CORAL REEF HABITATS
AND FISH CONNECTIVITY
Implications for coastal management and fishery

Tove Lund Jørgensen
Coral Reef Habitats and Fish Connectivity

Implications for coastal management and fishery

Tove Lund Jörgensen
This PhD thesis is dedicated to my family
Erik, Ophelia & Lyra

‘The edge of the sea is a strange and beautiful place’

Rachel Carson (1907-1964)
Coral reefs have one of the highest levels of biodiversity of all ecosystems in the world and are important for both human livelihood and food security throughout many tropical countries. However, due to increased anthropogenic pressure on marine ecosystems, especially during the last couple of decades, coral reefs have become critically over-fished and many reefs are now in a degraded state, and are facing additional future threats due to further over-exploitation, chemical pollution, sedimentation, and effects of climate change.

The main aim of this PhD thesis is to understand effects of anthropogenic disturbances on tropical coastal ecosystems and fish connectivity for coastal management purposes. Therefore, linkages between anthropogenic disturbance and corals were investigated (Paper I), as well as interactions between coral reef habitat and associated fish assemblage (Paper II). Furthermore, connectivity between coral reefs and other tropical coastal ecosystems was explored (Paper III), as well as fish migration to reproduction sites (Paper IV), and evaluations of spatial ecology methods (Paper V).

The result showed that coral reefs that are already exposed to disturbances, such as freshwater and nutrient run-offs, may be more sensitive to effects from climate change, in terms of increased sea surface temperatures (Paper I). In addition, there were also clear linkages between coral reef quality and fish assemblages, which
displayed high spatial variability and suggest patchy recovery after the 1997/1998 bleaching and subsequent coral mass mortality event (Paper II). This highlights the importance of understanding effects of disturbances on corals, especially in terms of synergistic effects between increased water temperatures and other coastal stressors such as decreased salinity and increased nutrients; and the indirect effects of habitat degradation on the fish community.

The results showed that coral reefs were strongly connected with mangrove and seagrass ecosystems, through ontogenetic migration of fish (Paper III). Migrations to spawning sites of groupers were related to lunar activities when thousands of fish gather for reproduction purposes during new moon, which increases the risk of over-exploitation (Paper IV). The results emphasises the importance of protecting key areas such as nursing grounds and reproduction sites. Furthermore, acoustic telemetry has become an increasingly common method in studies of fish movement, and the results showed that efficiency of acoustic arrays may increase depending on deployment strategies and habitat characteristics (Paper V).

In conclusion, the results from this PhD thesis emphasises the importance of protecting coral reef habitats, as well as identifying related susceptible tropical coastal areas, such as nursing grounds and reproduction sites. Indeed, a better scientific understanding of coral reef ecology and indirect and direct effects on fish assemblages are needed for efficient and accurate coastal management decisions and sustainable fishery.

*Keywords:* anthropogenic disturbance, coral reef habitats, fish community, coastal ecosystems, conservation management, spatial ecology, seascape approach
Assembling concrete foundations for deployment of acoustic receivers (Paper V).
1. LIST OF PAPERS

1.1 List of papers

This PhD thesis is based on the following five scientific manuscripts that are hereafter referred to by their Roman numerals in the text.*

**Paper I**
Faxneld, S., **Jörgensen, T. L.** and Tedengren, M. (2010)*
Effects of elevated water temperature, reduced salinity and nutrient enrichment on the metabolism of the coral *Turbinaria mesenterina.*

**Paper II**
Spatial variability in habitat structure and heterogenic coral reef fish assemblages inside a small-scale marine reserve after a coral mass mortality event.

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

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**Paper IV**
Robinson, J., Aumeeruddy, R., Jörgensen, T. L. and Öhman, M. C. (2008)*
Dynamics of camouflage (*Epinephelus polyphekadion*) and brown marbled grouper (*Epinephelus fuscoguttatus*) spawning aggregations at a remote reef site, Seychelles.

**Paper V**
Jörgensen, T. L. and Robinson, J.
Effectiveness of passive acoustic telemetry on coral reefs depends on deployment strategy and benthic substrate characteristics.
Submitted manuscript.

1.2 The author’s contribution to the papers

**Paper I**
Involved in initial planning and design of the study; led collection of organisms; responsible for execution of experiment; participated in interpretation of data and analyses; participated in the scientific discussion; wrote equal parts of the first draft of the manuscript together with the main author. Equal important contributor to the writing process together with the main author.

**Paper II**
Led the initial planning and design of the study; responsible for interpretation of data and analyses; led the scientific discussion; led the writing process; wrote the first draft of the manuscript; acted as corresponding author. Main contributor to the writing process (first author).
Paper III  Involved in initial planning and design of the study; shared responsibility for collection of organisms and field data on Mafia Island; led collection of organisms on Unguja Island; responsible for genetic analysis work; participated in interpretation of data and analyses; participated in scientific discussion; contributed to the writing process; wrote parts of the first draft of the manuscript; commented on the manuscript. Second most important contributor to the writing process.

Paper IV  Involved in initial planning and design of the study; responsible for collection of organisms and sampling; responsible for collection of field data; participated in interpretation of data and analyses; participated in the scientific discussion; commented on the manuscript.

Paper V  Led the initial planning and design of the study; led collection and handling of organisms; responsible for execution of experiment; led collection of field data; led interpretation of data and analyses; led the scientific discussion; contributed to the writing process; wrote the first draft of the manuscript; acted as corresponding author. Main contributor to the writing process (first author).
Table 1. Description of the different authors’ contribution to the manuscripts in this thesis.

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1.3 Additional relevant publications by the author


The blue planet: more than 70% of the Earth is covered by water.
2. INTRODUCTION

2.1 Coral reefs

Approximately 71% of the Earth’s surface is covered by oceans. Of the total area of the world’s oceans, 8% consists of shallow coastal systems, and only 0.01% (approximately 527,072 km²) consists of tropical coral reefs (Pauly, 2002; Mora et al., 2006; Day, 2014).* Coral reefs generally exist in tropical and subtropical seas around the equator (Pauly, 1997), where the water temperature is stable, around 26-28ºC, and are restricted to regions with water temperatures between 18-36ºC (Hubbard, 1997), while azooxanthellate cold water corals are found in cooler waters (reviewed by Roberts et al., 2009).

While tropical rainforests have higher biodiversity in terms of total numbers of species, coral reefs have the highest biodiversity of any ecosystem in the world in terms of the numbers of phyla and classes per hectare (Birkeland, 1997; Pauly, 1997; Knowlton and Jackson, 2008). Furthermore, around 800 of the world’s 1400 scleractinian coral species, which create the foundation for coral reef habitats, are associated with coral reefs (Pauly, 1997; Veron et al., 2009). In addition, a staggering 5,000-8,000 fish species can be found on coral reefs (Victor, 2015), representing a substantial proportion of all living fish species (Choat and Bellwood, 1991).

* The land area of the United Kingdom is 241,930 km².
Coral reefs are one of the most productive ecosystems and produce a wide range of ecosystem services essential to local human populations, e.g. fishery, shoreline protection, and recreational possibilities (Moberg and Folke, 1999; Barbier et al., 2011; Brander et al., 2012). Indeed, marine resources from coral reefs are economically important for many countries, especially in poorer regions, where marine organisms may provide the human population with crucial dietary proteins and fishing may provide the only monetary income (Jennings et al., 2001; Pauly and Zeller, 2014).

2.2 Disturbance, over-exploitation, and climate change

There are several threats to coral reefs, including natural disturbances such as hurricanes (Woodley et al., 1981; Hughes, 1994) and freshwater intrusions due to flooding (Banner, 1974), as well as anthropogenic disturbances, e.g. over-exploitation (Pauly, 1988; McManus et al., 1997; Riegl and Luke, 1998), sedimentation (Fabricius, 2005), eutrophication (Lapointe et al., 2004), and climate change (Hoegh-Guldberg, 1999).

Over-exploitation of marine resources has occurred since before the industrialisation (Jackson, 1997; Pandolfi et al., 2003; Hardt, 2008). Unsustainable fishing practices have been shown to affect the fish community in various ways and may result in, for example: lower fish biomass and density (Russ and Alcala, 1996; Knowlton and Jackson, 2008), skewed sex ratio (Beets and Friedlander, 1998), altered fish behaviour (Madin et al., 2010), lower quality of fish larvae (Berkley et al., 2004), as well as altered ecosystem functions (Bellwood et al., 2003; Hughes et al., 2013; Graham, et al., 2014).
Increased sedimentation and pollution have shown to have destructive influences on the growth and recruitment of coral species (reviewed by Fabricius, 2005). Indeed, reduced water quality has become more common and frequent, for example sedimentation loads on the Great Barrier Reef have increased five- to ten-fold since the European settlement in Australia due to changed land use practices, such as clearing and over-stocking of animals (McCulloch et al., 2003). In addition, studies have shown that recovery from natural short-term disturbances occur at a slower rate in areas where corals have been exposed to chronic impacts of anthropogenic disturbances (Loya, 1976; Connell, 1997).

Effects of climate change have put additional pressure on coral reefs in terms of increased sea surface temperatures (SST) (Carpenter et al., 2008) and ocean acidification (reviewed by Kleypas et al., 1999). Increased SST may cause coral bleaching, which is when the symbiosis between the coral host and the symbiotic zooxanthellae is disrupted and the zooxanthellae is expelled from the coral host (Glynn, 1996). The catastrophic 1997/1998 coral bleaching event, with consecutive coral mass mortality, destroyed approximately 16% of all coral reefs worldwide (Wilkinson, 2004). Increased temperatures and changes in climate systems have been predicted to become more common and severe in the future (Hoegh-Guldberg, 1999; IPCC, 2007; Feely et al., 2009; Bozec, et al., 2015), which may affect coral reefs worldwide, including remote and non-exploited reefs (Graham, et al., 2013). In addition, NOAA has recently predicted that a third historical global bleaching event may occur during 2015/2016,
which may result in one of the largest bleaching and coral mass mortality events on coral reefs in decades (Belva, 2015).

2.3 Coastal management

Different types of coastal management strategies have been established to protect coastal environments, for example: improved water quality by preventing coastal pollution and sediment run-offs, and protection of mangrove habitats that act as coastal filters (Banner, 1974; McCulloch et al., 2003; Fabricius, 2005). Direct habitat destruction may be caused by destructive fishing gears (Kaiser et al., 2003), anchoring damage (Öhman et al., 1993), dive tourism (Zakai and Chadwick-Furman, 2002), and ship grounding (Hatcher, 1984). Therefore, to reduce the risk of habitat destruction and over-exploitation, gear restriction and fishing quotas have been established (McClanahan et al., 2011).

Marine protected areas (MPAs) have been suggested as one of the most effective management tools for conservation biology and for protection of fish stocks (Gell and Roberts, 2003). As a management strategy MPAs have been proven to work in both developing and industrial countries (Cinner et al., 2009). However, studies have shown a variety of effects of MPAs, with both positive and negative impacts recorded, which indicates that effects of MPAs are not always predictable (reviewed by Halpern, 2003). Indeed, while small MPAs may provide suitable protection for sedentary species, mobile species may be less protected and may venture outside the MPAs border on a regular basis (Barrett, 1995; Sale et al., 2005; Le Quesne and Codling, 2009, Jörgensen, 2014). In addition, establishment of MPAs may
sometimes be controversial and lack local support from fishers, which may lead to poaching and lack of implementation (Wood, 2004; Christie and White, 2007).

With up to one third of reef-building corals threatened by increased risk of extinction (Carpenter et al., 2008) and with growing evidence of critical global over-fishing on coral reefs (Jackson, 2001; Berkes et al., 2006; Wilkinson and Salvat, 2012), more than 60% of the world’s reefs are under immediate threat (Bridge et al., 2013). It is therefore urgent to stop further coral reef degradation (Musick et al., 1999; Bellwood et al., 2004; Carpenter et al., 2008) and increase scientific knowledge regarding tropical marine ecosystems to ensure effective coastal management and sustainable fishery.
Local fishers inspect their catch from fishing in mangrove channels using traditional nets (Paper III). Photo from Mafia Island, Tanzania.
3. FRAMEWORK OF THE THESIS

3.1 Fish and habitat interactions

Tropical coral reefs are physically generated by corals, which consist of a coral animal host (Cnidaria), which lives in symbiosis with a symbiont (Dinoflagellata). Corals are considered to be so called “foundation species” or “ecosystem engineers” (Jones et al., 1996; Bruno and Bertness, 2001), as their secreted skeleton is made out of calcium carbonate (CaCO$_3$), which in turn creates complex and heterogeneous habitats and microhabitats for a vast numbers of marine organisms and fish (Sale et al., 1984). Many fish use corals as habitat for various activities, for example: shelter (Öhman et al., 1998; Bozec et al., 2005; Pratchett et al., 2008), protection against predators (Friedlander and Parrish, 1998; Almany, 2004), reproduction activities (Connell and Jones, 1991; Almany et al., 2007), and food source (Cox, 1994; Bozec et al., 2005).

Several studies have shown significant habitat interactions between coral coverage and fish assemblages, for example between live coral coverage or structural complexity and fish density (Syms and Jones, 2000; Garpe and Öhman, 2003; Messmer et al., 2011). However, results have been somewhat ambiguous, which may be explained by differences in dependency of live coral coverage within fish families (Halford et al., 2004; Pratchett and Berumen, 2008). For example, densities of obligate butterflyfish (Chaetodontidae) displayed strong
positive correlations with live coral coverage, however live coral-dependency has shown to vary between species depending on feeding specialisation (Sano, 2004, Berumen et al., 2005; Pratchett and Berumen, 2008).

Another explanation for unclear correlations between live coral coverage and fish may be due to lag effects after disturbances (Graham et al., 2007). Indeed, while most fish species may not be directly dependent on live coral coverage, if recolonisation of corals after a disturbance does not occur, the three-dimensional structure of the reefs will eventually be eroded, which may in turn have a large impact on the whole fish community (Syms and Jones, 2000; Gratwicke and Speight, 2005; reviewed by Pratchett et al., 2008).

3.2 Connectivity with other coastal ecosystems

While understanding linkages between disturbance, coral reef habitat quality, and fish assemblages creates a basic knowledge of coral reef ecology, fish are undeniably mobile organisms that move between and within habitat patches and corals may disperse their gametes over large areas. Therefore, increased scientific knowledge regarding connectivity between coastal habitats is vital.

The majority of all coral species are broadcast spawners and release their gametes into the water column, often in relation to optimal water temperatures and tidal regimes (Szmant, 1986). Coral recruitment may exhibit a high degree of spatio-temporal variation (Edmunds, 2000) and display high genetic connectivity (Souter et al., 2009) over large geographic areas (Veron, 2000). In contrast, other studies have shown that many coral reef fish species tend to settle close to their native
reefs (Jones et al., 2005), which indicate that these populations are not open as previously thought, and that many areas are in fact dependent on self-recruitment (Jones et al., 1999).

In addition to larvae dispersal and recruitment, coastal ecosystems are also directly interconnected on a seascape level through migration of fish between different habitats (McMahon et al., 2012; Chin et al., 2013). Several tropical coastal ecosystems have shown to be closely associated with coral reefs, e.g. mangroves (Unsworth et al., 2008) and seagrass beds (Dorenbosch et al., 2007; Kimirei et al., 2011). These ecosystems have been shown to be nursery grounds for many juvenile reef fish, or feeding grounds for adult fish (Robblee and Zieman, 1984; de la Morinière et al., 2002; Gullström, et al., 2008). Indeed, studies have shown that coral reefs that are located within the vicinity of mangrove or seagrass habitats support a different type of coral reef fish community and may increase adult fish biomass (Mumby et al., 2004; Nagelkerken et al., 2012).

3.3 Spatial ecology and fish movements

Studies of fish movements have shown that although many fish species display high site fidelity and limited home ranges, there are large disparities in sizes of home range between different species (Low, 1971; Chapman and Kramer, 2000; Werry et al., 2014).

There are different types of fish migration, such as fish movements within home ranges, for example daily migrations to feeding grounds or sleeping areas (Robblee and Zieman, 1984; Claydon et al., 2012; Howard et al., 2013). However, fish migration may also occur outside home ranges, e.g. through monthly or seasonal migration to
reproduction sites (Domeier and Colin, 1997; Bijoux et al., 2013b; Taylor and Mills, 2013), as well as migration between habitats through different life stages (Lecchini and Galzin, 2005). Indeed, a number of coral reef associated fish species perform ontogenetic shifts between different habitats (Luo et al., 2009), which highlight the importance of applying a holistic approach to coral reef management (Hughes et al., 2005). Similarly, species with larger home ranges or fish species that perform migrations to spawning sites may be less protected by management approaches such as MPAs if they venture outside the border of the MPAs (Le Quesne and Codling, 2009; Agardy et al., 2011; Grüss et al., 2011).

Different methodological approaches have been applied to study fish migration, from traditional tag-and-release methods, to more sophisticated methods such as stable isotope studies (Herzka, 2005) and active and passive telemetry (Kaunda-Arara and Rose, 2004; Moran et al., 2004; Welsh and Bellwood, 2012). Both active and passive telemetry have become more commonly used in marine science (Kessel et al., 2014). Despite the fact that telemetry is frequently used on coral reefs (Moran et al., 2004; Lindholm et al., 2006; Welsh and Bellwood, 2012), few large-scale studies have investigated efficiency of telemetry equipment in coral reef environments.

A challenge for future studies in spatial ecology will be to increase scientific knowledge regarding fish movement on spatial and temporary scales, as well as to evaluate research methods, which in turn could generate a better understanding of management of fish resources.
3.4 Definitions of conceptual keywords

**Biodiversity**
Biological diversity in terms of the variety and abundance of species in a defined unit of study (Magurran, 2013).

**Climate change**
Changes of climate that are attributed directly or indirectly to human activity that alters the composition of the global atmosphere and that are in addition to natural climate variability observed over comparable time periods (UNFCCC).

**Coral bleaching**
Loss of photosymbiotic microorganism and/or the pigments of these photosymbionts from tissues of host cnidarians (Williams and Bunkley-Williams, 1990).

**Connectivity**
Functional connectivity in terms of the degree to which the landscape [or seascape] facilitates or impedes movement among resource patches (Taylor et al., 1993).

**Disturbance**
A physical force, agent, or process, either abiotic or biotic, causing a perturbation (which include stress) in an ecological component or system (Rykiel, 1985).
<table>
<thead>
<tr>
<th><strong>Functional group</strong></th>
<th>A group of species that perform a similar function, regardless of their taxonomic affinities (Steneck and Dethier, 1994; Bellwood et al., 2004).</th>
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<tr>
<td><strong>Habitat quality</strong></td>
<td>The product of density, mean individual survival probability, and mean survival expectation of future offspring, for residents in an area as compared to other areas (Van Horne, 1983).</td>
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<td><strong>Home range</strong></td>
<td>An area traversed by an individual in its normal activities of food gathering, mating, and caring for young (Burt, 1943).*</td>
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<td><strong>Ontogenetic shift</strong></td>
<td>Shifts in diet or habitat usage depending on development or developmental history of an individual organism different life stages (Werner and Hall, 1988; Schellekens et al., 2010).</td>
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<tr>
<td><strong>Site fidelity</strong></td>
<td>An animal returning to a specific territory, e.g. a breeding territory, a feeding territory, or another type of territory (Switzer, 1993).</td>
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* Burt’s definition is aimed at mammals, but his definition is widely applied to marine organisms.
Spawning

A gathering of conspecific fish, for the purposes of spawning, that consists of fish densities significantly higher than are found during the non-reproductive period (Domeier and Colin, 1997).

Stress

A physiological or functional effect; the physiological response of an individual, or the functional response of a system caused by disturbance or other ecological process (Rykiel, 1985).

3.5 Abbreviations

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<tr>
<td>DNA</td>
<td>Deoxyribonucleic acid</td>
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<td>COI</td>
<td>Cytochrome c oxidase subunit 1</td>
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<tr>
<td>GP/R</td>
<td>Gross primary production/respiration</td>
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<td>GP/R(^{24})</td>
<td>Gross primary production/respiration per 24 h</td>
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<td>GSI</td>
<td>Gonadosomatic index</td>
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<td>IRMS</td>
<td>Isotope ratio mass spectrometer</td>
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<td>LIT</td>
<td>Line intercept transects</td>
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<td>MPA</td>
<td>Marine protected areas</td>
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<td>PCR</td>
<td>Polymerase chain reaction</td>
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<td>SST</td>
<td>Sea surface temperatures</td>
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<td>TL</td>
<td>Total length</td>
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<td>UVC</td>
<td>Underwater visual census</td>
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Experimental setup (Paper I).
4. OBJECTIVES

4.1 General objectives of the thesis

The general objective of this thesis was to investigate effects of anthropogenic disturbances on tropical coastal ecosystems and fish connectivity, ranging from species to seascape level (Fig. 1). Thus, effects of single and multiple stressors on corals were studied in Paper I, and interactions between coral reef habitat quality and associated fish assemblage were investigated in Paper II. Connectivity between coral reefs and other tropical coastal ecosystems was explored in Paper III, as well as fish migration to reproduction sites in Paper IV, while evaluations of effectiveness of spatial ecology methods were conducted in Paper V.

The results could have implications for coastal management and fishery, for example: a) by understanding effects of disturbances and coral and fish interactions (Paper I and Paper II), b) identifying vulnerable key areas for protection (Paper I-Paper IV), and c) understanding of fish movements, connectivity, and spatial ecology (Paper III-Paper V).
Fig. 1. Conceptual model over **Paper I-V** showing the different spatial scales that were investigated in the thesis and overlap between research areas.
Field picture from northern Vietnam, Cat Ba Island National Park.
5. STUDY SITES

The studies in this thesis were conducted in different types of tropical coastal ecosystems at the following locations in the Indo-Pacific region: Vietnam, the inner and outer islands of the Seychelles, and Tanzania (Fig. 2). The study sites were exposed to various disturbance regimes and levels of over-exploitation.

Fig. 2. Map of the Indian and Pacific Ocean showing the locations of where the studies were conducted. **Paper I** was carried out in Vietnam, **Paper II** and **Paper V** at the inner archipelago of the Seychelles, **Paper IV** at the outer island of the Seychelles, while **Paper III** was conducted in Tanzania.

Vietnam, Seychelles, and Tanzania are classified as developing countries, but with large variation in human population size and density, income, and life expectancy according to IMF and the World Bank (WEO, 2015; World Bank Population, 2015). For example, the
human population is high in Vietnam and Tanzania, with 91 million and 52 million people respectively, while the population in the Seychelles only reaches 92,000 persons (World Bank Population, 2015). This in turn puts different pressure on coastal ecosystems and marine resources, which many people highly depend on for food security and monetary income (Jennings et al., 2001; Iversen, 2012; Pauly and Zeller, 2014).
Mangroves are one of the least protected ecosystems in the world.
6. SUMMARY OF PAPERS

6.1 Paper I

The aim of Paper I was to investigate how a common coral species, *Turbinaria mesenterina*, responded to different stressors in nearshore reefs. Using a full factorial experiment, changes in net production and respiration rates were measured on *T. mesenterina* exposed to: (1) added nitrate (ambient vs. + 5 μM NO$_3^-$), (2) decreased salinity (30 vs. 20 psu), (3) increased temperature (25 vs. 31ºC), and combinations of these factors, after 24 h exposure.

The study was carried out in the northern regions of Vietnam at an outdoor laboratory in Do Son. Coral samples were collected from Cat Ba Island National Park, which is located within Halong bay; an area with high seasonal water temperature fluctuations (16-31.5ºC) (Faxneld et al., 2011). Nearshore coral reefs in Halong bay are frequently exposed to high levels of sedimentation, high nutrient levels, and coastal pollution (Lang et al., 2004; Tran et al., 2004; Latypov, 2005), such as arsenic, DDT, and PCB (Hong et al., 2008; Swennen et al., 2009). The area has low coral diversity, mainly consisting of massive coral species such as *Galaxea fascicularis* and *Porites lutea*.

Samples of *T. mesenterina* were collected using SCUBA at Co To Island, at a depth of 4-8 m. Changes in dissolved oxygen concentration in light (net production) and darkness (respiration) were
measured according to Moberg et al. (1997). Net production and respiration rate data were calculated per hour and cm² coral surface area. Live coral surface area was determined using the aluminium foil method (March, 1970). Respiration rate was added to net production values in order to achieve gross primary production rate. Gross primary production/respiration (GP/R) ratio over 24 h was calculated as a dimensionless estimate of the physiological status of the corals.

The results showed that T. mesenterina exposed to single stressors in terms of added nitrate or decreased salinity had little effect on physiological response, in terms of GP/R²⁴, while stressors acting in combination led to a GP/R²⁴ value of <1, which means that the corals were not energetically self-supporting and needed to import energy to fulfil their energy demands (Hopkinson and Smith, 2005) (Fig. 3.).

All treatments groups exposed to increased temperature (either alone or in combination with other stressors) had a GP/R²⁴ value of <1, which suggests that increased temperatures may have critical effects on coral health. All coral samples exposed to the triple combination of stressors in terms of increased temperature, added nitrate, and decreased salinity died after 24 h exposure, which suggests synergetic effects, since corals exposed to added nitrate and decreased salinity at ambient water temperature (25°C) did not show any stress response in GP/R ratio, respiration rate, or gross primary production rate and no mortality occurred.
In summary, effects of climate change may have a negative impact on coral reefs, especially in coastal areas where corals are already exposed to freshwater and nutrient run-offs.

6.2 Paper II

The aims of Paper II were to investigate spatial variability in coral reef habitat and fish community, as well as examine ecological linkages between habitat quality and coral reef fish assemblages within a small well-protected MPA. Five sites were selected for extensive surveys within the marine reserve at Cousin Island and by using various methods to investigate differences in: (1) biotic and abiotic benthic substrate, (2) rugosity, (3) coral recruitment, (4) fish density and functional groups, and (5) key invertebrate grazers.
**Paper II** was conducted at Cousin Island Special Reserve at the inner part of the archipelago of the Seychelles. Cousin Island is a small no-take marine protected area (1.2 km²) and has been under legal protection since 1975, which makes it one of the longest established MPAs in the Western Indian Ocean (McClanahan et al., 2009). The coral reefs in the Seychelles have been considered to be one of the regions least affected by local anthropogenic disturbances (Cinner et al., 2009; Burke et al., 2011), but the inner granitic islands were severely affected by the worldwide coral bleaching and mass mortality event in 1997/1998, with up to 95% coral mortality (Bigot et al., 2000; Wilkinson, 2004; Graham et al., 2006; Wilson et al., 2012). The marine area around Cousin Island is characterised by fringing reefs, granite reefs, patch reefs, and extensive areas of macroalgae.

Five different sites around Cousin Island were surveyed at 6-10 m depth to investigate spatial variation in coral reef habitats and associated fish communities. The following methods were used to collect data: a) 10 m line intercept transects (LIT) for benthic substrate (English et al., 1997), classified according to Leujak and Ormond (2007). Scleractinian corals were further classified to genus and morphology according to Veron (2000), b) 1 m² coral recruitment quadrates, c) 20 x 5 belt transects for surveying coral reef fish assemblage and key invertebrate grazers (English et al., 1997). Fish were identified to family level and categorised into functional groups (Froese and Pauly, 2014), and d) rugosity was measured using the chain-and-tape method (Risk, 1972; Luckhurst and Luckhurst, 1978; McCormick, 1994).
The results demonstrated that coral habitat quality was directly linked to fish density and composition of coral reef fish assemblages. Coral cover displayed a large spatial variation between the five surveyed sites, from 1.5% to 43.2% coral cover inside the MPA, and total fish abundance was 15 times higher on sites with high coral coverage in comparison to sites with low coral cover (Fig. 4.). Indeed, high numbers of piscivores and obligate corallivores were noted at the surveyed site with the highest level of coral coverage, while both functional fish groups were completely absent at the site with the lowest coral coverage.

To summarise, the results from **Paper II** demonstrate that coral reef habitat and fish assemblage may display high spatial variability and heterogenic differences after large-scale disturbances, such as the 1997/1998 bleaching event and subsequent coral mass mortality. Based on the distribution of coral rubble, coral recruits and colony size (**pers obs**), potential recovery appeared to occur in a patchy and non-linear fashion, which may depend on underlying stochastic
processes that affect coral recruitment and survivorship. The results highlight the importance of protecting coral reef habitats and that potential recovery processes from coral bleaching and mass mortality may be slow, even in regions which are otherwise exposed to low levels of local anthropogenic disturbances (Baker et al., 2008; Chong-Seng et al., 2012).

6.3 Paper III

The objectives of Paper III were to understand ontogenetic habitat shifts, feeding patterns, and resource partitioning of two commercially important species, *Lutjanus fulviflamma* and *L. ehrenbergii* in terms of: (1) diet and habitat usage, (2) diet composition (volume of food items and stable isotope signatures $\delta^{13}C$ ($^{13}C:^{12}C$) and $\delta^{15}N$ ($^{15}N:^{14}N$) ratios. In addition, genetic COI barcoding was conducted to correctly identify and verify the fish species.

The study was carried out at Mafia Island and Unguja Island (Zanzibar) in Tanzania. Mafia Island Marine Park (MIMP) was established 1995 and covers 822 km$^2$ (Andersson and Ngazi, 1995). The marine park has been divided into various management zones, including areas where only restricted fishing gears are allowed and several no-take areas where all fishing is prohibited (Horrill et al., 1996; Kamukuru et al., 2004). Chole Bay, which is located within MIMP, is a sheltered bay, protected from strong wave action by fringing coral reefs and surrounded by large areas of mangrove forest and extensive seagrass and intertidal flats.

Samples of *L. fulviflamma* and *L. ehrenbergii* from different habitats were collected or purchased directly from local fishers at
Mafia Island and Unguja Island. The following methods were used to collect data: a) COI barcoding (Ward et al., 2005), b) stomach analyses, where contents were identified to the lowest practical taxonomic level and proportion volume of stomach content was estimated (Hyslop, 1980; Berkström et al., 2012), and c) stable isotope studies of δ^{13}C and δ^{15}N ratios. For each fish specimen TL and weight were recorded. The fish were sexed macroscopically and gonad stages were noted. A fin clip was taken for genetic studies, a piece of muscle tissue for isotope studies, and the stomach and intestines were removed and preserved. Reference materials for the isotope study were collected from different habitats at Mafia Island.

The results showed that *L. fulviflamma* and *L. ehrenbergii* performed ontogenetic migrations between mangrove, seagrass, and coral reef habitats (Fig. 5.). Furthermore, although the two species overlapped in habitat usage, stomach contents differed significantly between the fish species in all comparable life stages and habitats, which suggests food resource partitioning. In addition, the results from the COI barcoding led to accurate verification of species, since the two species are notoriously difficult to tell apart (Garpe and Öhman, 2003), and visual characteristics may also become less apparent in dead fish.

In conclusion, the result from Paper III showed that the two closely related species *L. fulviflamma* and *L. ehrenbergii* performed ontogenetic migrations between spatially and ecologically different habitats. The study highlights the need to include multiple habitats in conservation and marine protected areas, since isolated management of coral reefs would not protect all life stages.
6.4 Paper IV

The objective of Paper IV was to derive key aggregation parameters of camouflage grouper, *Epinephelus polyphekadion* and brown marbled grouper, *E. fuscoguttatus* for management purposes. Specifically, the objectives were to: (1) verify fishers’ reports of grouper spawning aggregations, (2) investigate the spatial and temporal dynamics of aggregations, and (3) assess lunar and seasonal periodicity of reproductive activity.

**Paper IV** was carried out at a remote atoll in the southern parts of the outer islands of the Seychelles. Due to the sensitive data regarding spawning aggregation of groupers the exact location is not revealed. The study area consisted of patchy coral reefs and rock substrate separated by sandy channels.

Spatial and temporal dynamics of spawning aggregations of *E. polyphekadion* and *E. fuscoguttatus* were investigated at 7-13 m depth. Spawning aggregation sizes were calculated from fish
abundances in core and boundary areas, based on mean density counts from respective transects and area estimates. The following methods were used: a) 100 × 4 m permanent belt transects at the core and boundary area of the aggregation for recording discrete counts of camouflage groupers. In order to estimate fish densities of brown marbled grouper, logarithmic abundance classes were performed according to Colin et al. (2003), and a conservative approach and the minima of the abundance classes were used for estimation of overall aggregation abundances, b) video footage to investigate fish reproduction behaviour (Johannes et al., 1999; Rhodes and Sadovy, 2002), c) fish and gonad sampling. For each fish sample TL and weight were recorded. Sexual maturation stages were recorded according Rhodes and Sadovy (2002). Gonads were removed, weighed, and male/female classification was established through macroscopical investigation. In addition, a sub-sample of the gonads was collected for histological studies, and d) tagging of camouflage groupers to investigate site fidelity. Fish were tagged and released at the point of capture within the spawning site using T-bar anchor tags, which were inserted between the dorsal pterygiophores.

The results verified transient-type spawning aggregations (Domeier and Colin, 1997) of *E. polyphekadion* and *E. fuscoguttatus*, which had previously been reported by local fishers. The underwater visual surveys showed clear patterns in density, abundance, and fish behaviour within the core and boundary reef area of the aggregation site around the time of new moon, with peak aggregation abundances of more than 1900 individuals of fish (Fig. 6.). In addition, gonadosomatic index (GSI) and reproductive maturation were also
strongly associated with the new moon, and the spawning season lasted for 2-3 month between November and February each year. Furthermore, the results from the tagging studies showed that camouflage grouper exhibited site fidelity on scales of weeks to months, and that at least one individual returned to the aggregation site the following year.

Fig. 6. Abundance of groupers at spawning sites depending on lunar phase. a) Abundances of *Epinephelus polyphekadion* and b) *E. fuscoguttatus* at spawning aggregation site during spawning season (Dec-03, Jan-04, Dec-04, Jan-05) and non-aggregation (Nov-06) abundances on census days relative to the new moon (NM). (Dec-03, Jan-04, n=4; Dec-04, Jan-05, Nov-06, n=5). Black lines indicate the trend in abundance for the month (Jan-04) with the longest time series of observations.

In summary, the results from **Paper IV** verified spawning aggregations around the time of the new moon for both *E. polyphekadion* and *E. fuscoguttatus* at the site. The study highlights the importance of protecting spawning aggregation areas from over-exploitation.

### 6.5 Paper V

The aims of **Paper V** were to investigate effectiveness of acoustic telemetry in terms of deployment methods and factors that may affect detection rates and ranges of passive acoustic equipment deployed in
coral reef habitats. Using an experimental design with an array of acoustic receivers and stationary coded acoustic transmitters, the following factors were investigated: (1) deployment method, (2) benthic substrate, (3) rugosity, (4) background noise, and (5) depth. To verify findings, a second study was undertaken to determine the effects of deployment strategies and natural behaviour of two species of herbivorous rabbitfish (*Siganus sutor* and *S. argenteus*) on detection rates and ranges.

**Paper V** was conducted at Cousin Island Special Reserve at the inner part of the archipelago of the Seychelles in the same area as **Paper II**.

During the first part of the study, passive acoustic receivers (model VR2W 69kHz) and stationary V9 acoustic transmitters (V9-2x-069k-1, Vemco) were deployed at 5.8-14.9 m depth to investigate effects of deployment strategies, habitat characteristics, and other abiotic factors that may affect the performance of acoustic receivers, as well as calculating detection curves. Benthic substrate was estimated using underwater photos and the software Vidana, and rugosity was visually estimated according to Wilson et al. (2007). During the second part of the study, effects of deployment strategy on detection rates of live fish were investigated. 50% of the acoustic receivers were placed close to the bottom and 50% of the receivers were placed subsurface. Acoustic data was recorded for 72 h before the positions were reversed and data collection continued for another 72 h. 10 *Siganus sutor* and 17 *S. argenteus* were surgically fitted with V9 acoustic transmitters according to a modified protocol following Bijoux et al. (2013a).
The results showed that performance of passive acoustic arrays, both in terms of detection rates and ranges, could be increased depending on deployment method (Fig. 7.). Indeed, placing the acoustic receivers high in the water column resulted in approximately 45% more detections than when placing the receiver close to the bottom. This result was consistent using both stationary transmitters and live fish, displaying natural behaviour. In addition, benthic substrate in terms of hard substrate, rubble, and sand had an impact on detection rates and there was a clear diel pattern in detection rates between day and night. Furthermore, detection rate of acoustic signals decreased with distance in a non-linear way, exhibiting a clear S-shaped logistic relationship for both bottom mounted and subsurface mounted receivers.

![Fig. 7. Acoustic detection rates of bottom mounted and subsurface deployment of acoustic receivers.](image)
a) Mean numbers of total detection per hour/acoustic receiver for stationary acoustic tags (first array). (Bottom mounted receivers, n=19; Subsurface mounted receivers, n=20). b) Free-swimming fish, *Siganus sutor* and *S. argenteus* per hour/acoustic receiver for bottom mounted and subsurface mounted deployment (second array). (n=18). Error bars denote ±SE errors of the mean.
In conclusion, the results from Paper V suggest that to achieve optimal performance of passive acoustic telemetry, receivers should be placed subsurface using sturdy deployment methods that can tolerate harsh weather and strong currents. The study also emphasises the importance of using permanent transmitters as controls to evaluate effectiveness of receivers throughout acoustic studies on coral reefs, to calibrate for diel differences in background noise.
Fish tagging of *Siganus sutor*, just before the fish is released.
7. DISCUSSION

In this PhD thesis I investigate effects of anthropogenic disturbances on corals (Paper I), as well as interactions between coral reef habitat and associated fish assemblages (Paper II). Furthermore, I demonstrate how coral reefs are connected to other coastal ecosystems by ontogenetic fish migration (Paper III). Fish migrations, in terms of spatial and temporal patterns of spawning aggregations, are further investigated (Paper IV); while in the final paper (Paper V), I evaluate efficiency of passive acoustic telemetry, an increasingly common method in coral reef ecology.

7.1 Effects of disturbances and coral and fish interactions

To protect coral reefs for the future, a better understanding is needed of how coastal disturbances affect corals and how coral reef habitat quality in turn affects fish assemblages (Paper I and Paper II).

In Paper I Turbinaria mesenterina was negatively affected by increased water temperatures; and in combination with added nutrients and decreased salinity, effects were more severe and even lethal, which indicate synergistic effects. Several authors have reported negative physiological responses to increased water temperatures (Jokiel and Coles, 1977; Glynn and D’croz 1990; Levitan et al., 2014), added nutrients (Hallock and Schlager, 1986; Humphrey, et al., 2008;
Synergistic effects on corals and other organisms are not uncommon and have been reported by e.g. Coles and Jokiel (1978), who demonstrated synergetic effects between increased light intensity and decreased salinity in combination with increased temperatures on *Montipora verrucosa*. In addition, Hoegh-Guldberg and Smith (1989) reported synergetic effects due to changes in temperature, light, and salinity levels on *Stylophora pistillata* and *Seriatopora hystrix*. However, coral vulnerability to increased temperatures may also depend on coral species and genetic variations of the clade of the symbionts (Baker et al., 2004; Berkelmans and Van Oppen, 2006; Abrego et al., 2008; Jones et al., 2008). For example, in general *T. mesenterina* is considered to be a fairly tolerant coral species and are often found in turbid waters (Anthony et al., 2005; Sofonia and Anthony, 2008), while other fast growing species like *Acropora sp.* and *Pocillopora sp.* are considered to be more sensitive (Fabricius et al., 2004; McClanahan, et al., 2005).

The results suggest that in coastal areas where corals are already exposed to chronic disturbances, effects from climate change may be more drastic. Furthermore, Wooldridge et al. (2009) showed that the reverse result could be true too: hence, if water quality is improved, coral reefs may withstand higher temperatures. Since effects of climate change will continue even if CO₂ levels are decreased, these
results are important, since it shows that coral reefs’ ability to withstand increased temperatures could be improved. Thus, identifying thresholds levels and reversal effects on corals are of high importance (Graham et al., 2015), and by mitigating all other human induced stress factors it is likely that corals to a greater extent can survive predicted temperature increases. As coastal stressors often occur in combinations, it is clearly essential to understand how stress and disturbances affect corals, but also how coral reef habitat quality is connected to fish assemblages.

In Paper II coral reef habitat and fish assemblages displayed high spatial variability between surveyed sites after a large-scale coral mortality event. There were large heterogenic differences in fish densities and composition, which were directly linked to coral habitat quality, as coral coverage was significantly positively correlated with fish density and sea urchins, but negatively correlated with macroalgae.

Thus, if coral mass mortality occurs, as a result of natural disturbances or as a consequence of anthropogenic disturbances (Woodley et al., 1981; Hatcher, 1984), it may result in an initial decrease in live coral coverage and loss of three dimensional structure, which in turn could have a large impact on the fish communities (Syms and Jones, 2000; Graham et al., 2006). As long as the three dimensional structure remains however, several studies have shown that the fish community may remain more or less unaltered (Lindahl et al., 2001; Feary et al., 2007; Wilson et al., 2008).

The study also showed that establishment of MPAs may not always be sufficient, as MPAs may not protect against large-scale
disturbances such as climate change, even in areas exposed to low levels of disturbance.

Potential recovery in terms of coral recruit density seemed to occur in a patchy and non-linear manner, which may be due to stabilisation of coral rubble, which in turn may promote successful coral recruitment. Other authors have shown negative correlations between coral recruitment and rubble (Kuffner et al., 2006; Ritson-Williams et al., 2009), however positive or negative correlations between coral recruitment and rubble may depend on whether or not the rubble has stabilised, which has been suggested to be a bottleneck factor for coral recovery (Chong-Seng et al., 2012).

Several studies have shown significant habitat interactions between coral coverage and fish assemblages (Syms and Jones, 2000; Garpe and Öhman, 2003; Messmer et al., 2011), however, reports have been ambiguous. Thus, studies focusing on coral habitat interactions deserve further attention to investigate not only correlations with live coverage, but also to understand underlying mechanisms and driving forces behind coral recovery, for example effects of protection of grazers and factors that affect coral recruitment and survivorship.

7.2 Understanding fish movements, connectivity, and spatial ecology

For coastal management decisions it is important to understand fish movement and fish connectivity between habitats and identifying vulnerable areas for protection (Paper III-Paper V). Thus, it is not only important to focus on effects that affect habitat, but also interactions between other coastal habitats and protection of fish.
In Paper III two closely related lutjanids species, *Lutjanus fulviflamma* and *L. ehrenbergii* were shown to undergo ontogenetic shifts between different coastal ecosystems depending on life stage. In general, juveniles inhabited mangroves, subadults were found in seagrass beds, while adult specimens were found on coral reefs.

Other studies have shown that coral reef associated fish species change habitat depending on life stages (Lecchini and Galzin, 2005), a behaviour that has been suggested to decrease risks of predation and increase availabilities of resources (Dahlgren and Eggleston, 2000). Indeed, several other species within the snapper family have been reported to perform ontogenetic shifts, for example: *L. apodus* (de La Morinière, et al., 2003), *L. mahogoni* (Nagelkerken et al., 2000), and *L. griseus* (Nagelkerken et al., 2000; de La Morinière, et al., 2003). However, not all species perform ontogenetic shifts, which suggest that ontogenetic shifts are species-specific.

The results showed that coastal habitats were clearly interconnected, a result which is in concordance with other authors (Chin et al., 2013; Pittman et al., 2014). An improved understanding on the mechanisms of connectivity within and between coral reefs and other coastal habitats may lead to better protection and management (McCook et al., 2009). Furthermore, snappers are commercially important species (Lugendo et al., 2005; Shimose and Tachihara, 2005; Grandcourt et al., 2006) and in the region snappers and emperors (Lethrinidae) contribute to approximately 40% of local catches (1984 to 1992 Tanzanian Annual Fisheries Statistics).

Snappers are also important predators in coral reef ecosystems, and removal of predatory groups may have additional impacts on food
webs and ecosystem functions, as shown by Layman et al. (2007). Thus, to manage snapper stocks properly (and other fish species that perform ontogenetic shifts), protection and management of all habitats important for all life stages are essential, and not only protection of the coral reefs where the adults are found.

In summary, the study emphasises the importance of protecting various types of ecosystems for coastal management and not only areas with high biodiversity. Indeed, while the numbers of MPAs covering coral reefs have increased steadily, other “less attractive” ecosystems have not received the same level of protection. Mangroves are one of the least protected ecosystems in the world (Valiela et al., 2001), despite the fact that both mangroves and seagrass beds may be extremely important nursing grounds for many juvenile reef fishes (Mumby et al., 2004; Nagelkerken et al., 2012).

In Paper IV spatial and temporal patterns of abundances and sexual maturation of *Epinephelus polyphekadion* and *E. fuscoguttatus* were recorded at a spawning aggregation site at a remote atoll. The study showed that fish gathered during the new moon for several months and displayed high site fidelity throughout the spawning season. This is not unexpected, since many species reproduce selectively around the lunar cycle on coral reefs (Taylor, 1984; Park, et al., 2014; Abesamis, et al., 2015). Some species reproduce during the full moon (Lobel, 1978; Bolden, 2000; Rowell et al., 2015) to take advantage of beneficial tides that allows gametes to disperse quickly, which in turn enables coverage of larger areas and reduces the risks of predation of gametes (Heyman, et al., 2001). In contrast, other species reproduced during the new moon (Carter et al.,
2014; Claydon, et al., 2014), which has weaker tides, but may decrease the risk of predation of adults, due to the reduced light, since for example many shark species hunt more actively during full moon (Vianna et al., 2013). It therefore appears that there is a trade-off regarding spawning around full moon or new moon in terms of survival chance for the offspring or adult fish.

The results from the study suggest that there may be regional differences in spawning behaviour of groupers in comparison to other studies. For example, Rhodes et al. (2014) noted an increase in abundances at spawning sites *E. fuscoguttatus*, *E. polyphekadion*, and *Plectropomus areolatus* in Micronesia. While the spawning season was approximately as long as in our study, spawning in our study occurred during the new moon and during the warmer months of the year, while in the study from Micronesia, spawning occurred during the full moon and during the time of year when water temperatures were cooler. This result indicates that there are regional differences in spawning behaviour between populations of the same fish species and that management efforts should be applied on a local to regional level.

Spawning aggregations are highly vulnerable to over-exploitation, for example approximately 920 camouflage groupers were caught by island staff over four days, which represent 48% of the peak aggregation size. Indeed, many spawning sites have been heavily targeted by fisheries, which in several cases has led to a complete depletion of the spawning aggregations (Sadovy and Domeier, 2005; Russell et al., 2011; Erisman et al., 2015). However, studies have also shown that protection of spawning sites may be highly successful and
that fish sizes and sex ratios of groupers can reverse to normal levels after protection (Beets and Friedlander, 1998).

In Paper V the performance and efficiency of passive acoustic telemetry methods were evaluated as a tool for studying fish movements. The results showed that both detection rates and ranges could be significantly increased (with up to 45%) by placing the acoustic receivers high in the water column instead of close to the bottom, and that habitat structure could have a negative impact on detection rates and ranges.

Other telemetry studies have shown that a wide range of factors may influence detection rate and efficiency of acoustic receivers, which may be of biological, physical, and anthropogenic origin (Heupel et al., 2006; Espinoza et al., 2011; Simpfendorfer et al., 2008), for example: depth, tidal regimes, wave action, turbidity, salinity, temperature, habitat characteristic, biofouling, background noise, and animal behaviour (Voegeli and Pincock, 1996; Finstad et al., 2005; Heupel et al., 2006; Simpfendorfer et al., 2008; Espinoza et al., 2011).

The results showed significantly lower detection rates in comparison to other studies conducted in other aquatic habitats (Simpfendorfer et al., 2008), but were concordant to similar studies performed on coral reefs with the same type of acoustic transmitters (Welsh et al., 2012). This suggests that performance of passive acoustic telemetry may be less efficient on coral reefs than in other habitats, which could be a result of that coral reefs have high levels of acoustic background noise (Lammers et al., 2008; Simpson et al., 2008) and complex three dimensional structures, which may affect
detection rates (Jenkins and Wheatley, 1998; Kovalenko et al., 2012). In addition, the results displayed a significant difference in detection rates between day and night, a result that is in direct contrast to Welsh et al. (2012), who did not find any differences in detection rates due to diel variations. This may be a result of that individual coral reefs have different levels of background sound signatures, which may depend on activities and densities of soniferous animals, e.g. parrotfish and snapping shrimps (Kennedy et al., 2010; Lammers et al., 2008; Radford et al., 2010).

Therefore, we strongly recommend conducting pilot studies and using stationary transmitters throughout acoustic studies on corals reefs. Indeed, differences in performance of acoustic receivers could otherwise lead to flawed interpretations of fish movements and behaviour, as shown by Payne et al. (2010), who demonstrated that unless calibrations were carried out regarding effects of environmental factors on detection rates on tagged cuttlefish movements, this could lead to severely erroneous results.

Since acoustic telemetry can generate scientific knowledge and a deeper insight regarding aquatic animal movements connected to diel, tidal, lunar, or seasonal changes (Taquet et al., 2006; Mann et al., 2009; Bijoux et al., 2013a) and the method is becoming more commonly used for spatial ecology studies on coral reefs, it is fundamentally important to understand factors that could increase performance and reliability of passive acoustic methods in structurally complex habitats such as coral reefs.
7.3 Conclusions

Understanding direct causes of coral reef degradation due to anthropogenic disturbances, interactions between habitats and the fish community, and how coastal ecosystems are linked with each other are fundamental to coastal management and decision making.

In this thesis I have shown that it is important to understand how disturbances affects corals, investigated habitat and fish interactions, and shown that some coastal areas may be more vulnerable to disturbance than other areas (Paper I and Paper II). Furthermore, I have demonstrated that it is vital to protect key areas such as nursing grounds and reproduction sites (Paper III and Paper IV), which are essential for safe-guarding both biodiversity and fish resources. Studies of connectivity and fish movement may be challenging, and therefore telemetry methods are becoming more frequently used. However, performance of acoustic telemetry methods can be improved and the risk of erroneous interpretations of results may be reduced (Paper V).

In conclusion, coral reefs are dynamic and complicated ecosystems, which require complex management solutions. Thus, to protect coral reefs for the future it is therefore recommended to protect coastal environments and minimise all other anthropogenic disturbances to improve water quality, which may increase corals’ ability to cope with effects from climate change, in terms of increased water temperatures.

As coral reef habitat quality is directly linked to fish assemblages, these types of coastal management actions could also have indirect effects on the coral reef fish community. In addition, identifying and protect key habitats for fish are paramount, since coral reefs are
interconnected with other coastal ecosystems. This may include protection of less visually attractive areas with lower biodiversity, such as mangroves and seagrass beds.

A better understanding of how disturbances and recovery processes affect coral reefs and a wider understanding of fish movement and spatial ecology are of great importance. Indeed, more research and a better scientific understanding of coral reef ecology are needed to make future coastal management efforts as efficient as possible.

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Tropical coral reefs are tightly interconnected with mangrove and seagrass ecosystems. Photo from the Seychelles showing Cousin Island.
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