfin grouper - *Mycteroperca venenosa*	Gyell														
	Graysby - *Epinephelus cruentata*	Ggray														
	Coney - *Epinephelus fulvus/Cephalopholis fulva*	Gcone														
	Red hind - *Epinephelus guttatus*	Gred														
	Rock hind - *Epinephelus adscensionis*	Grock														
	Harlequin bass - *Serranus tigrinus*	Gharl														
	Hamlets - *Hypoplectrus spp.*	Ghaml														
JA	Horse eye jack - *Caranx latus*	Jhors														
	Bar jack - *Caranx ruber*	Jbar														
PREDATORS	Trumpetfish - *Aulostomus maculatus*	Trum														
	Spanish hogfish - *Bodianus rufus*	Hogf														
	Peacock flounder - *Bothus lunatus*	Flou														
	Morays - *Gymnothorax spp.*	Mora														
	Spotted scorpionfish - *Scorpaena plumieri*	Scor														
	Lionfish - *Pterois volitans*	Lion														
	Great Barracuda - *Sphyraena barracuda*	Barr														
	Sand diver / lizardfish - *Synodus intermedius*	Liza														
OTHER	Sergeant major	Smaj														
	Goatfish	Goat														
	Angelfish	Ange														
	File fish	File														
	Balloon fish	Ball														
	Soldierfish	Sold														
	Butterflyfish	Butt														
	Wrasse	Wras														
	Other …….															

Remarks site # ... :

Remarks site # ... :

BENTHOS DATA ENTRY SHEET

Date: .... May / June 2011

	Benthos diversity & abundance	**Code**	**Site # ...**		**Site # ...**		**Site # ...**		**Site # ...**		**Site # ...**		**Site # ...**		**Site # ...**	
			sand	reef	sand	reef	sand	reef	sand	reef	sand	reef	sand	reef	sand	reef
	GPS Weigh point	Wpt														
	Time in	In														
	Time out	Out														
CORAL	*Acropora palmata*	Apal														
	Acropora cervicornis	Acer														
	Montastrea annularis	Mann														
	Montastrea faveolata	Mfav														
	Max size colony *Montastrea*	CMS														
	Coral diversity (# of species)	CD														
	Coral mortality old	CMo														
	Coral mortality new	CMn														
	Bite marks	BM														
	Topographic complexity	TC														
SUBSTRATE	Coral cover (%)	CC														
	Macro algae cover (%)	MAC														
	Gorgonians	Gorg														
	Sponges	Spon														
	Cyanobacteria mats	Cyan														
	Tunicate mats (%): *Trididemnum solidum*	Tsol														
	Rubble (%)	Rubb														
	Sand/silt (%)	Sand														
	Hard ground/rock (%)	Rock														
O	*Diadema antillarum*	Dant														

Remarks site # ... :

Remarks site # ... :

Remarks site # ... :

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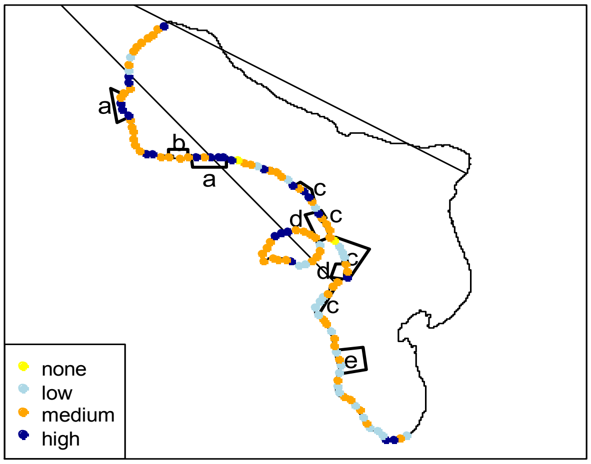
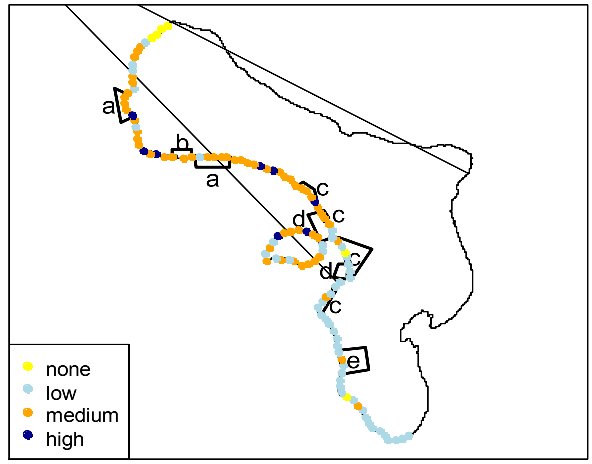
Remarks site # ... :

Appendix F – Functional value maps of habitats based on representation fish functional groups

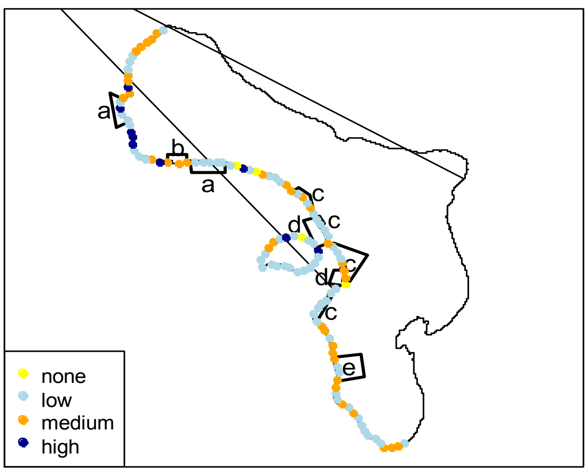
FG1.1 Scaridae - Shallow zone



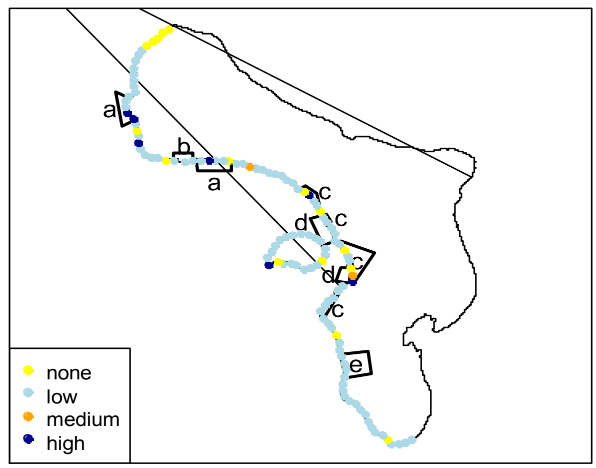
FG1.1 Scaridae - Reef zone



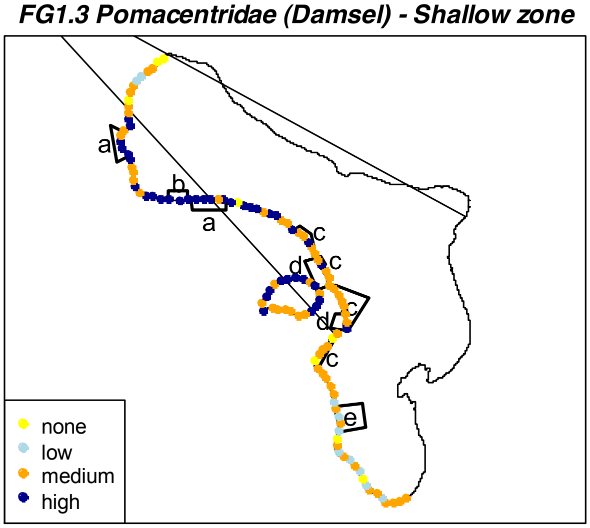
FG1.2 Acanthuridae - Shallow zone



FG1.2 Acanthuridae - Reef zone



FG1.3 Pomacentridae (Damsel) - Shallow zone



FG1.3 Pomacentridae (Damsel) - Reef zone

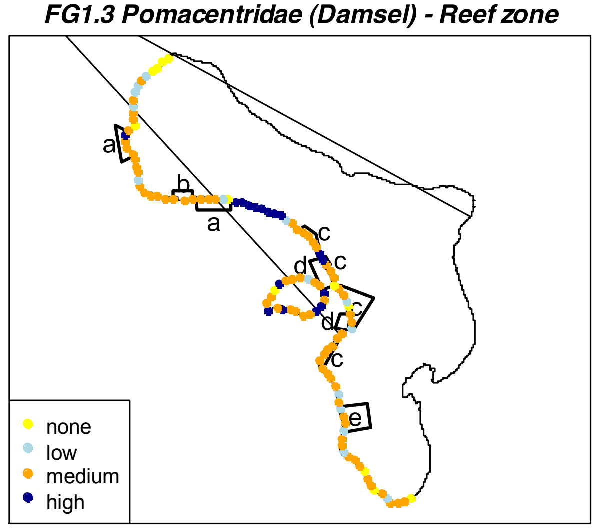


Figure 1. (See previous page) Maps of functional value of shallow and reef habitats measured by the representation of herbivorous fish functional groups (FG), whereby FG1.1 are escavating parrotfish – Scaridae spp. , FG1.2 are denuding surgeonfish – Acanthuridae spp., and FG1.3 are non-denuding damselfish – Pomacentridae spp. Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area, d=fish reserves and e=Cargill salt production.

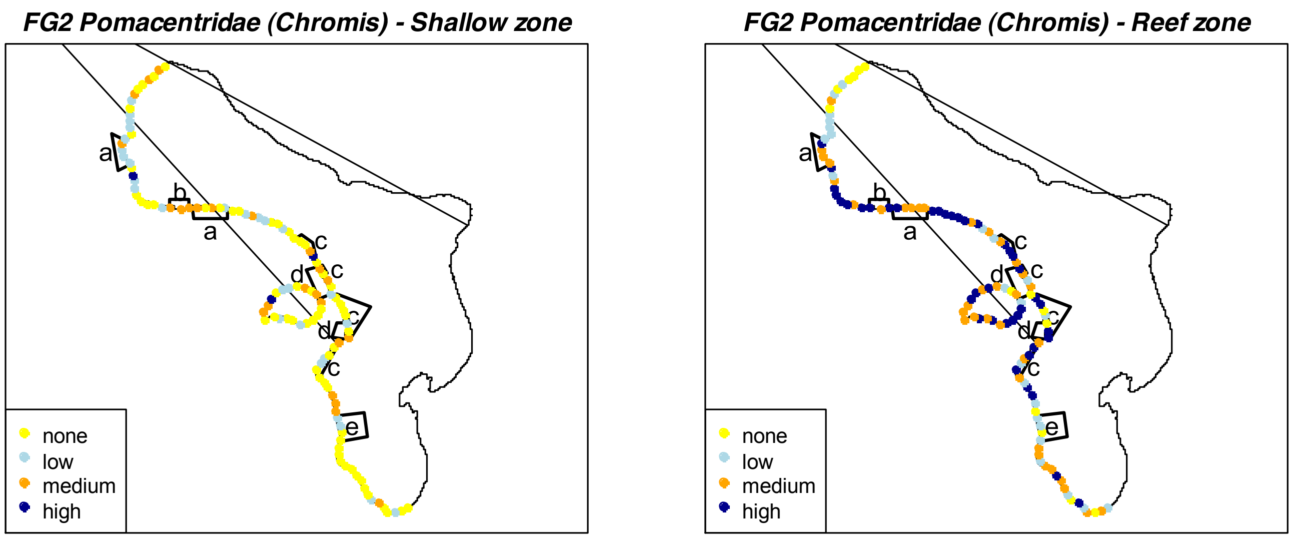
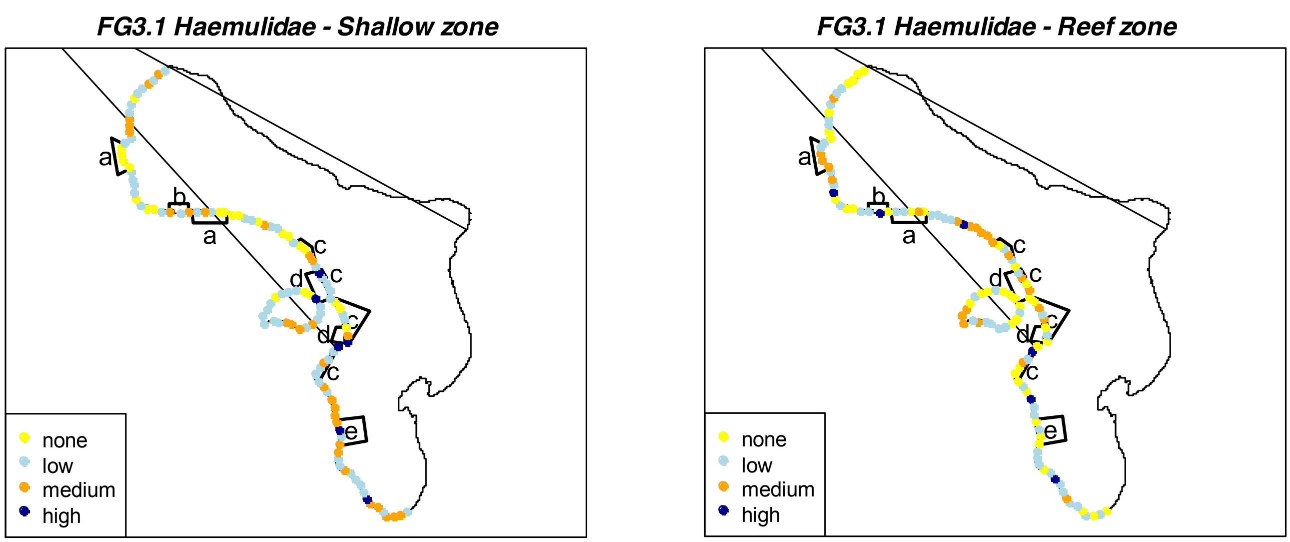


Figure 2. Maps of functional value of shallow and reef habitats measured by the representation of the planktivorous fish functional group FG2 chromis – Pomacentridae spp. Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area, d=fish reserves and e=Cargill salt production.



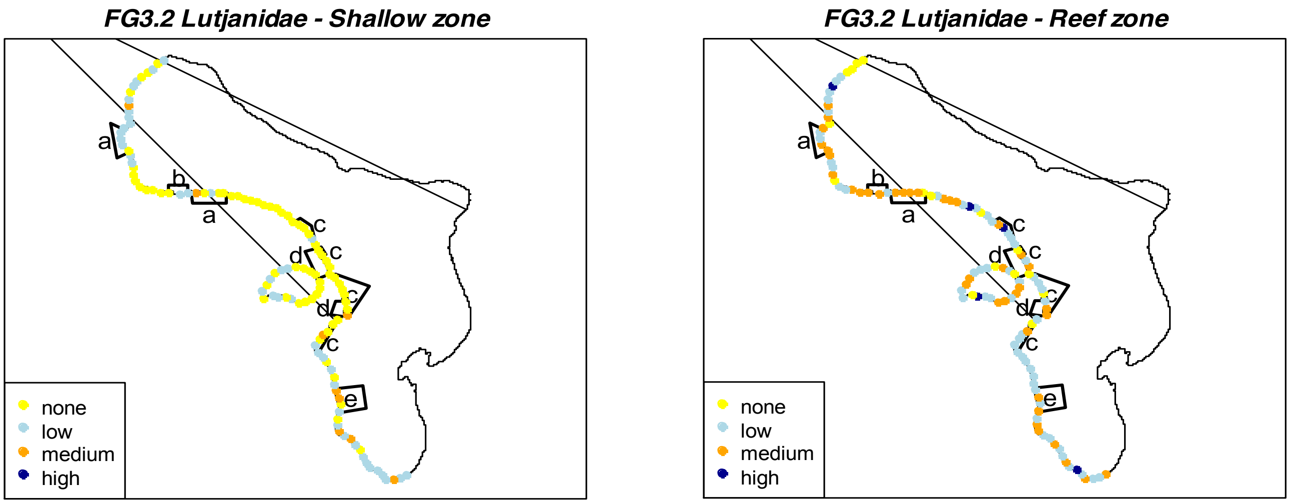
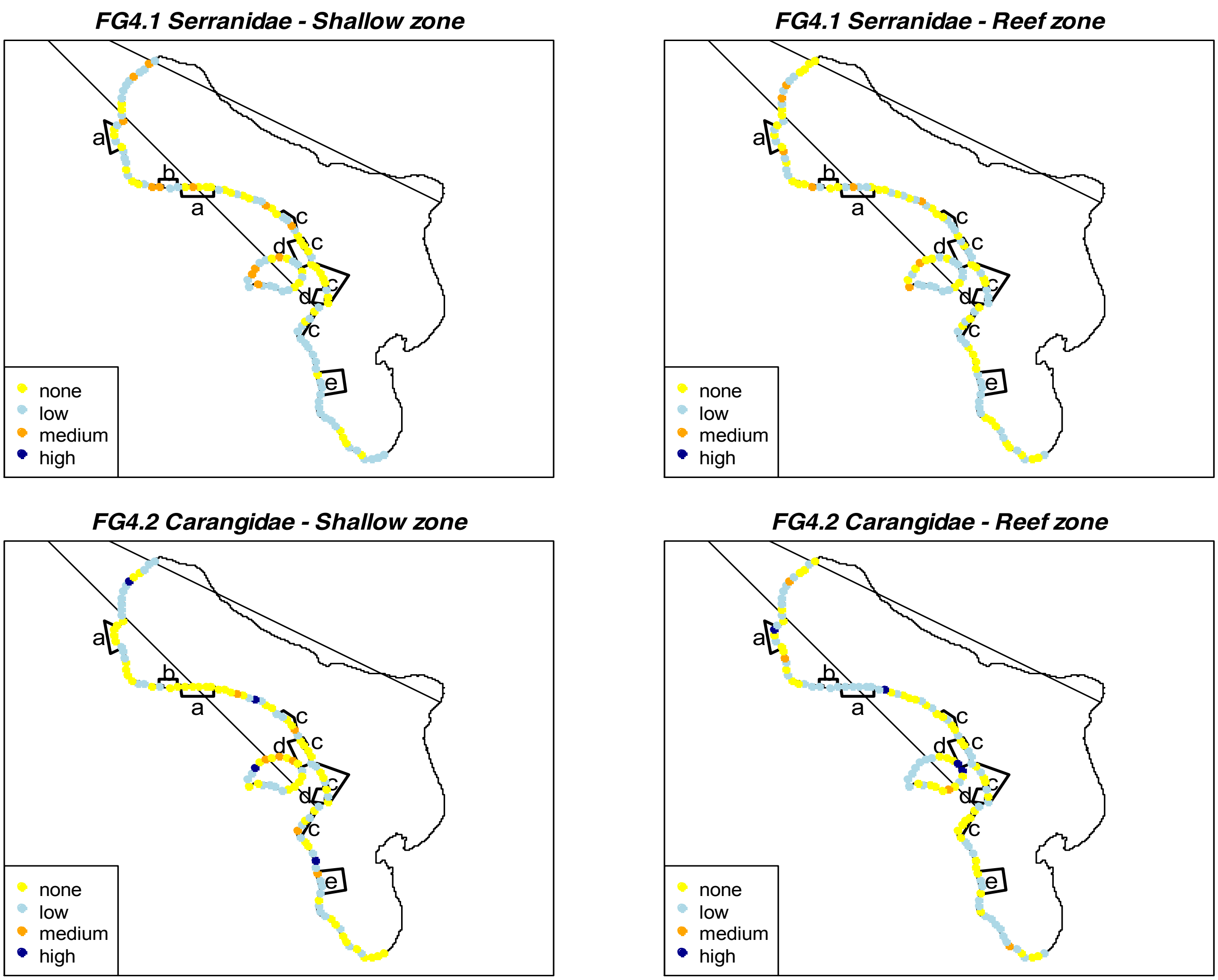


Figure 3. (See also previous page) Maps of functional value of shallow and reef habitats measured by the representation of omnivorous fish functional groups (FG) whereby FG3.1 are grunts – Haemulidae spp., and FG3.2 are snappers – Lutjanidae spp. Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area, d=fish reserves and e=Cargill salt production.



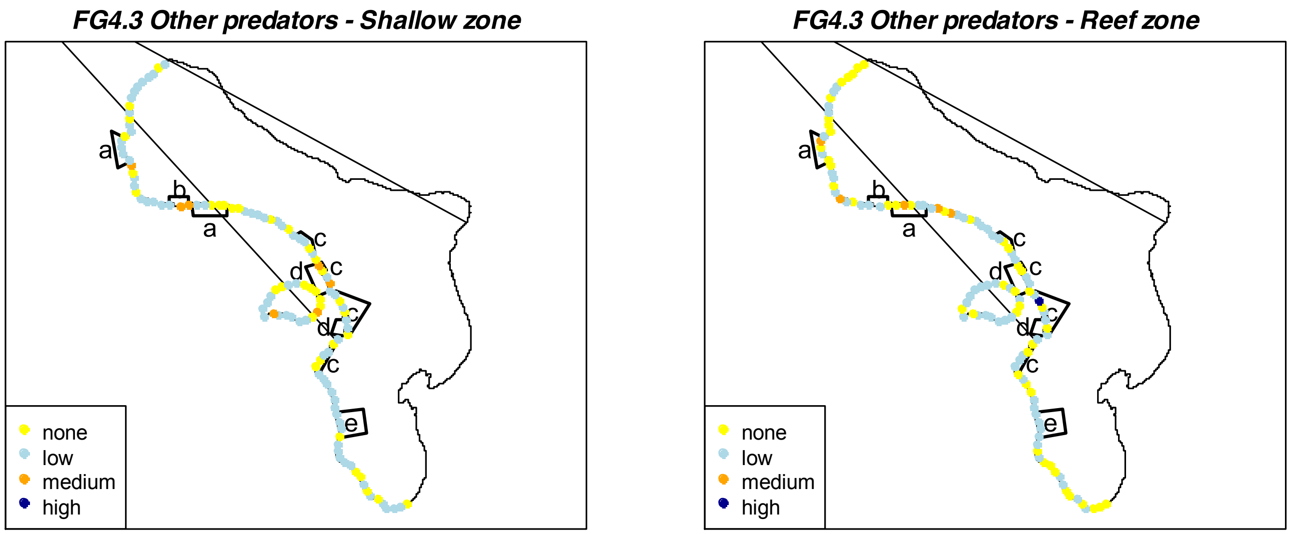


Figure 4. (See also previous page) Maps of functional value of shallow and reef habitats measured by the representation of predatory fish functional groups, whereby FG4.1 are groupers – Serranidae spp., FG4.2 are jacks – Carangidae spp., and FG4.3 are predators from 7 different families. Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area, d=fish reserves and e=Cargill salt production.

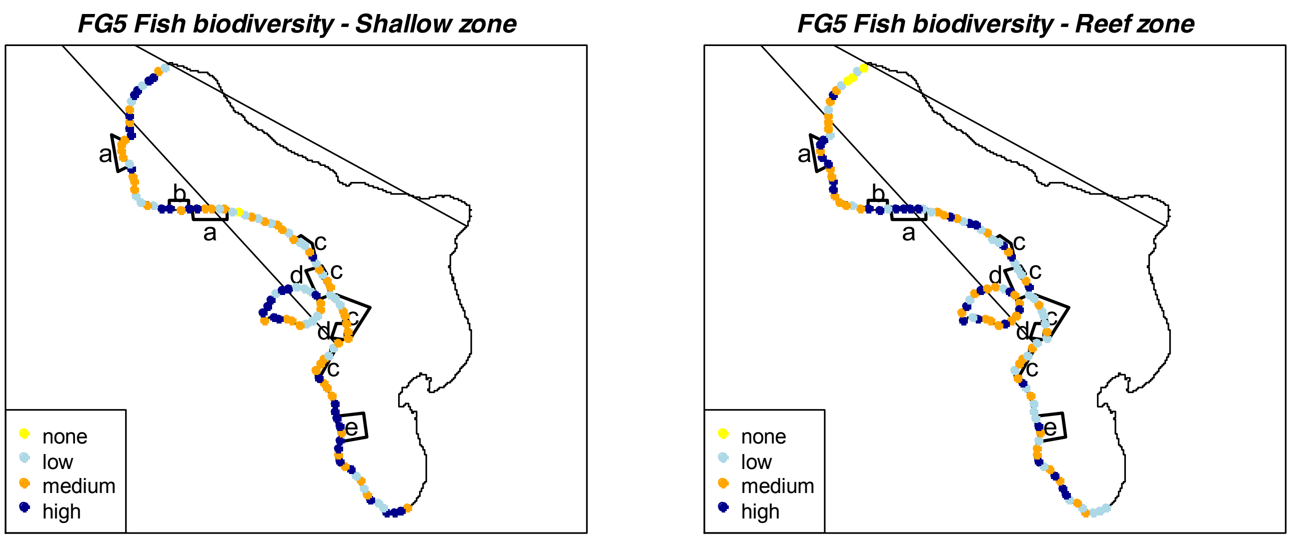


Figure 5. Maps of functional value of shallow and reef habitats measured by the representation of indicator FG5 biodiversity of fish species. Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area, d=fish reserves and e=Cargill salt production.

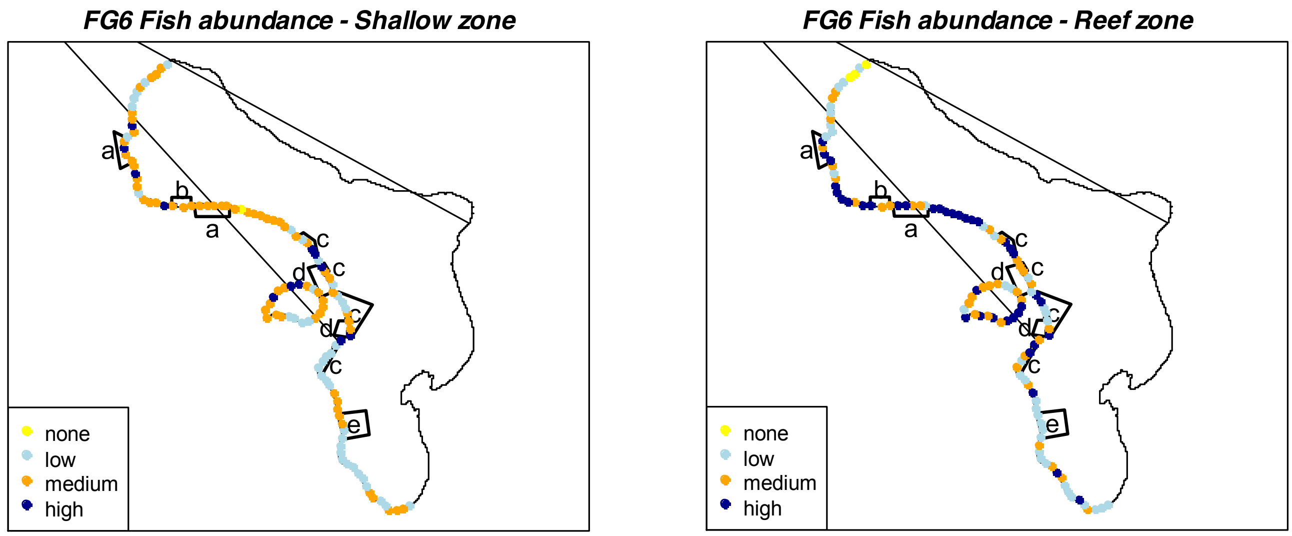


Figure 6. Maps of functional value of shallow and reef habitats measured by the representation of indicator FG6 total abundance of fish species. Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area, d=fish reserves and e=Cargill salt production.

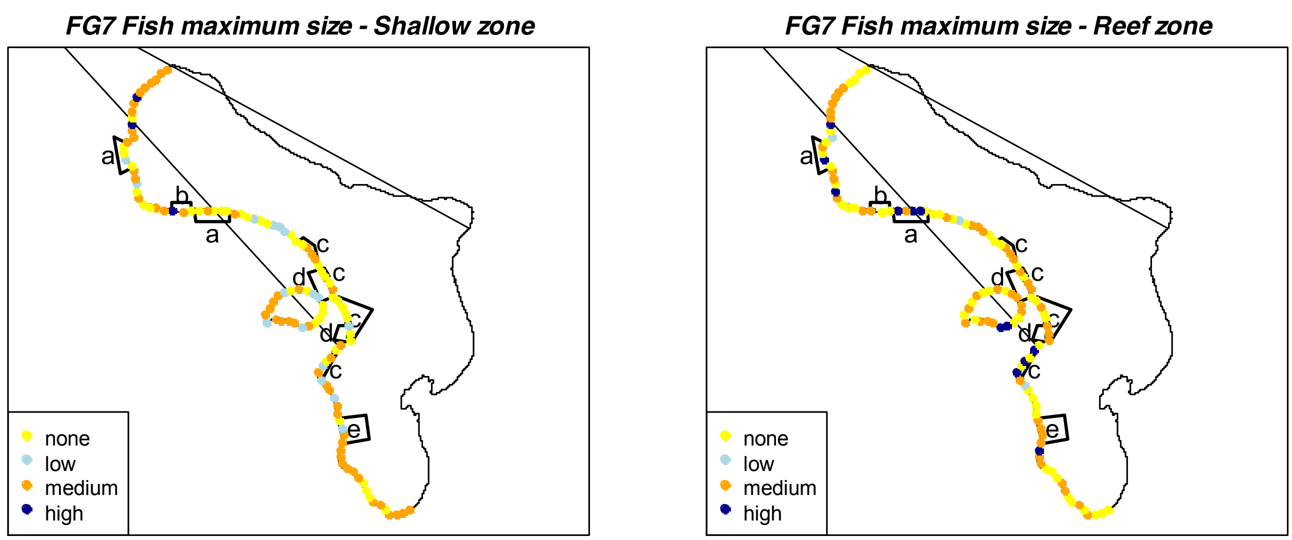
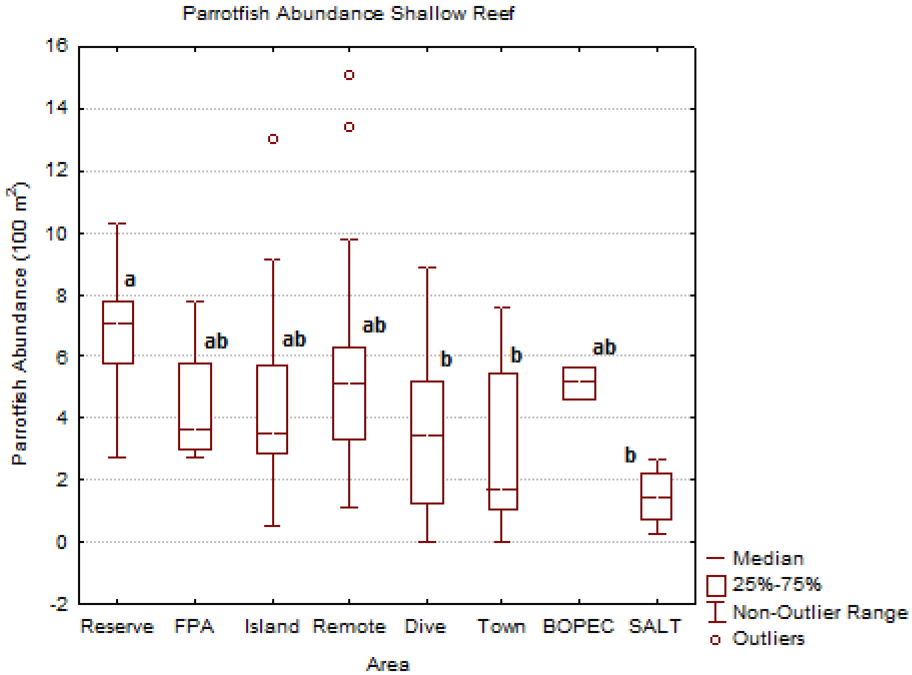


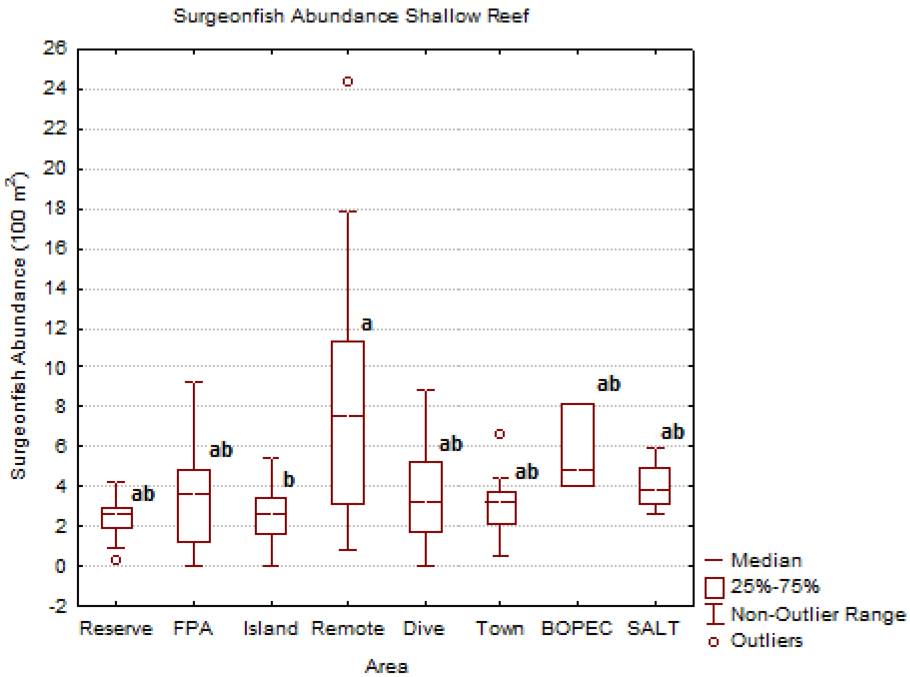
Figure 7. Maps of functional value of shallow and reef habitats measured by the representation of indicator FG7 Fish maximum size of predators including groupers (Serranidae spp.), jacks (Carangidae spp.) and Cubera snappers (Lutjanus cyanopterus). Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area, d=fish reserves and e=Cargill salt production.

Appendix G – Statistical analysis of group differences between resource use groups for fish functional values in shallow zones



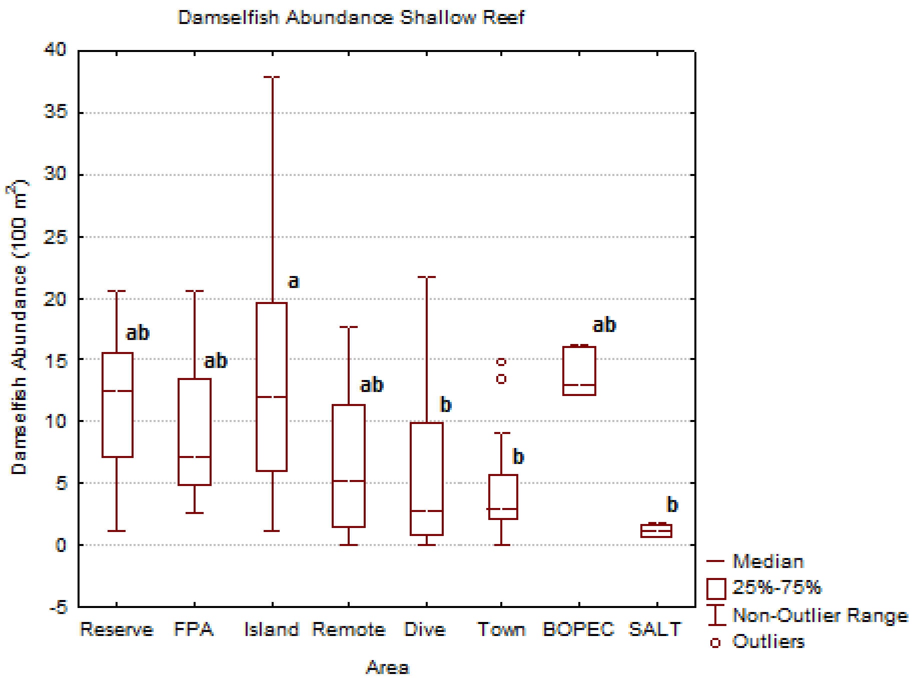
Parrotfish Abundance (100 m^2): KW-H(7;116) = 23,986; p = 0,0011

Depend.: Parrotfish Abundance (100 m^2)	Multiple Comparisons p values (2-tailed); Parrotfish Abundance (100 m^2) (DefinitiefF Independent (grouping) variable: Area Kruskal-Wallis test: H (7, N= 116) =23,98603 p =,0011							
	Reserve R:89,056	FPA R:61,313	Island R:60,810	Remote R:71,135	Dive R:48,250	Town R:41,853	BOPEC R:75,000	SALT R:20,000
Reserve		1,000000	0,98056	1,000000	0,04319	0,01853	1,000000	0,01772
FPA	1,000000		1,000000	1,000000	1,000000	1,000000	1,000000	1,000000
Island	0,98056	1,000000		1,000000	1,000000	1,000000	1,000000	0,73152
Remote	1,000000	1,000000	1,000000		0,349200	0,14688	1,000000	0,12992
Dive	0,04319	1,000000	1,000000	0,349200		1,000000	1,000000	1,000000
Town	0,01853	1,000000	1,000000	0,14688	1,000000		1,000000	1,000000
BOPEC	1,000000	1,000000	1,000000	1,000000	1,000000	1,000000		0,903040
SALT	0,01772	1,000000	0,73152	0,12992	1,000000	1,000000	0,903040	



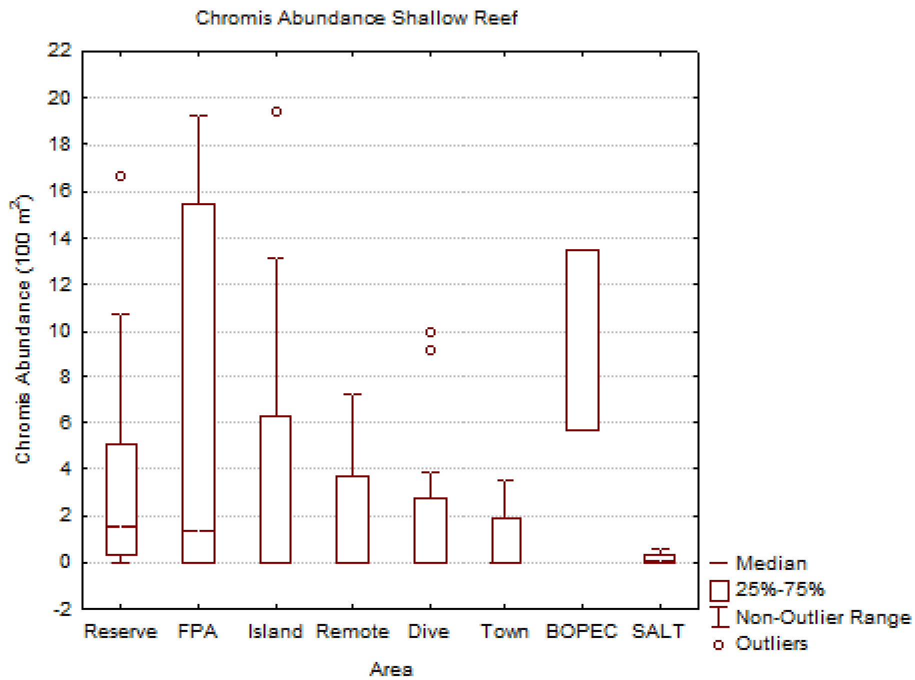
Surgeonfish Abundance (100 m^2): KW-H(7;116) = 17,5875; p = 0,0140

Depend.: Surgeonfish Abundance (100 m²)	Multiple Comparisons p values (2-tailed); Surgeonfish Abundance (100 m²) (DefinitiefFi Independent (grouping) variable: Area Kruskal-Wallis test: H (7, N= 116) =17,58754 p =,0140							
	Reserve R:45,889	FPA R:54,813	Island R:44,929	Remote R:79,115	Dive R:54,393	Town R:52,235	BOPEC R:84,000	SALT R:67,750
Reserve		1,000000	1,000000	0,297640	1,000000	1,000000	1,000000	1,000000
FPA	1,000000		1,000000	1,000000	1,000000	1,000000	1,000000	1,000000
Island	1,000000	1,000000		0,01485	1,000000	1,000000	1,000000	1,000000
Remote	0,29764	1,000000	0,01485		0,19463	0,29091	1,000000	1,000000
Dive	1,000000	1,000000	1,000000	0,19463		1,000000	1,000000	1,000000
Town	1,000000	1,000000	1,000000	0,29091	1,000000		1,000000	1,000000
BOPEC	1,000000	1,000000	1,000000	1,000000	1,000000	1,000000		1,000000
SALT	1,000000	1,000000	1,000000	1,000000	1,000000	1,000000	1,000000	

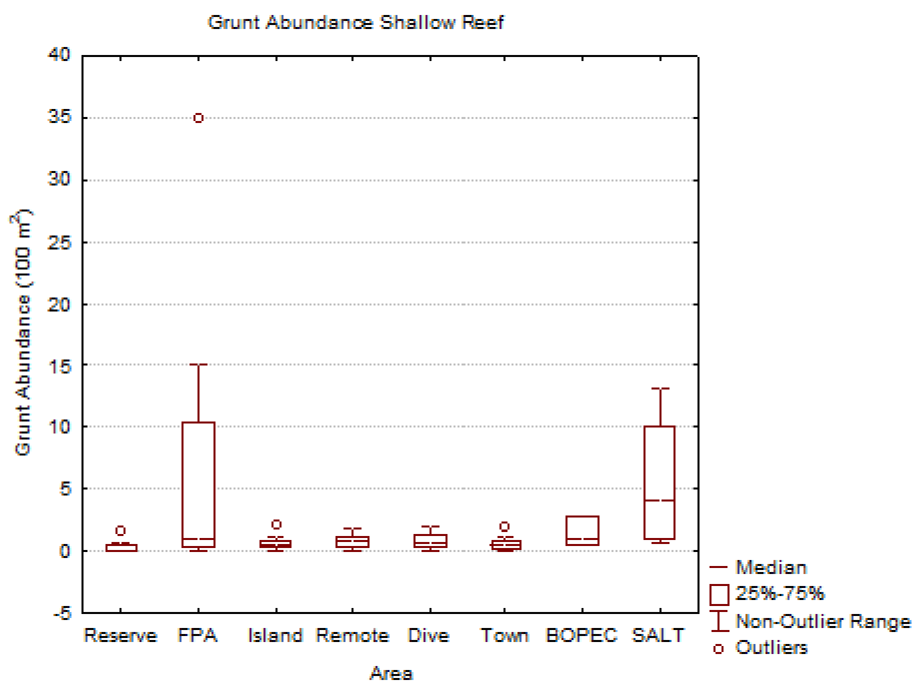


Damselfish Abundance (100 m^2): KW-H(7;116) = 26,6198; p = 0,0004

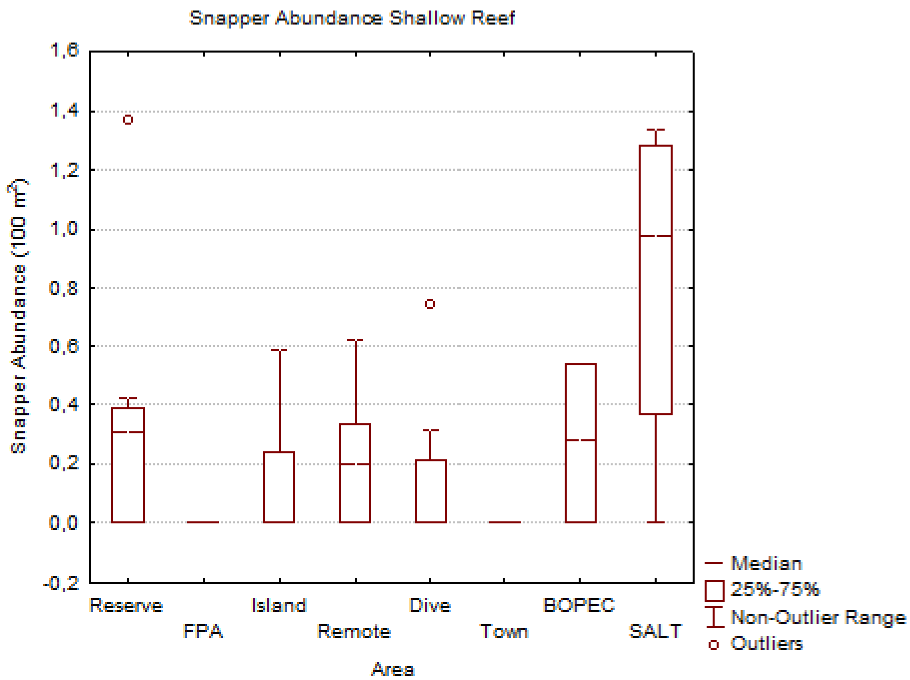
Depend.: Damselfish Abundance (100 m^2)	Multiple Comparisons p values (2-tailed); Damselfish Abundance (100 m^2) (Definitie Independent (grouping) variable: Area Kruskal-Wallis test: H (7, N= 116) =26,61979 p =,0004							
	Reserve R:77,000	FPA R:70,000	Island R:80,238	Remote R:54,192	Dive R:47,250	Town R:44,588	BOPEC R:91,000	SALT R:21,250
Reserve		1,000000	1,000000	1,000000	0,58698	0,54295	1,000000	0,16252
FPA	1,000000		1,000000	1,000000	1,000000	1,000000	1,000000	0,50190
Island	1,000000	1,000000		0,23234	0,01901	0,03241	1,000000	0,03650
Remote	1,000000	1,000000	0,23234		1,000000	1,000000	1,000000	1,000000
Dive	0,58698	1,000000	0,01901	1,000000		1,000000	0,90268	1,000000
Town	0,54295	1,000000	0,03241	1,000000	1,000000		0,77112	1,000000
BOPEC	1,000000	1,000000	1,000000	1,000000	0,90268	0,77112		0,18527
SALT	0,16252	0,50190	0,03650	1,000000	1,000000	1,000000	0,18527	



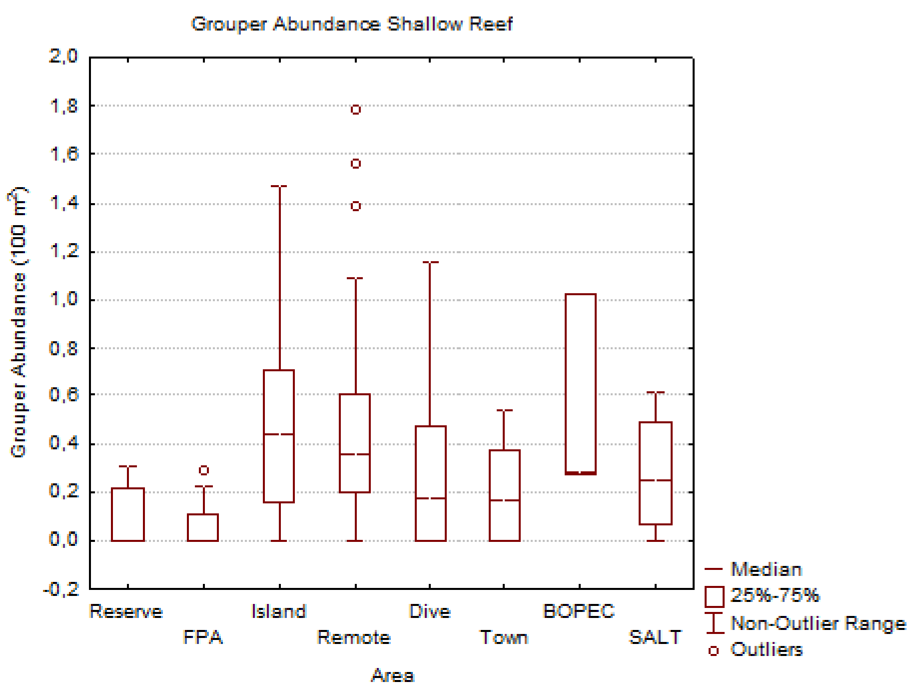
Chromis Abundance (100 m^2): KW-H(7;116) = 9,4702; p = 0,2206



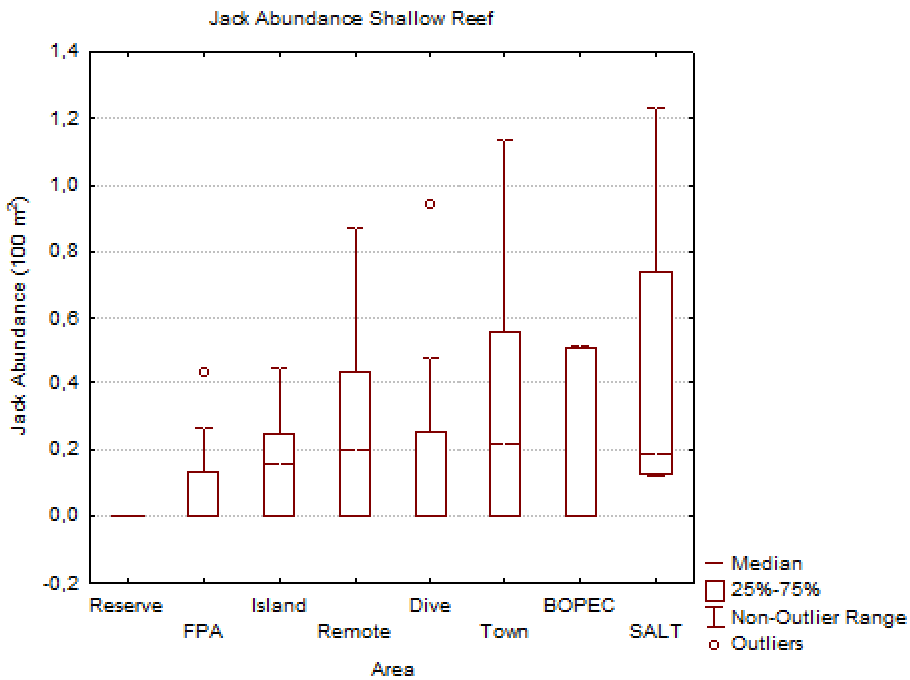
Grunt Abundance (100 m^2): KW-H(7;116) = 13,2617; p = 0,0660



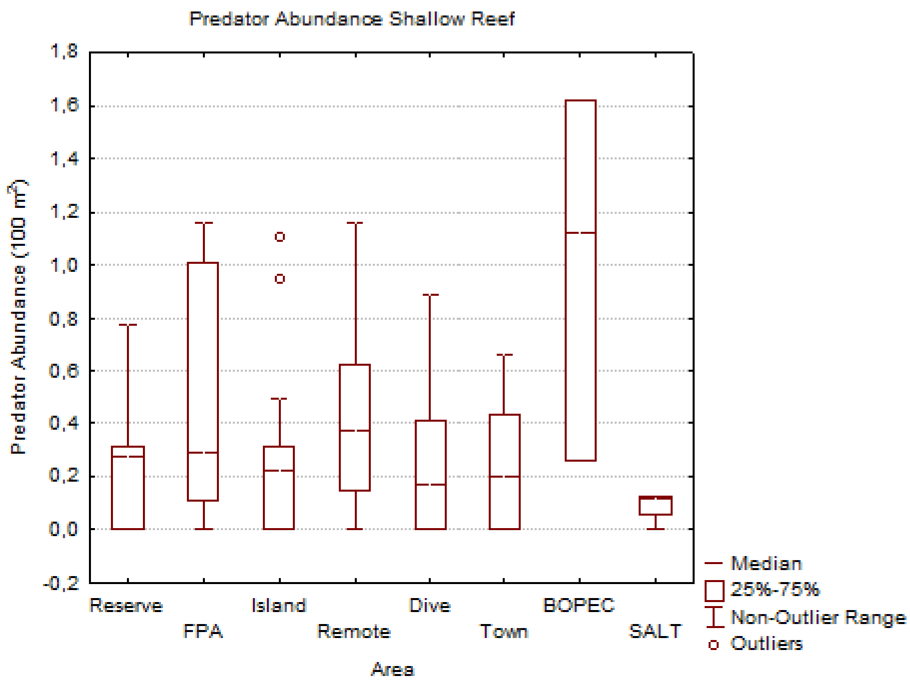
Snapper Abundance (100 m^2): KW-H(7;116) = 13,3374; p = 0,0643



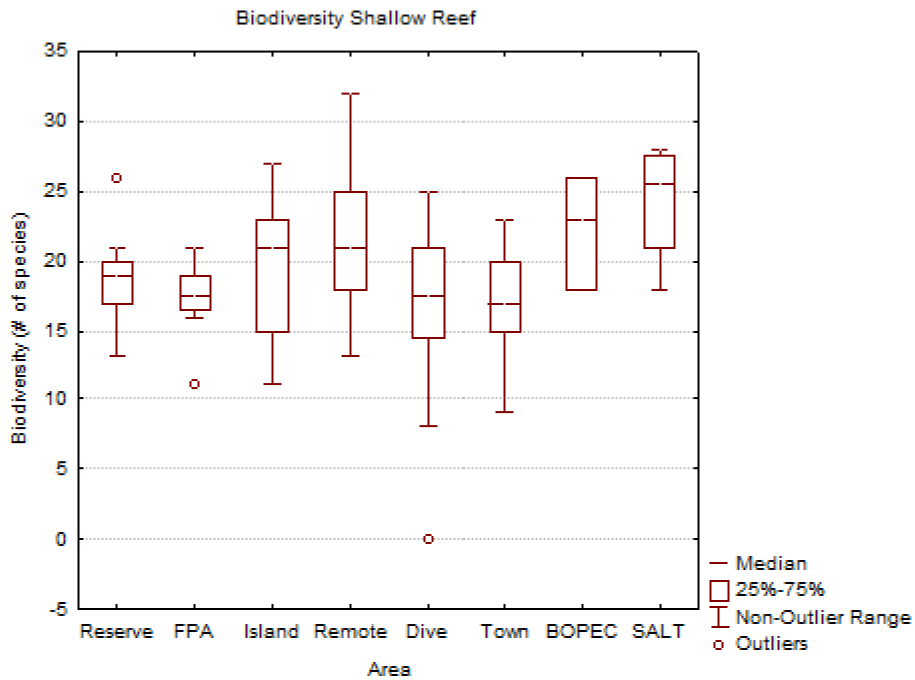
Grouper Abundance (100 m^2): KW-H(7;116) = 18,2195; p = 0,0110



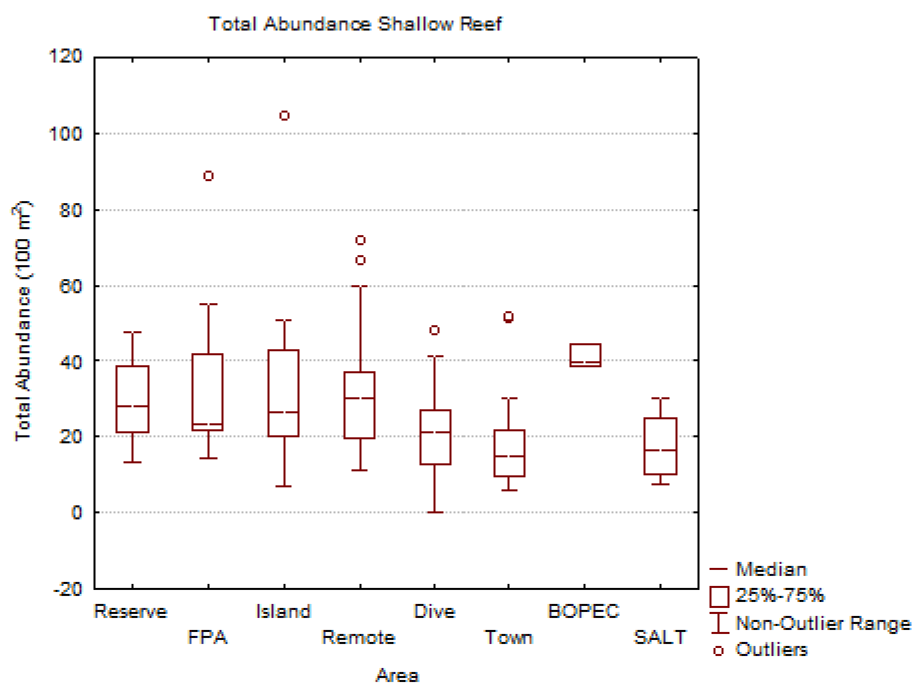
Jack Abundance (100 m^2): KW-H(7;116) = 10,2729; p = 0,1736



Predator Abundance (100 m^2): KW-H(7;116) = 11,5509; p = 0,1163

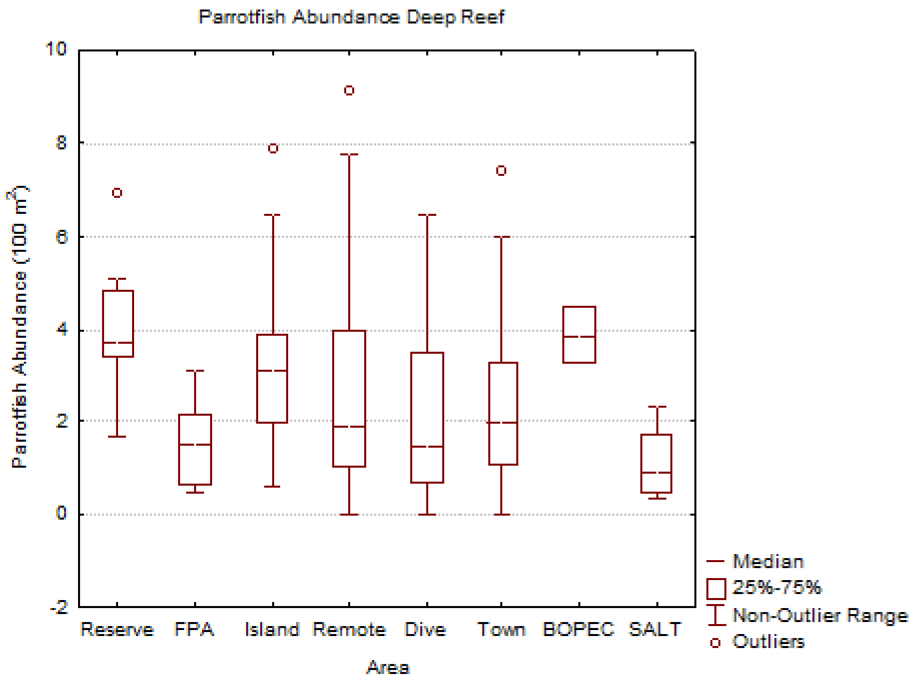


Biodiversity (# of species): KW-H(7;116) = 18,0239; p = 0,0119

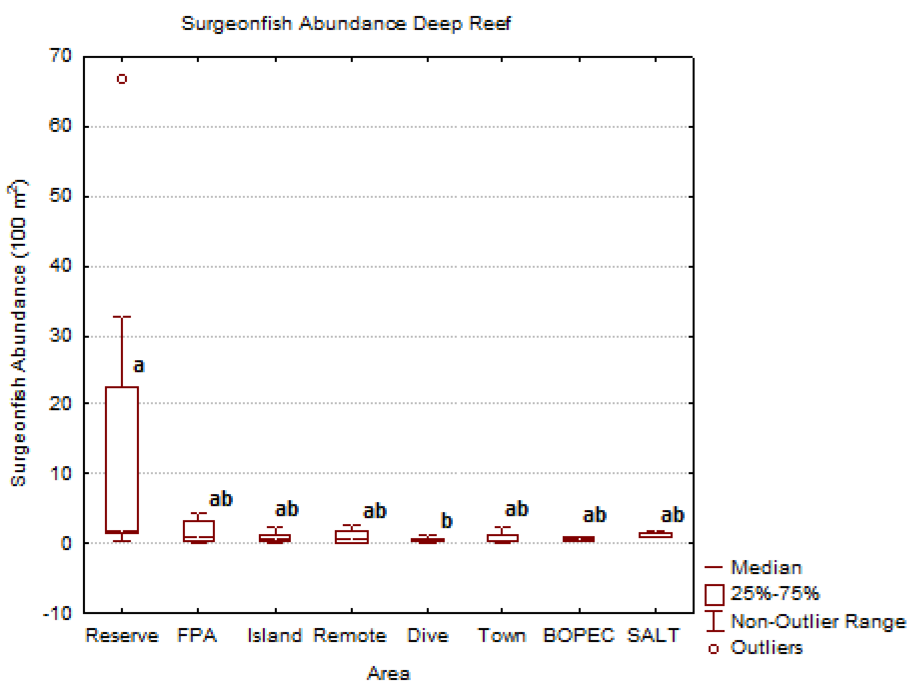


Total Abundance (100 m^2): KW-H(7;116) = 21,6527; p = 0,0029

Appendix H – Statistical analysis of group differences between resource use groups for fish functional values in reef zones

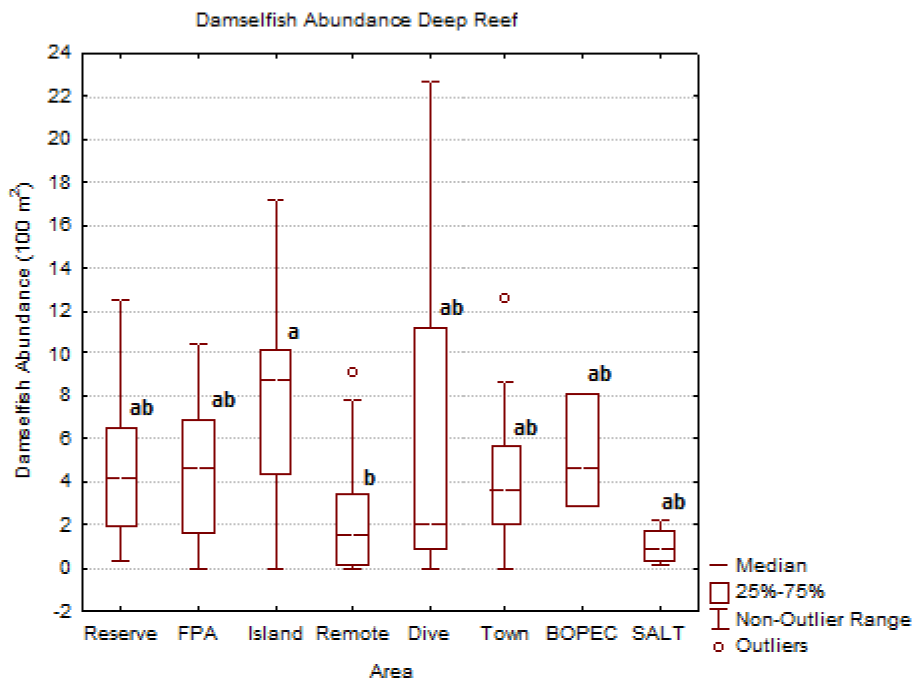


Parrotfish Abundance (100 m^2): KW-H(7;116) = 17,0981; p = 0,0168



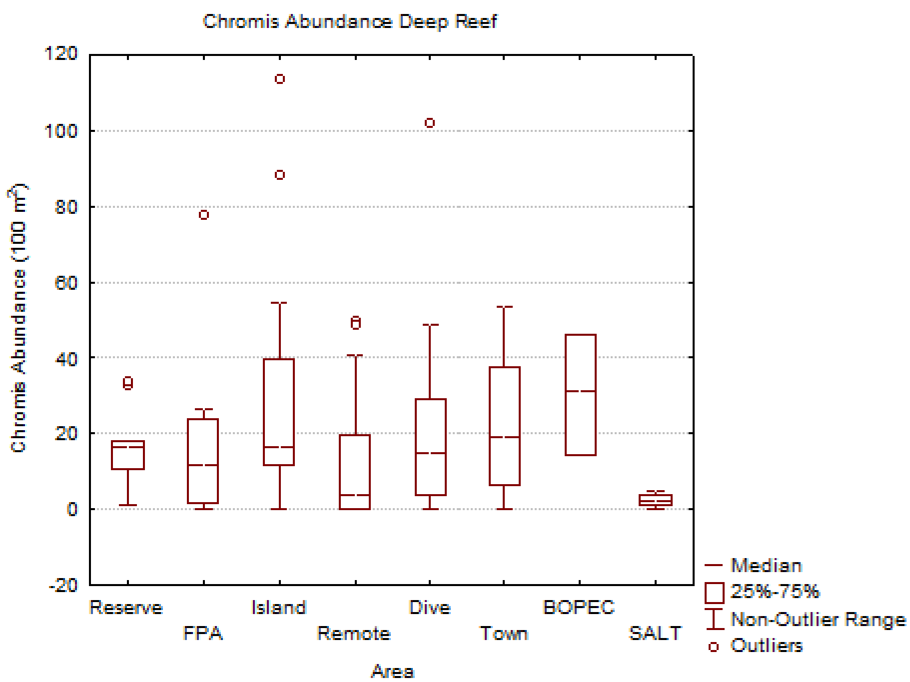
Surgeonfish Abundance (100 m^2): KW-H(7;116) = 12,5895; p = 0,0828

Depend.: Surgeonfish Abundance (100 m^2)	Multiple Comparisons p values (2-tailed); Surgeonfish Abundance (100 m^2) (Definitiefl Independent (grouping) variable: Area Kruskal-Wallis test: H (7, N= 116) =12,58947 p =,0828							
	Reserve R:89,778	FPA R:68,313	Island R:60,619	Remote R:55,423	Dive R:49,143	Town R:52,912	BOPEC R:48,333	SALT R:74,250
Reserve		1,00000	0,82703	0,23120	0,04520	0,21930	1,00000	1,00000
FPA	1,00000		1,00000	1,00000	1,00000	1,00000	1,00000	1,00000
Island	0,82703	1,00000		1,00000	1,00000	1,00000	1,00000	1,00000
Remote	0,23120	1,00000	1,00000		1,00000	1,00000	1,00000	1,00000
Dive	0,04520	1,00000	1,00000	1,00000		1,00000	1,00000	1,00000
Town	0,21930	1,00000	1,00000	1,00000	1,00000		1,00000	1,00000
BOPEC	1,00000	1,00000	1,00000	1,00000	1,00000	1,00000		1,00000
SALT	1,00000	1,00000	1,00000	1,00000	1,00000	1,00000	1,00000	

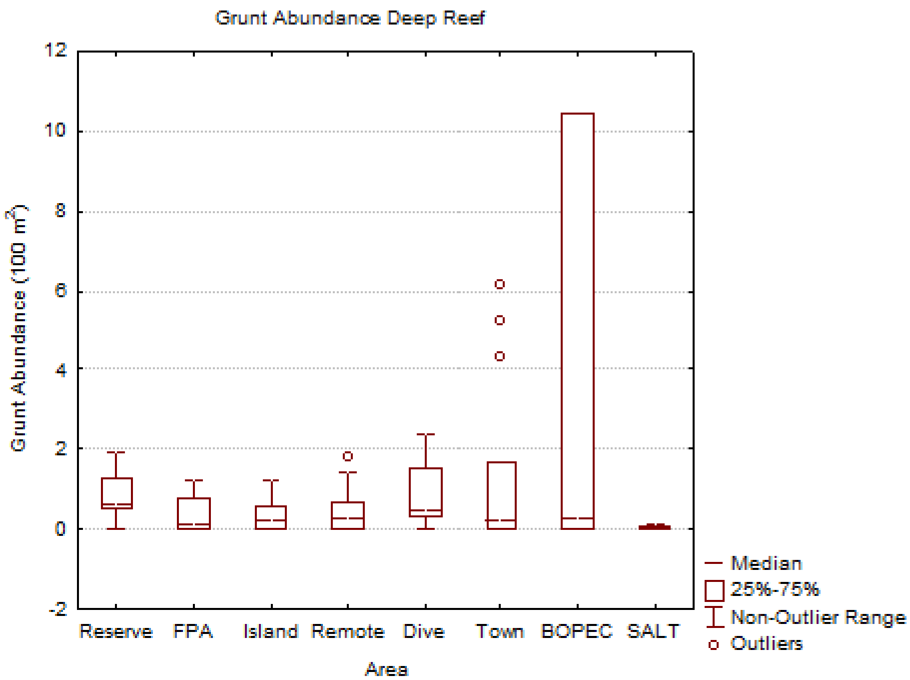


Damselfish Abundance (100 m^2): KW-H(7;116) = 20,5507; p = 0,0045

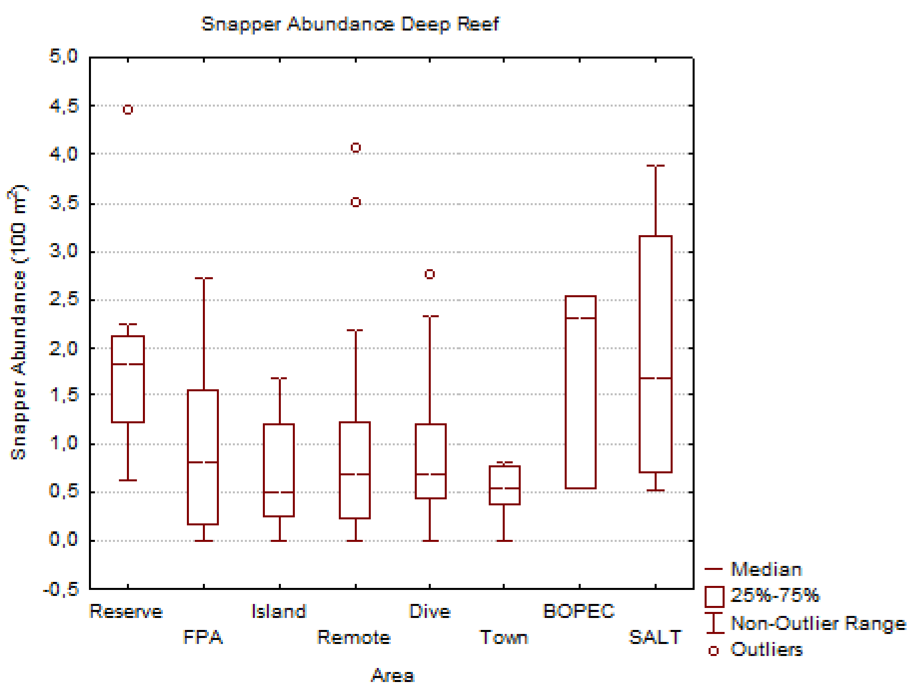
Depend.: Damselfish Abundance (100 m2)	Multiple Comparisons p values (2-tailed); Damselfish Abundance (100 m2) (Definitie Independent (grouping) variable: Area Kruskal-Wallis test: H (7, N= 116) =20,55071 p =,0045							
	Reserve R:66,778	FPA R:61,438	Island R:80,214	Remote R:40,346	Dive R:57,268	Town R:60,206	BOPEC R:72,000	SALT R:29,250
Reserve		1,000000	1,000000	1,000000	1,000000	1,000000	1,000000	1,000000
FPA	1,000000		1,000000	1,000000	1,000000	1,000000	1,000000	1,000000
Island	1,000000	1,000000		0,00149	0,50675	1,000000	1,000000	0,15322
Remote	1,000000	1,000000	0,00149		1,000000	1,000000	1,000000	1,000000
Dive	1,000000	1,000000	0,50675	1,000000		1,000000	1,000000	1,000000
Town	1,000000	1,000000	1,000000	1,000000	1,000000		1,000000	1,000000
BOPEC	1,000000	1,000000	1,000000	1,000000	1,000000	1,000000		1,000000
SALT	1,000000	1,000000	0,15322	1,000000	1,000000	1,000000	1,000000	



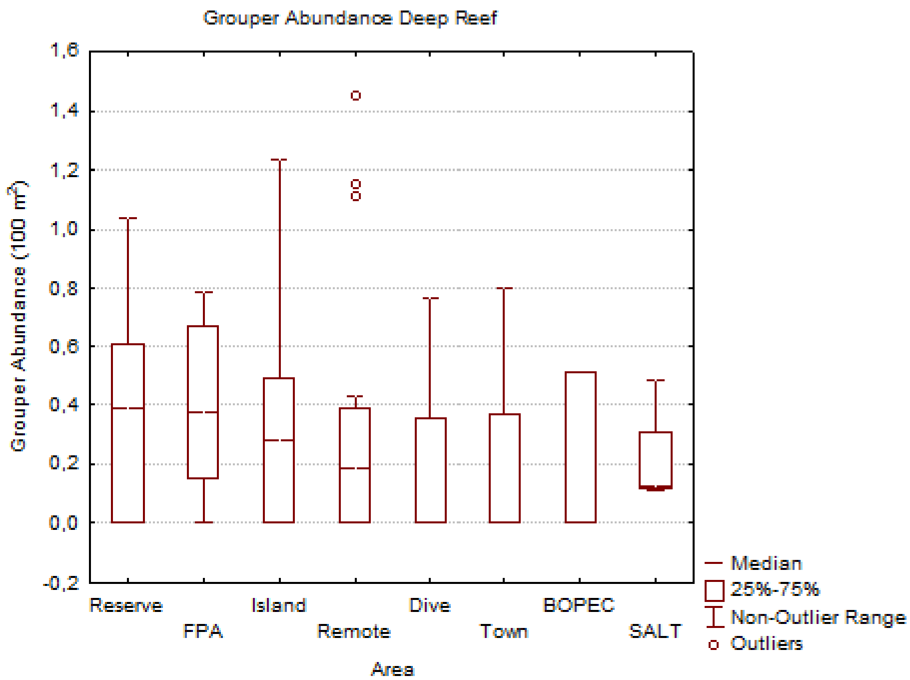
Chromis Abundance (100 m^2): KW-H(7;116) = 16,0459; p = 0,0247



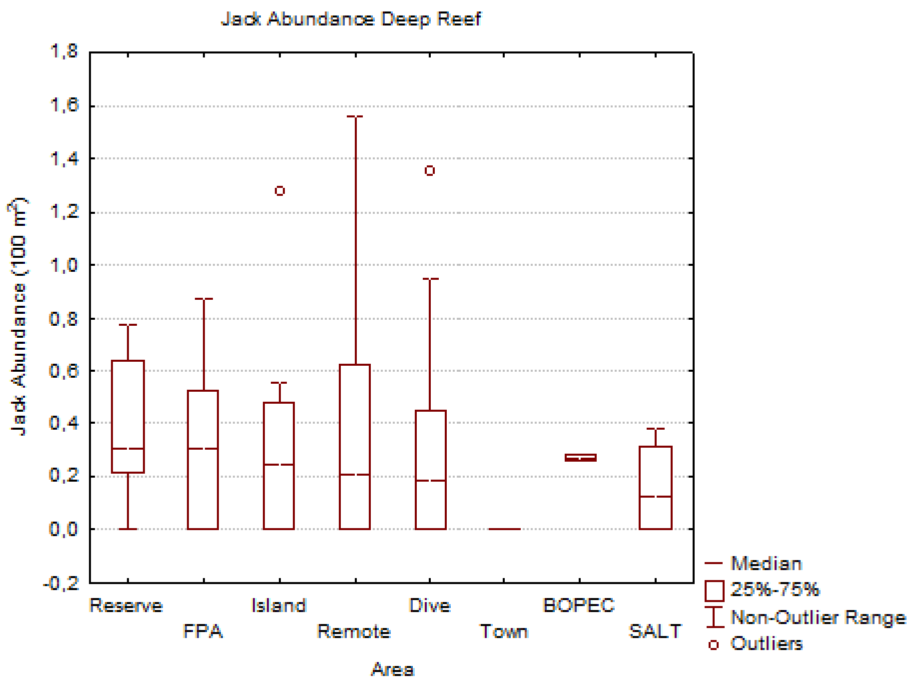
Grunt Abundance (100 m^2): KW-H(7;116) = 14,5036; p = 0,0429



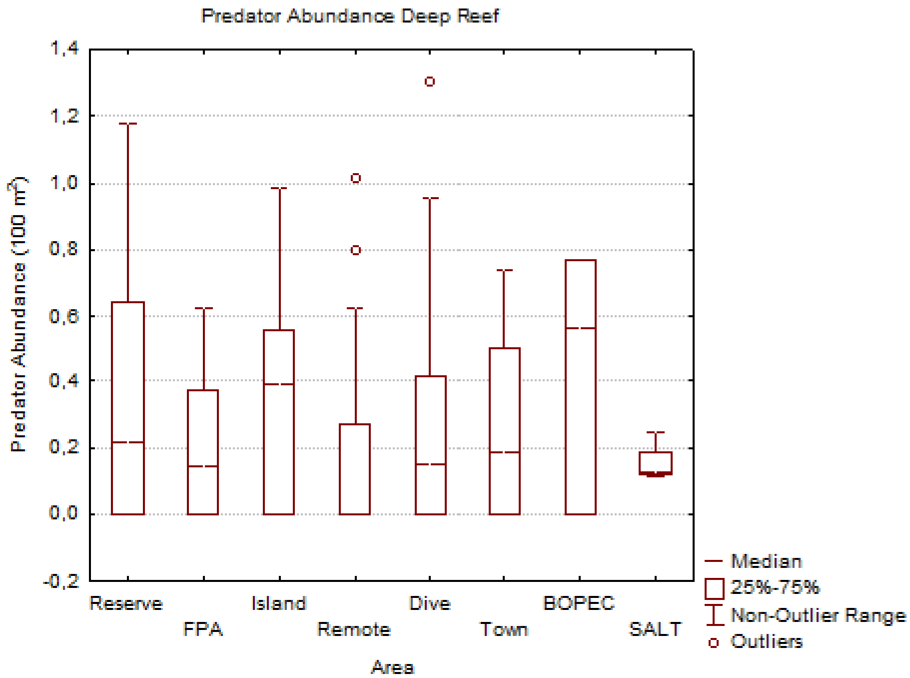
Snapper Abundance (100 m^2): KW-H(7;116) = 11,951; p = 0,1022



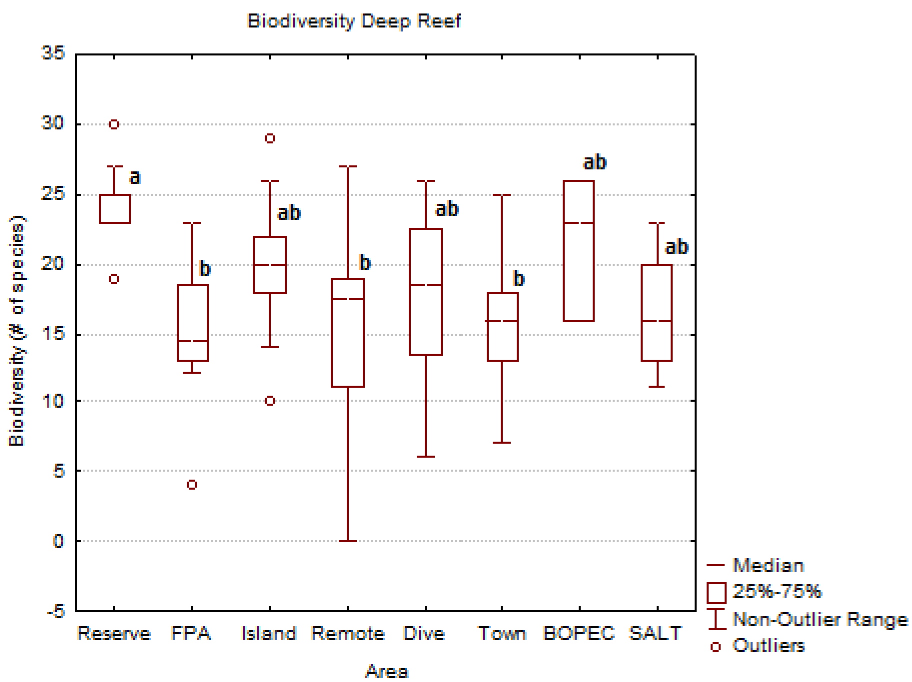
Grouper Abundance (100 m^2): KW-H(7;116) = 7,0249; p = 0,4263



Jack Abundance (100 m^2): KW-H(7;116) = 8,7911; p = 0,2680

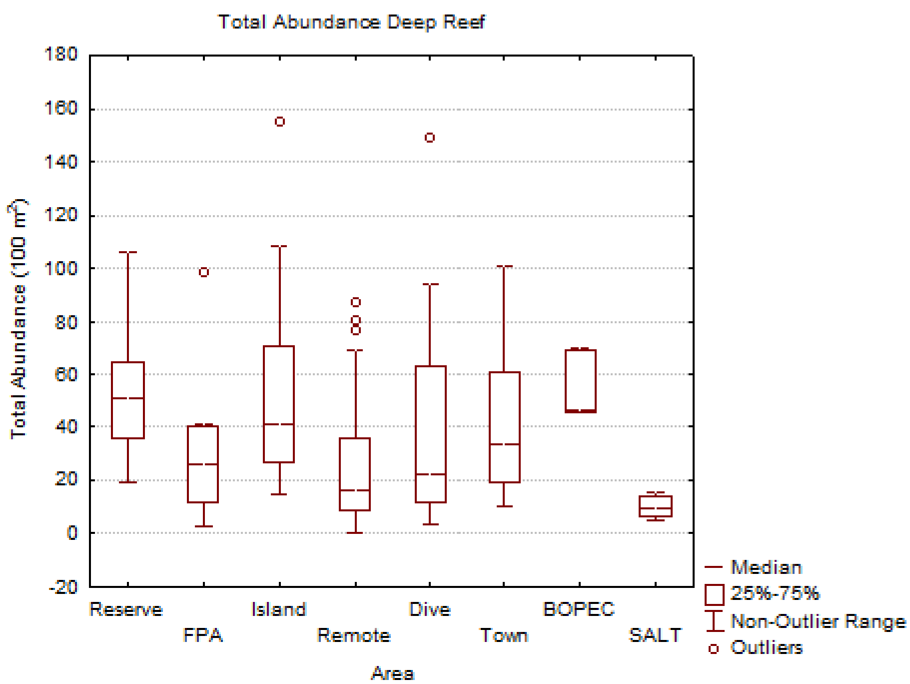


Predator Abundance (100 m^2): KW-H(7;116) = 7,6133; p = 0,3679



Biodiversity (# of species): KW-H(7;116) = 26,6393; p = 0,0004

	Multiple Comparisons p values (2-tailed); Biodiversity (# of species) (DefinitiefFi Independent (grouping) variable: Area Kruskal-Wallis test: H (7, N= 116) =26,63930 p =,0004							
Depend.: Biodiversity (# of species	Reserve R:98,333	FPA R:41,375	Island R:72,381	Remote R:45,962	Dive R:59,339	Town R:44,794	BOPEC R:81,000	SALT R:47,250
Reserve		0,013753	1,000000	0,001584	0,069391	0,003150	1,000000	0,321464
FPA	0,013753		0,741510	1,000000	1,000000	1,000000	1,000000	1,000000
Island	1,000000	0,741510		0,207649	1,000000	0,333976	1,000000	1,000000
Remote	0,001584	1,000000	0,207649		1,000000	1,000000	1,000000	1,000000
Dive	0,069391	1,000000	1,000000	1,000000		1,000000	1,000000	1,000000
Town	0,003150	1,000000	0,333976	1,000000	1,000000		1,000000	1,000000
BOPEC	1,000000	1,000000	1,000000	1,000000	1,000000	1,000000		1,000000
SALT	0,321464	1,000000	1,000000	1,000000	1,000000	1,000000	1,000000	

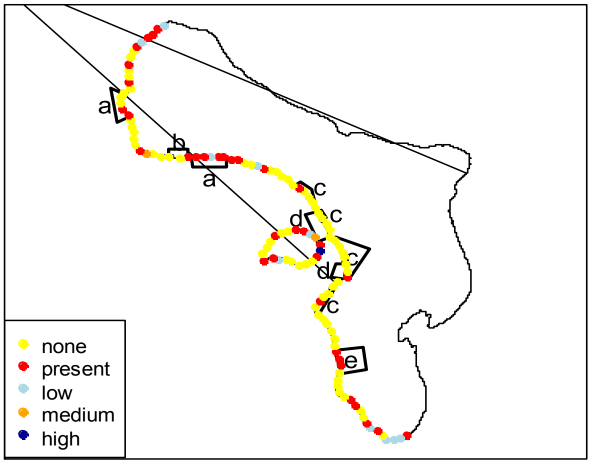


Total Abundance (100 m^2): KW-H(7;116) = 20,8619; p = 0,0040

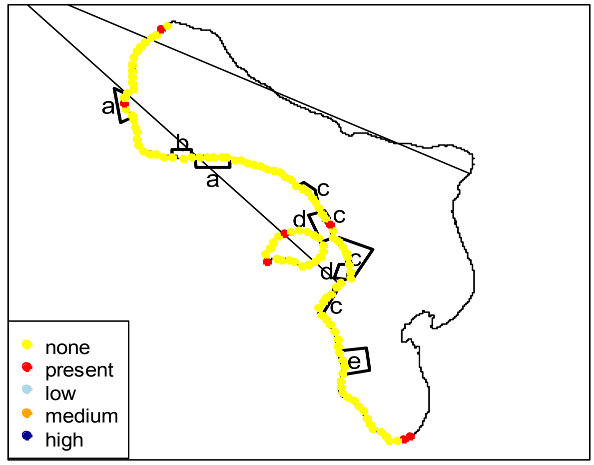
Appendix I –Habitat functional value maps based on representation benthic functional groups

Figures below present functional value maps of shallow and reef habitats measured by the representation of benthic functional groups (FG8-FG20). Labels a-e refer to the following marine and coastal area: a=marine reserves, b=Bopec oil terminal, c=residential area, d=fish reserves and e=Cargill salt production.

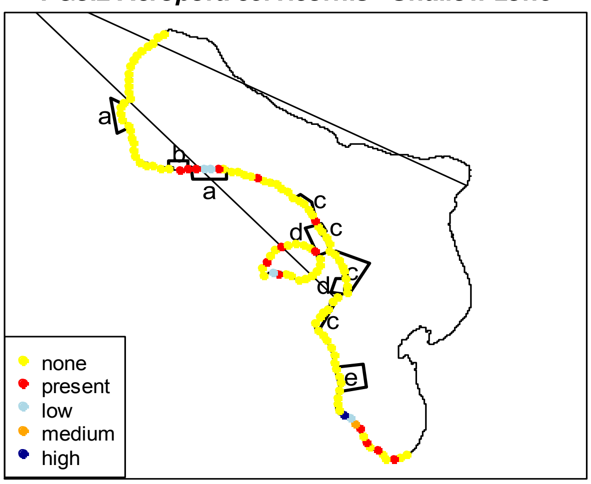
FG8.1 Acropora palmata - Shallow zone



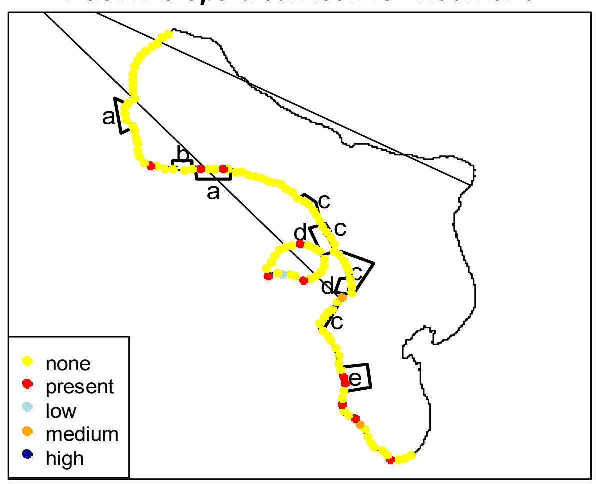
FG8.1 Acropora palmata - Reef zone



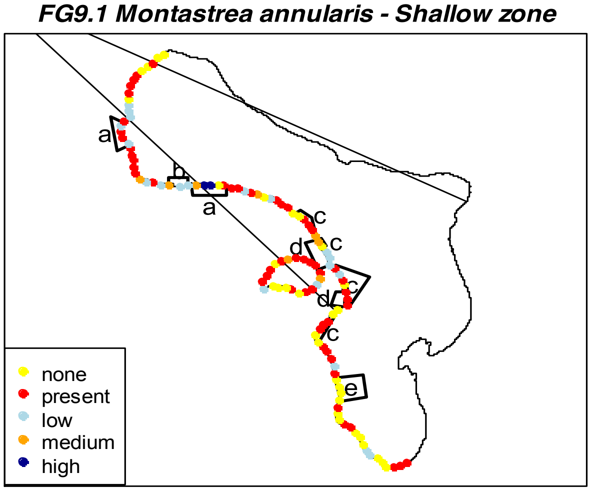
FG8.2 Acropora cervicornis - Shallow zone



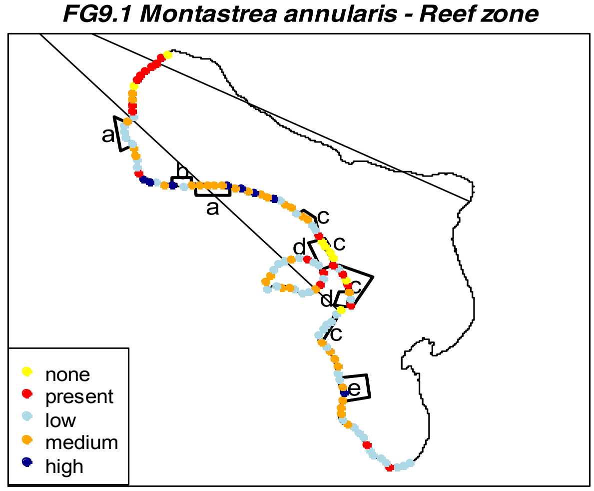
FG8.2 Acropora cervicornis - Reef zone



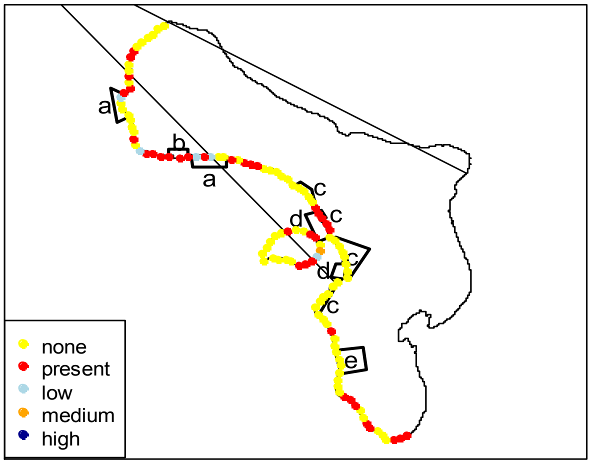
FG9.1 Montastrea annularis - Shallow zone



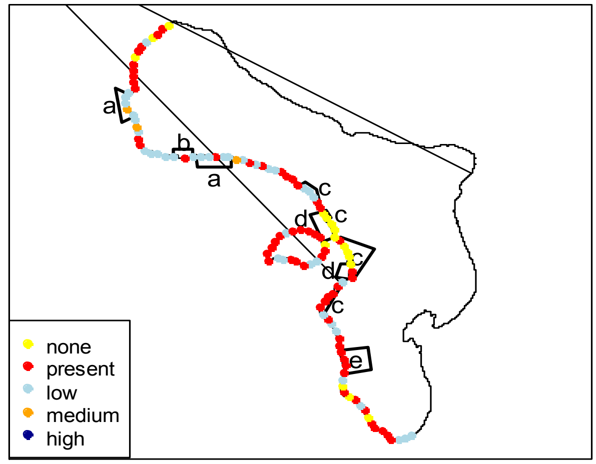
FG9.1 Montastrea annularis - Reef zone



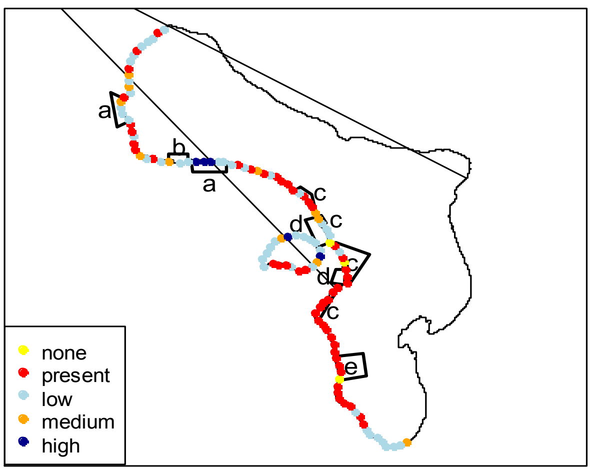
FG9.2 Montastrea faveolata - Shallow zone



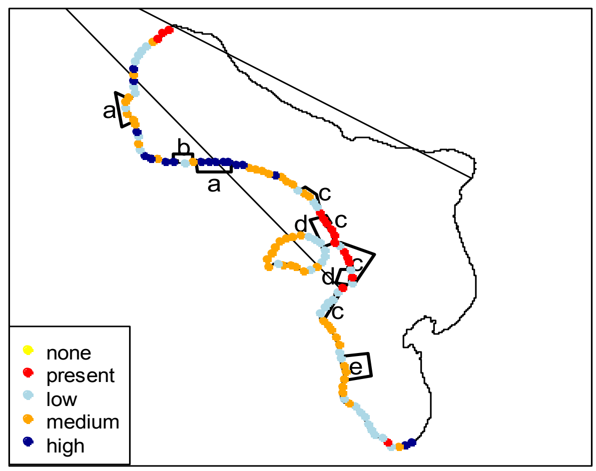
FG9.2 Montastrea faveolata - Reef zone



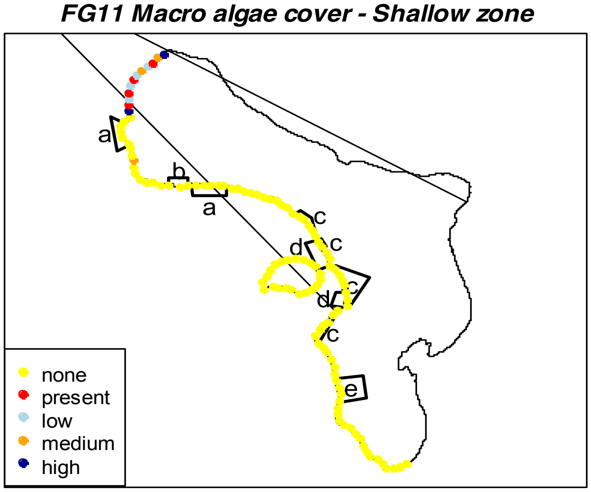
FG10 Coral cover - Shallow zone



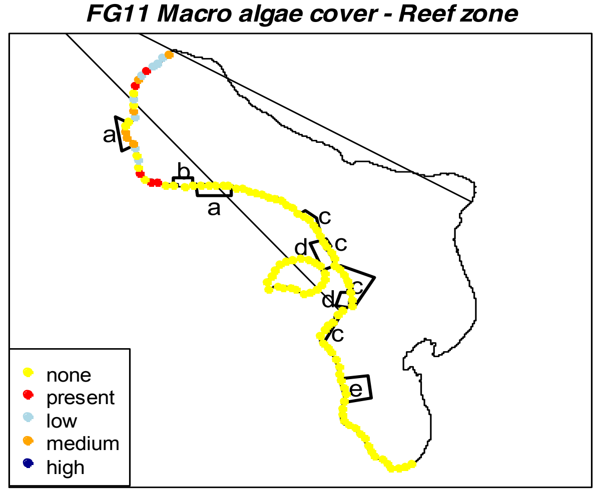
FG10 Coral cover - Reef zone



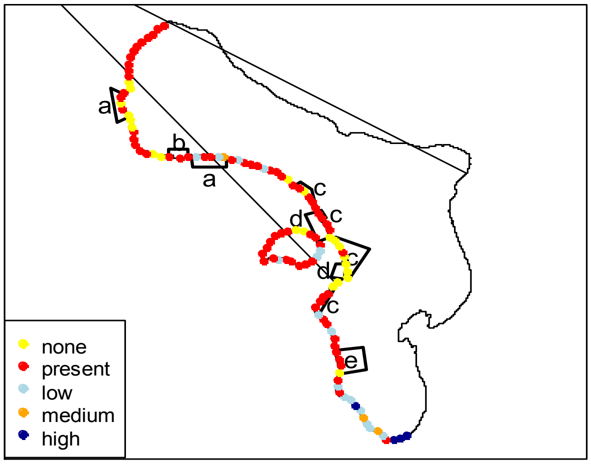
FG11 Macro algae cover - Shallow zone



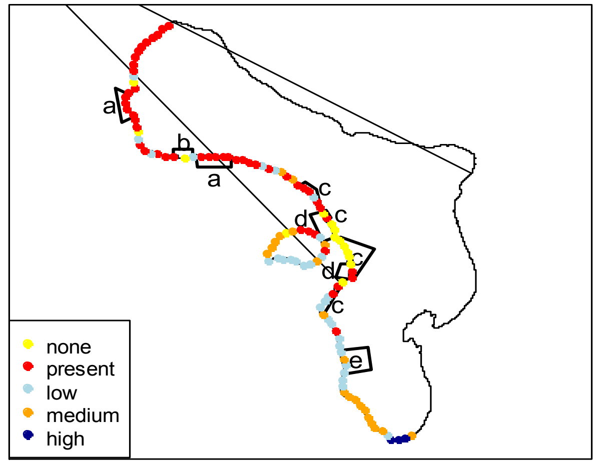
FG11 Macro algae cover - Reef zone



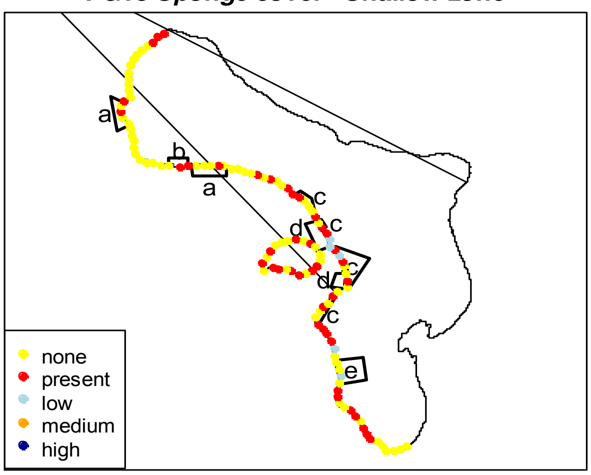
FG12 Gorgonian soft coral cover - Shallow zone



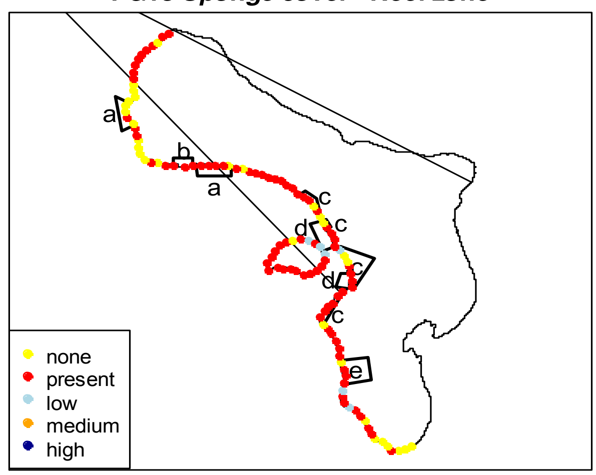
FG12 Gorgonian soft coral cover - Reef zone



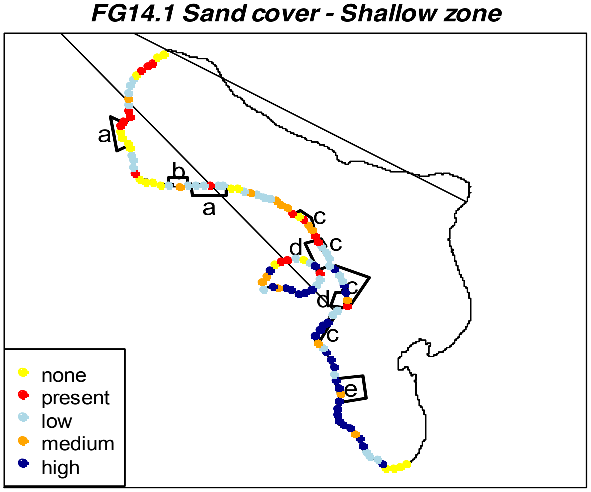
FG13 Sponge cover - Shallow zone



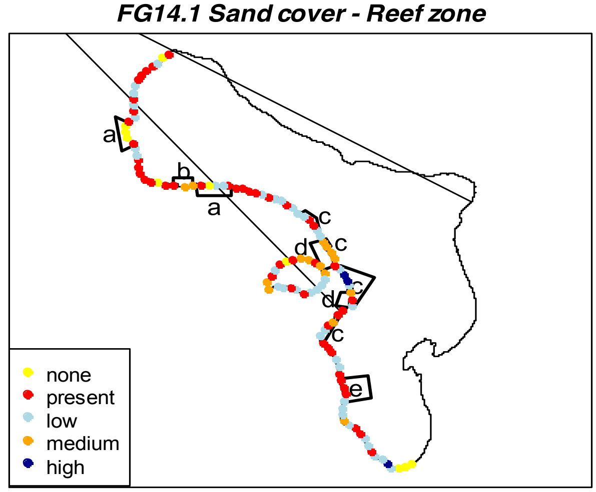
FG13 Sponge cover - Reef zone



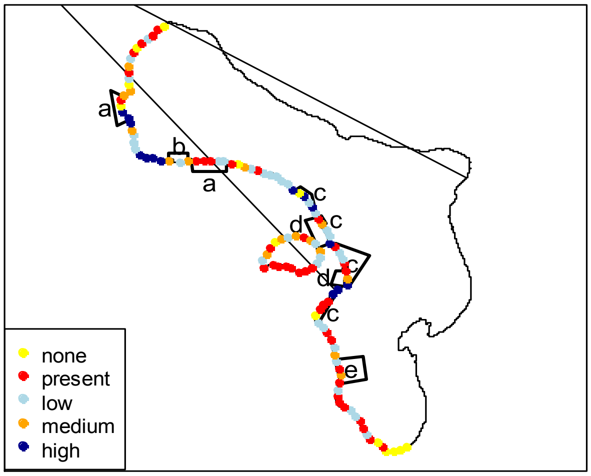
FG14.1 Sand cover - Shallow zone



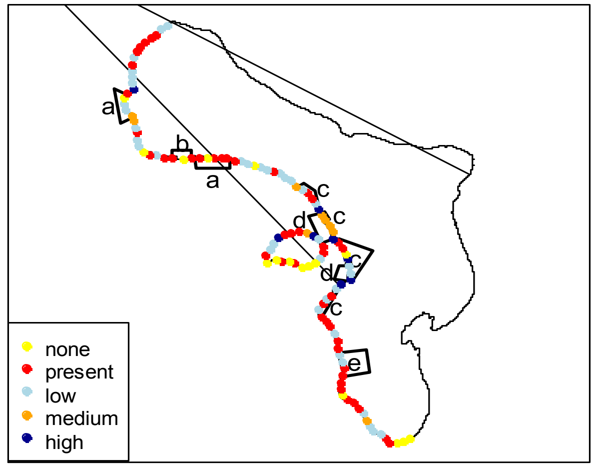
FG14.1 Sand cover - Reef zone



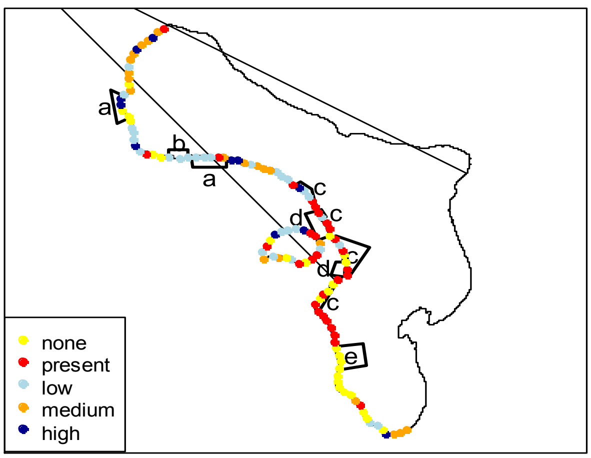
FG14.2 Coral rubble cover - Shallow zone



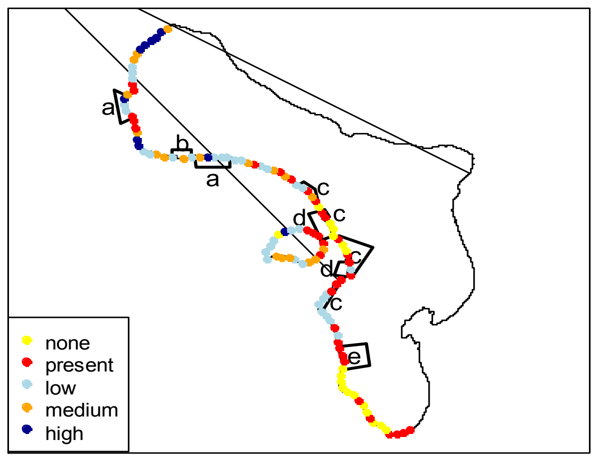
FG14.2 Coral rubble cover - Reef zone



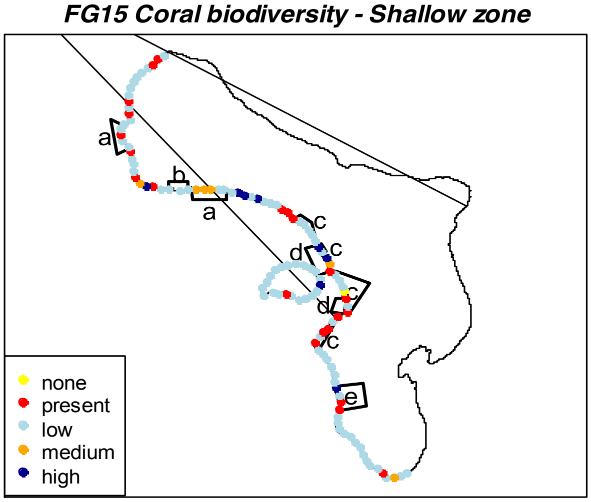
14.3 Rock cover - Shallow zone



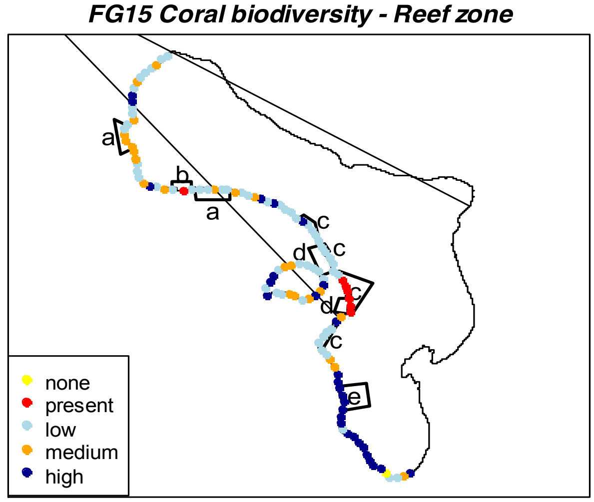
14.3 Rock cover - Reef zone



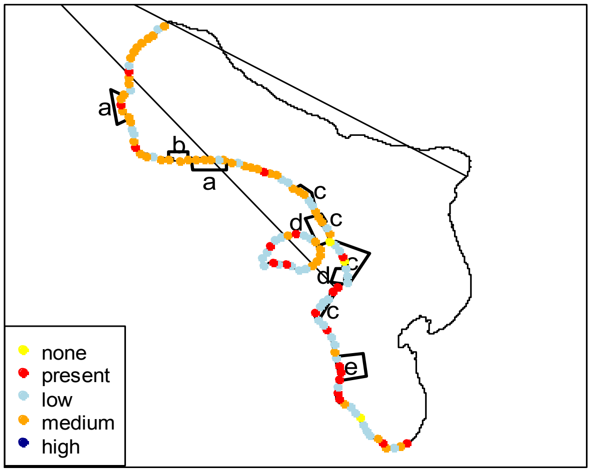
FG15 Coral biodiversity - Shallow zone



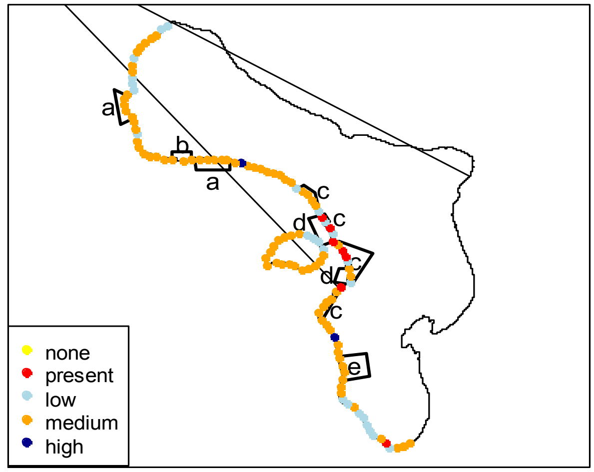
FG15 Coral biodiversity - Reef zone



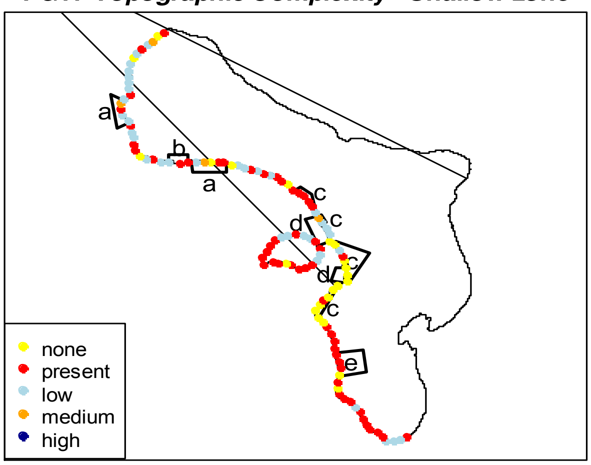
FG16 Coral maximum size - Shallow zone



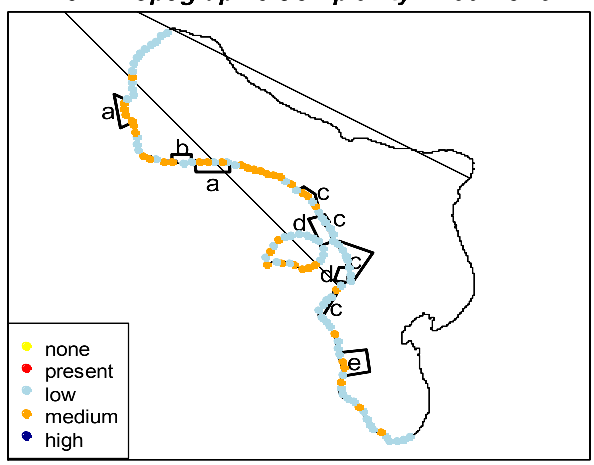
FG16 Coral maximum size - Reef zone



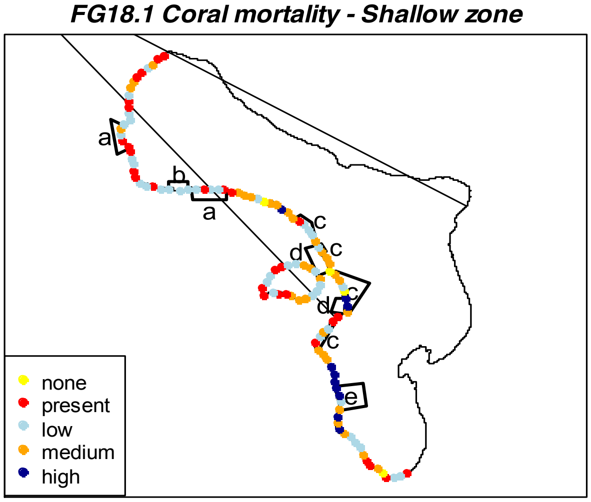
FG17 Topographic Complexity - Shallow zone



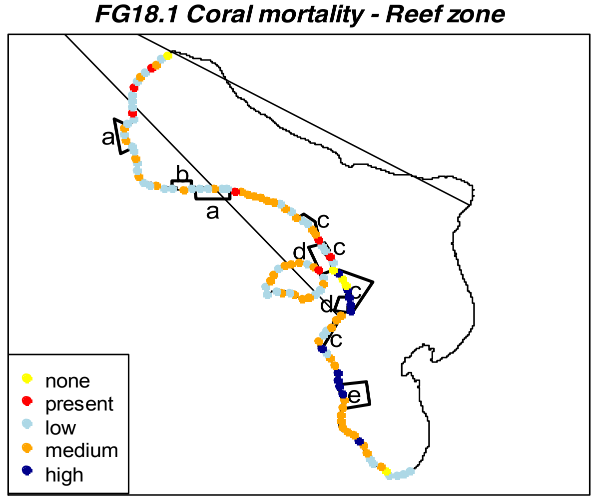
FG17 Topographic Complexity - Reef zone



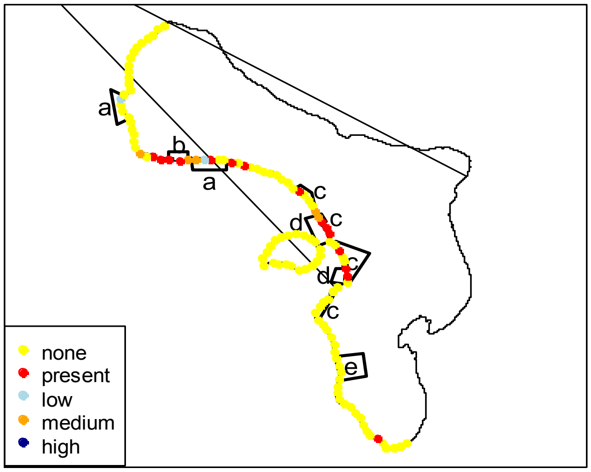
FG18.1 Coral mortality - Shallow zone



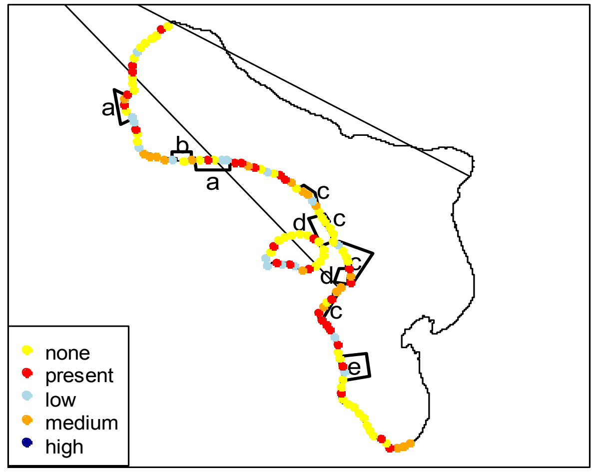
FG18.1 Coral mortality - Reef zone



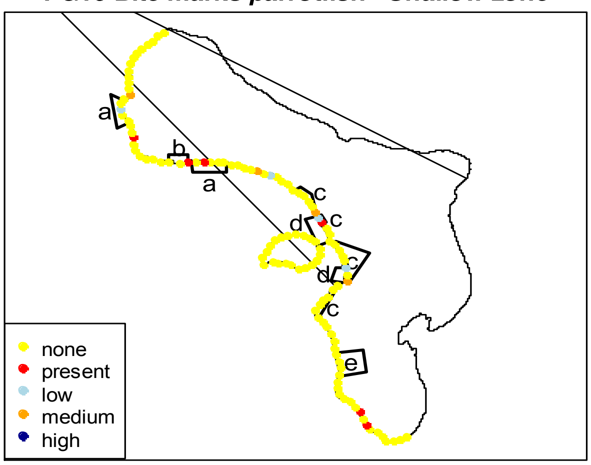
FG18.2 Coral bleaching - Shallow zone



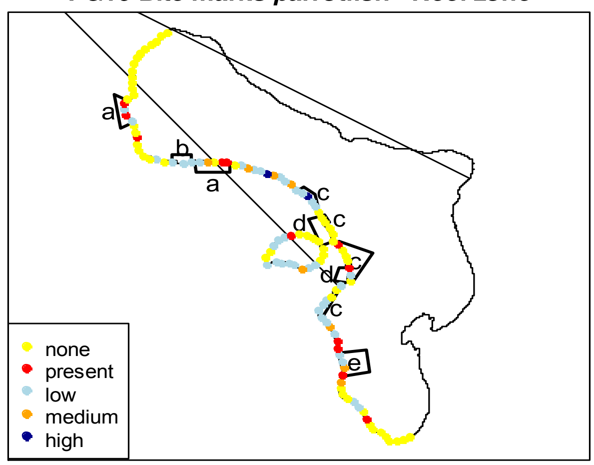
FG18.2 Coral bleaching - Reef zone



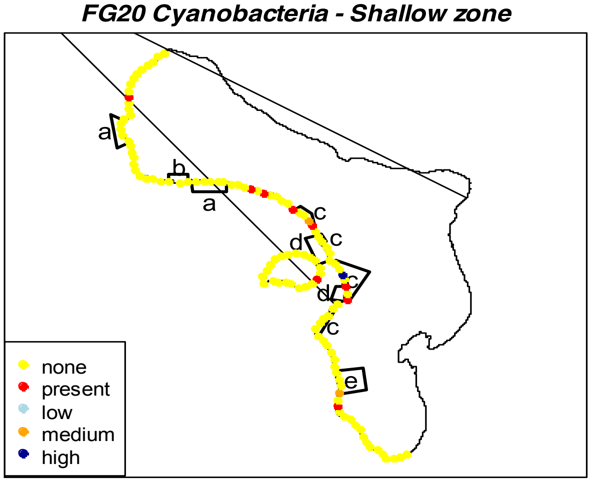
FG19 Bite marks parrotfish - Shallow zone



FG19 Bite marks parrotfish - Reef zone



FG20 Cyanobacteria - Shallow zone



FG20 Cyanobacteria - Reef zone