Faculty of Biosciences, Fisheries and Economics
Norwegian College of Fishery Science

The ecology of a tropical bay and social aspects of small-scale fisheries: Implications for management

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Hector A. Andrade R.

A dissertation for the degree of Philosophiae Doctor – September 2015

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Dedication

I dedicate this dissertation to my parents, Maria and Hector for whom my education has always been a priority. Thanks for all your support and efforts during the difficult and expensive private school years and later on, during my undergraduate degree in Guatemala. Also to my sons, Adrian and Sebastian who have brought new meaning to my life.

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Finally to my Trude who has been so supportive through all these years, even when 7 months after our marriage, I left her for a year of fieldwork. This project started as an investment for a common future, thinking that a PhD degree was the way forward to secure a job in Norway. Although the job did not arrive as planned (luckily!), the investment paid off and now we can enjoy our latter recruits, Adrian and Sebastian!

Foreword

In 1999, I started working in the Rio Dulce National Park, an area in Livingston, Izabal that connects Lake Izabal and Amatique Bay, on the Caribbean coast of Guatemala. This was part of an internship to finish my degree in aquaculture at the University of San Carlos. My main task was to perform a pilot project exploring the aquaculture potential of a native fish species. I was feeding juveniles of this fish in a cage to find out how well they grow. The general idea was that if successful, the rearing of this fish could provide steady income and food to the inhabitants of the Rio Dulce National Park.

Several of the impoverished indigenous communities located here made a living out of subsistence agriculture and/or natural resource extraction. In need of arable land or construction material, people would cut down the forest in spite of prohibitions stated in the environmental laws. Fishing, in contrast, was virtually unregulated so everybody could fish and get their food with a larger sense of legality. Fish landings were nevertheless diminishing according to some fishers, and the central government authorities foresaw that some form of management actions were needed to curb this trend. However, much scientific information was needed to execute a revised management plan. The situation was similar and more complex than I had previously experienced while working with fisheries on the Pacific coast of Guatemala. There were increased challenges because of the longer distances from the largest cultural centers of the country, as well as poor research infrastructure. I realized that the challenges of simultaneously achieving sound management, conservation and food security goals were huge. That thrust inspired me to pursue research on these topics.

In 2001, the Norwegian Agency for Development Cooperation (NORAD) awarded me a scholarship to study a Master's Degree in Tromsø where I was able to participate in research cruises, do lab work, analyze data and report the results giving me the feeling of what research was really about. I wanted to continue my studies and carry out research in tropical fisheries. Therefore, in 2005, I applied for a PhD scholarship from the World Wildlife Fund. I got the scholarship and traveled back to Livingston, Guatemala, where I spent the next 13 months collecting fish gonads and otoliths. I returned to Norway with about 2000 otoliths in a bag knowing nothing about how to work with them. This changed after I traveled to Saint Petersburg, Florida to learn processing and ageing with Ron Taylor and Janet Tunnel at the Fish and Wildlife Research Institute. In 2007, Svein Jentoft, at the Norwegian College of Fishery Sciences, invited me to work as a researcher in the newly financed project "Unravelling the Vicious Circle - Poverty Alleviation and Sustainable Livelihoods in Small-scale Fisheries (PovFish)”. I was paired with Georges Midré, also at the University of Tromsø, who taught me some of the research techniques in social sciences, like using a tape recorder in an interview.

I revisited Livingston in 2008, to interview several of the fishers and mongers that I had met previously during biological sampling. Upon returning to Tromsø funding ceased, living costs in Norway were very high and I was now starting a family in the Arctic. In order to continue my tropical research, I took several part-time jobs. These included cleaning floors, washing dishes, sorting sediment samples, occasional teaching, cruises during the polar nights, and for one time only, as a football referee. Finally, in 2010, I became a full time employee at Akvaplan-niva AS where I currently work as an environmental consultant. After securing a salary, it became easier to concentrate on the PhD work during my spare time. It was then that the long gestation period of the data collection and assimilated background knowledge began to take form for publications and this thesis.

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1. Introduction

The inherent ecological and social importance of coastal ecosystems requires that management plans pursue both environmental and socioeconomic sustainability goals (Gladstone 2009, Lebel 2012, Kolding et al. 2014a). For this purpose, the integration of scientific information regarding ecosystem functioning and the knowledge about the welfare of individuals and communities is of paramount importance (Granek et al. 2010, Cochrane et al. 2011, de Graaf et al. 2011, Ferrol-Schulte et al. 2013). This represents a major challenge for effective management of the river-estuary-coast complex in tropical areas where the complex interactions between the ecological, biological, physical and socio-cultural processes are normally poorly understood (Barletta et al. 2010, Christie 2011, Lebel 2012).

Ecologically speaking, estuaries and coastal lagoons are among the most productive environments worldwide, interconnecting freshwater rivers and wetlands to marine and oceanic habitats (Nagelkerken 2009, Basset et al. 2013, Hyndes et al. 2014). In the tropics, important habitats include coral reefs, mangrove forests, and seagrass beds. All these environments sustain high species diversity and maintain key ecosystem processes demanding special conservation attention and efforts (Blaber 2002, Nagelkerken 2009). At the same time, the production of food from fisheries is considered a primary service derived from coastal ecosystems (Gladstone 2009). In the developing world, the small-scale fisheries operating in near-shore waters often provide labour and cash income to resource-poor households lacking alternative means of support (Blaber 2009, Allison et al. 2011, Ferrol-Schulte et al. 2013).

This thesis is concerned with developing primary scientific knowledge that can be used to inform coastal management plans, particularly in the context of tropical estuaries and small-scale fisheries (Figure 1). In this concern, a multi-disciplinary approach was judged imperative. Estuarine ecosystems are often characterized by high abiotic variability (e.g. run-off, salinity, temperature, oxygen, etc.). These environmental cycles strongly influence the structure of species assemblages, their life histories and how humans obtain ecosystem services (Barletta et al. 2005, Gillson 2011, Basset et al. 2013). Within the field of natural ecology, this dissertation concentrates on the functioning of tropical marine estuarine ecosystems. Major emphasis is placed on environmental cycles and how these relate to the life history of species with different ecological traits. The conceptual and theoretical underpinnings of this investigation stem from life-history theory, as well as theories relating to the effects of fishing on spawning aggregations and the balanced harvest of different trophic levels and size categories. Modern representatives of these approaches include but are not limited to Blaber (2000), King & McFarlane (2003), Nagelkerken (2009), Sadovy et al. (2012), and Kolding et al. (2014a, 2014b).

From a social perspective, the present work emphasizes the access regulation of common pool resources. A primary focus is the way multiethnic fisher groups operate their diverse fishing gear, how this can give rise to space conflicts due to physical interactions, and how institutional arrangements to mitigate open conflicts are negotiated. The welfare function of the small-scale fisheries, which is defined as the capacity to provide labor and cash income to resource-poor households (Béné et al. 2010) is also investigated. The theoretical background for the understanding of the complex interactions of these social systems was obtained primarily from the works of Béné (2003), Chuenpagdee & Jentoft (2009) Jentoft et al. (2009), Béné et al. (2010), Jentoft & Eide (2011) and Kooiman & Bavinck (2013)

The social and ecological processes and their interactions analyzed in the present work were largely disclosed by means of fieldwork and empirical data, which required direct biological sampling and interviews in the fishing communities. Thus, it can be argued that the primary approach of this thesis is inductive. Due to the lack of previous detailed knowledge on the Amatique system, the surveys were performed by means of semi-structured interviews, and quantitative data were subjected to exploratory, rather than confirmatory analyses. Thus, hypotheses and theories were developed *a posteriori*: in a bottom-up approach, patterns were identified and matched to patterns observed elsewhere. A number of analyses were performed, that had as a point of departure the available perceptions of the evolution and dispersal of different organisms during the formation of Central America, which led to developing some conjectures about possible causes of extant organism distribution. Analyses rooted in small-scale fisheries management theory led to the development of conjectures on social relationships. These analyses were tested against available information, which included literature studies, remote (satellite) sensing and traditional fishers' knowledge. Interpretation of these data resulted in inferences with regard to how the evolutionary path of different species have been, and still are, molded by the changing environment of the Caribbean. In this respect, the presence/absence of patterns of organisms are telling. This approach, which starts from overarching questions and hypotheses and attempts to collate empirical data that may falsify them, has a more deductive character. With respect to small-scale fisheries governance, the interactions between different fishing groups were analyzed to disclose how management consensus has been pursued and implemented. The interview data revealed also why the fishing regulations that have been agreed upon are not fully observed. Finally, the present approach is multidisciplinary and makes use of different time scales (months to decades) and spatial scales (Amatique and Caribbean to other tropical regions of the Atlantic and Pacific) to achieve validation and useful generalization.

This dissertation begins by defining the research questions that motivated this investigation and how these were addressed in the three papers constituting the thesis. This is followed by a section that provides a general overview of the study area and the materials and methodology chosen to collect the data. Then, a summary of the three papers and their main findings is provided. The final chapter discusses opportunities and challenges of combining knowledge from the ecological and social settings for the development of a coastal management plan with particular emphasis on fisheries. In an attempt to bring the findings from the present work into an immediate practical application, some aspects of the current fisheries management regime (i.e. seasonal closures, fishing across trophic levels and sizes) are examined under the light of new findings disclosed in this thesis.

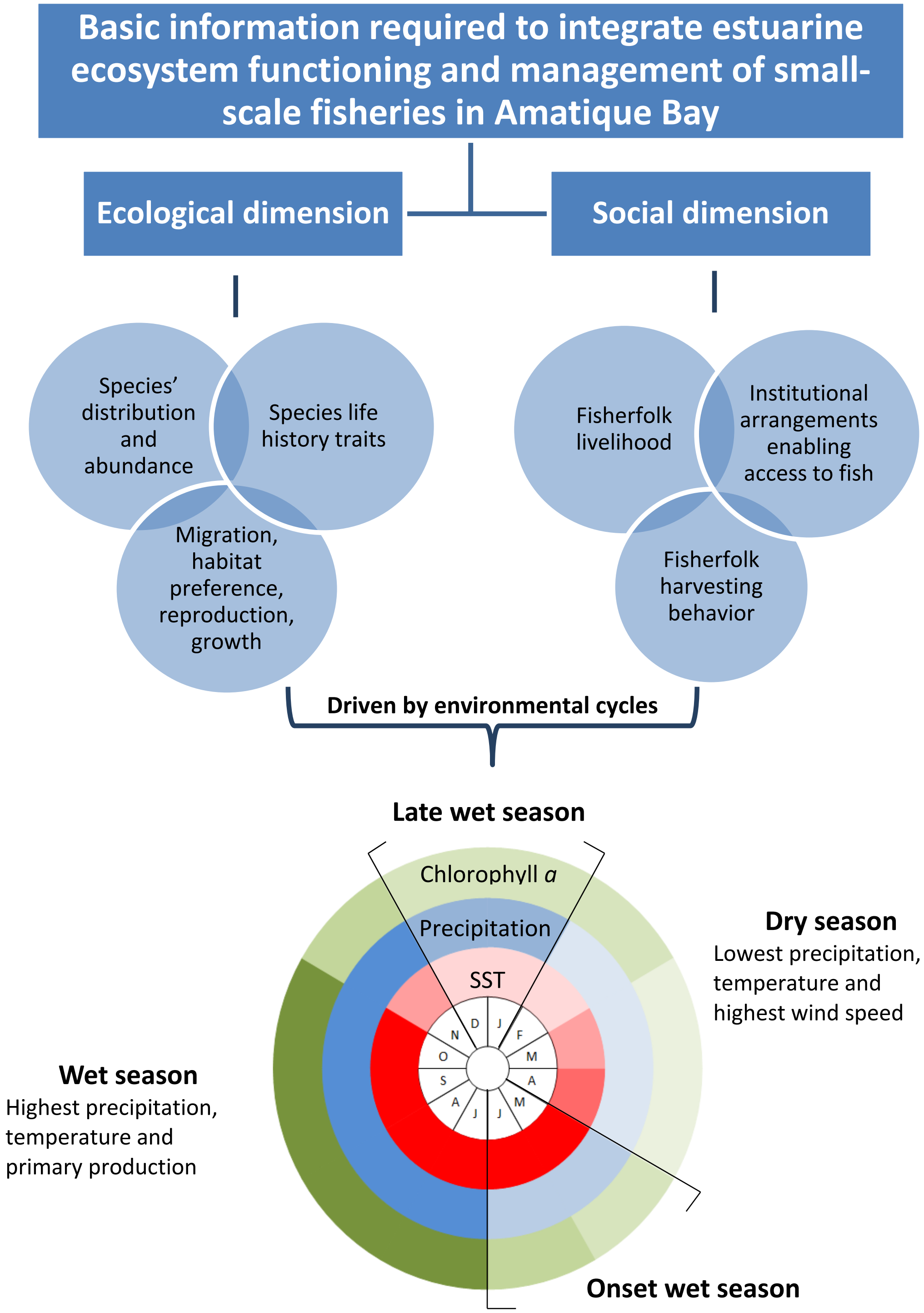

Figure 1. Basic information needed for the integration of ecosystem functioning and small-scale fisheries management in Amatique Bay. Intensity in color denotes relative strength of sea surface temperature (SST), precipitation and chlorophyll *a*. The onset of the wet season is defined as the month when precipitation increases from the average annual minimum (150 mm). By July, the monthly precipitation is about 400 mm and the wet season is well established (**Paper 1**)

2. Research questions

A multidisciplinary investigation was performed, based on a variety of ecological and social aspects of Amatique Bay. The data were then combined to understand how the implementation of technical measures affects small-scale fishery management outcomes, especially with regard to regulation compliance. Specifically, the following questions are answered in this dissertation:

1. What are the main ecological drivers of Amatique Bay and how do these drivers influence the life history of iconic and commercially important species targeted by the small-scale fishers?

2. What are the main social factors driving fisheries in Amatique Bay?

3. How can socio-ecological aspects be integrated for more effective small-scale fisheries management in Amatique Bay?

The first question is addressed in **Paper 1** and **Paper 2**.

In **Paper 1**, we investigate:

- fluctuations of the main environmental cycles having an effect on the physical-chemical properties of Amatique Bay;
- how these cycles drive species abundances in the Bay and how they could have driven the evolution of extant taxa in the last 3 Ma;
- how fishers adapt to target the most abundant species; and
- how such cycles affect the life history of commercially important fish species.

Paper 2 focuses on the common snook (*Centropomus undecimalis*), an abundant fish species not only in Amatique Bay, but also across the Western Atlantic. This was just one of the fish species surveyed in detail, and focus is given to it here because of its commercial and recreational value. Despite its importance, relatively little is known about the biology of this species across its distribution range. The life history and the seasonal patterns of the fish biology are investigated in detail. Longevity, population growth and spawning, as well as reproductive traits related to sex change are addressed in this paper. The results are then compared across latitudinal clines to identify similarities and differences of life history traits, effects of fishing on such traits, as well as to demonstrate how large-scale biogeographic patterns can be utilized in the formulation of management advice.

The second question is addressed in **Paper 3.** Here, fishers' livelihoods and fisheries management are investigated from a social perspective, including: how and why the multiethnic fisher groups fish; the interactions between fleets; how conflicts and economic hardships affect fisher groups and the development of coping mechanisms; and lastly, how all of the above drive and shape compliance with the current fisheries management regime.

The third question is an aggregating issue that is dealt with in the present discussion.

3. Materials and Methods

3.1. Study area

Fieldwork was conducted in Amatique Bay, Guatemala (Figure 2), specifically in the towns of Livingston and Puerto Barrios during two separate periods to perform biological sampling (2006-2007), and to conduct semi-structured interviews with fishers (2008). Fieldwork had a total duration of 14 months.

Amatique Bay is a tropical shallow (< 10 m) estuary rich in coastal lagoons, sea-grass meadows, reefs, mangroves, swamps and marshes (Yañez-Arancibia et al. 1999, Fonseca & Arrivillaga 2003). The bay is surrounded by natural protected areas with different management goals that shelter the watershed and parts of the marine systems. Despite protection efforts, and being considered an area of great tourism potential, environmental degradation is occurring rapidly. Causes for this degradation include inadequate agricultural practices, overfishing, increased industrial infrastructure, oil and gas exploration and mining (Yáñez-Arancibia et al. 1999). This development has been attributed to the lack of management plans, and also socioeconomic issues including poverty and income inequality (Yáñez-Arancibia et al. 1999, Heyman & Graham 2000, **Paper 1**).

Amatique Bay is part of the Livingston district, Izabal, and home to 65,000 inhabitants. In this district, agriculture is the primary activity, but poverty and extreme poverty are relatively high (59 and 20% respectively), and escalating (OMP 2006, INE 2013). There is also a lack of basic infrastructure (e.g. hospitals), and illiteracy is the reality for up to 40% of the population (OMP 2006). The land distribution is highly skewed, with 5% of the people owning 95% of the total area, diverting land use mainly to forestry or cattle ranching. The remaining arable land is employed for slash-and-burn subsistence agriculture, with a common 6-year cycle. Such characteristics have contributed to human desertification and migration from rural communities into the more urbanized municipal center called "Livingston" (OMP 2006).

Livingston (hereafter used as a synonym for the municipal center) has a thriving small tourism industry based on its attractive natural and cultural landscapes. Its multiethnic population is comprised mainly of Q'eqchi, Ladino, Garífuna, and Hindu descendants. Situated in the mouth of Rio Dulce, this town also has a strategic location for the small-scale fishers operating in Amatique Bay. These fishing grounds are relatively close and commercialization channels are well-developed, providing good access to the domestic market. More than 1,000 small-scale fishers operate in Amatique Bay benefiting from the relatively high productivity brought about by nutrient run-off, local retention and re-cycling in the estuary (Heyman & Kjerfve 2001, Heyman & Granados-Dieseldorff 2012).

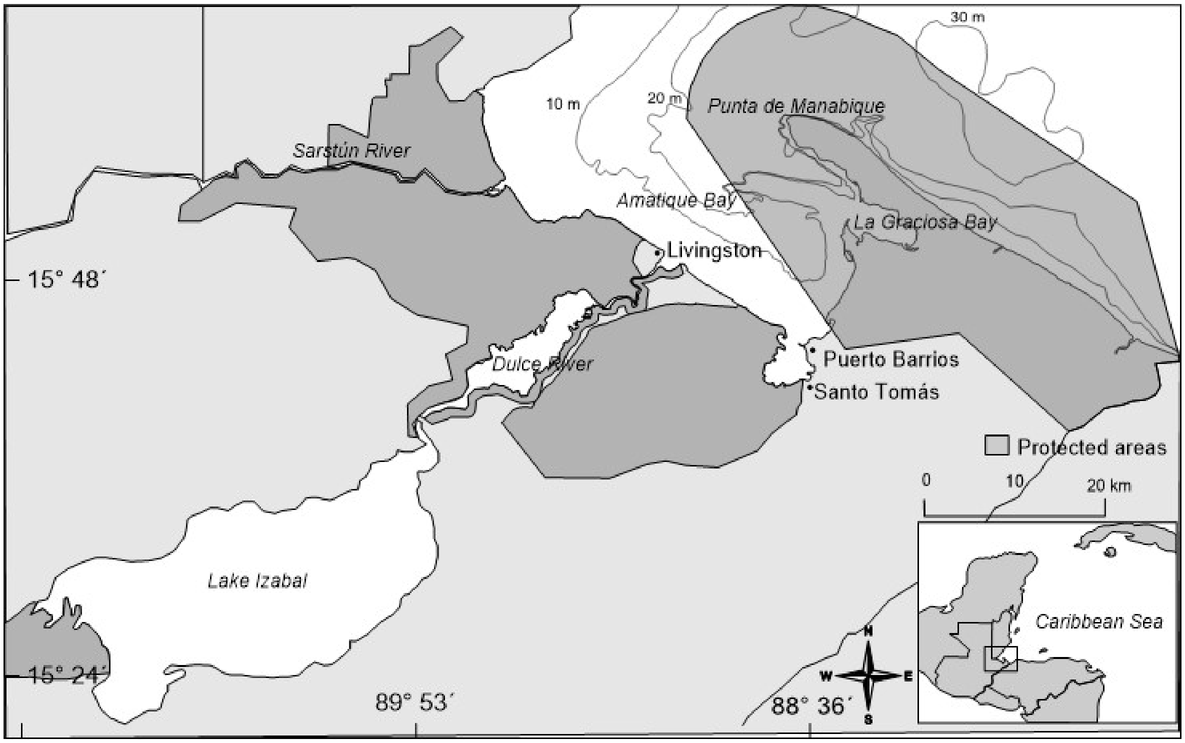

Figure 2. Map of Amatique Bay, Guatemala and current protected areas (shaded). Source: **Paper 1**.

3.2. Biological sampling

Biological sampling of important commercial fish species such as the common snook (*Centropomus undecimalis)*, gafftopsail catfish (*Bagre marinus)*, grey snapper (*Lutjanus griseus)* and lane snapper (*Lutjanus synagris)* was undertaken in the period March 2006 to April 2007. Purposive (landing-dependent) sampling took place at the largest landing compound in the town of Livingston, and at the fish market in the town of Puerto Barrios, which is Guatemala's main harbour in the Caribbean (Figure 2). The amount of fish sampled on a daily basis was dependent on the total volume of the landings and the time available before the product got sold (see below). If the catch was small, all fish were sampled. Otherwise, a random selection of sizes was carried out. In very few cases (n<20), special attention was given to fish of particularly large sizes, as otoliths were required for age and growth studies.

Biological sampling consisted of biometric measurements of different length dimensions and fish mass, macroscopic inspection of gonads for sex, mass and maturity determination, and the collection of otoliths for ageing purposes, following standard methodology (Zale et al. 2013). Only a part of all the biological material collected was used or described in this thesis. The species sampled tended to have high commercial value, therefore there were limitations to the acquisition of fish. Whenever manipulation of the fish was required, attempts were made to follow non-invasive techniques and avoid otherwise damaging data collection methods such that the fish could be further processed and traded. For instance, most of the snook and gafftopsail catfish were sampled while fish workers, who are paid on a processed-unit basis, quickly cleaned and salted the fish in Livingston.

At the Puerto Barrios market, where snappers are more common than in Livingston, sampling could only be performed when, and if, the mongers cleaned the fish for their customers. Snappers were also sampled after direct purchase from boats in Livingston, and later on sold in town to recover the investment. In spite of these complications, more than 1,800 fish were sampled over a period of 14 months. A positive spin-off from this sampling process was that it allowed more personal contact and interactions with fishers, mongers, and other community residents.

3.3. Interviews with fishers

Between September-October 2008, after 13 months of biological research, 24 semi-structured interviews were performed and recorded with fishers in Livingston. These interviews addressed the fishers’ livelihoods, specifically their perceptions of poverty, well-being, fishery resource abundance, and resource management. The sampling design was purposive and the interviewees were mainly the volunteer fishers who were met during the biological fieldwork. Most fishers interviewed were adults and had at least 5 years of fishing experience. These fishers were interviewed in Spanish in their homes or in public places, such as the landing pier or at the fish processing facility. Respondent answers were treated as describing external realities (facts, events) or internal experiences (feelings, meanings) (Silverman 2005).

Finally, to seek corroboration of the views expressed by the different fishers interviewed, a general fishers meeting organized by the NGO FUNDAECO was attended[1]. Here, fishers from Amatique gathered in Livingston to discuss the implementation of management policies, their perception on the status of fish stocks and the applicability of FAO's code of conduct as a local tool for fisheries management. This was a unique opportunity to observe the interaction among the different groups of fishers.

3.4. Secondary data

Supplementary local data on environmental parameters, fish landings, species distributions and social issues were obtained from official records, freely open internet sources, published articles and research reports available as "grey literature", which were often obtained after direct contact with the authors or institutions:

- Meteorological and oceanographic data, obtained from the national meteorological institute (INSIVUMEH, Guatemala), the National Oceanic and Atmospheric Administration (NOAA, USA), and the National Aeronautics and Space Administration (NASA, USA).

- Seasonal abundance of fish species in Amatique Bay, available from official shrimp trawler landing records at the national fisheries directorate (DIPESCA, Guatemala). For other small-scale fisheries, official landings do not exist and estimates of the monthly catches made by the fishers themselves were available for 1998 in Heyman and Graham (2000) and Heyman and Granados-Dieseldorff (2012).

- Oceanographic and biological observations including salinity profiles and fish density, obtained from Ixquiac-Cabrera et al. (2008).

[1] Meeting held at the “Buga Mama Restaurant”, Livingston, Izabal in October 2008.

- "Grey literature" in the form of final reports of research projects, consultancy reports, graduate or undergraduate theses obtained from the internet, funding agencies, private consultants, environmental institutions and universities in Guatemala.

- Social background data including demographic parameters and poverty indexes obtained directly from the Livingston municipality (OMP 2006), or the Guatemalan National Statistics Institute (www.ine.gob.gt/).

4. Results

In **Paper 1**, the evolutionary and ecological settings for Amatique Bay are introduced providing a description of ecosystem functioning. In **Paper 2**, an example of the biology of the common snook (*Centropomus undecimalis)* is provided, showing interesting adaptations to the riverine and estuarine life. This is a valuable species that is considered an economically important coastal fish species for the whole Western Central Atlantic. Total landings may exceed the amount of 1,500 tons reported for 2009 (FAO 2011), and this figure does not account for its importance as a recreational species. **Paper 3** describes the interactions and adaptations of the different social and ethnic groups that make use of these resources and the fisheries management regime. Following this presentation of results, the Discussion section will take the results presented here a step further and examine how the ecological and social data generated in this dissertation can be integrated in the broader context of management of small-scale fisheries.

4.1. Summary of the main results

The main results of the articles constituting this thesis are as follows:

4.1.1. Paper 1

Andrade H, Santos J, Ixquiac M (accepted) Ecological linkages of a tropical estuary bay in the Caribbean. Mar Ecol-Prog Ser Doi:10.3354/meps11342

In this paper, a general view of the ecological functioning of Amatique Bay is provided, and this is perhaps the first integrated account of any estuary in the Caribbean. The main results are descriptions of the environmental cycles that drive both the species abundances and the small-scale fisheries, as local fishers adapt their efforts to target the most abundant and valuable species. Special emphasis is placed on the eco-physiological adaptations of the different species (reproduction, growth, migration) to these driving forces. Organisms analyzed under this framework included crustaceans, mollusks, fish, migratory shorebirds and manatees.

Important abiotic factors of the Bay and other estuaries in the Caribbean, are the marked precipitation and wind regimes, as well as the weak tidal forcing. Seasonal increases in temperature (April-October) and precipitation (July-November) prompt the reproduction of marine, catadromous and estuarine fish species, suggesting that the ensuing increase in primary production provides larval fish with an abundant food source. The lane snapper (*Lutjanus synagris)* and the grey snapper (*Lutjanus griseus)* showed well-defined spawning peaks prior to the start of the rainy season in the period March-July. Contrastingly, the common snook (*Centropomus undecimalis)* presented a more prolonged spawning season commencing in April and continuing throughout November, i.e. at the core of the rainy season.

A shorter study of the gafftopsail catfish data indicated that, like snook, it spawns at the onset or during the rainy season from March to September. The reverse (oceanic) input to the estuary is triggered by the massive migration of several species of penaeid shrimp, which use the mangroves as a nursery, and by engraulids, which probably use the Bay for spawning. These aggregations attract a great number of transient coastal and oceanic predators comprising, among others, the species of the families Carangidae, Loliginidae, Lutjanidae, Scombridae and Sphyraenidae. Also, these occur mainly during the dry season.

Yet other groups of fish, like the caitipa mojarra (*Diapterus rhombeus)*, utilize the Bay permanently, apparently unaffected by the runoff and the primary-production cycles. A contrasting and more limited utilization is made by most shorebirds. These depend mostly on Amatique Bay and surrounding estuaries as a perennial refuge, and contribute less to nutrient cycling. The abundance of freshwater, the sheltered environment, the water clarity, and particularly the very low tidal amplitude, may have contributed to the abundance of extant seagrasses and manatees. The study emphasizes how the particular coastal environment of the

Caribbean, which has developed since the formation of the Central American isthmus in the Pliocene 3 Ma, has had contrasting impacts on the evolution and ecology of the different taxa analyzed. This is important ecological information required for conservation-based management of fisheries.

4.1.2. Paper 2

Andrade H, Santos J, Taylor R (2013) Life-history traits of the common snook *Centropomus undecimalis* in a Caribbean estuary and large-scale biogeographic patterns relevant to management. J Fish Biol 82:1951-1974

The second paper has a more specific focus and addresses the ecology and life history of an economically important, but little studied fish species in Amatique Bay, the common snook (*Centropomus undecimalis*). This fish species is diadromous and spawns in the marine waters of Amatique Bay, demonstrating thereby the importance of the freshwater-coastal ecosystem connectivity. After spawning, males facultatively change sex into females (protandry). The research for this paper resulted in a description of the reproduction cycle, age and growth of the population based on almost 600 fish sampled over 14 months, from 2006-2007.

Spawning of *C. undecimalis* in Amatique Bay, as disclosed by gonadosomatic index and macroscopic analysis, was prolonged (April-November) and strongly related to the precipitation cycle. Peak spawning occurs in October after the onset of the summer rains. During October, adult growth is slow, as reflected by the low body condition and the formation of dark edges on the otoliths. Protandric sex reversal occurred early in the dry season (December) before somatic recovery from spawning. Generally, growth was fast as many individuals reached >70% of the maximum observed total length (LT, 102 cm) after 3 years. Sex transition occurred within a relatively narrow LT range (70–79 cm), but over a wide range of ages, indicating plasticity in this respect. The youngest fish analyzed was 2 years of age and the oldest 10 years, but most of the 456 individuals aged were between 3 and 4 years old. The total mortality averaged 0·62 year^{-1} and the exploitation rate was grossly estimated to 60%, which may be too high for a fish with a medium life span.

To validate and widen the scope of the study, a multivariate zoo-geographical analysis of the life-history traits of snook was made across its whole distribution range. This is one of the most valuable species for artisanal and recreational fisheries in the Americas, from Florida to Brazil, and no such comparative study has been attempted before. The analysis indicates a latitudinal-temperature gradient in some life-history traits, as well as different response patterns to local temperature and hydrographical cycles. *C. undecimalis* from cooler winter waters (e.g. Florida) reach larger sizes, have greater gonado-somatic indices, change sex at larger sizes, and attain longer life spans. Further, this study suggests that increased fishing mortality results in sex reversal at a younger age, as well as male predominance in the different populations. These findings are, in general, consistent with life-history theory and help in the formulation of management advice across the area of occurrence of snook. Data from this comparative study can provide guidance for other regions, even where little knowledge about the species exists.

4.1.3. Paper 3

Andrade H, Midré G (2011) The Merits of Consensus: Small-Scale Fisheries as a Livelihood Buffer in Livingston, Guatemala. In: Jentoft S, Eide A (eds) Poverty Mosaics: Realities and Prospects in Small-Scale Fisheries. Springer, Netherlands.

The main result of the third paper is a comprehensive description of how fisheries in Amatique Bay provide a livelihood to the multiethnic population of the town of Livingston and nearby communities where poverty is high and other income generating activities are scarce. Interviews with fishers and observation of the fishers' livelihoods, which are marked by their ethnicity, culture and and/or fishing traditions, allow for a better understanding of some of the determinants of the relationships among groups. The study also highlights some of the difficulties of an emerging institution, i.e. the fisheries co-management regime. These include:

i) The challenges brought about by the poverty hardships and the scarcity of income generating alternatives outside the fisheries sector.

According to interviewees, this scarcity attracts new entrants to the semi-open access fisheries, a process that leads to reduced individual landings, possible overfishing and escalating competition. With reference to what appears to be, as expressed by most participants, an excessive growth in the number of fishers, this escalation is termed Malthusian overfishing in the paper. Ethnic groups develop different strategies to cope with poverty and/or declining incomes: Q'eqchi peoples from nearby move into Livingston to work as crew in trawlers because fishing ensures a daily meal while providing some income, as opposed to agriculture activities; Garífuna people, who traditionally use only hand lines - the simplest of all fishing gears - abandon the fishery, emigrate and send remittances that ensure the subsistence of their remaining relatives; Ladino and Hindu-descendants might remain in the fishery. They do so by investing in new gear to diversify their catch and target smaller, but more abundant fish. The latter group can, due to family ties, also access fishing grounds in Belize where resources are more abundant. Thus, most groups show some ability to diversify economic activities, and this is primordial for wellbeing of their households and communities. Simultaneously, most groups showed some form of specialization with little competitive overlap with regard to gear type and livelihoods.

ii) The deficient monitoring, control and surveillance system to enforce rules and dissuade offenders.

According to fishers, governmental authorities should increase patrolling and even increase penalties for non-compliance; however limited operational budgets and the few fish inspectors working in the area constrain dissuasive actions, such as inspections at sea or landing sites across Lake Izabal-Punta de Manabique. During the closed season, for example, informants from all the fisher groups reported that they continue to fish, even if they acknowledge that this practice contributes to overfishing and declining incomes.

iii) The scanty compliance with the existing fishing regulations, even when rules were created by the participants themselves or with their collaboration.

Regulations include a "Gentlemen’s Pact" which is an agreement between fisher groups that divides Amatique Bay into fishing zones to avoid conflicts between passive and active fishing gear; and seasonal fishing closures. Lack of compliance seems to be a consequence of the partial legitimization of fishing rules and true empowerment; and the lack of alternative means of support during e.g. the closed season.

This paper has shown that in spite of economic hardships and the limited support from the central governance, multiethnic groups with a community bond may have achieved a minimum of management consensus in Amatique Bay that safeguards the welfare function of fisheries (Béné et al. 2010). It is possible that improvements in adherence and compliance can be reached if efforts are directed towards empowering fishers' organizations, integrating them in participatory research, and providing support on governance issues.

5. Discussion

5.1. Collation of data for fisheries management purposes

Much of the material collected for this dissertation was a combination of biological sampling and direct interviews with fishers. These observations restricted in time to a collection period of 1 ½ years, could have given a narrow and static vision of the main ecological and social interactions driving species composition in the catches, species abundances, and fishing activities in Amatique Bay. However, the consolidation of these observations with secondary information such as environmental data derived from satellite imagery, official landings, published and unpublished reports, as well as fishers’ ecological knowledge collected from fishery surveys performed by Heyman & Graham (2000) and Heyman & Granados-Dieseldorff (2012) has proven instrumental in better defining some of the more prominent socio-ecological system dynamics. Additional data sources were imperative for this type of systems analysis, as there is a great lack of integrated social and ecological information for this region, but also in other parts of the tropical world (Sheaves et al. 2013). This calls for holistic approaches that make use of the scant and disperse scientific information from different disciplines or geographical areas, to identify patterns and propose testable hypotheses.

In this regard, the exploratory meta-analysis performed for the common snook revealed how environmental factors influence the species' life history (spawning, age, and growth) across wide geographical gradients (**Paper 2**). This implies that conservation-based fishery management measures (e.g. closed fishing season), for this and similar species, should take into account local life history traits rather than attempting to copy regulations from better studied but inherently different areas and populations (e.g. Florida). The present zoo-geographic analysis predicts life-history traits even for areas where previous biological information is lacking for the species, it has, therefore, application in other poorly investigated tropical regions. Suspicions were confirmed in this study that increased fishing intensity drives earlier sex reversal and male predominance across the species range. This raises some concern about possible evolutionary changes induced by fishing, particularly selective fishing of large individuals. Sequential hermaphroditism is a common reproductive strategy in tropical teleosts, and many of them are commercially important species. These are factors that require further experimental and theoretical investigation. However, the results from the present and other studies on sex-changing commercial species already provide some guidelines with regard to conservation-oriented population management.

5.2. Implications for aquatic management: Coastal zone and watershed

Comparative analyses from **Paper 1** and from previous ecological and paleontological studies performed along both coasts of Central America, allowed for the synthesis of ideas on the evolutionary forces and relationships that shaped, and still shape, the ecosystem of Amatique Bay. Identifying such relationships provides valuable information for the management of not only Amatique Bay, but also the Mesoamerican Reef and specially the Gulf of Honduras, as these systems are ecologically interconnected (Soto et al. 2009, Muhling et al. 2013). This is in line with the conservation efforts that are being undertaken by the governments of the Mesoamerican Reef regional ecosystem, who recently engaged in the project "Integrated Transboundary Ridge-to-Reef Management of the Mesoamerican Reef" (WWF 2014). The objective of this project is to "*support regional collaboration for the integrated ridge-to-reef management of the transboundary Mesoamerican Reef, by demonstrating its advantages and improving regional, national and local capacities for the integrated management and governance of its freshwater, coastal, and marine resources*" (Waigwa 2014).

The development of a regulatory plan accounting for socio-ecological interactions in the Guatemalan Caribbean was first considered by Yañez-Arancibia et al. (1999). In 2009, a policy encouraging the implementation of an integrated coastal zone management plan was approved by the national authorities with the general goal of protecting, managing and promoting the sustainable use of coastal ecosystems and their watersheds (MARN 2009). The protection of the watershed draining into coastal zones is expected to contribute to the maintenance of the quantity and quality of fresh water entering as runoff, and thereby indirectly supporting the production of estuarine and coastal systems and fisheries (Gillson 2011, Meynecke & Lee 2011). Freshwater flow controls many important traits and functions in remote estuarine and coastal systems bringing increased input of nutrients that affect primary and secondary production. In exchange, these can impact population traits of several species such as recruitment, growth, and survival dynamics (Meynecke et al. 2006, Gillson 2011, Meynecke & Lee 2011).

It has been postulated in this thesis that rainfall in Amatique Bay, closely followed by freshwater runoff, regulates production cycles, species distribution and life histories of both commercially important and iconic species that inhabit or make seasonal use of the bay (**Papers 1, 2**), extending across the entire Mesoamerican Reef (Soto et al. 2009, Muhling et al. 2013). Maintaining adequate freshwater quality and flow should therefore be a management priority for the whole watershed. In fact, the greatest threats to the aquatic system of Amatique Bay, and even the Mesoamerica reef, may well be the influx of sediments, nutrients and pollutants resulting from the increase of industrial activities and expanding agricultural practices (Thattai et al. 2003, Pérez et al. 2011), or the diversion of water for other purposes in very remote areas upstream. The importance of natural protected areas for the maintenance of ecosystem functioning is vital and cannot be discounted. Although these protected areas are not primordial feeding area for migratory birds, they have importance as secondary stop-over spots. They play, thereby, a significant role in the migration routes between high-latitude ecosystems in North America, and the ecosystems in South America. More crucial for the connectivity of local ecosystems, is the fact that these protected areas are home to diverse mangrove and seagrass stands that play a significant ecological role in the life-history of many commercial species.

The migration cycle of manatees suggested by previous authors (and illustrated in this study) calls for a management system that protects adults and juveniles from netting in the calving grounds in the inner Lake Izabal (UNEP 2010), as well as the outward migratory individuals during the rainy season. Manatees also become exposed to coastal fishing and shipping. In this respect, the voluntary declaration in 2012 by fisher groups mediated by the government and NGOs of no-take fishing zones inside La Graciosa Bay, where abundant seagrass stands persist, is a promising step for the conservation of this iconic sirenian species. As this example demonstrates, for the long-term conservation of both species and fisheries, a systems approach must be pursued.

5.3. Fisheries co-management and the use of fishers' ecological knowledge

Interview data revealed that the aquatic area outside the protected zone in Amatique is regulated by voluntary agreements among fishers and gear groups, the "Gentlemen's Pact", which later became recognized by the central government and embodied in the fisheries law (**Paper 3)**. In addition, drafts of new fishing regulations (e.g. closed seasons, permanent no-take fishing zones) are now being discussed between the government and the heterogeneous fisher groups. This contrasts starkly with the previous top-down attitude practiced by the central government, which was minimally effective in practice because it lacked both enforcement and legitimacy. Fisheries management in the Guatemalan Caribbean has been slowly moving to a co-management regime (**Paper 3)**. This has been a long-term response to conflicts arising between competing fleets (Heyman & Graham 2000), concerns about the exploitation state of the fisheries, the support from official and non-governmental organizations to fisher associations, and the willingness of the national government to merge fishers' agreements into national law (**Paper 3**). A co-management regime is expected to improve fisheries management in two basic ways: by incorporating local knowledge into fishery science; and by enhancing law compliance among resource users when they perceive the arrangements to be legitimate (Jentoft 2000). Further, co-management may provide a framework for stakeholders with different values, images and principles to unite and negotiate expected governance outcomes (Jentoft et al. 2009, Song et al. 2013).

Some of these attributes have been highlighted in Amatique Bay by studying four ethnic fisher groups' livelihoods, action space and pursuit of wellbeing. The goal was to understand how compliance with fishery rules can be enhanced within the co-management regime, given that weak central government law enforcement is expected to be a factor for many years to come. This lack of central interference can even be seen as an opportunity for development of voluntary and sound local solutions. The accepted rules include the Gentlemen's Pact described earlier, which establishes periodic area restrictions to avoid the operation of antagonistic gears, as e.g. gillnets (passive gear) and trawlers (active gears), no-take areas that have been proposed by fisher groups, and time closure (closed seasons) strategies. It was our observation that the timing and coverage of these closures is variable and probably more often related to cultural practices than to biological cycles of some species or guilds of species.

Fishery regulations in the Guatemalan Caribbean have relied heavily on fishers' ecological knowledge (Heyman & Granados-Dieseldorff 2012) as a means to enhance legitimacy and governance. This is in line with findings from other parts of the world: fishers' ecological knowledge has been increasingly recognized as an important component of scientific research, conservation and resource management, especially in small-scale fisheries (Thornton & Scheer 2012). However, it has also been recognized that local knowledge and experiences may not correspond accurately to the scientific understanding of ecosystem processes, where this one exists (Berkes 2009, Mathew 2011, Ruddle & Davis 2011). Thus, multiple information sources and critical analyses are required to understand fisheries dynamics and complement participatory management regimes (Andrew & Evans 2011, Daw et al. 2011). The collation of all these pieces of information can contribute to form an arena where different types of knowledge meet and mix (Holm 2003, Bjørkan 2011), providing a fertile ground from which to develop adaptive management plans. This discussion is important in Amatique. The present work highlights some of the apparent contradictions found in this field survey with regard to the seasonal cycle of fish reproduction and the ecological knowledge transmitted in some instances by fishers to Heyman & Graham (2000) and Heyman & Granados-Dieseldorff (2011).

Lane snapper (*Lutjanus synagris)*, for example, may spawn in October, when catches from dories and skiffs peak (Heyman & Graham 2000), and this is probably the reason for the implementation of a closure in October 2012. These authors consider October to be the end of the rainy season. However, the simple reproductive analysis performed in **Paper 1** suggests that spawning of this species seems to be cued to increasing temperatures occurring prior to, or at, the start of the rainy season, that is in the months of March-July. Thus, the apparent mismatch in the exact spawning season of lane snapper (*Lutjanus synagris)* as perceived in biological sampling (**Paper 1**), and as perceived by traditional ecological knowledge must be resolved and discussed to optimize management actions (see section 5.5). A great step in this direction would be to e.g. involve fishers in research projects to validate and legitimize research results that later could be incorporated into management plans (Bjørkan 2011).

5.4. Critical aspects for fisheries management: socio-ecological interactions

Tropical coastal ecosystems are challenging to govern as these are highly dynamic systems, interlinked to distant habitats across a land-sea interface, and often support a wide variety of competing or interfering human activities (Lebel 2012, Blaber 2013). A first step to deal with such complexity is to understand the three different components of interactive governance as applied to fisheries and coastal systems: the natural and social system to be governed (SG – the fish chain from catching to consumption); the governing system (GS – state, market and civil society institutions governing this chain); and the interactions between these two (GI) (Kooiman 2008, Chuenpagdee & Jentoft 2009, Kooiman & Bavinck 2013). Biological diversity, species abundances, ecosystem productivity and functioning among other variables pertain to the natural system. Issues referring to the socioeconomic system include the composition of stakeholder groups with regard to interests, demography, ethnicity, their organization and the interactions between such groups (Chuenpagdee & Jentoft 2009).

With the socio-ecological information uncovered in **Paper 1** and **Paper 3** a model coupling the human and natural system and their interactions can be constructed for Amatique (Figure 3). These interactions are highly complex and dynamic due to the inherent variability of estuarine processes and the socioeconomic conditions that influence how people derive a living from them.

Starting with the natural system, the main environmental driver of production is the flood pulse brought about by the increased precipitation during the rainy season. The increased productivity drives fish migrations and other life aspects of their life history, species composition and abundances. Some fishers adjust their gears to target the most productive or available species (**Paper 1**).

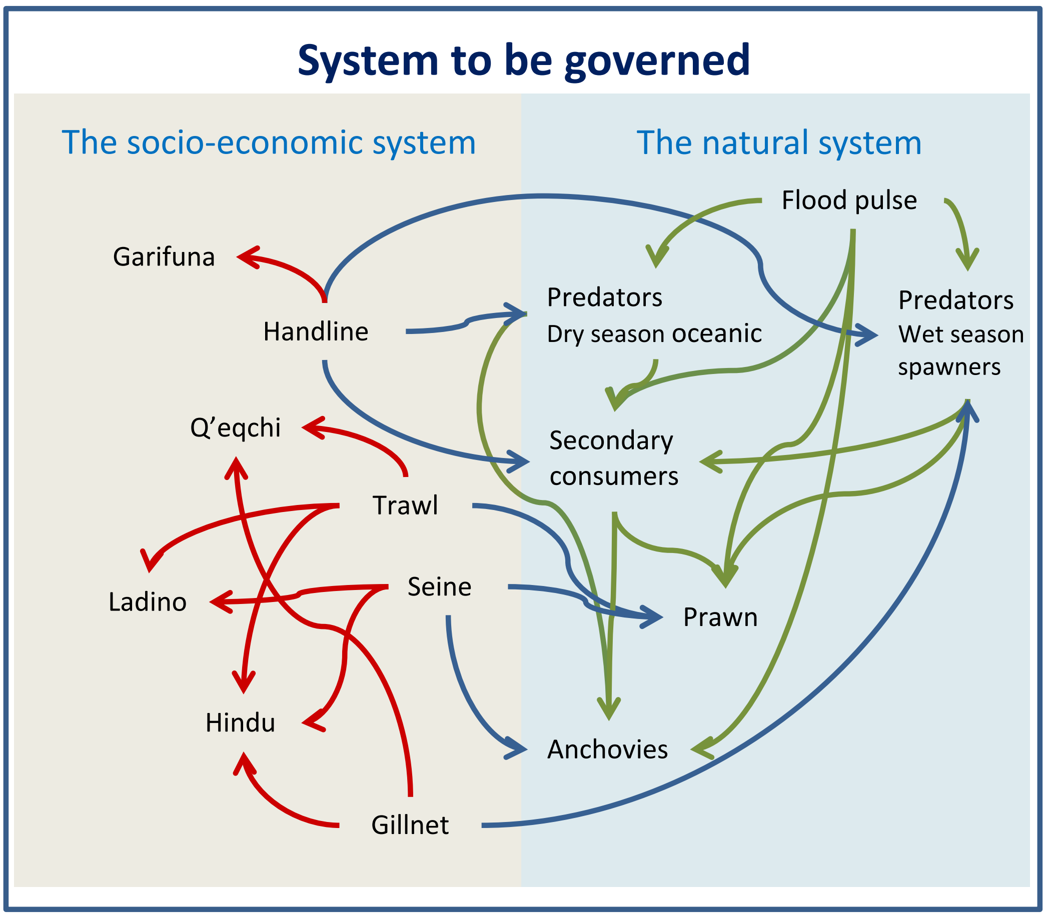

Figure 3. Simplified social and ecological relationships in Amatique Bay for aquatic management purposes. Green arrows denote the natural interactions among species or trophic levels. Blue arrows denote the technological relationships and associated fishing gears and targeted species. Red arrows depict the socio-technological component - the gear types most often used by the different ethnic groups, which has a cultural element.

The socio-economic system includes the demographic groups representing fishers, who in Amatique can be related to ethnicity, the fishing gears they employ and the interactions with other fishers (through e.g. conflict and cooperation). These ethnic groups demonstrate different livelihoods, and these are related to traditions and mobility (geographic and social), which might not be fully dependent on fishing (Figure 4). An example of mobility, people of the Q'echi ethnic group are moving into Livingston town due to the impoverished conditions found in nearby rural areas, hoping to find jobs in the fishing and/or construction sector. Within fisheries, they happen to find jobs as crew in the shrimp trawlers. It is therefore argued that fisheries in Amatique function as a buffer for people displaced from other income generating opportunities (**Paper 3**). For the very few owning land, subsistence agriculture is an alternative occupation. Similarly Hindu descendants and ladino fishers attributed the increasing number of fishers to the lack of alternative income. They cope with the current stock situation by investing in new gear, targeting the most abundant species within a season, or complementary access coastal fisheries in Belize. For the Garifuna, however, emigration and reception of remittances from their kin abroad are important sources of income outside the fisheries sector (**Paper 3**). In this regard, the system to be governed and the governing interactions in Amatique are influenced not only by the socio-ecological interactions imbedded within the fisheries realm, but also by external socioeconomic factors such as poverty which pervades the whole country (**Paper 3**). These interactions demonstrate some of the complexity and dynamics of the socio-ecological system which are challenging to govern. Clearly, policies and actions for mitigation and reduction of poverty require that other opportunities and doors remain open for the existing fishers but also people entering the fisheries. Change must occur at different scales, often outside the scope of the traditionally defined systems to be governed. The study of the linkages and complexity in such an open system is an interesting topic for future studies. These studies can be in the form of a system analysis or of comparative analyses across natural and cultural contexts.

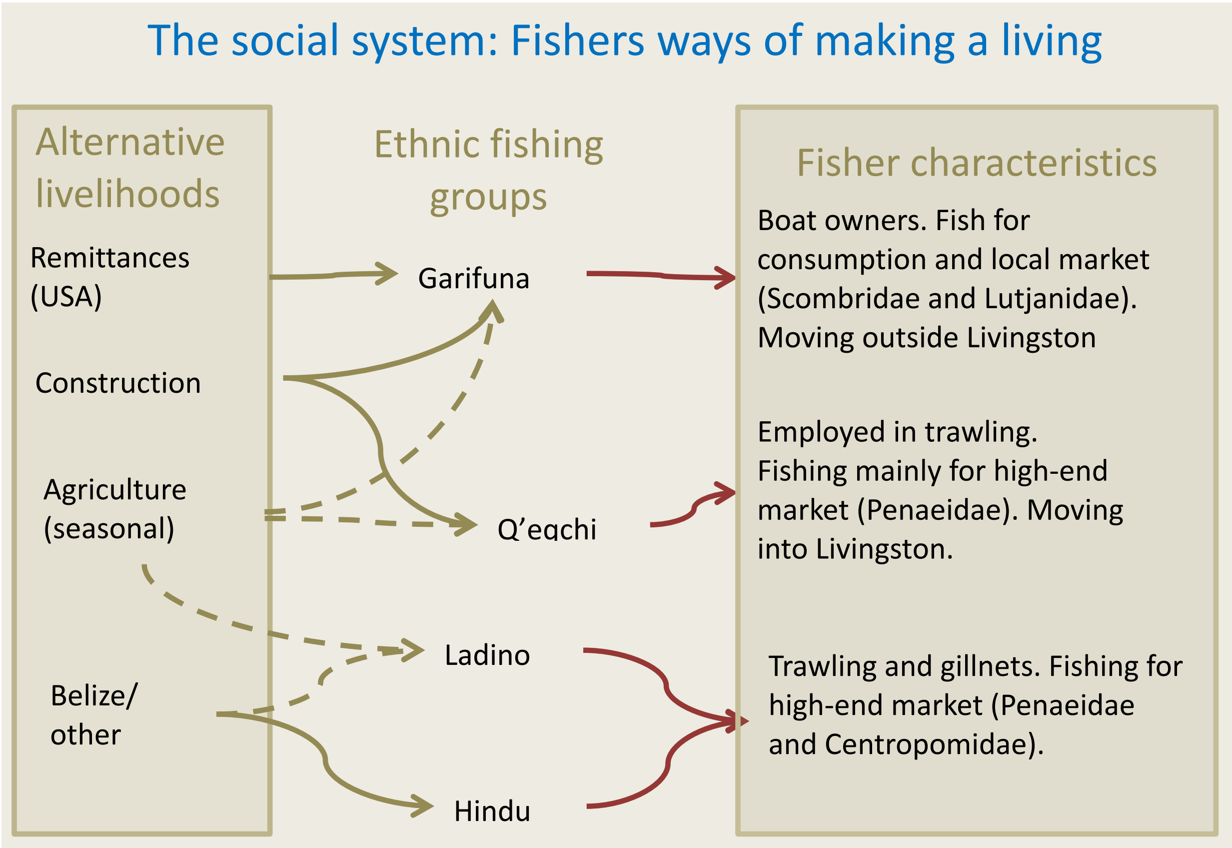

Figure 4. The ways in which different fishing ethnic groups derive a livelihood in Livingston. The red lines denote how ethnic fisher groups derive a living out of fishing. Brown lines denote the alternative occupations of the different ethnic groups. Stipple lines denote possible, non-confirmed relationships. The boxes denote different social and institutional elements related to the external (livelihood) spheres and the internal spheres (fisher characteristics).

Within the current partially regulated fishery management system, there are two types of technical or agreed measures that deserve particular attention: the seasonal closures implemented to protect species under their reproductive period, and restrictions on the integrated fishing effort pattern that involves fishing across trophic levels and sizes. Seasonal closures have been historically applied in Guatemala since the fisheries law of 1932 and are currently the foremost management tool in the Caribbean, with closures pronounced each year, as exemplified by the regulations in October 2012 (MAGA 2102). Controlling fishing effort across trophic levels and sizes has been a controversial topic between fisher groups, occasionally requiring the intervention of the central government to handle confrontations (**Paper 3**). These technical measures influence how fishers derive a living from fisheries.

5.5. Critical aspects for management: seasonal regulations

The implementation of closed seasons as a management tool is spread worldwide; however, direct evidence for their benefit is mainly restricted to species forming dense and ephemeral spawning aggregations (van Overzee & Rijnsdorp 2015). Closed seasons have been applied in the Guatemalan Caribbean with the aim of restricting fishing effort on the spawning stocks and, by extension, to increase recruitment. The closures are perceived as beneficial by fishers. However, the present interviews revealed a clear gap between this positive perception and the practical enactment of the rule. Often these closures are not fully complied with, according to the fishers. They attribute this to both the poverty situation of many families, who may lack alternative sources of cash and food, and a general lack of enforcing mechanisms (patrolling) to dissuade irregular fishing (**Paper 3**). The fishing closures are arranged by groups of species or higher taxa, e.g. shrimps, snappers. Their duration varies between 1-3 months depending on the year. As late as 2012, the closed seasons for shrimp trawling were implemented in May-June and November. In September-October the system was closed for finfish (e.g. catfish, snappers, cichlids and snook) (Table 1) (MAGA 2012).

The data analyzed in **Paper 1** suggest that the closed season for shrimp trawlers, if enforced in the month of November (Table 1), offers partial protection to sub-adult shrimp in their migration offshore and mitigates the by-catch of juvenile fish (e.g. lane snapper). It is likely that these rejected fish juveniles experience high discard mortality. In this regard, the closed season, if complied with by the fishers, could help prevent growth overfishing, and thereby contribute to a better potential catch (alternatively, predation) in the future.

Contrastingly, the closed season for finfish, if enforced in the months September-October, may give some protection to wet-season spawners, like snook (**Paper 2**), and may help in the prevention of recruitment overfishing. Contrastingly, the closed season for finfish, if enforced in the months September-October, may give some protection to wet-season spawners, like snook (**Paper 2**), and may help in the prevention of recruitment overfishing.

Table 1. Timing of closed fishing seasons in 2012 for selected fish species in the Guatemalan Caribbean. Source: MAGA (2012)

Species	**Family**	**Timing of Closure**
Shrimps	Penaeidae	1st May -15th June 1st Nov – 30th Nov
Catfish Snappers Snook Tarpon Jacks Mullets Grunts Drums Groupers Barracuda Cichlids	Ariidae Lutjanidae Centropomidae Megalopidae Carangidae Mugilidae Pomadasyidae Sciaenidae Serranidae Sphyraenidae Cichlidae	15th Sept – 31st Oct
Anchovies (manjua) and sardines	Clupeidae Engraulidae	1st May – 15th Jul
Gastropods	Strombidae Melongenidae	1st July – 31st July

As shown in **Paper 1**, the reproduction of the gafftopsail catfish (*Bagre marinus*), the lane snapper (*Lutjanus synagris)* and particularly the grey snapper (*Lutjanus griseus)* seem to occur just before or at the onset of the rainy season. In 2012, the expected spawning season occurred about 2-3 months prior to this fishing closure (Figure 5).

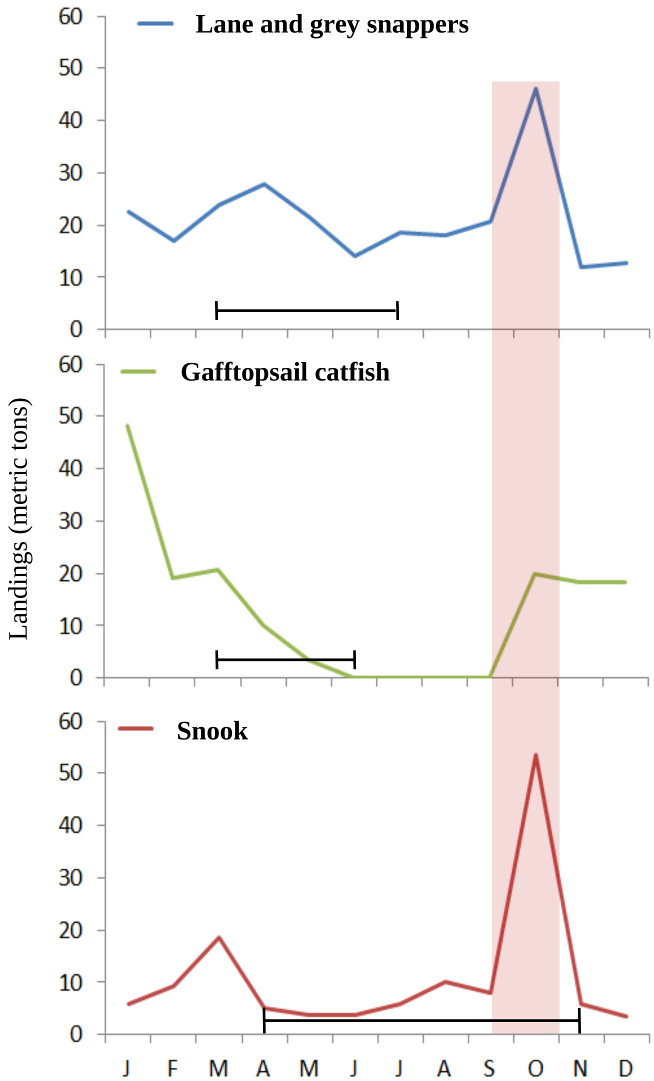

Figure 5. Artisanal landings of the species lane (*Lutjanus synagris*) and grey snapper (*Lutjanus griseus*) (pooled), Gafftopsail catfish (*Bagre marinus*) and common snook (*Centropomus undecimalis*) in Amatique Bay. Abundances were derived from fisher's ecological knowledge by Heyman and Graham (2000) and Heyman and Granados-Dieseldorff (2012) in 1997. The superimposed bar denotes the 2012 closed season (MAGA 2012). Black lines denote spawning seasons (**Paper 1, Paper 2**).

It is likely that the present management pattern may, when duly enforced and complied with, provide the best protection to the adult stocks of species with typical spawning late in the rainy season. These include stocks of the most valuable species, as the common snook. Landings of common snook are probably tightly connected to their increased availability when these fish migrate from freshwater habitats to the coastal waters of Amatique Bay for spawning. It is known that snook forms spawning aggregations in other geographical areas that are predictable in space and time, making the spawning stocks vulnerable to overfishing (Young et al. 2014).

Fishing dense aggregations provides fishers with increased catches at diminished costs and therefore elicits a clear economic dividend. However, due to the ease of catch, such aggregations can be substantially extirpated by excess fishing with consequent biological (e.g. reduced reproductive output) and socio-economic (e.g. decline in total catches) implications (de Mitcheson & Erisman 2012). Management tools for protecting spawning aggregations include a combination of temporal and spatial closures followed by controls on fishery input (e.g. number of fishers) and output (e.g. maximum and/or minimum sizes) (Russell et al. 2012). It has been recently postulated that spawning aggregations can be harvested sustainably, provided that juveniles are excluded, fish are harvested at an optimal intermediate size, and older, fecund individuals are spared (Erisman et al. 2014). This approach differs from the traditional view of a selectivity pattern for fisheries that targets only the largest individuals, and actually admits a non-selective but regulated fishing pattern. Such an approach could contribute to a more easily understood and implemented fishing regime in Amatique. This is because under such a fishing pattern, fishers might continue to fish, providing food for their families as well as receiving some income. These were the main caveats leading to failure to comply with the fishing closure, as revealed by interview data (**Paper 3**). It is not unlikely that regulations of this type allowing restrictive fishing, rather than full prohibition, might be more easily adopted and complied with by fishers.

Another alternative venue that could win the fishers' support would be to modify the closed season system into a less restrictive system that allowed fishers to target species that are not spawning. For example under the October closure, when snook are spawning, fishers observing the closure could possibly target snappers for personal consumption instead. As a technical measure, a temporary gillnet ban could be introduced, still allowing fishers to use hook and line. Moreover, a finer adjustment of the closed season to other productive activities and social events could bring better acceptance. Again, during the October closed season, fishers might enroll in subsistence agriculture as corn and other crops produced in the area are harvested in this month

(OMP 2006). Agriculture might provide other means of support to those fishers with access to arable land. Identification and support for the enrollment of fishers in such alternatives should be a development goal priority. As often heard during interviews, such regulatory approaches that consider the trade-offs and production alternatives for households, are more likely to be observed by all fishing groups.

5.6. Critical aspects for management: fishing across trophic levels and sizes

Recently, the idea that harvesting all components of the ecosystem in proportion to their productivity has been revived, and has been suggested to be more in line with the ecosystem-based approach to fisheries management (EAF) – (Kolding & van Zwieten 2014, Kolding et al. 2014a,b). The balanced harvesting principle is a fisheries management strategy that distributes a moderate mortality from fishing across the widest possible range of species, stocks, and sizes in an ecosystem, in proportion to their natural productivity (Garcia et al. 2012). The FAO technical guidelines on the ecosystem approach to fisheries (FAO 2003) define EAF as "*an ecosystem approach to fisheries strives to balance diverse societal objectives, by taking into account the knowledge and uncertainties about biotic, abiotic and human components of ecosystems and their interactions and applying an integrated approach to fisheries within ecologically meaningful boundaries*", which is a relatively vague concept.

The mentioned authors argue that a balanced fishing pattern will more likely contribute to sustainable fisheries and food security. This contrasts to the conventional fisheries wisdom that relies on the conflicting principle of strongly selective single-species fisheries, often reflected in the mentioned FAO guidelines. This historical practice has allegedly resulted in problematic outcomes at both the single-species and community level (Kolding et al. 2014b).

It would be interesting to analyze the fisheries of Amatique Bay in terms of trophic levels, as suggested by the proponents of the balanced fisheries. It is possible to estimate the total fisheries production (landings) by dories and skiffs disaggregated by trophic levels. Anchovies, locally known as "manjua" (Engraulidae) and shrimps (Peneidae) comprise 57% of the total weight landed in the Guatemalan Caribbean and form the base of a Lindeman trophic pyramid (Figure

6). These species are considered primary consumers at the bottom of the trophic pyramid as they are frequently described to consume plankton and detritus (Froese & Pauly 2014). Secondary consumers comprise 35% of the landings and include species that feed on small fish, detritus and crustaceans like mojarras, cichlids, carangids, scombrids and most snappers. Tertiary consumers comprise 8% of the landings and are represented by snook, barracudas, groupers and mutton snapper. Thus, the landings of dories and skiffs in Amatique Bay indicate that fishing occurs at all trophic levels, and apparently reflect a trophic pyramid. Although these simple estimates are not conclusive evidence, these observations suggest that some form of balanced harvesting may be taking place. In this respect, the fisheries of Amatique Bay could be following a satisfactory fishing pattern, but further studies are required to understand the adequacy of the aggregated fishing intensity (effort).

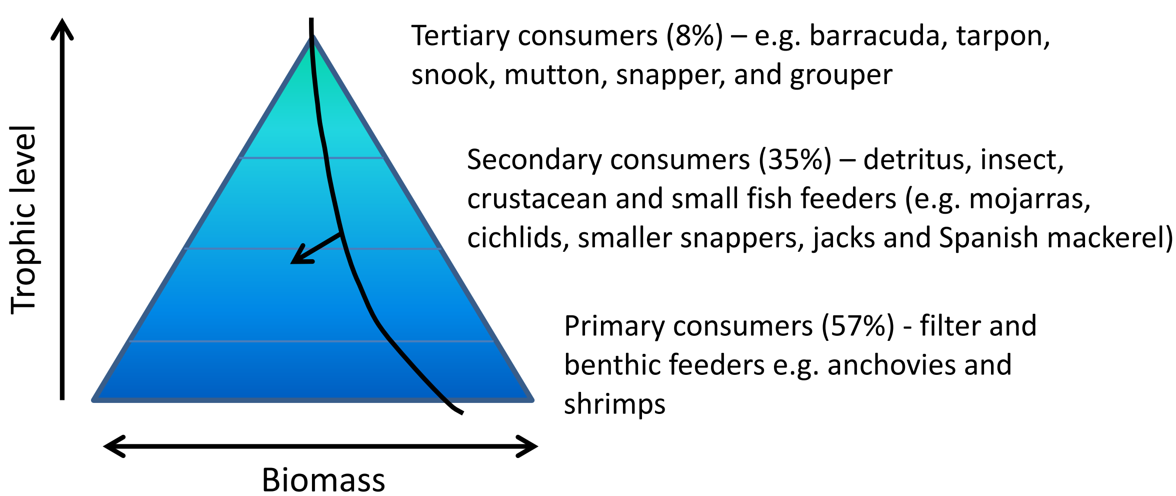

Figure 6. The hypothetical Lindeman trophic pyramid constructed from dory and skiff landings in the Guatemalan Caribbean. Source of data: Heyman & Granados-Dieseldorff (2012). Diagram based on Kolding et al. (2014b)

Two issues remain controversial among the fishers with regard to the appropriateness of the aggregated fishing regime (**Paper 3**). The first conflict arises from the observation that some fisher groups specialize and target a particular species or trophic level, as is the case of shrimp trawlers, snook gillnetters or Garifuna hook and line fishers. By employing antagonistic fishing practices i.e. passive and active gear, conflicts for space arise (Table 2). While this is, in essence, a purely physical conflict, it is difficult to dissociate it from the ecological conflict at the base of the un-balanced fisheries problem. The second conflict relates to the unselective nature and discards practices of the operators of active gear (Table 2). This conflict relates to the catch operations and is not accounted for by the simple harvest balance sheet described earlier, which focused on landings.

Table 2. Gear and species conflicts between fishing groups operating in Amatique Bay.

	Garifuna hook and line	**Gillnets**
Trawlers	Trawling leads to mortality of juveniles of commercially important species like lane snapper which are targeted as adults or semi-adults by the Garifuna	Physical interactions between passive (stationary) and active (moving) gear targeting different species have created conflicts in the past. Conflicts have been partially addressed by the Gentlemen's Pact which separates the Bay into alternating fishing zones.
Seines	Seines target *manjua* which is preyed upon by kingfishes and mackerels (Scombridae). Fishers complain that low manjua abundance results in low Scombridae landings. Seines and gillnets can be employed as surrounding nets in the reefs to catch Scombridae. This practice conflicts with the Garifuna and was made illegal in the Gentlemen's Pact	No interactions

Conflicts between *manjua* (Engraulidae) and other fisheries have represented a problem for management authorities. Although this fishery has a high socio-economic importance by providing inexpensive food and good quality protein to many communities in the hinterland, as well as an occupation and income to entire families in the bay, it is often blamed for its negative ecosystem impacts (Boix et al. 2008, Heyman & Granados-Dieseldorff 2011). This lead to several efforts in the past to close the fishery permanently (de Noak et al. 2015). The *manjua* (Engraulidae) may comprise up to 15 fish species with unclear taxonomic status (Boix et al. 2008). Generally, engraulids are filter feeders occupying a basic trophic level in the fish food chain, and are strongly targeted by larger predators (Blaber 2000, Ganias 2014). In Livingston, several fishers claim that the landings of transient marine species such as barracuda (*Sphyraena* sp.), Spanish mackerel and Kingfish (Scombridae), have decreased as a consequence of the high fishing mortality suffered by the *manjua* (Engraulidae) (Table 2) (**Paper 3).** In addition, the "mosquito seines" used in the *manjua* fishery, with mesh sizes of about 0.5 cm, unselectively capture and kill juveniles of several other species (Heyman & Granados-Dieseldorff 2011).

The first argument against *manjua* fishing expressed in the interviews is probably the only one that falls into the realm of the balanced-harvest paradigm – i.e. the prey-predator relationship. *Manjua* fishers may counter-argue that the fishery is simply extracting the surplus anchovies not consumed by the predators removed by the other fisheries. The by-catch issue is, however, more complex to deal with and can hardly be resolved without further quantitative research. The fishing mortality of the larvae of other species killed by the mosquito nets (Heyman & Granados-Dieseldorff 2011) must be compared to the massive natural mortality that these larvae would otherwise experience in the absence of fisheries (Law et al. 2012).

The by-catch problem is also a concern in the shrimp trawler fisheries (**Paper 3)**. Rough estimates indicate that about 80% of the shrimp trawlers' catches is comprised of species other than shrimp (Manuel Ixquiac, former fisheries officer, personal communication, April 2015), mostly juveniles of commercial and non-commercial species that are returned dead to the sea.

Although by-catch mortality is an unwanted outcome in the *manjua* and shrimp fisheries, these are the most harvested and most valuable species in the Gulf of Honduras (Heyman & Granados-Dieseldorff 2012). Technical measures may be necessary to improve selectivity properties of the gear employed in these fisheries. The introduction of by-catch reduction devices in the shrimp fisheries, have shown some success in the Caribbean (Maniarres et al. 2008, Silva et al. 2012). For the *manjua* fisheries, mortality of non-target species can be lowered by adopting more careful fishing operations and rapid discard practices (Heyman & Granados-Dieseldorff 2011). Interview data revealed that fisher organizations are willing to increase mesh sizes to harvest larger organisms and/or reduce by-catch (**Paper 3**). Recently, trawler fishers agreed upon using the legal cod-end mesh size of 3.8 cm instead of the commonly employed 2.5 cm cod-end (Manuel Ixquiac, former fisheries officer, personal communication, April 2015). A similar cooperative move has been taken by *manjua* fishers who agreed to restrict the fishery outside grounds where *manjua* juveniles abound. The background for their decision is their claim that adults and juveniles use different habitats (de Noak et al. 2015).

For other species with complex life-cycles like the snook, the appropriate regime of size regulations must be investigated in order to find acceptable ecological and evolutionary compromises. This may even include an exclusive protection of the largest spawners (females) as these can contribute disproportionately to recruitment (**Paper 2**). This strategy would also be compliant with the principles of balanced harvesting.

In summary, fishing in Amatique occurs across all trophic levels and sizes, in a fashion (multispecies, multi-gear fisheries) that might be closer to a balanced ecosystem exploitation than conventional single-species selective fisheries (Koldning et al. 2014a). Fisheries have developed in this direction, rather than as a result of centralized management measurement, as fishers follow the seasonal productivity pulses in the Bay. It must be borne in mind that fisheries in Amatique Bay, and also in many other parts of the Caribbean, take place in a context where a principal agent (regulating and controlling authorities) is often absent. If compliance bears any chance of achievement, any new regulation must account for fishers' ways of making a living and be duly legitimized by fisher groups (Russel et al. 2012, McClanahan et al. 2014). In this regard, it is interesting and encouraging to observe that many local regulations have been agreed upon in the past (i.e. the Gentlemen's Pact) after hard negotiations between the different stakeholders. Efforts should then be placed on empowering fishers' organizations and working with them in participatory research.

6. Conclusions

The interdisciplinary approach employed in this thesis has revealed the natural and socio-economic drivers of the fisheries and their complex interactions in the ecosystem in Amatique Bay. As a permanently open estuary, the Bay interconnects the Lake Izabal-Rio Dulce complex to the Caribbean Sea. The strength of this geographic interconnection is modified by abiotic factors such as the precipitation, runoff and wind regimes combined with weak tidal forcing.

During the dry season (February to May), precipitation is low and river discharge is at its yearly minimum. In this period, an increase in air temperature and evaporation give rise to higher salinities as marine water dominates the Bay - brought about by a steady onshore (NE) breeze. During the wet season (July-December), freshwater runoff increases lowering the salinities and bringing nutrients from land. The primary production responds quickly to these inputs showing a marked increase, with a probable subsequent rise in secondary production. Species life histories are influenced by these cycles. Spawning of fish like the grey snapper, lane snapper, the snook and probably the gafftopsail catfish occur just prior to or during the rainy season in the months of March-November, when the increase in primary and secondary production may favor larval survival and growth. Migration to and from this Bay are related to long- and short-term movements due to reproduction, feeding and ontogeny. The most conspicuous linkage between the freshwater system and the estuary in Amatique are the movements of snook, the blackbelt cichlid and, in part, the manatees.

These movements are associated with both spawning cycles and the precipitation cycle. The reverse (oceanic) input to the estuary is triggered by the massive migration of several species of penaeid shrimp and by engraulids, which probably use the Bay for spawning. These aggregations attract a great number of transient coastal and oceanic predators comprising, among others, the families Carangidae, Loliginidae, Lutjanidae, Scombridae and Sphyraenidae, especially during the dry season. Some fishers modify their fishing practices to target the most abundant commercially important species. In this regard, fishing in Amatique occurs across all trophic levels and sizes resembling the "balanced harvesting" principle, where individuals are exploited in proportion to their productivity.

The socio-economic drivers of these fisheries are mainly related to the necessity to earn a living; the economic hardships experienced by people in Livingston and nearby rural areas; the interactions between fisher groups to solve conflicts related to fishing; and lastly, the regulations agreed upon between such groups and central government to manage these fisheries. Both the scarcity of alternative income-generating opportunities and the labor immigration from poor adjacent areas are the main factors explaining the increased number of active fishers. In this regard, fisheries provide a social as well as economic buffer to people experiencing poverty hardships. However, the increased number of fishers has exacerbated conflicts between different ethnic/fishing gear groups. Area conflicts arise when fishing takes place in the same fishing grounds with active (trawler) and passive (gillnets) gears simultaneously. Species conflicts occur due to the high juvenile by-catch mortalities induced by non-selective gears (e.g. trawlers), when fishing groups target the same species employing different techniques, or when a fishing group targets a species which is thought to be an important food item for other commercially important species (e.g. Engraulidae for Scombridae). To solve these conflicts, area and time closures have been agreed upon by fishing groups preluding a co-management regime supported by the central government. While area conflicts have diminished due to fisher's acceptance of the rotatory regime agreed to in “the Gentlemen’s Pact”, closed seasons are not fully complied with due to the lack of alternative income-generating opportunities for fishers, and the lack of rule enforcement.

The integration of ecological and social data gathered in this thesis provides input for a more effective small-scale fisheries management regime. Scientific information has been provided as input to the technical measurements which can now be implemented. For example, the spawning seasons of the four commercially important species disclosed above can be employed for selecting the period when closed seasons are implemented thereby potentially increasing protection of aggregating spawning adults. At the same time, this thesis explores how such technical measures impact the ways in which fishers derive a living. Regulations that include temporal bans on all fishing resources simultaneously are unlikely to be observed by fisher groups because of their reliance on such resources for income and food. Similarly, the permanent closure of important fisheries e.g. *manjua* (Engraulidae) would result in unwanted social outcomes, including increased unemployment, and shortage of low-cost high-quality protein. The technical measures that seem to be more accepted among fishers are the implementation of area closures to protect nursery grounds, and the implementation of more selective fishing gear.

Successful fisheries management in Amatique Bay will depend upon the active enrollment of fishers across all decision-making levels and processes. Efforts should then be placed on empowering fishers' organizations and working with them in participatory research for the resolution of governance issues. Due to this region’s ecological and social importance, the area should be managed to achieve both conservation and food security goals.

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