

**Habitat driven responses of reef fish: temporal change,
niche partitioning and selection**

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A thesis submitted for the degree of Doctor of Philosophy

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Date of Submission (March 2018)

Dedicated to my mother

Abstract

Shallow water tropical and temperate marine habitats are changing dramatically in response to many stressor-driven effects. The change in turn threatens the associated fish communities relying on their maintenance for habitat provision. At present, a much better understanding of the interaction between changing habitats and the associated fish is necessary. To address the lack of understanding of the habitat – fish association, mechanisms which underpin the habitat driven responses of reef fish were examined, from entire communities down to species level, across tropical and temperate ecosystems. Using a highly biodiverse ecosystem as the model system, effects of changing habitat on the associated fish community were observed, consequently demonstrating how important, in terms of shelter and food resources, the overall habitat is in structuring the fish community. Furthermore, patterns of habitat use of certain fish species within and across tropical and temperate ecosystems were examined. Variation in the size of the habitat used and its overlap between species within systems, and uniform patterns in habitat use and comparable fish habitat size and overlap across systems, were discovered. By looking at fish habitat use within systems, invaluable knowledge was gained on ecological interactions between habitat and fish on a small scale. At the same time, detection of similar mechanisms of fish habitat use across ecosystems indicates to possible uniform response of fish communities to habitat change at a large-scale. Finally, by looking at fish habitat selection using olfaction, in a temperate model system, a range of subtle behavioural responses displayed during habitat selection were detected. These results highlighted the extent of complexity of the mechanisms used in fish habitat selection and the ubiquitous importance of the habitat and its properties for the associated fish. In addition to, and based on the ecological significance of the findings, a number of potential management and conservational applications of the research were given within the thesis.

Acknowledgements

Draga majko, bez tvoje ljubavi, pomoći i beskrajnog hrabrenja, siguran sam da bi mi bilo teže i da bi mi trebalo mnogo duže da završim ovaj doktorat. Beskrajno ti hvala na podršci, moralnoj i prehrambenoj. Joan Moranta, sense tu aquesta tesi no seria possible. Mai et podré agrair prou per acceptar de ser el meu director. Per a mi has estat una gran influencia, tant científicament com personalment. Espero ser teu amic per sempre. Dave Smith, thank you for starting me on this PhD journey and being a “yes type of supervisor”, always encouraging and supporting my scientific ideas. Hilmar Hinz, although you were not my official supervisor, more than often your scientific input into the PhD matched that of one. You significantly improved the quality of my research, as well as me as a scientist. I am really glad we also became friends along the way. Olga Reñones, sin tu ayuda con el trabajo del campo, organización de campañas y recogida de datos, todavía estaría pendiente de muestreo. Tampoco hubiese disfrutado de él, tanto. Aparte, a lo largo de los últimos años siempre has estado pendiente de mí y me has apoyado muchas veces cuando el más lo he necesitado. Lucia Rueda, tu extenso conocimiento de R y constante disponibilidad frente mis preguntas me han ahorrado muchísimo tiempo y nervios a lo largo de la tesis. Manolo Hidalgo y Cova Orejas dedicaron su tiempo e interés a escuchar sobre mi trabajo científico y me ayudaron con sus consejos expertos. Emma Revill, University of Essex graduate administrator, showed limitless patience with my inquiries and requests, often going out of her way to help me. University of Essex contributed in funding several of my scientific trips and conferences. My stay at the Spanish Institute of Oceanography (Instituto Español de Oceanografía) and the resulting opportunities within this research environment increased the quality of my PhD and formed an invaluable part in my scientific development. Klemen Vute, tvoje drugarstvo mi je pomoglo da ostanem veseo tokom doktorata, ali šta je za mene možda i važnije, fizički spreman. Finally, Heather Baxter, from being the best expedition

buddy to being the best life buddy I could wish for, your presence, love and support made this PhD journey a lot happier for me.

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Publications and conferences

PUBLICATIONS

Gouraguine, A., Díaz-Gil, C., Reñones, O., Otegui, D. S., Palmer, M., Hinz, H., Catalán, I. A., Smith, D. J. and Moranta, J. (2017) 'Behavioural response to detection of chemical stimuli of predation, feeding and schooling in a temperate juvenile fish', *Journal of Experimental Marine Biology and Ecology*, 486, pp. 140–147.

Gouraguine, A., Reñones, O., Baxter, H., Hinz, H., Smith, D. and Moranta, J. (2016) 'Individual Based Analysis of the Functional Overlap Among Four Temperate Fish Species', in 41st Mediterranean Science Commission (CIESM) conference proceedings.

PUBLICATIONS IN PREPARATION

Citizen science as a tool to detect long-term environmental changes in data-poor/resource-limited areas

The role of intra- and inter-specific behavioural variation in niche partitioning

Sensitivity of two current choice flume methodology in fish behaviour studies

CONFERENCES AND WORKSHOPS

World Conference on Marine Biodiversity, Montreal, Canada, May 2018

10th Indo-Pacific Fish Conference (IPFC), Tahiti, French Polynesia, October 2017

Underwater Video Techniques Workshop, Barcelona, Spain, May 2017

41st CIESM Congress, Kiel, Germany, September 2016

List of abbreviations

a	Intraspecific aggression
A	Open horizontal surface
ad	Advertising
AIC	Akaike's Information Criterion
alg	Algae
b	Interspecific aggression
B	Open vertical surface
BCI	Bayesian Credibility Intervals
br	Branching
c	Cleaning
C	Underside surface
D	Concealed surface
df	Diffused feeding
DHM	Degree Heating Month
ERSST	Extended Reconstructed Sea Surface Temperature

et	Erect tree-like algae morphotype
f	Focused feeding
fl	Filamentous algae morphotype
GLMM	Generalized Linear Mixed-effects Model
h	Hovering
JAGS	Just Another Gibbs Sampler
m	Massive
MCMC	Markov Chain Monte Carlo
MDS	Nonmetric Multidimensional Scaling
NOAA	National Oceanic and Atmospheric Administration
OISST	Daily Optimum Interpolation Sea Surface Temperature
p	Seagrass
PADI	Professional Association of Diving Instructors
PCA	Principal Component Analysis
PCoA	Principal Co-ordinate Analysis
PVC	Polymerising Vinyl Chloride

r	Rock
rb	Rubbing
rm	Roaming
RN	Realised Niche
rub	Rubble
s	Searching
SCUBA	Self-Contained Underwater Breathing Apparatus
SE	Standard Error
SEA	Standard Ellipse Area
TA	Total Area of the Convex Hull
tf	Turf algae morphotype
UV	Ultraviolet
wc	Water column feeding
WNP	Wakatobi National Park

1 Chapter 1: General introduction

1.1 The habitat

1.1.1 Description

The central theme of this thesis is based on shallow tropical and temperate Mediterranean reef habitats, defined as marine habitats of hard substrate, including carbonate reefs in tropical and rocky reefs in the Mediterranean Sea (Figure 1). The overall benthic community composition of these habitats is greatly influenced by the slope of the bottom and the nature of the substrate, with horizontal and gently sloping substrates often dominated by corals, macroalgae and/or seagrass beds (Pequegnat, 1964; Bertness, Gaines and Hay, 2001). In the tropical regions, shallow, well lit, horizontal and sloping surfaces of hard substratum are often dominated by scleractian coral cover (Witman, 1992). Scleractian corals are rare in the temperate Mediterranean and the high light, horizontal and gently sloping environments of these regions tend to be inhabited mainly by erect and turf macroalgae and seagrass beds (Dayton, 1985; Margalef, 1985; Sales and Ballesteros, 2009).

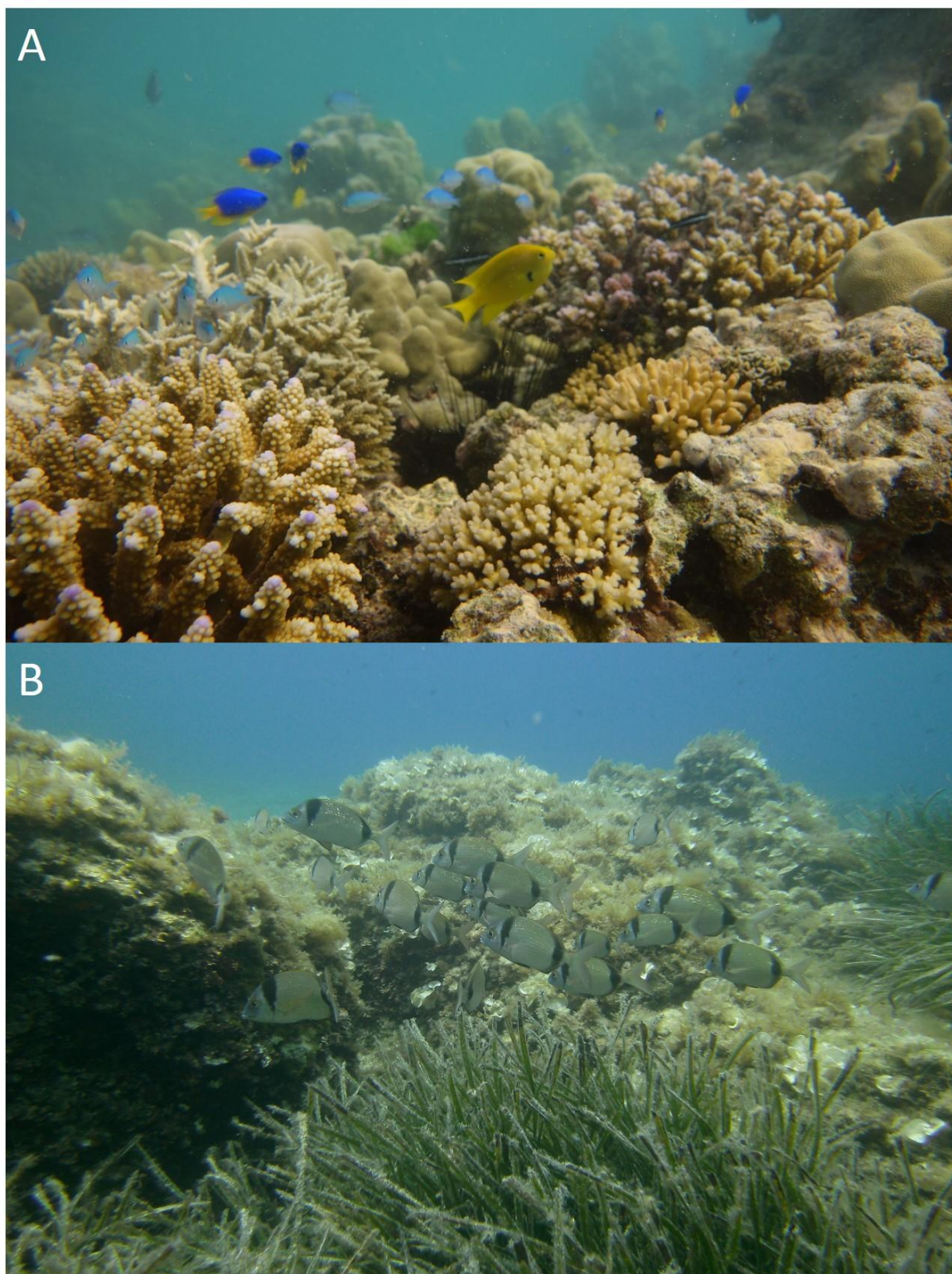


Figure 1: Biological reefs, creating complex habitats which provide organisms with numerous niches and refuge from predation; A) Indo-Pacific coral-dominated tropical and B) Mediterranean algal-dominated temperate reef (photos by A Gouraguine from thesis' sampling sites).

Coral reefs, also known as the “rain forests of the sea,” are among the most biologically rich and productive ecosystems on earth (Burke *et al.*, 2011). They are the world’s largest

biogenic structures and first appeared over 3.5 billion years ago (Wood, 1998). The structure of the reefs is formed through long-term build-up of calcium carbonate excreted by coral polyps living in colonies (Burke *et al.*, 2012). Reef-building corals can be found in areas with suitable light conditions and high salinity, in tropical coastal areas, thriving where sediment loading and freshwater input is minimal (Duraiappah *et al.*, 2005). Coral reefs are widely distributed in the tropical Atlantic, Pacific and Indian oceans, located between approximately 30°N and 30°S, where the minimum sea surface temperature does not fall below 18°C (Done *et al.*, 1996). They are characterised by a wide range of forms of different biological composition, diversity and structural organization, occurring as atolls, fringing, barrier or patch reefs. (Duraiappah *et al.*, 2005). A number of islands in the Pacific and Indian oceans, as well as the Caribbean Sea have reef systems which can combine all reef types.

The Mediterranean Sea, unlike many other temperate seas, is characterised by extremely reduced tides, oligotrophy, high salinity and high mean summer temperatures (Margalef, 1985). The shallow reef habitats of the Mediterranean tend to be dominated in cover by algae, specifically those of the genus *Cystoseira* (Fucales) (Sales and Ballesteros, 2009). The abundance of *Cystoseira* is determined by multiple factors, including sea urchin grazing, coastal development and water quality, and historical and current fishing pressure (Gianni *et al.*, 2013). Although also found in the Atlantic, the genus *Cystoseira* is especially diverse in the Mediterranean, where over 50 species of this genus are observed (Sales and Ballesteros, 2012). Different species are found in different habitats, depending on their depth, degree of exposure to wave action, and other environmental factors (Sales and Ballesteros, 2009).

1.1.2 Coral and macroalgae roles and ecosystem services

Shallow tropical and temperate reef habitats produce more services relating to human well-being than most other systems, even those of much larger total areas (e.g. open oceans) (Duraiappah *et al.*, 2005). These ecosystems are responsible for food supply, numerous economic, biological, cultural and social benefits (Costanza *et al.*, 1997).

In tropical latitudes, corals create highly diverse habitats, capable of sustaining great biomass within their complex three-dimensional structure. While they cover less than 0.01 % (280 000 km²) of the world ocean surface area, coral reefs harbour approximately one quarter of all marine fish species along with numerous other life forms (mollusks, crustaceans, sea urchins, starfish, sponges, tube-worms), totalling in excess of 1 million species (Alevizon *et al.*, 1985). Coral reefs provide ecological services which act as life support systems to society. They produce a variety of seafood products including fish, crustaceans, mussels, sea cucumbers and seaweeds (Burke *et al.*, 2011). As a result, catches from reef fisheries make up around 10% of the global fishery catch (Smith, 1978), while in many parts of the Indo-Pacific the reef fishery constitutes up to 25% of the total catch (Cesar *et al.*, 1997). Over 100 countries have coastlines with coral reefs in which the reefs sustain the livelihood of tens of millions of people (Burke *et al.*, 2011). Coral reefs also provide many local communities with coastal protection, from currents, waves and storms, without which there is loss of land due to erosion (Moberg and Folke, 1999). In Indonesia for example, it has been estimated that between US\$ 820 – 1 000 000 per km of coastline was lost due to reduced coastal protection as a consequence of coral destruction (Cesar *et al.*, 1997). In addition to protecting the existing, coral reefs build up new land, creating islands inhabited by large human populations, especially in the Indian Ocean and the Pacific (Moberg and Folke, 1999). The recreational value of coral reefs is enormous and results in billions in income from tourism

(Burke *et al.*, 2011). Coral reefs hold also aesthetic, medicinal and cultural values (Smith, 1978).

In temperate zones, many macroalgae species are regarded to be among some of the most important marine ecosystem-engineers, forming extended canopies, comparable in physical structure to land forests (Gianni *et al.*, 2013). Containing “only” several hundred species, temperate reefs are less biodiverse than coral reefs, however they are highly productive and their biomass can attain several kilograms per square meter. Benthic macroalgae, dominating temperate reef habitats, are important ecosystem engineers, providing structural base for many coastal habitats and associated food webs (Orfanidis, Panayatidis and Stamatis, 2001). They have been estimated to contribute to 10% of the world's marine primary production (Charpy-Roubaud and Sournia, 1990). These habitats harbour large numbers of invertebrates which in turn offer a valuable food source to many commercially and otherwise important fish species. Further economic value of the algal-dominated temperate reefs is their high potential as sources of chemical compounds with wide medicinal and industrial uses, as well as harvest or cultivation of algae for human and animal food and fertilizers (Salomidi *et al.*, 2012). Temperate reef macroalgae often serve as bioindicators of water quality, as they integrate and respond predictably and rapidly to nutrient pollution and other environmental impacts (Orfanidis, Panayatidis and Stamatis, 2001). Furthermore, reflecting anthropogenic stress, they are also used in long-term environmental quality monitoring studies (Sales and Ballesteros, 2009). Many algal species found on temperate rocky reefs have been characterised as highly efficient in removing CO₂, nutrients, and heavy metals from the seawater (Salomidi *et al.*, 2012).

1.1.3 Threats

Despite their importance, shallow tropical and temperate reef habitats and the services they provide are becoming increasingly vulnerable (Duraiappah *et al.*, 2005). These habitats are subject to a wide range of impacts which are substantially contributing to their damage.

Geographically, the most wide-spread consequences of impacts are those caused by global climate change and ocean acidification (Duraiappah *et al.*, 2005; Harvell *et al.*, 2008; Boyd, 2011; Frieler *et al.*, 2013; Riebesell and Gattuso, 2015; Hughes *et al.*, 2017, 2018). As the rates of warming and acidification are likely to increase in the future, the related impacts are also expected to rise (Houghton *et al.*, 2001; Hoegh-Guldberg *et al.*, 2007). The increase in sea surface temperature and ocean acidification of the world's seas degrades shallow water ecosystems and affects the habitat building species in a number of ways: it changes relative sea level faster than most organisms can adapt to (Nicholls and Cazenave, 2010); causes stress, followed by deterioration and susceptibility to disease, to temperature-sensitive organisms, including corals, algae and seagrasses (Duraiappah *et al.*, 2005) and reduces the rate of calcification of marine organisms, such as reef-building corals (Raven *et al.*, 2005). Corals are highly sensitive to changes in temperature and during unusually warm conditions they exhibit a stress response known as bleaching, resulting in complete loss of the algal symbionts living within the coral (Hughes *et al.*, 2003; Baker, Glynn and Riegl, 2008; Spalding and Brown, 2015). Prolonged absence of the symbiotic algae leads to high levels of coral mortality and subsequent breakdown of their structure (Glynn, 1984; Berkelmans *et al.*, 2004). Mass bleaching of corals, caused by increased sea surface temperature is becoming more frequent, more intense and more widespread, as abnormally high temperatures keep recurring (Glynn, 1993; Hoegh-Guldberg, 1999; Eakin, Lough and Heron, 2009). Severe or prolonged bleaching events can kill corals, while less extreme

events are likely to affect their immune response, leaving them prone to disease and can, in addition, reduce corals' growth rates and reproductive potential (Burke *et al.*, 2012). The rising temperatures also affect macroalgal species across various biogeographic regions (Koch *et al.*, 2013). Many macroalgae are characterised by relatively low thermal tolerance and are growing closer to their thermal limits, making them highly vulnerable to climate warming (Berry and Raison, 1981). Sustained elevated temperatures are likely to reduce their distribution and may result in replacement by different organisms, which are better adapted to high temperatures (Koch *et al.*, 2013). In the coming decades it is expected that rising sea temperature will significantly affect the survival and distribution of many macroalgal species (Sarà *et al.*, 2014). The result of these impacts, for both coral and temperate reefs, will be less diverse communities and habitat structures that fail to be maintained (Harvell *et al.*, 2008).

Locally, benthic communities of shallow tropical and temperate reef habitats are threatened by a number of disturbances; with habitat destruction, declining water quality and damaging fishing practices emerging as the greatest threats (Airoldi and Beck, 2007; Halpern *et al.*, 2007; Airoldi, Balata and Beck, 2008; Burke *et al.*, 2011). Habitat destruction and reduced water quality are underpinned by coastal construction, which causes sedimentation, terrestrial runoff and direct loss of the shallow water benthic habitats in many areas of the world, as well as changes in coastal processes maintaining these ecosystems (Richmond, 1993; Duraiappah *et al.*, 2005). Damaging fishing practices locally affecting benthic shallow water marine habitats include the use of destructive fishing gear and poison (Duraiappah *et al.*, 2005). For coral reefs, the two common forms of destructive fishing damaging the coral involve the use of explosives (bomb fishing) and cyanide (Mcmanus, Reyes and Nañola, 1997). They significantly contribute to coral reef destruction in many countries or island dependencies (Allen and Werner, 2002). Bomb fishing is used worldwide on coral reefs in

at least 40 countries (Mcmanus, Reyes and Nañola, 1997) and is believed to be one of the most important causes of reef destruction in South East Asia (Yap and Gomez, 1985). Cyanide, causing significant damage to the coral, is used illegally to capture fish in at least 15 countries or dependencies (Mcmanus, Reyes and Nañola, 1997). Furthermore, the damage due to anchors associated with a variety of reef fishing methods is prevalent in most countries with coral reefs (Burke *et al.*, 2011). Destructive fishing techniques are also thought to be, in part, responsible for the continuing decline of canopy-forming macroalgae, posing serious threats to the future of rocky reefs in general (Tudela, 2004). For example, despite the legal ban, the collection of the date mussel *Lithophaga lithophaga* by use of hammers and chisels, pneumatic hammers and explosives is still a common practice in most Mediterranean countries (Airoldi and Beck, 2007). This practice causes the loss of canopy-forming algae and the formation of barrens, directly and irreversibly destroying the rocky environment (Tudela, 2004). The alteration of both, coral- and algal-dominated habitats, over long periods through destructive practices reduces the biodiversity of these systems, ultimately resulting in losses based on the intrinsic value of individual taxa and in further losses of ecosystem services (Duraiappah *et al.*, 2005).

The intrinsic value of species is often based on opinions and the rationale for protecting biodiversity based on its intrinsic worth is generally not considered a scientific issue. On the other hand, the impact of species loss on ecosystem function can be measured using scientific testing and experimentation (Rosenfeld, 2002). As a result, the loss of ecosystem services resulting from the accelerated loss of biodiversity has become one of the main concerns in ecology (Loreau *et al.*, 2001; Hooper *et al.*, 2005). It has since been recognised that the assurance of long-term functioning of ecosystems depends on the number of species providing unique functions to the ecosystem (Rosenfeld, 2002). The loss of certain species can thus dramatically change the functioning of ecosystems through the alteration of

functional diversity (Petchey and Gaston, 2006). Many species can however have very similar functional roles and support the same or similar ecological functions. Those species, playing the same functional roles in ecosystems, termed functional redundancy, are key to the resilience of ecological processes when strong disturbances deplete or remove species from communities (Brandl and Bellwood, 2014). The impact of the loss of species on ecosystem function depends on the degree of redundancy in the species' functional roles and can range from profound to minimal. If many species perform the same functions, the impacts on the ecosystem functioning are reduced, compared to when the functions are supported by one or few species (Petchey and Gaston, 2006; Villéger, Novack-Gottshall and Mouillot, 2011). As the threats to shallow water reef habitats continue to grow, depletions of individuals and species from these communities will continue to occur. The losses may in turn have significant consequences for functional diversity and the ecosystem services provided by these habitats.

1.2 Fish community

There are many views on how habitat degradation and subsequently loss of benthic biodiversity will affect the function of shallow marine habitats and their service provision (Gray, 1997; Paulay, 1997; Bianchi and Morri, 2000; Worm *et al.*, 2006; Halpern *et al.*, 2008; Thrush and Dayton, 2010). Although service provision is well studied, the factors that drive and maintain the ecological services provided by these habitats are generally poorly understood and the studies concerning the issues are relatively scarce (Rozas and Odum, 1988; Birkeland, 1997; de Groot *et al.*, 2010; Selig and Bruno, 2010).

While global and local stressors directly affect habitat-forming organisms, such as corals, algae and seagrasses in the tropics and temperate regions, a number of studies indicate that fish communities, due to their relationship with the habitat, are also showing dramatic

changes (Carr, 1989; Halford *et al.*, 2004; Jones *et al.*, 2004; Graham *et al.*, 2006; Wilson *et al.*, 2006).

The habitat created by reef forming organisms of shallow seas plays a central role in shaping fish communities, with structural features providing shelter from physical stress and foraging predators and competitors, and changing the availability of resources and their rate of acquisition (Carr, 1989; Safriel and Ben-Eliahu, 1991; Garcia-Charton and Pérez-Ruzafa, 1998). Thus, these habitats increase survivorship by providing fish with refuge from predation, as well as offer more potential niches to be utilised (Hixon & Beets 1989; Sogard 1989; Beukers & Jones 1997) (see Figure 1). The reef also provides habitat for a biodiverse invertebrate assemblage, many species of which represent food resources for fish (Schiel and Foster, 1986; Friedlander and Parrish, 1998; Thibaut *et al.*, 2005). According to this, the abundance and distribution of many fish species are greatly determined by the habitat available (Kopp *et al.*, 2010).

Previous studies demonstrate that overall, shallow tropical and temperate reef habitats support high fish species abundance, diversity and biomass (Schiel and Foster, 1986; Hixon and Beets, 1989; Reñones *et al.*, 1997; Friedlander and Parrish, 1998; García-Charton and Pérez-Ruzafa, 2001; Garcia-Charton *et al.*, 2004; Gratwicke and Speight, 2005). A wealth of data also exists on how changes in reef habitat benthic composition, including loss of live benthic cover and changing structural complexity, affect fish assemblages (e.g., Paddack *et al.*, 2009; Coker *et al.*, 2014). However, many studies only look at the short term response and examine selected taxa in one habitat type, with final outcomes often opposed and inconsistent with limited conclusions being made regarding the relationship between habitat and associated fish community. For example, there is opposing evidence that physical properties of the reef substratum type have strong positive (Garpe and Öhman, 2003) and

limited influence on the diversity and abundance of fish (Roberts and Ormond, 1987). Similarly, biological nature of the substratum was also found to have both positive (Bell & Galzin 1984; Sano *et al.* 1984; Schiel & Foster 1986; Bell & Galzin 1988; Charton & Ruzafa 1998; García-Charton & Pérez-Ruzafa 2001) and poor influence on fish diversity and abundance (Luckhurst and Luckhurst, 1978). Thus, despite increasing evidence that these habitats influence local assemblages of fishes, our knowledge of how assemblage structure changes with variation in particular microhabitat features is comparatively limited (Holbrook, Brooks and Schmitt, 2002).

As shallow water tropical and temperate reef ecosystems are complex, and the impacts on them vary, a better understanding of the interaction between changing habitats and the associated fish communities, over larger temporal and spatial scales, are essential for future research. The importance of habitat structure in driving and maintaining biodiversity is a key ecological question directly relevant to conservation and future management of marine systems. Thus, the knowledge on processes underlying fish distribution within these habitats, their partitioning and selection is essential in order to understand patterns of the association between the fish community and the habitat. As a result, subsequent sections review and identify gaps in the existing information and highlight the need for further research of these interactions.

1.3 Long-term habitat change

As the current research has been mainly inconsistent and short-term, in order to better understand how habitat drives fish structure, further observations of ecosystem change, over larger time scales are necessary. The effect of habitat change over time could indeed be more substantial and driven by processes such as loss of the physical matrix or changes in the physiological condition of fish following the degradation of the habitat (Pratchett *et al.*,

2004; Graham *et al.*, 2006). However, due to many difficulties in establishing research projects covering ecosystem change over time, the effects which long-term changes in habitats have on the structure of fish communities are poorly understood (Madduppa *et al.*, 2012). Empirical data necessary to gain insight into the impacts that disturbances on shallow water tropical and temperate reefs are having on the associated fish communities is lacking (Magurran *et al.*, 2010; Galzin *et al.*, 2016). With universally accepted predictions of large-scale degradations of these habitats in coming decades, long-term observation data is of particular interest in order to determine adequate future management practices (Duraiappah *et al.*, 2005). Within this context, to conserve tropical and temperate shallow water reef ecosystems through time, a significant improvement in the understanding of long-term changes affecting fish-habitat relationships and their capacity to recover from disturbance is imperative. To achieve this, we must rely on and ensure robust, long-term datasets, which are generally uncommon and seldom available in many regions of the world (Magurran *et al.*, 2010; Mieszkowska *et al.*, 2014).

1.4 Habitat use

The influence of habitat on organism distribution has been a long-term focus in ecology, with many studies reporting species-specific habitat associations (Jones, 1991; Nanami *et al.*, 2005). Alteration of habitats can result in decrease of ecosystem services, while the subsequent change in the associated community has the potential to impact ecosystem function (Schlapfer, Schmid and Seidl, 1999). With widespread factors affecting fish communities, a large amount of research has been focused on understanding how changes in fish communities may affect ecosystem functioning and resulting ecosystem services (Loreau *et al.*, 2001; Hooper *et al.*, 2005). However, in order to predict how ecosystems and their functioning will evolve with changing fish communities, knowledge about processes

underlying the use and partitioning of the very habitats is necessary. Globally, surprisingly, there are very few empirical studies quantifying fish species' niches and evaluating their ecosystem function based on these measurements (Hooper *et al.*, 2005; Petchey and Gaston, 2006; Villéger, Novack-Gottshall and Mouillot, 2011).

Measurements of a fishes' ecosystem function can be obtained empirically, by conducting field observations, estimating the size of the space (realised niche) occupied within a functional hyperspace (fundamental niche) (Brandl and Bellwood, 2014). The realised niche size of the species studied can subsequently also be used to infer the degrees of the functional overlap between individual species within a community (space shared between species in the functional hyperspace) (Brandl and Bellwood, 2014). Thus, the empirically measured species' niche, and degree of the niche overlap between species in the community, will likely determine the effects which loss of species would have on the ecosystem considered. According to theoretical models in ecology, ecosystem functioning is determined by fish community species richness, the abundance of generalist or specialist species within each functional group, and the degree of saturation of functional space (Lawton and Brown, 1994). At present however, there is paucity of information on whether the same principles apply across different ecosystems and communities (Rosenfeld, 2002).

1.5 Fish habitat selection

Settlement and post-settlement processes play a fundamental role in the maintenance of adult fish populations in the marine environment (Jones, 1991; Hixon, 1998). After spawning and fertilisation of eggs the surviving larval stages of most demersal species of fish generally remain in the water column to complete part or the entire larval development phase (Hannan and Williams, 1998; Jenkins, Keough and Hamer, 1998). During this pelagic stage, larvae are dispersed by currents, followed by settlement onto a benthic habitat and subsequent

development into juveniles (Thresher, Colin and Bell, 1989). Several factors determine how suitable the habitat is for the newly settled juveniles, because once settled they face a number of challenges. In order to ensure future recruitment into adult populations, fish must be able to find food, successfully compete with other organisms and avoid predation within the settlement habitat (Beck *et al.*, 2001). Accordingly, locating microhabitats in which those processes are optimised, as well as the ability to successfully disperse to other habitats in subsequent life stages, is highly advantageous in terms of the growth and survival (Igulu *et al.*, 2011). Thus, fish fitness and survival partly depend on the ability to acquire information from the environment in order to orientate toward the most suitable habitat. In the ocean, this information can be acquired through a number of environmental cues which subsequently guide a fish through different habitats with the aim of reaching those optimised for survival (Cardona, 2000; Huijbers *et al.*, 2012).

Guidance mechanisms which rely on the detection of environmental cues, and thus facilitate successful movement between locations and habitats, may utilise acoustic, visual and chemical cues via specifically adapted sensory systems (Staaterman, Paris and Helgers, 2012; Paris *et al.*, 2013). A number of studies have identified the attraction of fish to biological reef noise (Leis *et al.*, 2003; Simpson *et al.*, 2004). In addition, it has been discovered that different components of the acoustic signature of a reef are important at different life stages, suggesting that the stimulus may also change with ontogeny. Juveniles and adults are attracted to low-frequency fish sounds (Simpson *et al.*, 2008), while the settlement stage fish respond to the higher frequency invertebrate crackle (Simpson *et al.*, 2004). These auditory cues can be detected at long distances, highlighting their importance in guiding directional movement towards a habitat (Simpson *et al.*, 2010; Radford *et al.*, 2011). On the other hand, visual cues are used by fish over short distances for microhabitat selection during settlement, and to some extent over the subsequent demersal life cycle for

foraging, reproduction and anti-predator behaviour (Guthrie, Muntz and Pitcher, 1993; Igulu *et al.*, 2011). The use of the visual sensory system is of particular importance in areas of high water transparency (McCormick and Manassa, 2008).

1.5.1 Chemical cues and habitat selection

Habitat selection, including predator avoidance, directed searching and prey location beyond visual range, is possible through chemical detection using the olfactory system (Atema, 1980). Many studies suggest that olfaction may be the most important cue for locating habitats over both, large and small spatial scales (Baird, Johari and Jumper, 1996; Dittman and Quinn, 1996; Lecchini, Planes and Galzin, 2005). The olfactory system in fish is highly sensitive and is, in terms of organisation, similar to that of the higher vertebrates, with some species having the ability to sense chemicals in the water at concentrations as weak as 10^{-9} M (Hara, 1992).

Throughout the last decade, a number of studies have been published addressing the topic, and despite this effort, the question whether olfactory mechanisms are critical in habitat selection remains under – researched (Coppock, Gardiner and Jones, 2013). On the other hand, bio-chemical research into fish detection and discrimination between chemical cues is extensive. The many compounds involved have been known for a long time and range from simple amino acids to complex mixtures of molecules from both biological and environmental origin. Compounds such as pheromones, peptides, amino acids, proteins, lipids and several other products of decomposition have been identified among the important ones (Hara, 1992; Derby and Sorensen, 2008). Other compounds which can be detected and may produce a response in fish include mannitol from algae, tannins from terrestrial plants and anthropogenic pollutants including industrial waste, sewage and insecticides (Kingsford and Gray, 1996; Dixon, Munday and Jones, 2010; Havel and Fuiman, 2015). Factors

influencing chemical stimuli distribution vary spatially and temporally, dependent on environmental events and biology of organisms (Kingsford *et al.*, 2002). Oceanographic features influence the concentrations of chemical stimuli and the directional information that the stimuli provide, often corresponding to the specific ecosystem. Fish olfaction can provide information on the identity of the water mass encountered when there is a lack of other stimuli. For example, the ability of larval fish to process information once a signal is recognised is dependent on the frequency of the encounter with the patches of chemicals and the concentration of the chemical cue (Vergassola, Villermaux and Shraiman, 2007). Fish select qualitatively different habitats for particular factors such as reproduction, foraging and predator avoidance and will display a preference for habitats which will benefit them during key life stages (Arnold and Targett, 2002). Studies by Atema *et al.* (2002) and Dixson *et al.* (2008) tested orientation preference according to water mass and discovered that larval fish are able to discriminate between different reefs on the basis of water-borne chemical cues. Fish are also able to respond to specific chemical signals from coral tissue and conspecifics, symbiotic partners and predators (Sweatman, 1983; Arvedlund *et al.*, 1999; Lecchini *et al.*, 2005; Lecchini, Planes and Galzin, 2005).

Once settled, the ability of fish to sense both beneficial and detrimental olfactory cues is critical to survival. An aversion to disadvantageous habitats, such as those with high presence of predators, or a selection for optimal conditions, as seen in attraction to refuge and prey cues, will further an individual's chances of reaching sexual maturity, (reviewed by Kingsford *et al.* 2002). Whilst over the last decade there has been an increase in fish olfactory-based research, there is still a limited number of studies on the use of olfactory cues in habitat selection, with the focus of the research being mainly on tropical fish species. In addition, most olfactory habitat selection studies focused on larvae and adults, while juvenile life stage behaviour is poorly understood (Gouraguine *et al.*, 2017).

1.6 Conservation

All of the stressor-driven effects on the functioning of shallow tropical and temperate reef ecosystems highlighted here are likely to increase in the future (Harborne *et al.*, 2017). As a result, the ability to maintain critical ecosystem properties will be seriously threatened (Hughes *et al.*, 2003). Following the alteration, it is highly uncertain whether these ecosystems will be able to continue to provide key ecosystems services (Moberg and Folke, 1999). As degradation and decline of shallow tropical and temperate reef ecosystems continue, there is much emphasis to establish effective conservation strategies that will ensure continued survival and future service provision. Despite global ubiquity and numerous efforts however, it is well known that up to date, marine conservation management is often opportunistic, utilising precautionary principles with limited direct strategic approaches being applied (Pomeroy *et al.*, 2005). Many studies argue that measures addressing declines in the condition of coastal systems are currently ineffective and are commonly too few and too late (Duraiappah *et al.*, 2005).

Effective coastal area management requires a) integration and coordination of activities across many separate sectors, b) consideration of interspecific interactions across a range of habitats, c) knowledge of how changes to habitat structure drives key fish community characteristics and services provided from that system so that management benchmarks and performance criteria can be identified (Agardy, 2000). Traditionally, as a result, areas prohibiting the exploitation of marine organisms have been established in a variety of marine habitats (Rowley, 1994; Bohnsack and Ault, 1996). Following the establishment, studies generally focused on the locally isolated effects of protection and lack comparisons across regions (Roberts and Polunin, 1991; Rowley, 1994). The success of conservation effort is commonly measured by the difference in densities of the organisms found inhabiting the

protected area and the densities of the organisms found in the ecologically similar sites in the nearby affected areas (Jones *et al.*, 2004; Selig and Bruno, 2010). These comparisons however, do not take into the account other factors affecting the distribution of the marine organisms, including differences in habitat quality between the two areas (Polunin and Roberts, 1993; Burke *et al.*, 2011). The abundance of the organisms within a habitat is often directly related to the variation in characteristics of the environment, including topographic complexity (Luckhurst and Luckhurst, 1978) and the live benthic cover itself (Bell and Galzin, 1984; Carr, 1989). Whenever possible, quantification of the effect of protection on communities should include controls for both temporal and spatial distribution (Russ and Alcala, 1996), as well as the effect on local and regional scales (Bertness, Gaines and Hay, 2001). Policymakers, agencies and managers in charge of protecting shallow tropical and temperate reef ecosystems need more effective ways to minimise the decline and aid their recovery (Hoegh-Guldberg *et al.*, 2007). Ultimately, such solutions must include biological aspects which drive the ecosystems in question (Hughes *et al.*, 2005). Without a better understanding of these aspects it is difficult to determine the most appropriate practices and goals for management (Agardy, 1994). For management to move forward, it must integrate the scientifically relevant information, and adapt efforts toward the evolving best practices. To enable a more strategic and targeted approach to management, particularly as it concerns the conservation of extremely important ecosystem services to humankind, approaches and policies need to be supported by an understanding of how biodiversity and productivity is partitioned across the habitat. Thus, an understanding of the interaction between benthic features and the surrounding community is essential for present day, as well as future management approaches that must be aimed to best protect these systems.

There is now clear evidence of serious changes to the habitat structure and subsequent functioning of shallow tropical and temperate reef ecosystems across the globe. Basic

ecological research on ecosystem functional relationships needs to be expanded in order to broaden our understanding of the linkages between ecosystem functions and services. Therefore, for future research it is essential to integrate the findings of the effect of benthic habitat alteration on the corresponding animal community. In addition, the knowledge about the processes underlying the specific habitat partitioning and selection is essential in order to understand the patterns of the association between the animal community and the habitat.

1.7 Aims of the thesis

To address major ecological questions of the habitat driven responses of reef fish in tropical and temperate ecosystems, this thesis used a highly diverse mix of field and laboratory-based data, obtained over large temporal and spatial scales, from a range of different habitats. The main aims of the thesis were as follows:

- To understand how changes in benthic habitat composition influence the associated fish communities, using a long-term dataset and a highly biodiverse tropical reef environment as the model system (Chapter 2).
- To understand how habitat influences ecological interactions between fish species, within and across ecosystems, using empirical behavioural data to estimate the size of the habitat occupied and compare the habitat overlaps between species in tropical and temperate reef habitats (Chapter 3).
- To explore the mechanisms responsible for fish habitat selection and observe behavioural responses involved in olfactory selection and avoidance of certain habitats by conducting a series of laboratory experiments on juveniles of a common temperate reef fish species as the model organism (Chapter 4).

- To provide ecological significance of each of the results chapters individually, as well as their synthesis, and argue the ecological and conservational significance of the findings and the potential for future studies stemming from this research (Chapter 5).

2 Chapter 2: The effect of habitat change on the associated fish community in a tropical coral reef ecosystem

2.1 Introduction

In this chapter, using coral – dominated tropical reef as the model ecosystem, the importance of habitat for fish was investigated through observation of the effect which changing habitat had on the associated fish community.

While tropical coral reefs represent one of the most diverse marine ecosystems on Earth, they have also been most severely impacted by a milieu of natural and anthropogenic stressors, resulting in loss of coral, both globally and locally (Bellwood *et al.*, 2004). Declines in hard coral cover have been reported throughout the tropics, causing an alteration of the structure of the benthic habitat (Gardner *et al.*, 2003).

Globally, one the most threatening stressors to coral reef ecosystems is the climate-induced increase in sea surface temperature (SST), thermally stressing corals and often resulting in loss of photosynthetic algal symbionts (*Symbiodinium* spp.) living within the coral tissues (Hughes *et al.*, 2003; Baker, Glynn and Riegl, 2008; Spalding and Brown, 2015). The stress response is called coral bleaching, since it results in coral tissue paling, following the loss of the symbionts (Burke *et al.*, 2012). Prolonged absence of the symbiotic algae can lead to coral mortality and subsequent breakdown of their structure (Glynn, 1984; Berkelmans *et al.*, 2004). Thermally stressed corals can also experience a decreased immune response, which may benefit a number of coral pathogens leading to disease and further coral mortality (Raymundo *et al.*, 2007; Harvell *et al.*, 2008).

Beside climate induced coral bleaching, other impacts which affect coral – dominated habitats are related to the expanding coastal populations bringing about multiple local stressors, which combined inflict dramatic damage in a short period of time (Hughes *et al.*, 2003, 2017). In particular, the use of destructive practices, such as blast fishing, as well as sewage and industrial pollution and increased sedimentation, are considered to be the main causes of coral reef habitat degradation locally (Burke *et al.*, 2011).

Evidently, the change in habitat through the decline in coral cover has far reaching consequences for the associated fauna as well, in particular to fish communities (Jones *et al.*, 2004; Graham *et al.*, 2007). A number of fish species are highly dependent on the coral habitat providing them with food and shelter, thus suggesting a structural and biological association to the habitat (Plass-Johnson *et al.*, 2016). The death of coral following disturbance events can alter the composition of fish communities in the short-term by affecting species reliant on living corals as food resources (Bellwood *et al.*, 2006), while subsequent gradual loss of habitat complexity thorough coral skeleton breakdown can result in further and long-term ecosystem changes by affecting those species reliant on corals for shelter (Graham *et al.*, 2007). In addition, in early life stages, most reef fish settle and recruit directly to live coral habitat, demonstrating a high degree of the habitat association at some point in their life cycle (Jones *et al.*, 2004). Thus, the loss of habitat and its structural components may have direct ramifications on the size and recovery potential of future adult stocks (Halpern, Gaines and Warner, 2005).

The short-term effect of habitat change through coral degradation on the associated fish community has been investigated in a number of studies with somewhat opposing results. Several authors pointed to the resilience of reef fish to habitat disturbance, with the assemblages exhibiting only a limited response to the loss of corals (Hart and Russ, 1996;

Booth and Beretta, 2002). Other authors, on the other hand, reported significant changes in the community composition of many coral-associated fishes (Pratchett *et al.*, 2004), with some indicating that the declines in coral cover resulted in parallel declines of fish, both in density, as well as in the number of species (Halford and Caley, 2009).

In addition to the reported acute and local habitat alterations and its consequences for associated reef fishes from various regions (Alvarez-Filip *et al.*, 2015), there are also predictions for chronic and large-scale coral habitat degradation over the coming decades related to climate-induced change (Hoegh-Guldberg, 1999; Sheppard, 2003; Hughes *et al.*, 2017). Currently, however, there is a lack of long-term empirical data to explore how this coral habitat degradation will affect the associated fish communities (Wilson *et al.*, 2006). As a result, our knowledge of long-term habitat changes is at large rudimentary, yet understanding of the responses of entire fish assemblages to them is needed in order to determine appropriate conservation strategies (Galzin *et al.*, 2016). The lack of long-term data not only for coral reefs, but also for other marine habitats has long been recognized, highlighting the importance of the few existing datasets (Magurran *et al.*, 2010; Mieszkowska *et al.*, 2014). The shortage in long-term data series is often related to unsustainable funding and a lack of institutional commitment over long time periods (Mieszkowska *et al.*, 2014).

In this study, an 11 year long coral reef monitoring data set (2002–2012) was used, collected by a mix of experienced researchers and scientifically trained volunteer graduate assistants, from a previously poorly documented area of the Tukang Besi archipelago in the South-east Sulawesi, Indonesia. Coral reefs of Indonesia are known to be among the richest and most diverse in the world, for both corals and reef fish (Edinger *et al.*, 1998). These reefs are currently under enormous pressure from the dense human populations living in close

proximity, exploiting them unsustainably (Burke *et al.*, 2011). Within the present study, annual visual transect benthic habitat and fish surveys were carried out, thus documenting and describing the temporal change of the habitat and its associated fish community. Specifically, the temporal variation in the structure of the habitat benthic cover and its effect on the associated fish community as a whole, as well as specific families and number of fish species within families were investigated. It was hypothesised that i) over a decadal time scale, significant changes to habitat structure would occur, as a result of which; ii) fish community would suffer changes in abundance and species composition, however; iii) not all fish families and species within the community would be affected equally.

2.2 Materials and methods

2.2.1 Study site

Sampling took place on the coral reefs around the islands of Hoga and Kaledupa, within the Wakatobi National Park (WNP), located in the Tukang Besi archipelago, South-east Sulawesi, Indonesia (Figure 2). The park was established in 1996 and comprising surface area of 13,900km² is the one of the largest in Indonesia. With a resident community of around 100,000 people, WNP is the most populated in Indonesia (Clifton, Unsworth and Smith, 2010). WNP has historically been characterized by a lack of sufficient funding, ineffective enforcement, minimal community participation in management activities and inappropriate zonation of the park (Elliot *et al.*, 2001). Local people of the WNP are highly dependent upon coastal resources, with marine products being the most important protein source, resulting in widespread overfishing and unsustainable resource usage (Cullen *et al.*, 2007).

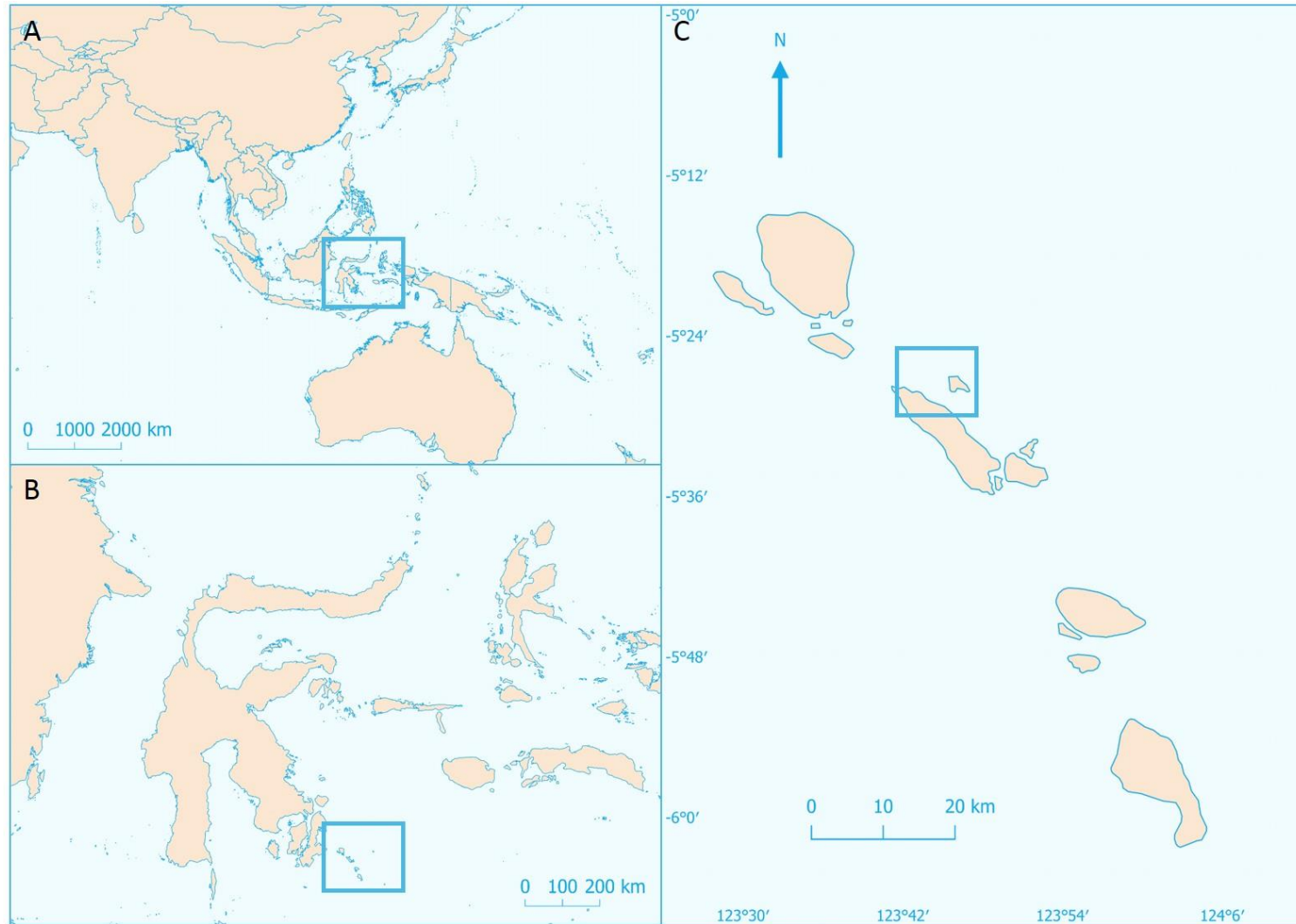


Figure 2: Sampling location. Boxed areas represent: A) Sulawesi, B) Wakatobi National Park, C) the monitoring area.

2.2.2 Sampling

A long-term monitoring program was implemented in the WNP in 2002 (Clifton, Unsworth and Smith, 2010). The data used in the study included the monitoring survey data gathered annually between June – August, from 2002 to 2012. Fifty-one 50 m permanent transects were established in the study area using a nested design, in replicates of three (except at one location where there was no reef flat habitat), on the reef flat (5m horizontal distance on the landward side from the reef crest), the reef crest and the upper reef slope (defined by habitat type and a depth of 10m). At the start and the end, permanent transects were marked with steel pickets and each transect was separated by a minimum distance of 20m. This arrangement facilitated the laying of measuring tapes along transects during surveys to act as a reference line. Transects were sampled annually for fish and benthos.

Data from a total of 495 transects sampled over the 11 year period were included in the analyses. Due to logistical constraints not all permanent transects established were sampled each year. In years 2004, 2006 and 2007 transect samples missed represented 49%, 33% and 22% of the total possible combinations of year by locations, respectively. For the remaining years in which transects were missed (2002, 2003, 2008 and 2009), they represented less than 10% of the total possible combinations. Overall, almost an identical number of transects was sampled for crest and slope habitats, while the flat habitat was represented by 27% less transects (Table 1).

Table 1: Total number of transects sampled per year and habitat type.

Year	Flat	Crest	Slope	Total
2002	15	17	14	46
2003	15	17	18	50
2004	5	11	10	26
2005	15	18	18	51
2006	9	11	14	34
2007	4	18	18	40
2008	12	18	18	48
2009	12	17	18	47
2010	15	18	18	51
2011	15	18	18	51
2012	15	18	18	51
Total	132	181	182	495

2.2.3 Temperature data and benthic habitat surveys

The study period encompassed El Niño–Southern Oscillation (ENSO) events. These events have been demonstrated to have a dramatic impact on the key coral types due to the associated sea surface temperature variations (Lindahl, Öhman and Schelten, 2001). Therefore, to investigate if any of the trends observed in benthic cover were related to high temperature anomalies, area-specific temperature information was obtained from the National Oceanic and Atmospheric Administration (NOAA) website (<https://www.nesdis.noaa.gov/>). Datasets containing Daily Optimum Interpolation Sea Surface Temperatures (OISST) and monthly means Extended Reconstructed Sea Surface Temperatures (ERSST) were downloaded. In order to consider the temperatures before, during and immediately after the sampling period, 20 yearlong datasets were downloaded (1996 – 2016). Using the OISST data, continuous temperature trend was plotted to demonstrate the temperature peaks which exceeded the coral bleaching threshold. ERSST data was used to test for thermal stress likely to cause coral bleaching by identifying the months, termed Degree Heating Months (DHMs), in which the coral bleaching temperature threshold exceeded the monthly temperature mean during the monitoring period. Whenever

positive temperature anomalies occur and these are above the coral bleaching temperature threshold for an extended period, they are often accompanied by bleaching. Temperatures in excess of the coral bleaching temperature threshold with an elevation of $+1^{\circ}\text{C}$ and sustained for a month suggest that potential bleaching activity is most likely underway (Strong *et al.*, 1997). Regional Virtual Station for South-east Sulawesi was used to provide information about the coral bleaching temperature threshold in the sampling area (Glynn and D’Croze, 1990).

Continuous Line Intercept Transect technique was used to assess the benthic habitat. The area intercepting the transect tape was classified according to the benthic category system from the methodology of English *et al.*, (1997). The percentage cover of each category was then calculated by dividing by the total transect length and multiplying by hundred. The cover was estimated for four broad categories; hard coral, soft coral, algae and abiotic category (including dead coral, rock, rubble and sand). The category, hard coral, was further separated into the following morphological categories: branching, massive, submassive, tabulate, foliose and encrusting (English, Wilkinson and Baker, 1997).

2.2.4 Fish surveys

Reef fish communities were assessed by underwater visual census (English, Wilkinson and Baker, 1997). The same transect used for benthic surveys was used for fish surveys. After laying the tape, the transect was given a wide berth and left for a minimum of 10 minutes prior to data collection, to allow fish to settle after the disturbance caused by the observers’ presence. Subsequently, the observer swam along the transect line over an approximately 25 minute period. All the fish sighted within 2.5m to each side and 5m above the transect were recorded and identified to species level. The sampling was conducted between the hours of 09.00 and 16.00, excluding the high activity periods of early morning and late afternoon,

thus reducing variability in fish densities due to diurnal influence on behaviour (Colton and Alevizon, 1981). A preliminary study in 2002 identified no significant differences in fish abundance between morning and afternoon, within the chosen sampling times (Clifton, Unsworth and Smith, 2010).

2.2.5 Monitoring participants and data treatment

Both, benthic surveys and visual censuses were conducted by a mix of experienced researchers and volunteer graduate assistants. Volunteers did not necessarily have previous diving and/or sampling experience. If the volunteers were not SCUBA proficient, they completed a PADI Open Water course at the local dive centre and then went on to the reef ecology course. The reef ecology course consisted of a week-long, location-specific reef course, combining classroom and field-based coral, macroalgae and fish identification tutorials. Volunteers were tested at the end of their training period and in order to participate in data collection they had to achieve a minimum of 90% test score. To improve data quality, volunteers' first identifications were cross-checked against experienced researchers.

Benthic data collected was of consistent quality as the surveys were based on easily distinguishable broad benthic categories. Conversely, the fish data recorded showed a much higher variability. This was related to the large number of fish species present and the difficulty of correctly identifying and counting these by a multitude of observers of different experience levels.

To reduce this observer-related variability, various data procedures for minimising the presence of any erroneous or false data were introduced. All the fish species which occurred in a single transect and did not repeat in previous or subsequent years were removed. These species amounted to approximately 35% of all the species reported, but had less than 1%

contribution to the total abundance. FishBase (<http://www.fishbase.org/>) was subsequently used to match the species' geographical distributions – if a species recorded had never previously been reported in the study area it was marked as a possible erroneous identification. All erroneously identified species were photographically compared to the species within the dataset with confirmed occurrences in the sampling area and their abundances were added to the physically most similar species of the same fish family. This mainly occurred with Pomacentridae, Scaridae, Labridae and Chaetodontidae species. The process reduced the number of species by further ~ 20%, however it preserved the overall abundance. Because of known problems with sampling (Ahmadi, Pezold and Smith, 2012), initial programme design did not include a number of small cryptic (e.g. Gobidae, Gobiesocidae, Scorpaenidae) and transient pelagic species (e.g. Scombridae), thus accidentally recorded species of these families were also removed; ~ 5% species, < 0.1% total abundance.

2.2.6 Statistical analysis

Pearson's correlation coefficient was calculated to test the associations between Year, Abiotic, Hard coral, Soft coral and Algae. The correlation coefficient was also calculated to test the relationships between Year, Massive, Submassive, Branching, Tabulate, Encrusting and Foliose hard coral morphotypes in different reef habitats (Crest, Flat and Slope).

To estimate to what extent fish community composition changed through time, nonmetric multidimensional scaling (MDS) was performed on non-transformed annual mean abundance data per year, using software PRIMER v6 (Clarke and Gorley, 2006). The data was not transformed due to the interest in capturing trends related to absolute abundances. The resulting ordination was tested for seriation i.e. if there was a statistically significant sequential pattern with consecutive years having a higher similarity compared to years

separated by longer time periods. Furthermore, a Simprof test was applied to ascertain if some years formed statistically significant clusters (year groups) due to their similarity in species composition. Stress value was used to indicate how faithfully the high dimensional relationships among the samples were represented in the two dimensional ordination plot (Clarke and Gorley, 2006). Furthermore, the similarity percentage analysis (SIMPER) was performed on significant year groups in order to determine which species characterised different groups and contributed most to dissimilarity, both with respect to contributions to average similarity within a group and average dissimilarity between groups (Clarke and Gorley, 2006). The routine was based on breaking down the Bray-Curtis dissimilarity between two samples into contributions for each species ($\delta \bar{i}$). This is a useful measure of how consistently a species contributes to $\delta \bar{i}$ across all pairs of samples is the ratio $\delta \bar{i}/SD$. When this ratio is larger, than the species not only contributes greatly to the dissimilarity between two groups but it also does so consistently in inter-comparisons of all samples in the two groups (Clarke and Warwick, 2001).

Poisson or negative binomial generalized linear mixed-effects models (GLMMs) were used to test the degree of influence of hard coral cover on the fish community abundance and species richness. Zero-inflated Poisson or zero-inflated negative binomial generalized linear mixed models (GLMMs) were used to investigate the relationship between hard coral cover and fish family abundance, as well as fish feeding guild abundance. For the fish families, if the relationship was statistically significant and the family had >1% community abundance contribution, species within the family were also tested for the hard coral cover – abundance relationship. Due to the large number of species within certain families, the relationships were tested for the most abundant species which together made up a minimum of 90% of the total family abundance contribution. The process allowed for exclusion of occasional and non-dominant species and representation of all other species with statistically significant

hard coral cover – abundance relationships. Zero-inflated GLMMs were chosen for these analyses as the zero inflation was evident in the transect data. Visual transect data of mobile fish inherently contain many zero observations. The non-detection of a species may in many circumstances be unrelated to the explanatory factor investigated and thus resemble false zeros. As an example, a fish with a generally high association to hard coral may, due its mobility, could have been missed because when the transect was surveyed, the species was swimming over a different part of the reef. The recorded zero value is thus false and does not capture the real relationship. Zero-inflated models provide the means to account for false or excess number of zero observations (Zuur *et al.*, 2009), thus providing a more realistic estimate in the relationship between coral cover and fish abundances. All GLMMs were random intercept models where the random factor was year. Through this modelling approach the dependence of transects sampled within the same year was taken into account (Zuur *et al.*, 2009). Selection between Poisson and negative binomial models was undertaken by calculating the Akaike's information criterion (AIC), based on the trade-off between model deviance and parsimony (Crawley 2007). All model data were analysed with the package glmmTMB and AIC calculations were carried out in bbmle package in the statistical software R (Bolker and Team, 2013; Brooks *et al.*, 2017; R Core Team, 2017).

2.3 Results

2.3.1 Temperature anomalies and benthic habitat

Both OISST and ERSST data revealed anomalies associated with high temperatures in the sampling area. South-east Sulawesi Coral Reef Watch Regional Virtual Station, indicates the temperature of 30.38 °C as the coral bleaching temperature threshold. According to the OISST data, a large number of the temperature points exceeded the bleaching threshold,

before, during and after the monitoring period (Figure 3). Using the ERSST dataset, during the monitoring, 3 years with DHMs were identified (2002, 2005 and 2006) (Table 2).

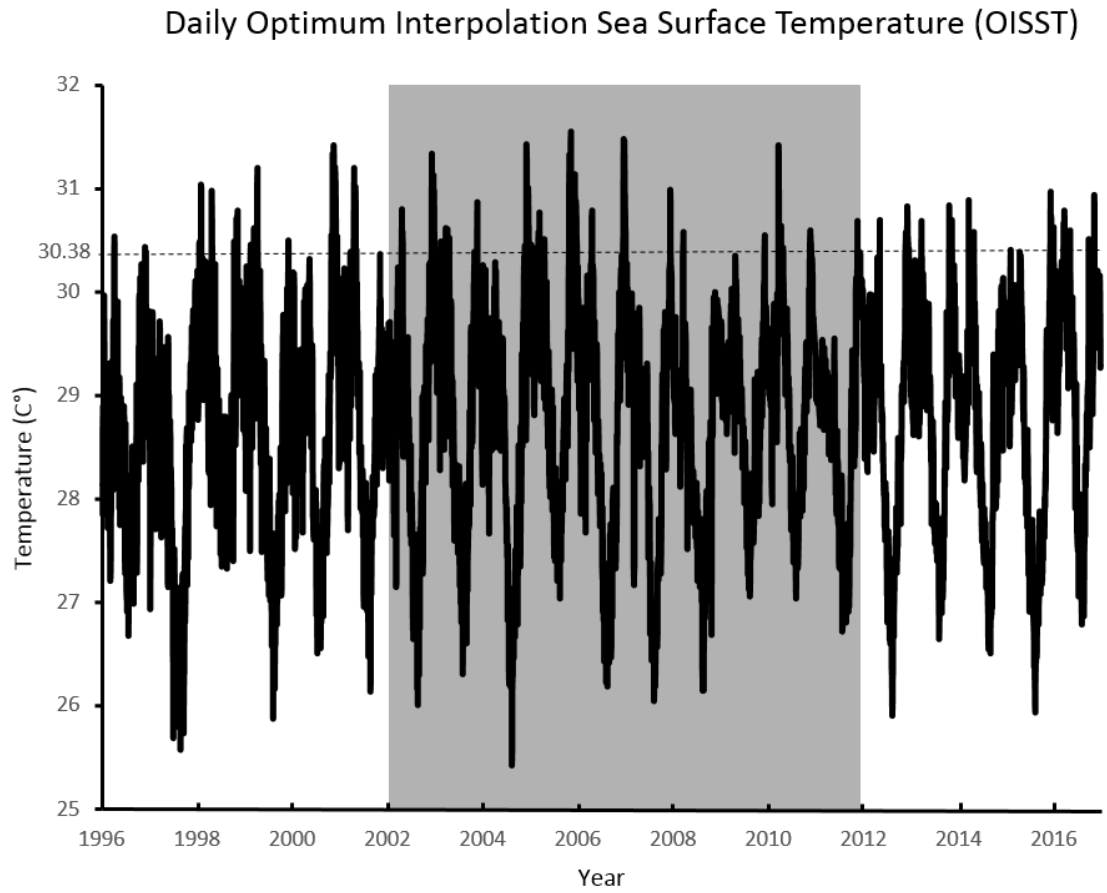


Figure 3: Daily optimum interpolation Sea Surface Temperature (OISST) trend from 1996 to 2016. Shaded area depicts the temperature trend during the monitoring period (2002 – 2012). Dashed line represents the coral bleaching temperature threshold for South-east Sulawesi.

Table 2: Extended Reconstructed Sea Surface Temperature (ERSST) data showing monthly temperature means and a number of months in which the coral bleaching temperature threshold was exceeded (DHM), for each year from 1996 to 2016.

Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	DHM
1996	28.66	28.52	28.57	29.47	28.44	28.34	27.35	27.71	28.11	29.38	29.76	29.31	0
1997	28.54	28.3	28.74	28.72	28.41	27.83	26.62	26.46	26.71	28.12	29.17	29.66	0
1998	29.68	29.62	29.39	29.4	28.86	28.47	27.93	28.09	28.2	29.27	29.9	29.28	0
1999	29.05	29.43	29.36	29.74	28.54	28.14	27.34	26.9	27.43	28.47	28.92	29.35	0
2000	28.79	28.7	28.76	29.61	29.44	28.11	27.11	27.39	28	29.2	30.65	29.41	1
2001	28.98	29.35	29.04	30.07	29.5	28.17	27.55	26.97	28.03	28.97	29.25	28.99	0
2002	29.12	28.38	29.16	29.92	28.87	28.48	27.38	26.85	27.69	28.84	29.6	30.42	1
2003	29.6	29.53	29.36	29.76	28.83	28	27.5	27.51	27.88	29.33	29.9	29.62	0
2004	29.4	28.84	29.06	29.42	29.12	28.74	27.1	26.45	27.27	28.27	29.6	30.2	0
2005	29.62	29.64	29.91	29.59	29.02	28.45	27.76	27.65	28.45	29.54	30.25	30.41	1
2006	29.18	28.9	29.24	29.95	29.14	28.3	27.3	26.62	27.24	27.79	29.4	30.44	1
2007	29.78	29.5	29.02	29.2	28.82	28.51	27.16	26.6	27.34	28.77	29.42	29.98	0
2008	29.13	28.94	29.29	28.97	28.55	27.91	27.61	26.94	27.55	28.38	29.42	29.62	0
2009	29.18	28.83	29.39	29.47	29.39	28.78	28.04	27.55	28.06	28.56	29.21	29.77	0
2010	29.22	29.26	29.84	30.15	29.48	28.68	27.83	27.6	28.29	28.9	29.93	29.82	0
2011	29.05	29.17	29.12	28.95	28.88	28.15	27.48	27.28	27.51	28.81	29.65	30.09	0
2012	29.3	29.28	29.21	29.83	29.31	28.03	27.07	26.63	27.67	28.41	29.6	30.14	0
2013	28.95	29.57	29.39	29.68	29.21	28.4	27.74	27.21	27.83	29.21	29.63	29.41	0
2014	29.06	28.71	29.4	29.77	29.25	28.5	27.72	27.13	27.34	28.23	29.35	29.6	0
2015	29.37	29.17	29.63	29.84	29.1	28.04	27.39	26.48	27.2	27.56	28.96	29.95	0
2016	29.97	29.53	30.27	29.93	29.82	28.85	27.69	27.39	28.6	29.21	29.93	29.89	0

The reefs in 2002 were characterised by high hard coral cover and low abiotic cover. Subsequently, annual surveys documented a continuous decline from the initial mean hard coral cover of 45.8% (SE±1.5%) in 2002 to a low mean of 14% (SE±1.1%) in 2012. The most notable changes were observed between 2004 and 2005, with 10.3% decline, and between 2007 and 2008, when mean hard coral cover declined by 8.5%. Overall, a decline of 69.3% in mean hard coral over the 11 year period, relative to the initial cover was evidenced. Conversely, over the same period the mean abiotic cover increased by 70.5%, from 19% (SE±2%) in 2002 to 63.4% (SE±1.7%) in 2012. Algae experienced an increase in mean cover from 16.4 % (SE±1%) in 2002 to 22.5% (SE±1.7) in 2006, followed by a gradual decrease to 4.9 % (SE±0.4%) in 2012. Mean cover of soft coral demonstrated little fluctuation and appeared to be relatively stable over the study period (Figure 4).

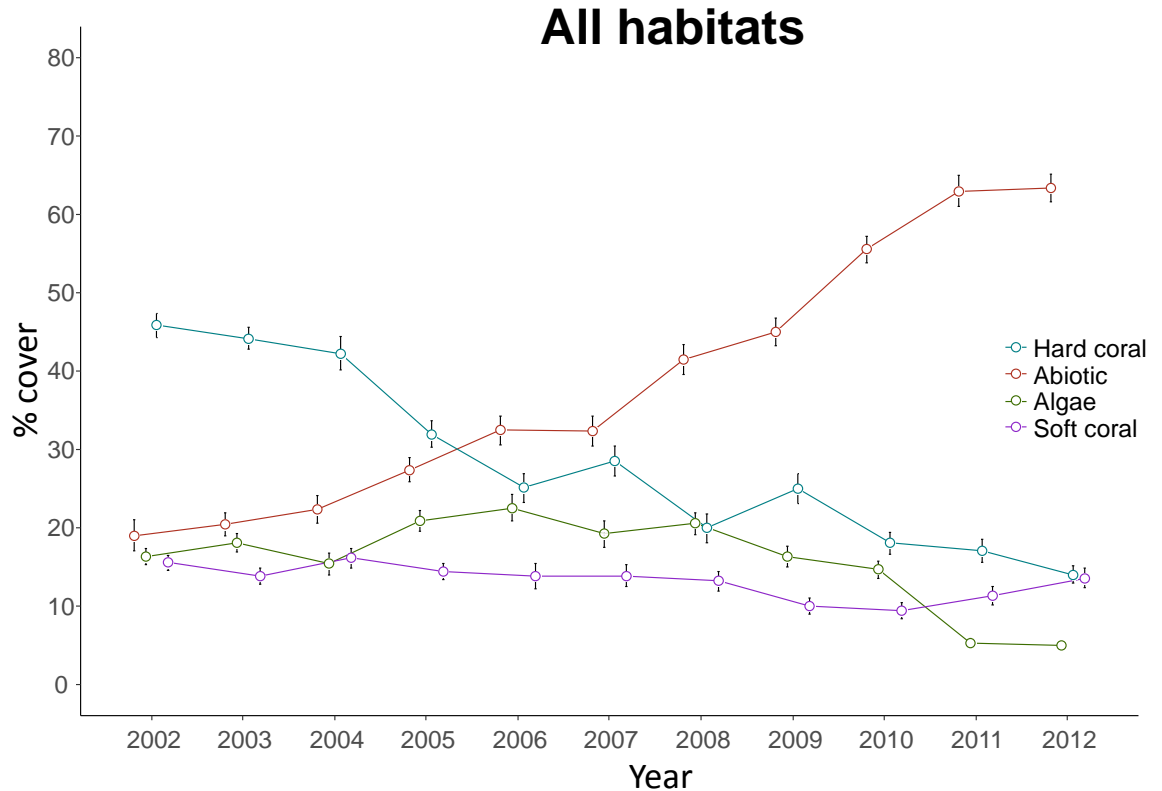


Figure 4: Changes in mean cover of the main benthic categories in all habitats combined over the 2002 – 2012 monitoring period (the vertical lines represents standard error). The total number of transects analysed by year and habitat was 495 (see Table 1).

Pearson's correlation analysis identified a number of statistically significant relationships between benthic habitat categories (Table 3). The correlation coefficients relating Year and Hard coral, as well as Abiotic and Hard coral were highly negative and statistically significant.

Table 3: Pearson's correlation coefficients between sample year and benthic categories for all habitats combined. The total number of transects analysed by year and habitat was 495 (see Table 1). Statistically significant relationships ($P < 0.05$) are marked with *.

All habitats				
	Year	Abiotic	Algae	Hard coral
Abiotic	0.79*			
Algae	-0.39*	-0.41*		
Hard coral	-0.68*	-0.80*	0	
Soft coral	-0.17*	-0.37*	-0.18*	0.09

For individual habitats, the mean hard coral cover on the reef flat varied between 42.2% (SE±3%) and 10.8% (SE±1.3%), reef crest had mean hard coral cover values between 47.2% (SE±2.1%) and 13.6% (SE±2.1%), while the mean values on the reef slope ranged between 48% (SE±2.7%) and 17.1% (SE±2%). Hard coral cover had a ubiquitous downward trend with strong decreases between 2004 and 2006. The abiotic cover increased gradually in all reef habitats over the course of the study period. Highly similar trends in change of algal cover were also observed in all three reef habitats. Finally, with the exception of the reef flat, where the soft coral cover increased between 2003 and 2004, before stabilising again at a lower value, similar habitat-related cover trends were also observed for this category (Figure 5).

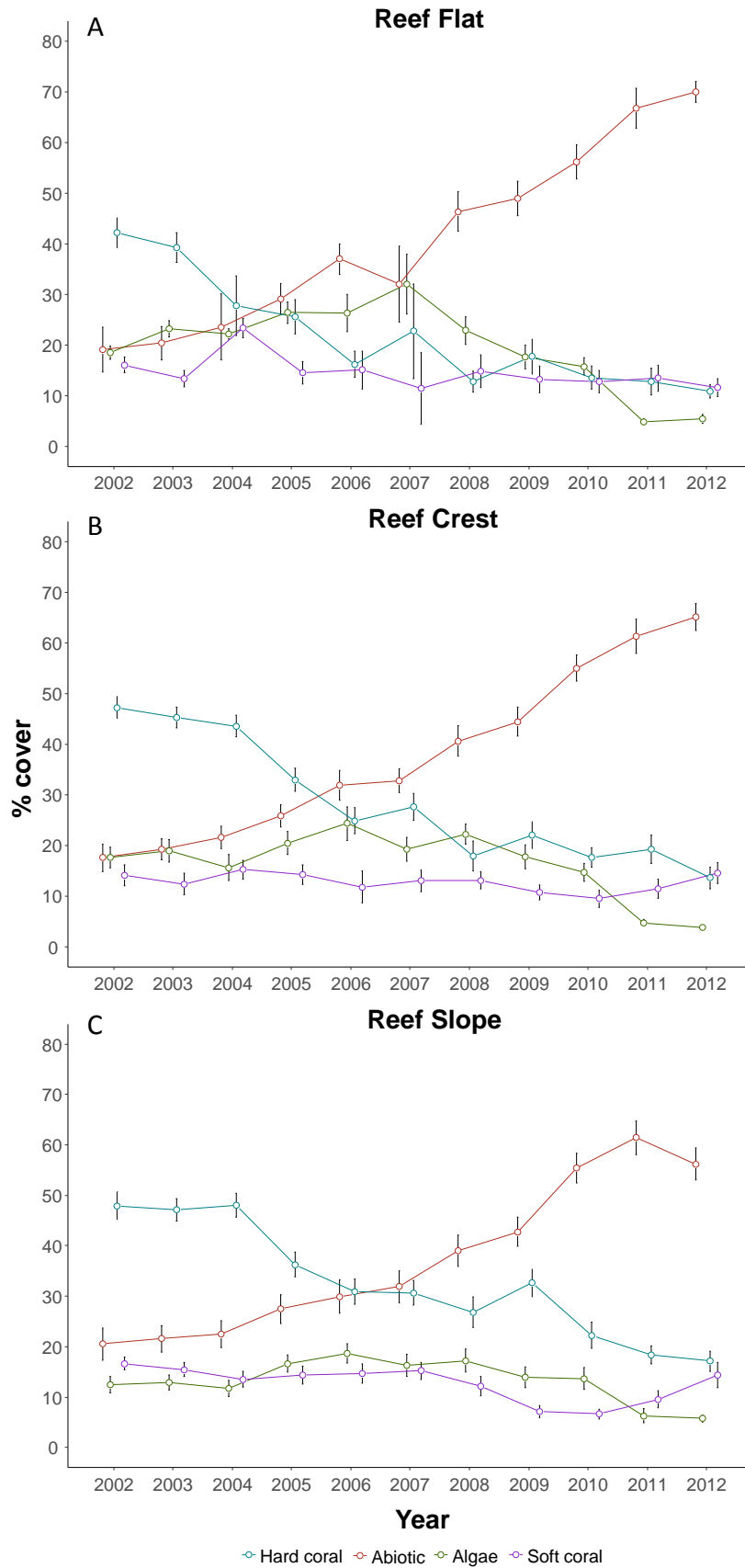


Figure 5: Changes in mean cover of the benthic categories on A) Reef Flat, B) Reef Crest and C) Reef Slope, over the 2002 – 2012 monitoring period (the vertical lines represents standard error). The total number of transects analysed by year and habitat was 495 (see Table 1).

Live massive, branching and encrusting corals were overall the most abundant morphotypes present and were subsequently the categories which had the most profound declines. They experienced gradual decline over the period studied, resulting in reduction of the mean cover, relative to the initial cover, of 62.2% for massive, 71.8% for branching and 81.5% for encrusting morphotype. Starting from a lower initial cover, other morphotypes considered (submassive, tabulate and foliose) also experienced gradual decline. At the start of the sampling period, the reef flat and crest were characterised by the highest percentage abundance of branching coral morphotype (12.7%, SE \pm 2.1% and 13.8%, SE \pm 2%, respectively), while the reef slope had the highest percentage abundance cover of encrusting hard coral morphotype (13.8%, SE \pm 1.9%). Overall, regardless of the habitat type, all hard coral morphotypes sampled experienced gradual decline in percentage cover over the sampling period (Figure 6). In summary, as a result of the uniform decrease in hard coral and the increase in abiotic cover, the habitat experienced profound changes, going from a habitat represented by high live cover of many coral morphotypes, to a habitat dominated by dead coral, rock, rubble and sand.

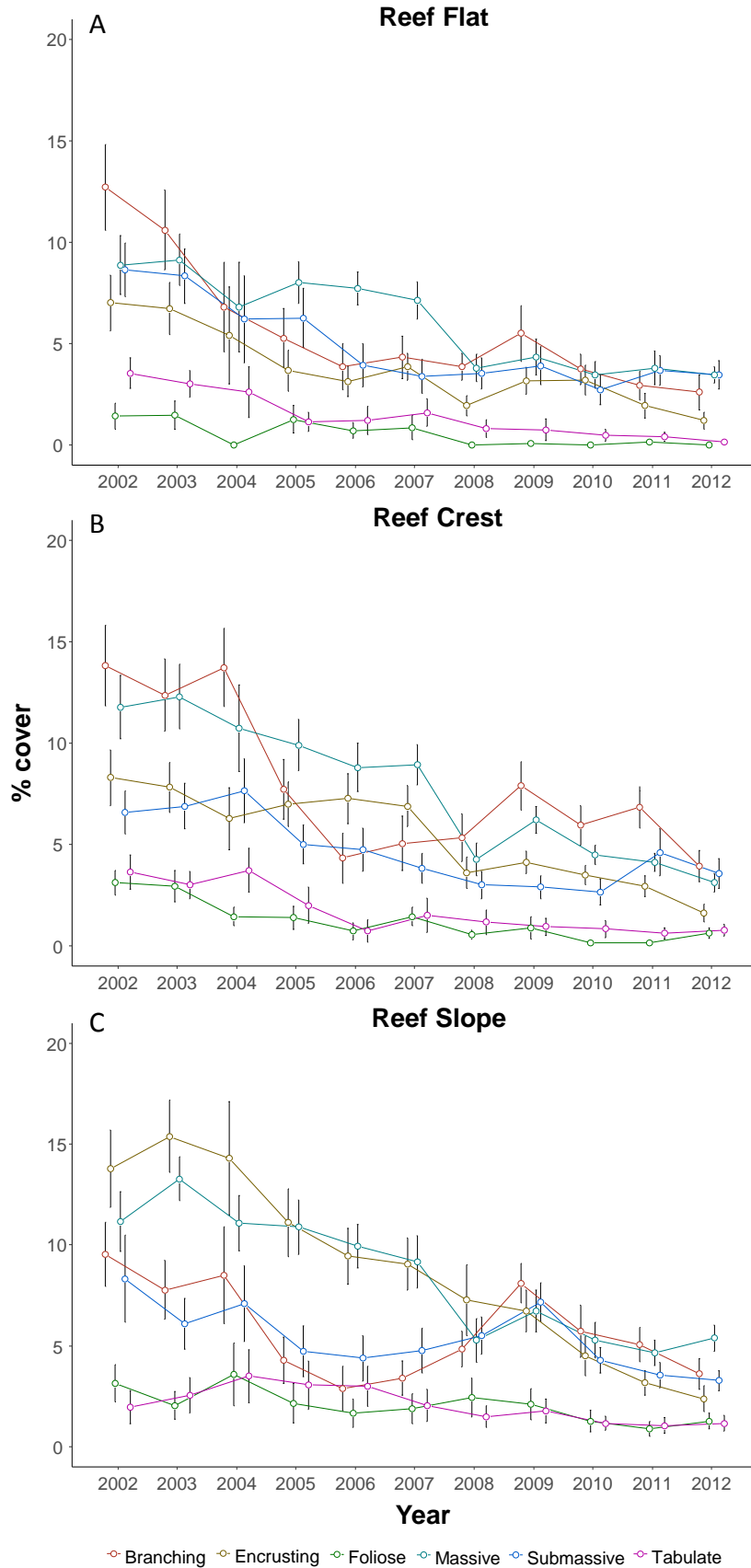


Figure 6: Changes in mean cover of the hard coral morphotypes on A) Reef Flat, B) Reef Crest and C) Reef Slope, over the 2002 - 2012 monitoring period (the vertical lines represents standard error). The total number of transects analysed by year and habitat was 495 (see Table 1).

The results of Pearson's correlation analysis of individual reef habitats were highly similar to the overall habitat correlation analysis. Many statistically significant relationships between benthic habitat categories in each reef habitat were identified (Table 4). The correlation coefficients relating Year and Hard coral and Abiotic and Hard coral were also highly negative, as well as statistically significant in all three habitats.

Table 4: Pearson's correlation coefficients between sample year and benthic categories for Reef Flat, Reef Crest and Reef Slope habitats. The total number of transects analysed by year and habitat was 495 (see Table 1). Statistically significant relationships ($P < 0.05$) are marked with *.

Reef Flat				
	Year	Abiotic	Algae	Hard coral
Abiotic	0.82*			
Algae	-0.54*	-0.54*		
Hard coral	-0.69*	-0.82*	0.17	
Soft coral	-0.15	-0.40*	-0.13	0.09
Reef Crest				
	Year	Abiotic	Algae	Hard coral
Abiotic	0.82*			
Algae	-0.40*	-0.39*		
Hard coral	-0.73*	-0.83*	0.03	
Soft coral	-0.08	-0.28*	-0.35*	0.09
Reef Slope				
	Year	Abiotic	Algae	Hard coral
Abiotic	0.73*			
Algae	-0.24*	-0.37*		
Hard coral	-0.70*	-0.79*	-0.04	
Soft coral	-0.28*	-0.48*	-0.08	0.14

2.3.2 Fish community

Over the entire monitoring period, a total of 246,412 individuals were counted, belonging to 213 different species from 34 fish families (Table 5). Pomacentridae (42 species), Chaedontidae (25 species) and Labridae (25 species) were the most species rich families, across all sites and reef habitats.

Table 5: List of species observed during the monitoring period with total abundance (total), total abundance percentage contribution (% a), mean abundance per transect (250 m²) with standard error of the mean (\pm SE), percentage frequency of occurrence indicating the proportion of transects in which the species was observed (% f) and species' feeding guild (guild). Superscripts indicate ¹ family and ² species tested within the family which experienced statistically significant abundance – hard coral relationship (species relationships were tested only within those families which had >1% total abundance contribution).

N°	FAMILY/Species	total	% a	250m ²	SE	% f	guild
1	ACANTHURIDAE¹	17667	7.17	2.38	0.25		
1	<i>Acanthurus auranticavus</i>	77	0.03	0.16	0.07	4.24	Her
2	<i>Acanthurus grammoptilus</i>	69	0.03	0.14	0.06	2.43	Her
3	<i>Acanthurus pyroferus</i>	2195	0.89	4.43	0.23	74.14	Her
4	<i>Acanthurus thompsonii</i>	1597	0.65	3.23	0.63	18.99	Plank
5	<i>Ctenochaetus binotatus</i>	637	0.26	1.29	0.13	29.29	Her
6	<i>Ctenochaetus striatus²</i>	6833	2.77	13.8	0.76	80.2	Her
7	<i>Ctenochaetus strigosus</i>	350	0.14	0.71	0.12	9.49	Her
8	<i>Naso brevirostris</i>	99	0.04	0.2	0.11	1.82	Her
9	<i>Naso caeruleacauda</i>	532	0.22	1.07	0.35	4.44	Plank
10	<i>Naso caesius</i>	67	0.03	0.14	0.08	2.02	Plank
11	<i>Naso hexacanthus</i>	665	0.27	1.34	0.39	8.69	Plank
12	<i>Naso lituratus</i>	286	0.12	0.58	0.07	23.64	Her
13	<i>Naso vlamingii²</i>	934	0.38	1.89	0.3	25.25	Plank
14	<i>Zebrasoma scopas²</i>	3173	1.29	6.41	0.33	78.79	Her
15	<i>Zebrasoma veliferum</i>	153	0.06	0.31	0.04	12.73	Her
2	ANTHINAE¹	21413	8.69	8.65	1.68		
16	<i>Pseudanthias huchtii</i>	12059	4.89	24.36	4.5	28.48	Plank
17	<i>Pseudanthias pleurotaenia</i>	637	0.26	1.29	0.31	7.27	Plank
18	<i>Pseudanthias squamipinnis²</i>	3790	1.54	7.66	1.69	12.32	Plank
19	<i>Pseudanthias tuka²</i>	4284	1.74	8.65	1.46	18.99	Plank
20	<i>Pseudanthias parvirostris</i>	643	0.26	1.3	0.46	3.23	Plank
3	APOGONIDAE	3596	1.46	3.63	1.24		
21	<i>Apogon aureus</i>	1572	0.64	3.18	1.46	4.04	Car
22	<i>Cheilodipterus quinquelineatus</i>	2024	0.82	4.09	1.02	19.8	Car
4	AULOSTOMIDAE	293	0.12	0.59	0.09		
23	<i>Aulostomus chinensis</i>	293	0.12	0.59	0.09	22.02	Car
5	BALISTIDAE¹	4538	1.84	1.15	0.19		
24	<i>Balistapus undulatus</i>	900	0.37	1.82	0.1	60.61	Omv
25	<i>Balistoides conspicillum</i>	62	0.03	0.13	0.04	3.03	Car
26	<i>Balistoides viridescens</i>	5	0	0.01	0	1.01	Car
27	<i>Melichthys niger²</i>	292	0.12	0.59	0.21	10.51	Plank
28	<i>Melichthys vidua²</i>	367	0.15	0.74	0.07	31.92	Omv
29	<i>Odonus niger²</i>	2750	1.12	5.56	1.06	16.97	Omv
30	<i>Sufflamen bursa</i>	89	0.04	0.18	0.02	12.53	Omv
31	<i>Sufflamen chrysopterus</i>	73	0.03	0.15	0.03	7.88	Car

6	BLÉNIDAE	183	0.07	0.37	0.1		
32	<i>Plagiotremus rhinorhynchos</i>	183	0.07	0.37	0.1	10.51	Car
7	CAESIONIDAE	29594	12.01	14.95	2.17		
33	<i>Caesio cuning</i>	3726	1.51	7.53	1.67	20.81	Plank
34	<i>Caesio lunaris</i>	643	0.26	1.3	0.39	4.85	Plank
35	<i>Caesio teres</i>	5636	2.29	11.39	1.97	14.55	Plank
36	<i>Pterocaesio tile</i>	19589	7.95	39.57	4.64	37.37	Plank
8	CARANGIDAE	123	0.05	0.08	0.02		
37	<i>Caranx ignobilis</i>	5	0	0.01	0.01	0.4	Car
38	<i>Caranx melampygus</i>	67	0.03	0.14	0.04	5.86	Car
39	<i>Caranx sexfasciatus</i>	51	0.02	0.1	0.03	3.23	Car
9	CHAETODONTIDAE¹	8560	3.47	0.69	0.08		
40	<i>Chaetodon auriga</i>	122	0.05	0.25	0.04	12.53	Cor
41	<i>Chaetodon baronessa²</i>	509	0.21	1.03	0.07	42.02	Cor
42	<i>Chaetodon ephippium</i>	92	0.04	0.19	0.03	10.3	Cor
43	<i>Chaetodon kleinii</i>	1290	0.52	2.61	0.16	58.59	Cor
44	<i>Chaetodon lunula</i>	124	0.05	0.25	0.04	11.11	Cor
45	<i>Chaetodon lunulatus²</i>	723	0.29	1.46	0.1	45.45	Cor
46	<i>Chaetodon melannotus</i>	394	0.16	0.8	0.07	30.51	Cor
47	<i>Chaetodon meyeri²</i>	126	0.05	0.25	0.03	12.93	Cor
48	<i>Chaetodon ocellicaudus</i>	45	0.02	0.09	0.02	5.25	Cor
49	<i>Chaetodon ornatissimus</i>	104	0.04	0.21	0.03	11.52	Cor
50	<i>Chaetodon punctatofasciatus²</i>	411	0.17	0.83	0.06	32.53	Cor
51	<i>Chaetodon rafflesi</i>	174	0.07	0.35	0.04	18.59	Cor
52	<i>Chaetodon speculum</i>	108	0.04	0.22	0.04	10.1	Cor
53	<i>Chaetodon trifascialis</i>	98	0.04	0.2	0.03	10.91	Cor
54	<i>Chaetodon trifasciatus</i>	179	0.07	0.36	0.06	10.91	Cor
55	<i>Chaetodon ulietensis</i>	156	0.06	0.32	0.04	14.55	Cor
56	<i>Chaetodon unimaculatus</i>	241	0.1	0.49	0.06	19.39	Cor
57	<i>Chaetodon vagabundus</i>	363	0.15	0.73	0.06	34.14	Cor
58	<i>Forcipiger flavissimus²</i>	1107	0.45	2.24	0.13	57.37	Cor
59	<i>Forcipiger longirostris</i>	375	0.15	0.76	0.21	17.58	Car
60	<i>Hemitaurichthys polylepis</i>	991	0.4	2	0.43	12.93	Plank
61	<i>Heniochus acuminatus</i>	48	0.02	0.1	0.02	5.86	Cor
62	<i>Heniochus chrysostomus²</i>	238	0.1	0.48	0.04	24.85	Cor
63	<i>Heniochus varius²</i>	449	0.18	0.91	0.06	39.6	Cor
64	<i>Heniochus singularius</i>	93	0.04	0.19	0.03	8.89	Cor
10	CIRRHITIDAE	226	0.09	0.46	0.04		
65	<i>Paracirrhites forsteri</i>	226	0.09	0.46	0.04	24.44	Car
11	CLUPEIDAE	412	0.17	0.83	0.81		
66	<i>Spratelloides sp</i>	412	0.17	0.83	0.81	1.21	Plank
12	CONGRIDAE	391	0.16	0.79	0.33		
67	<i>Heteroconger hassi</i>	391	0.16	0.79	0.33	3.64	Car
13	EPHIPPIDAE	188	0.08	0.19	0.08		

68	<i>Platax pinnatus</i>	53	0.02	0.11	0.05	2.22	Omv
69	<i>Platax teira</i>	135	0.05	0.27	0.11	3.23	Omv
14	FISTULARIDAE	225	0.09	0.45	0.08		
70	<i>Fistularia commersonii</i>	225	0.09	0.45	0.08	12.32	Car
15	HAEMULIDAE	85	0.03	0.09	0.02		
71	<i>Plectorhinchus lineatus</i>	40	0.02	0.08	0.02	3.64	Car
72	<i>Plectorhinchus vittatus</i>	45	0.02	0.09	0.02	5.66	Car
16	HOLOCENTRIDAE¹	936	0.38	0.32	0.04		
73	<i>Myripristis murdjan</i>	120	0.05	0.24	0.05	8.89	Plank
74	<i>Neoniphon sammara</i>	298	0.12	0.6	0.09	15.96	Car
75	<i>Priacanthus hamrur</i>	2	0	0	0	0.2	Car
76	<i>Sargocentron caudimaculatum</i>	482	0.2	0.97	0.09	31.31	Car
77	<i>Sargocentron diadema</i>	11	0	0.02	0.02	0.61	Car
78	<i>Sargocentron spiniferum</i>	23	0.01	0.05	0.02	2.22	Car
17	LABRIDAE¹	14072	5.71	1.14	0.14		
79	<i>Anampses melanurus</i>	24	0.01	0.05	0.01	3.03	Car
80	<i>Anampses twistii</i>	132	0.05	0.27	0.03	14.55	Car
81	<i>Bodianus diana</i>	133	0.05	0.27	0.05	13.33	Car
82	<i>Bodianus mesothorax</i>	100	0.04	0.2	0.03	12.96	Car
83	<i>Cheilinus fasciatus</i>	286	0.12	0.58	0.05	30.91	Car
84	<i>Cheilinus trilobatus</i>	133	0.05	0.27	0.04	12.73	Car
85	<i>Cheilinus undulatus</i>	45	0.02	0.09	0.02	4.85	Car
86	<i>Cheilinus chlorourus²</i>	197	0.08	0.4	0.06	16.36	Car
87	<i>Choerodon anchorago</i>	166	0.07	0.34	0.05	13.94	Car
88	<i>Cirrhilabrus solorensis</i>	415	0.17	0.84	0.33	3.44	Plank
89	<i>Coris gaimard</i>	195	0.08	0.39	0.07	14.17	Car
90	<i>Epibulus insidiator</i>	127	0.05	0.26	0.03	16.77	Car
91	<i>Gomphosus varius</i>	162	0.07	0.33	0.04	17.17	Car
92	<i>Halichoeres hortulanus²</i>	822	0.33	1.66	0.12	48.08	Car
93	<i>Halichoeres melanochir</i>	62	0.03	0.13	0.06	3.84	Car
94	<i>Halichoeres prosopeion²</i>	775	0.31	1.57	0.31	33.74	Car
95	<i>Hemigymnus fasciatus²</i>	263	0.11	0.53	0.05	25.25	Car
96	<i>Hemigymnus melapterus²</i>	334	0.14	0.67	0.17	26.26	Car
97	<i>Labroides bicolor</i>	628	0.25	1.27	0.1	40.61	Car
98	<i>Labroides dimidiatus</i>	1687	0.68	3.41	0.17	68.48	Car
99	<i>Oxycheilinus digrammus</i>	97	0.04	0.2	0.03	12.53	Car
100	<i>Oxycheilinus rhodochrous</i>	44	0.02	0.09	0.04	2.02	Car
101	<i>Thalassoma amblycephalum²</i>	4028	1.63	8.14	1.17	29.7	Plank
102	<i>Thalassoma hardwicke</i>	1316	0.53	2.66	0.23	45.25	Car
103	<i>Thalassoma lunare</i>	1901	0.77	3.84	0.35	57.98	Car
18	LETHRINIDAE	826	0.34	0.28	0.06		
104	<i>Gnathodentex aureolineatus</i>	390	0.16	0.79	0.2	5.86	Car
105	<i>Lethrinus harak</i>	96	0.04	0.19	0.07	3.84	Car

106	<i>Lethrinus olivaceus</i>	8	0	0.02	0.01	0.61	Car
107	<i>Lethrinus ornatus</i>	1	0	0	0	0.2	Car
108	<i>Lethrinus erythropterus</i>	58	0.02	0.12	0.02	8.69	Car
109	<i>Monotaxis grandoculis</i>	273	0.11	0.55	0.06	24.65	Car
19	LUTJANIDAE¹	1190	0.48	0.27	0.07		
110	<i>Aphareus furca</i>	13	0.01	0.03	0.01	1.82	Car
111	<i>Lutjanus biguttatus</i>	116	0.05	0.23	0.06	6.26	Car
112	<i>Lutjanus bohar</i>	138	0.06	0.28	0.2	3.03	Car
113	<i>Lutjanus decussatus</i>	318	0.13	0.64	0.06	26.26	Car
114	<i>Lutjanus ehrenbergii</i>	153	0.06	0.31	0.11	3.64	Car
115	<i>Lutjanus gibbus</i>	43	0.02	0.09	0.02	3.03	Car
116	<i>Lutjanus semicinctus</i>	35	0.01	0.07	0.03	2.22	Car
117	<i>Macolor macularis</i>	294	0.12	0.59	0.12	16.36	Car
118	<i>Macolor niger</i>	80	0.03	0.16	0.04	5.66	Car
20	MULLIDAE	1279	0.52	0.43	0.07		
119	<i>Mulloidichthys flavolineatus</i>	124	0.05	0.25	0.08	3.43	Car
120	<i>Mulloidichthys vanicolensis</i>	87	0.04	0.18	0.1	1.41	Car
121	<i>Parupeneus barberinus</i>	288	0.12	0.58	0.07	22.02	Car
122	<i>Parupeneus bifasciatus</i>	113	0.05	0.23	0.03	13.74	Car
123	<i>Parupeneus crassilabris</i>	122	0.05	0.25	0.05	6.67	Car
124	<i>Parupeneus multifasciatus</i>	545	0.22	1.1	0.09	37.37	Car
21	NEMIPTERIDAE¹	959	0.39	0.65	0.08		
125	<i>Scolopsis bilineata</i>	563	0.23	1.14	0.07	46.26	Car
126	<i>Scolopsis lineata</i>	264	0.11	0.53	0.13	11.31	Car
127	<i>Scolopsis trilineata</i>	132	0.05	0.27	0.04	10.51	Car
22	OSTRACIIDAE	48	0.02	0.1	0.05		
128	<i>Ostracion cubicus</i>	48	0.02	0.1	0.05	3.23	Omv
23	PLOTOSIDAE	2890	1.17	5.84	2.85		
129	<i>Plotosus lineatus</i>	2890	1.17	5.84	2.85	1.41	Omv
24	POMACANTHIDAE¹	2753	1.12	0.62	0.1		
130	<i>Centropyge bicolor</i>	396	0.16	0.8	0.09	26.67	Omv
131	<i>Centropyge bispinosus</i>	110	0.04	0.22	0.03	12.53	Omv
132	<i>Centropyge tibicen²</i>	416	0.17	0.84	0.08	31.11	Her
133	<i>Centropyge vroliki²</i>	727	0.3	1.47	0.1	48.08	Her
134	<i>Pomacanthus imperator</i>	25	0.01	0.05	0.01	4.65	Omv
135	<i>Pomacanthus navarchus</i>	27	0.01	0.05	0.01	4.44	Omv
136	<i>Pomacanthus sexstriatus</i>	29	0.01	0.06	0.01	4.44	Omv
137	<i>Pomacanthus xanthometopon</i>	455	0.18	0.92	0.5	5.66	Omv
138	<i>Pygoplites diacanthus²</i>	568	0.23	1.15	0.07	49.7	Omv
25	POMACENTRIDAE¹	120573	48.93	5.8	0.73		
139	<i>Abudefduf vaigiensis</i>	1188	0.48	2.4	0.39	13.74	Omv
140	<i>Amblyglyphidodon aureus</i>	960	0.39	1.94	0.39	18.02	Plank
141	<i>Amblyglyphidodon curacao</i>	8207	3.33	16.58	1.42	53.94	Omv

142	<i>Amblyglyphidodon leucogaster</i>	7362	2.99	14.87	1.17	58.18	Plank
143	<i>Amphiprion clarkii</i>	1121	0.45	2.26	0.3	41.41	Plank
144	<i>Amphiprion perideraion</i>	464	0.19	0.94	0.09	22.22	Plank
145	<i>Chromis amboinensis</i> ²	5210	2.11	10.53	1	41.41	Plank
146	<i>Chromis analis</i> ²	2955	1.2	5.98	1.09	18.83	Plank
147	<i>Chromis caudalis</i>	2577	1.05	5.21	1.2	19.39	Plank
148	<i>Chromis lepidolepis</i> ²	2196	0.89	4.44	0.56	29.49	Plank
149	<i>Chromis margaritifer</i>	2353	0.95	4.75	0.69	23.43	Plank
150	<i>Chromis retrofasciata</i> ²	2149	0.87	4.34	0.66	26.87	Plank
151	<i>Chromis ternatensis</i>	12972	5.26	26.21	4.06	26.06	Plank
152	<i>Chromis viridis</i>	7665	3.11	15.48	2.56	20.2	Plank
153	<i>Chromis weberi</i>	2266	0.92	4.58	0.71	23.23	Plank
154	<i>Chromis xanthochira</i>	397	0.16	0.8	0.2	7.27	Plank
155	<i>Chromis xanthura</i>	1296	0.53	2.62	0.37	23.43	Plank
156	<i>Chrysiptera cyanea</i>	2633	1.07	5.32	0.75	24.44	Plank
157	<i>Chrysiptera rollandi</i>	1580	0.64	3.19	0.32	31.92	Plank
158	<i>Chrysiptera talboti</i>	2101	0.85	4.24	0.39	34.34	Plank
159	<i>Dascyllus aruanus</i>	2050	0.83	4.14	0.75	16.36	Omv
160	<i>Dascyllus reticulatus</i> ²	7886	3.2	15.93	1.42	44.44	Omv
161	<i>Dascyllus trimaculatus</i>	1624	0.66	3.28	0.56	26.26	Omv
162	<i>Dischistodus melanotus</i>	358	0.15	0.72	0.14	13.33	Her
163	<i>Neoglyphidodon melas</i>	1783	0.72	3.6	0.52	35.96	Omv
164	<i>Neoglyphidodon oxyodon</i>	18	0.01	0.04	0.01	1.82	Plank
165	<i>Neoglyphidodon nigroris</i>	7461	3.03	15.07	1.02	51.92	Plank
166	<i>Plectroglyphidodon lacrymatus</i>	1387	0.56	2.8	0.29	30.51	Omv
167	<i>Pomacentrus adelus</i>	2241	0.91	4.53	0.83	18.38	Plank
168	<i>Pomacentrus alexanderae</i>	1063	0.43	2.15	0.31	23.03	Omv
169	<i>Pomacentrus amboinensis</i>	472	0.19	0.95	0.16	12.12	Her
170	<i>Pomacentrus auriventris</i>	998	0.41	2.02	0.39	14.14	Plank
171	<i>Pomacentrus brachialis</i>	6483	2.63	13.1	0.88	66.46	Plank
172	<i>Pomacentrus lepidogenys</i> ²	1999	0.81	4.04	0.48	27.47	Plank
173	<i>Pomacentrus littoralis</i>	1328	0.54	2.68	0.65	8.48	Her
174	<i>Pomacentrus moluccensis</i>	7704	3.13	15.56	1.62	47.68	Omv
175	<i>Pomacentrus nigromanus</i>	265	0.11	0.54	0.15	6.46	Omv
176	<i>Pomacentrus philippinus</i>	426	0.17	0.86	0.11	17.78	Plank
177	<i>Pomacentrus reidi</i>	1249	0.51	2.52	0.3	27.07	Plank
178	<i>Pomacentrus simsiang</i>	34	0.01	0.07	0.03	1.01	Her
179	<i>Pomacentrus vaiuli</i> ²	4154	1.69	8.39	0.9	49.9	Omv
180	<i>Pomacentrus auriventris</i>	1938	0.79	3.92	0.64	17.17	Plank
26	PSEUDOCHROMIDAE ¹	5995	2.43	4.04	0.39		
181	<i>Labracinus cyclophthalmus</i>	406	0.16	0.82	0.07	35.35	Car
182	<i>Manonichthys splendens</i>	191	0.08	0.39	0.04	19.8	Car
183	<i>Pictichromis paccagnellae</i> ²	5398	2.19	10.91	1.05	41.82	Car

27	PTERELEOTRIDAE	543	0.22	0.55	0.14		
184	<i>Nemateleotris magnifica</i>	280	0.11	0.57	0.16	8.89	Plank
185	<i>Ptereleotris evides</i>	263	0.11	0.53	0.13	7.07	Plank
28	SCARIDAE	2803	1.14	0.81	0.09		
186	<i>Cetoscarus bicolor</i>	79	0.03	0.16	0.03	7.47	Her
187	<i>Chlorurus bleekeri</i>	495	0.2	1	0.09	34.34	Her
188	<i>Chlorurus sordidus</i>	1031	0.42	2.08	0.23	43.43	Her
189	<i>Hipposcarus longiceps</i>	47	0.02	0.09	0.03	4.65	Her
190	<i>Scarus dimidiatus</i>	246	0.1	0.5	0.07	17.58	Her
191	<i>Scarus flavipectoralis</i>	388	0.16	0.78	0.07	33.74	Her
192	<i>Scarus niger</i>	517	0.21	1.04	0.08	40.2	Her
29	SCORPAENIDAE	139	0.06	0.14	0.03		
193	<i>Pterois antennata</i>	35	0.01	0.07	0.02	5.25	Car
194	<i>Pterois volitans</i>	104	0.04	0.21	0.04	9.9	Car
30	SERRANIDAE¹	1591	0.65	0.46	0.12		
195	<i>Anyperodon leucogrammicus</i>	28	0.01	0.06	0.01	5.05	Car
196	<i>Belonoperca chabanaudi</i>	659	0.27	1.33	0.63	2.63	Car
197	<i>Cephalopholis argus</i>	195	0.08	0.39	0.04	24.44	Car
198	<i>Cephalopholis urodeta</i>	245	0.1	0.49	0.05	27.88	Car
199	<i>Epinephelus fasciatus</i>	122	0.05	0.25	0.03	14.95	Car
200	<i>Epinephelus merra</i>	321	0.13	0.65	0.08	22.42	Car
201	<i>Gracila albomarginata</i>	21	0.01	0.04	0.01	3.43	Car
31	SIGANIDAE	373	0.15	0.15	0.03		
202	<i>Siganus corallinus</i>	66	0.03	0.13	0.03	5.86	Her
203	<i>Siganus doliatus</i>	74	0.03	0.15	0.03	6.46	Her
204	<i>Siganus guttatus</i>	111	0.05	0.22	0.06	5.86	Her
205	<i>Siganus puellus</i>	98	0.04	0.2	0.03	10.1	Omv
206	<i>Siganus punctatissimus</i>	24	0.01	0.05	0.01	2.42	Her
32	SPHYRAENIDAE	4	0	0.01	0		
207	<i>Sphyraena barracuda</i>	4	0	0.01	0	0.61	Car
33	TETRADONTIDAE	970	0.39	0.39	0.2		
208	<i>Arothron hispidus</i>	47	0.02	0.09	0.06	1.82	Omv
209	<i>Arothron nigropunctatus</i>	134	0.05	0.27	0.05	15.56	Omv
210	<i>Arothron stellatus</i>	1	0	0	0	0.2	Omv
211	<i>Canthigaster papua</i>	376	0.15	0.76	0.43	9.29	Omv
212	<i>Canthigaster valentini</i>	412	0.17	0.83	0.47	8.69	Omv
34	ZANCLIDAE¹	974	0.4	1.97	0.22		
213	<i>Zanclus cornutus</i>	974	0.4	1.97	0.22	50.1	Omv

Of all fish recorded, 63% belonged to 25 species, with the ten most commonly occurring species making up 40% of the total abundance (Table 6 and Supplementary material). With the exception of *Plotosus lineatus* (Plotosidae), all other species belonged exclusively to 5 fish families: Caesionidae, Pomacentridae, Acanthuridae, Labridae and Serranidae subfamily Anthiinae.

Table 6: Twenty-five most abundant species observed over the monitoring period, ordered from most to less abundant (N°), along with their percentage contribution to the total number of individuals sampled (% contribution). Pictures of the species included in section 2.5 – Supplementary material.

N°	Species	% contribution
1	<i>Pterocaesio tile</i>	7.95
2	<i>Chromis ternatensis</i>	5.26
3	<i>Pseudanthias huchtii</i>	4.89
4	<i>Amblyglyphidodon curacao</i>	3.33
5	<i>Dascyllus reticulatus</i>	3.2
6	<i>Pomacentrus moluccensis</i>	3.13
7	<i>Chromis viridis</i>	3.11
8	<i>Neoglyphidodon nigroris</i>	3.03
9	<i>Amblyglyphidodon leucogaster</i>	2.99
10	<i>Ctenochaetus striatus</i>	2.77
11	<i>Pomacentrus brachialis</i>	2.63
12	<i>Caesio teres</i>	2.29
13	<i>Pictichromis paccagnellae</i>	2.19
14	<i>Chromis amboinensis</i>	2.11
15	<i>Pseudanthias tuka</i>	1.74
16	<i>Pomacentrus vaiuli</i>	1.69
17	<i>Thalassoma amblycephalum</i>	1.63
18	<i>Pseudanthias squamipinnis</i>	1.54
19	<i>Caesio cuning</i>	1.51
20	<i>Zebrasoma scopas</i>	1.29
21	<i>Chromis analis</i>	1.2
22	<i>Plotosus lineatus</i>	1.17
23	<i>Odonus niger</i>	1.12
24	<i>Chrysiptera cyanea</i>	1.07
25	<i>Chromis caudalis</i>	1.05

A large number of the most abundant species experienced dominance throughout the monitoring period, with high abundances observed each year. There were, however, several new species which with time appeared and subsequently generally remained dominant. The most important species included *Ctenochaetus striatus*, belonging to the family Acanthuridae, and *Thalassoma amblycephalum* of the family Labridae, since prior to 2006 neither of the species, nor any species other than those belonging to families Caesionidae, Pomacentridae, Pseudochromidae and Anthiinae were observed among the 5 most abundant. Accordingly before 2006, despite an occasional change in dominance of certain species, in most cases the species were subsequently replaced by a species of the same family. The community dominance structure changed with the introduction of Acanthuridae in 2006 and Labridae in 2011 (Figure 7A). Similarly, when the change in dominance of the fish community feeding guilds were examined, 2006 marked the introduction of herbivorous guild which subsequently remained one of the dominant guilds. Prior to 2006 the community was dominated by planktivorous and carnivorous feeding guilds (Figure 7B).

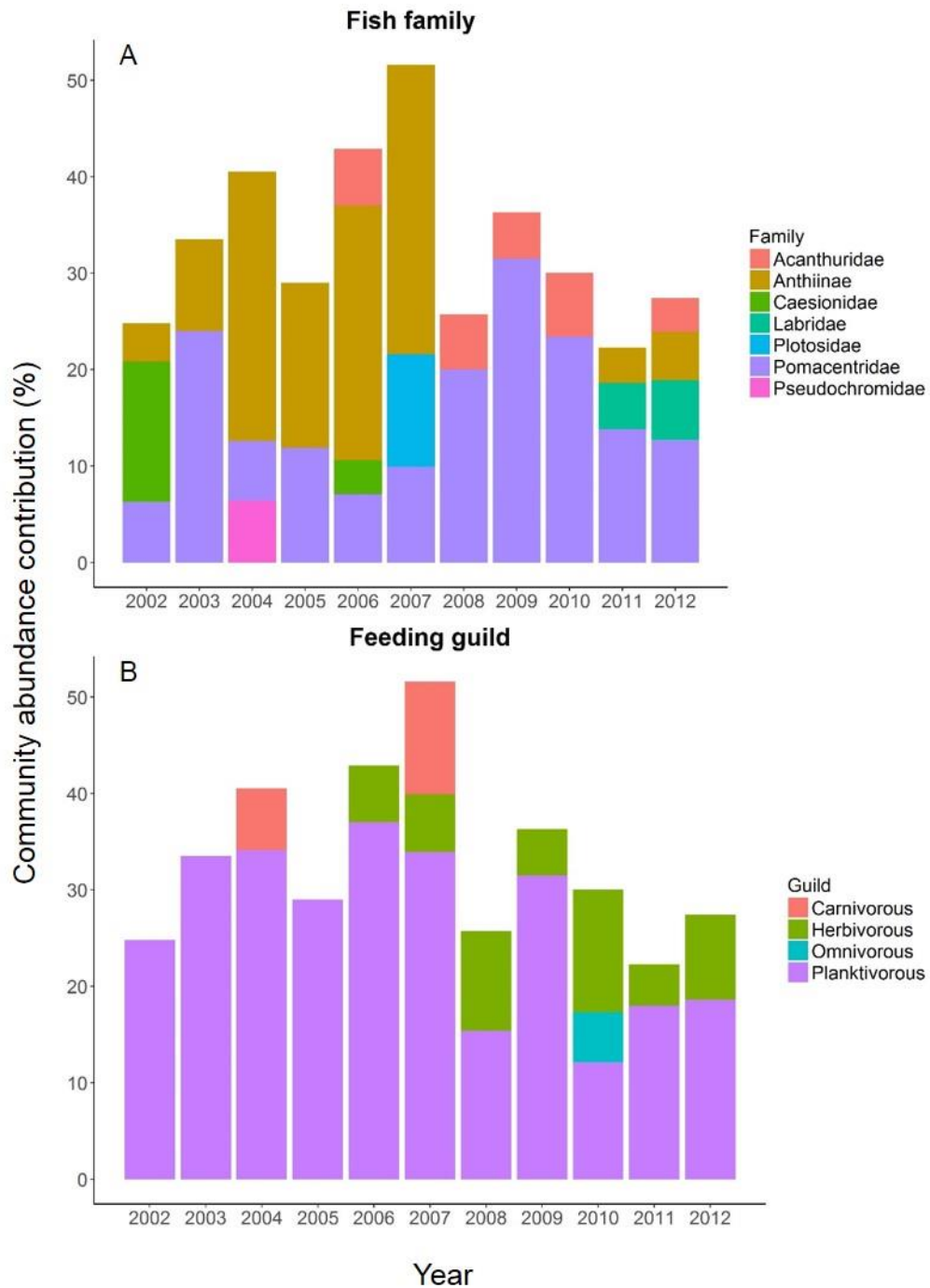


Figure 7: Dominance of fish A) Families and B) Feeding guilds in terms of % abundance contribution to the total number of individuals sampled. Graphs are plotted using the 5 most abundant species observed in each year, categorised into fish families and feeding guilds.

The fish community abundance experienced similar pattern to that of hard coral cover, decreasing over time, with decreases in abundances coinciding with decreases in hard coral cover for a number of years. The fish community abundance followed the opposite trend to that of abiotic cover, which continuously increased through time. The mean fish abundance per transect ranged from the maximum of 890.3 to the minimum of 267.1 (Figure 8).

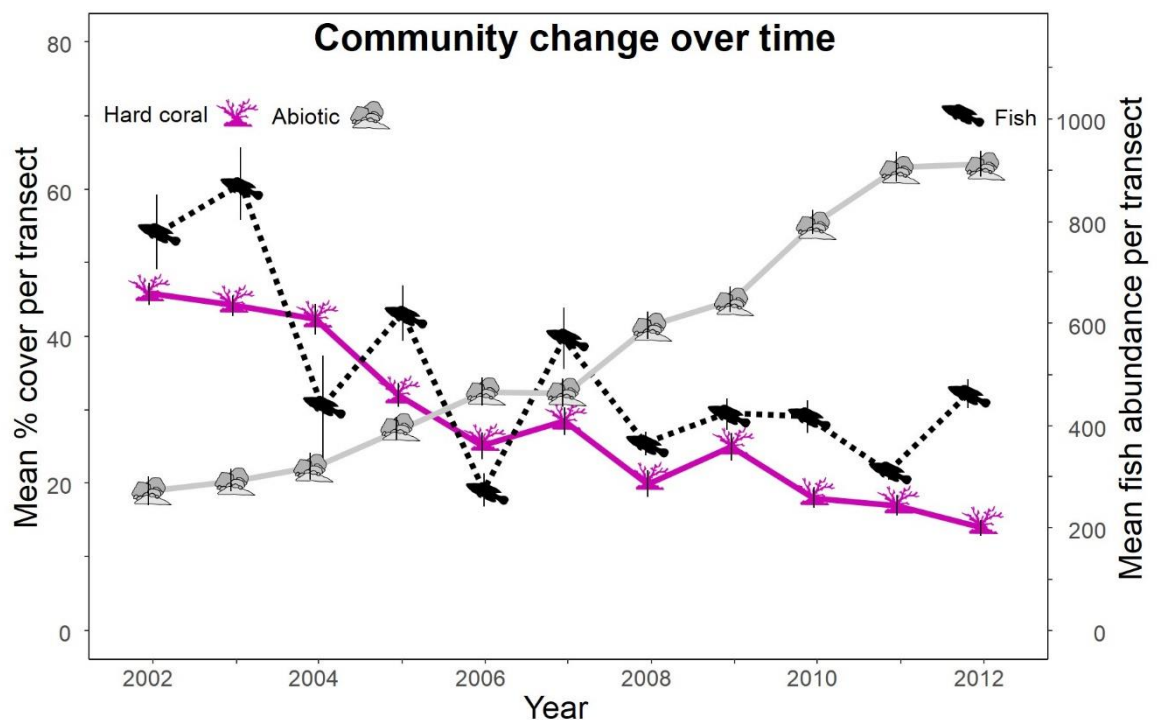


Figure 8: Summary of changes in fish community abundance and mean cover of hard coral and abiotic benthos (mean \pm standard error).

The seriation test on the nonmetric MDS, representing the change of fish community composition through time, showed that a significant sequential patterns existed in fish community composition ($Rho=0.24$, $p<0.05$), while the Stress value of 0.05 was sufficiently low to give an excellent representation of the high-dimensional data represented in the two-dimensional plot. Furthermore, the Simprof test identified significant groupings of years (years with high similarity) at $p<0.05$. The 1st group consisted of years at the start of the sampling period (2002, 2003 and 2005) while the 2nd group consisted of years at the end of the monitoring period (2008, 2009, 2011 and 2012). Year 2004 did not belong to the Simprof

classified group but clustered more closely to the 1st group. The two year groupings were connected by years which were notably distinct from both groups, 2006 and 2007, representing a transition period. Year 2010 was highly distinct from all other years and did not clearly fit into the trajectory or within any conspicuous groups (Figure 9). The fish community abundance trajectory and groups can be compared to the time trend in the hard coral cover, coinciding with initial years of high hard coral cover, followed by years of dramatic decline and culmination in years of low hard coral cover. The community composition shift from the start to the end of the survey period via the two transition years also coincided with the DHMs identified in 2005 and 2006.

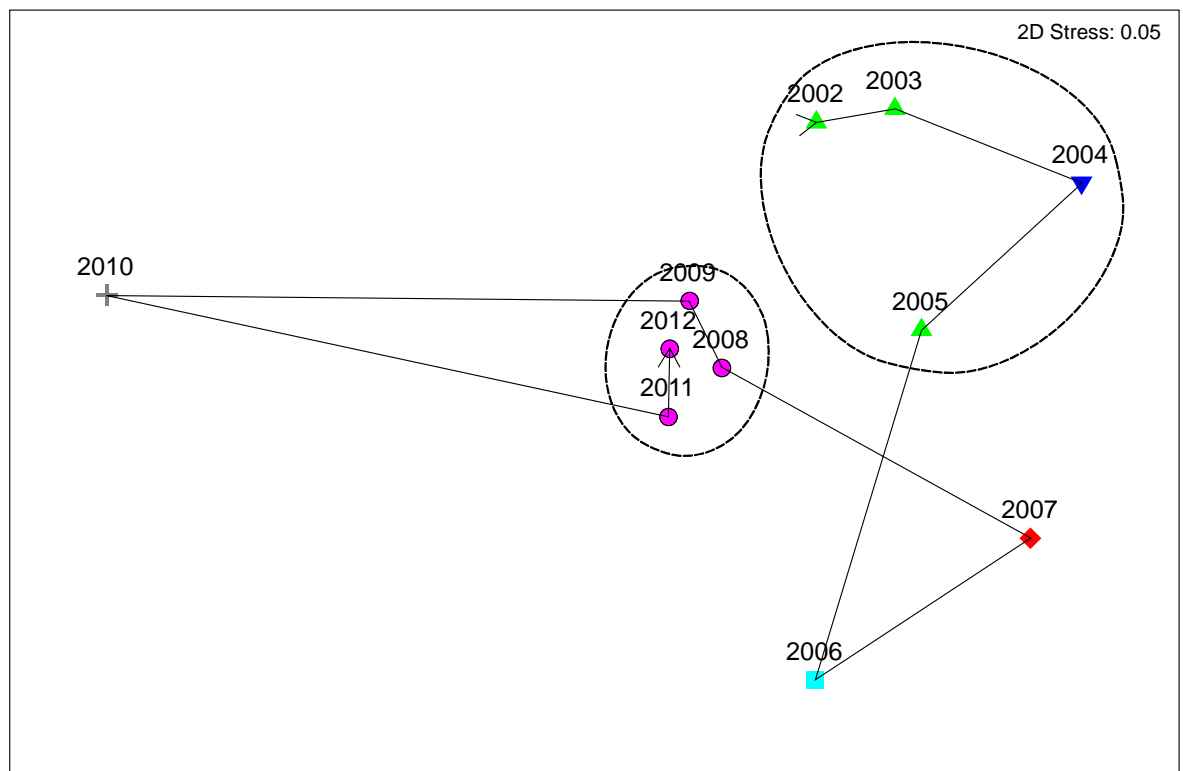


Figure 9: MDS ordination plot with years sequentially connected by an arrow. Same colours and shapes represent years classified by the Simprof routine as statically significant year groups. The dashed circles represent a similarity level of 50%.

Within year group similarity identified by SIMPER was 58.18% for the 1st group and 68.14% for the 2nd group. The most representative species of the 1st group were *Pseudanthias huchtii* (9.8%), *Pterocaesio tile* (7.3%) and *Chromis viridis* (6.2%), while *Chromis ternatensis*

(5.6%) *Ctenochaetus striatus* (5.6%) and *Pomacentrus moluccensis* (4.9%) were most representative of the 2nd group. Between year group dissimilarity was 51.43%. The species which contributed most to the dissimilarity included *Pseudanthias huchtii* (8.4%), *Chromis viridis* (6.3%) and *Chromis ternatensis* (5.3%) (Table 7).

Table 7: Results of the SIMPER analysis showing the contributions in similarity composition of the species within each year group and the contributions in dissimilarity of species between year groups. The species are ordered by decreasing contribution. $\bar{\delta}_i$: average dissimilarity, $\bar{\delta}_i\%$: contribution of each species to the average dissimilarity, SD: standard deviation.

1st group avg. similarity = 58.18			2nd group avg. similarity = 68.14			Between group avg. dissimilarity = 51.43		
Species	$\bar{\delta}_i\%$	$\bar{\delta}_i$ /SD	Species	$\bar{\delta}_i\%$	$\bar{\delta}_i$ /SD	Species	$\bar{\delta}_i\%$	$\bar{\delta}_i$ /SD
<i>P. huchtii</i>	9.79	2.02	<i>C. ternatensis</i>	5.61	1.28	<i>P. huchtii</i>	8.4	1.88
<i>P. tile</i>	7.31	2.83	<i>C. striatus</i>	5.58	3.99	<i>C. viridis</i>	6.31	1.81
<i>C. viridis</i>	6.18	4.03	<i>P. moluccensis</i>	4.88	4.05	<i>C. ternatensis</i>	5.34	1.36
<i>P. moluccensis</i>	4.41	1.85	<i>D. reticulatus</i>	4.81	6.79	<i>P. tile</i>	4.83	1.63
<i>C. teres</i>	4.02	2.71	<i>P. tile</i>	4.39	10.33	<i>C. teres</i>	4.32	2.09
<i>N. nigroris</i>	3.9	4.46	<i>A. curacao</i>	4.38	6.16	<i>C. cuning</i>	2.84	1.38
<i>C. ternatensis</i>	3.82	1.03	<i>N. nigroris</i>	4.35	6.02	<i>D. reticulatus</i>	2.83	1.89
<i>A. curacao</i>	3.74	2.33	<i>T. amblycephalum</i>	3.7	2.44	<i>P. squamipinnis</i>	2.57	1.46
<i>P. paccagnellae</i>	3.4	2.84	<i>C. amboinensis</i>	3.66	11.56	<i>P. tuka</i>	2.54	1.14
<i>P. brachialis</i>	3.06	2.89	<i>P. brachialis</i>	3.62	4.89	<i>P. moluccensis</i>	2.45	1.45
<i>A. leucogaster</i>	2.84	2.16	<i>P. huchtii</i>	3.04	4.03	<i>T. amblycephalum</i>	2.34	1.41
<i>D. reticulatus</i>	2.64	0.97	<i>A. leucogaster</i>	3.02	6.79	<i>A. curacao</i>	2.2	1.85
<i>P. squamipinnis</i>	2.17	1.62	<i>P. vaiuli</i>	2.43	6.16	<i>C. striatus</i>	2.17	1.52
<i>C. cuning</i>	2.11	2	<i>P. paccagnellae</i>	2.18	2.85	<i>P. paccagnellae</i>	2.06	1.21
<i>C. analis</i>	1.82	6.12	<i>Z. scopas</i>	2.09	3.72	<i>C. caudalis</i>	1.77	0.78
<i>P. tuka</i>	1.82	2.31	<i>C. margaritifer</i>	1.77	3.28	<i>P. adelus</i>	1.75	1.17
<i>C. amboinensis</i>	1.8	1.73	<i>C. cyanea</i>	1.65	2.09	<i>Spratelloides sp</i>	1.63	0.56

Since Pearson's correlation analysis indicated highly negative and statistically significant correlation between time and hard coral cover, Year was included as random and Hard coral as fixed effect, in all GLMM models used in the fish analyses.

GLMM for fish community abundance showed statistically significant negative effect of decreasing hard coral cover on the number of individuals (Figure 10, z statistic = 4.09, $P < 0.05$).

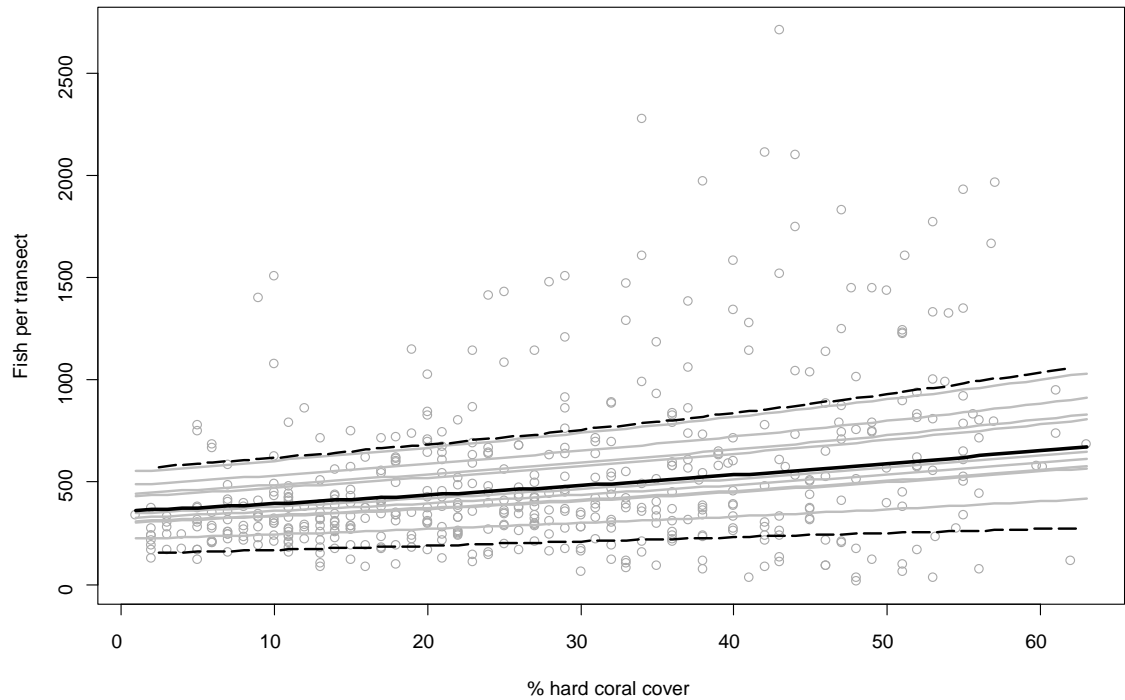


Figure 10: Negative binomial generalized linear mixed effect model fitted to the relationship between fish community abundance and hard coral cover for each year separately (solid grey lines) and mean of all years (solid black line) and confidence intervals of the mean (dashed black lines). Grey circles represent data points.

A high degree of variability in the data was observed for the fish community species richness. Nonetheless, GLMM analysis identified a statistically significant negative effect of decreasing hard coral cover on the number of species, with the same trend observed in all years sampled (Figure 11, z statistic = 4.83, $P < 0.05$). The highest species number observed was 57.3 ($SE \pm 3.1$) species/transect, while the lowest was 19.4 ($SE \pm 5.5$) species/transect.

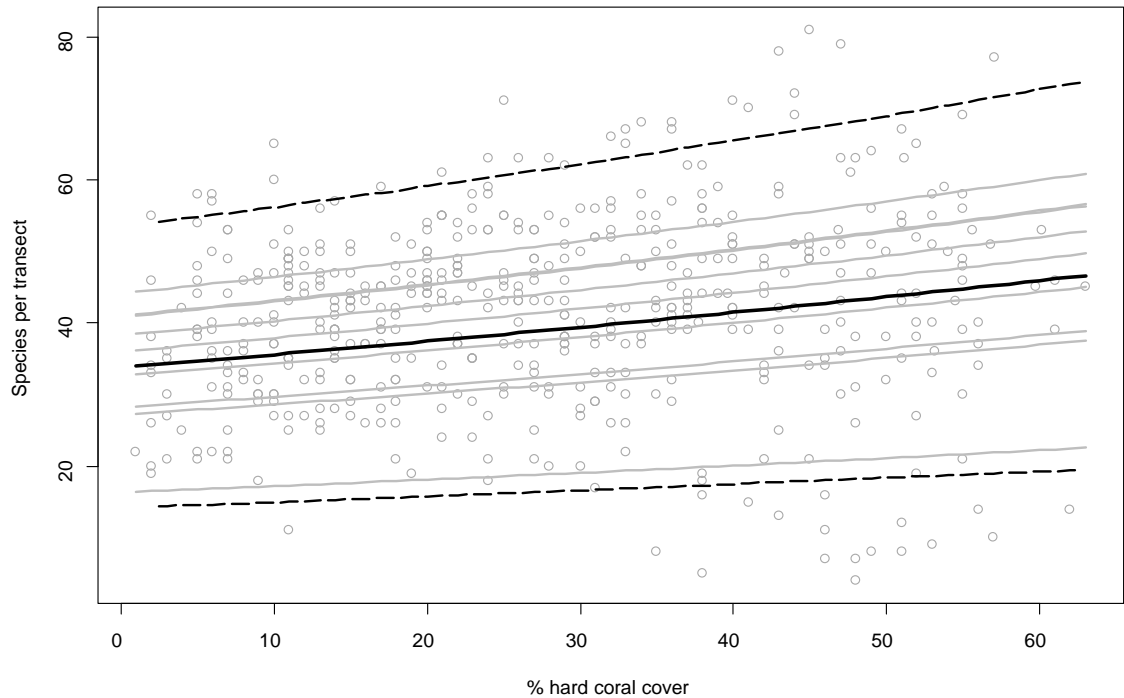


Figure 11: Negative binomial generalized linear mixed effect model fitted to the relationship between fish community species richness and hard coral cover for each year separately (solid grey lines) and mean of all years (solid black line) and confidence intervals of the mean (dashed black lines). Grey circles represent data points.

Zero-inflated GLMMs identified statistically significant abundance relationships with hard coral cover for 13 fish families (Table 8). Acanthuridae, Nemipteridae and Pomacanthidae experienced a negative effect of increasing hard coral cover on abundance (Figure 12A and Figure 13A and B, respectively) and so did Serranidae subfamily Epinephelinae, but to a lesser extent and with a much lower number of samples observed (Figure 12B). Hard coral cover had a positive effect on the abundance of all remaining fish families, with most prominent increases observed in Anthiinae, Chaetodontidae and Pseudochromidae (Figure 12B, D and Figure 13D, respectively).

Table 8: Summary of zero-inflated negative binomial generalized linear mixed effect model showing the effect of hard coral cover and year on fish family abundance. The table shows the best-selected model indicating parameter means with standard errors for fixed effects mean (FEM), and variance terms with standard deviation for random effects variance (REV). Hard coral cover is fixed effects and Year represents random effects. Significance codes: '*' 0.001 '**' 0.01 '*' 0.05.**

Selected model: fish abundance ~ hard coral + random (year)					
FAMILY		FEM ± (SE)	z statistic	P	REV ± (SE)
ACANTHURIDAE	intercept	3.73(0.17)	22.46	***	0.21(0.46)
	hard coral	-0.01(0)	-3.24	**	
ANTHINAE	intercept	3.13(0.34)	9.22	***	0.2(0.45)
	hard coral	0.03(0.01)	3.8	***	
BALISTIDAE	intercept	0.84(0.3)	2.82	**	0.52(0.72)
	hard coral	0.04(0.01)	5.9	***	
CHAETODONTIDAE	intercept	2.35(0.11)	21.7	***	0.05(0.22)
	hard coral	0.02(0)	5.57	***	
HOLOCENTRIDAE	intercept	0.01(0.23)	0.03	0.1	0.06(0.25)
	hard coral	-0.03	0.01	***	
LABRIDAE	intercept	3.07(0.16)	19.28	***	0.18(0.42)
	hard coral	0.01(0)	2.04	*	
LUTJANIDAE	intercept	-0.25(0.29)	-0.85	0.3	0.27(0.52)
	hard coral	0.04(0.01)	5.27	***	
NEMIPTERIDAE	intercept	1.51(0.26)	5.92	***	0.35(0.59)
	hard coral	-0.04(0.01)	-6.29	***	
POMACANTHIDAE	intercept	1.85(0.12)	14.96	***	0.05(0.22)
	hard coral	-0.01(0)	-2.8	**	
POMACENTRIDAE	intercept	5.33(0.13)	39.91	0.4	0.12(0.35)
	hard coral	0(0)	1.72	*	
PSEUDOCHROMIDAE	intercept	0.58(0.42)	1.37	1.1	1.22(1.11)
	hard coral	0.05(0.01)	6.61	***	
SERRANIDAE	intercept	0.99(0.27)	3.67	***	0.51(0.71)
	hard coral	-0.02(0.01)	-3.52	***	
ZANCLIDAE	intercept	-0.18(0.38)	-0.47	0.1	1.11(1.05)
	hard coral	0.02(0.01)	3.9	***	

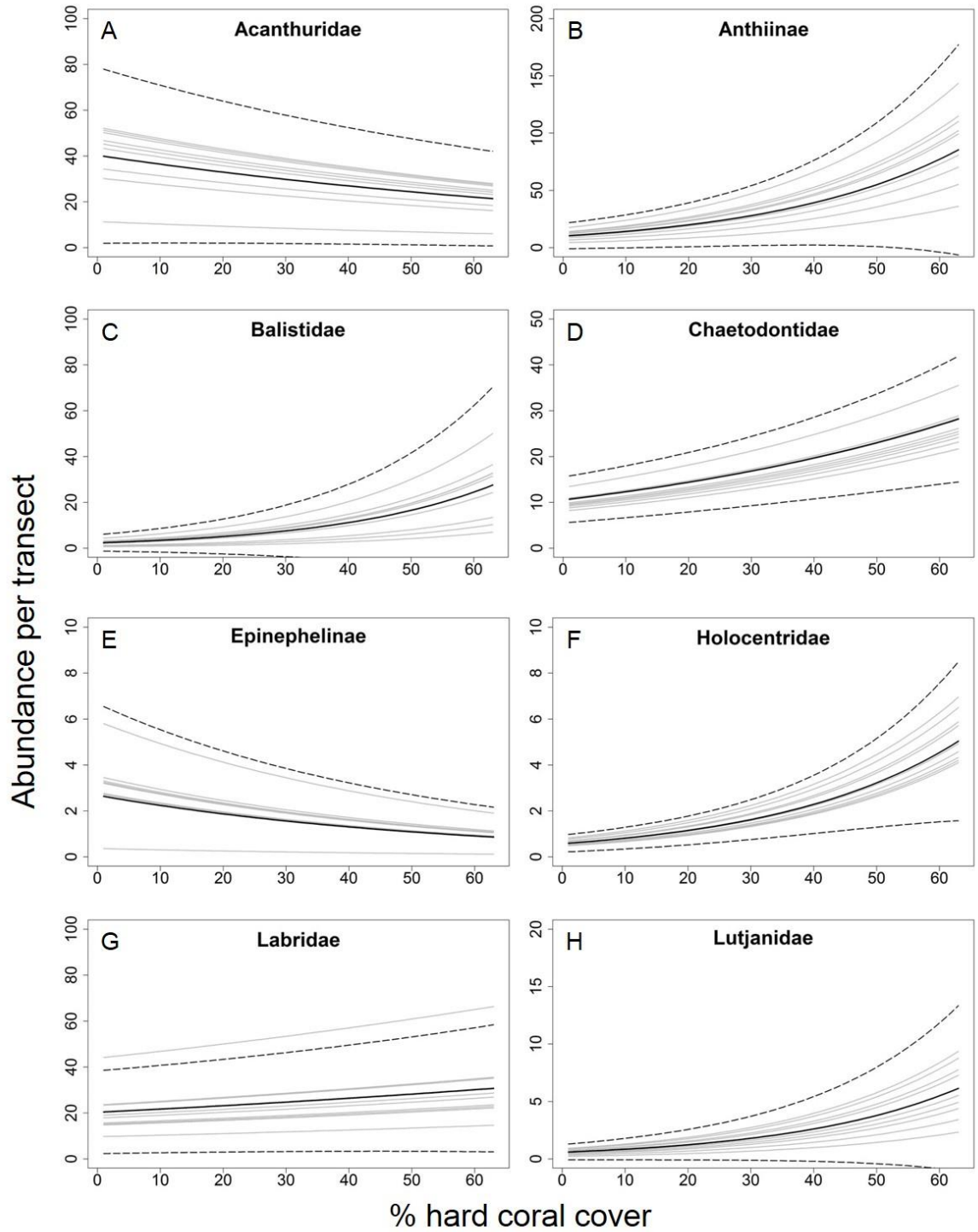


Figure 12: Zero-inflated negative binomial generalized linear mixed effect models fitted to the relationship between fish families' abundance and hard coral cover for each year separately (solid grey lines) and mean of all years (solid black line) and confidence intervals of the mean (dashed black lines): A) Acanthuridae, B) Anthiinae, C) Balistidae, D) Chaetodontidae, E) Epinephelinae, F) Holocentridae, G) Labridae, H) Lutjanidae.

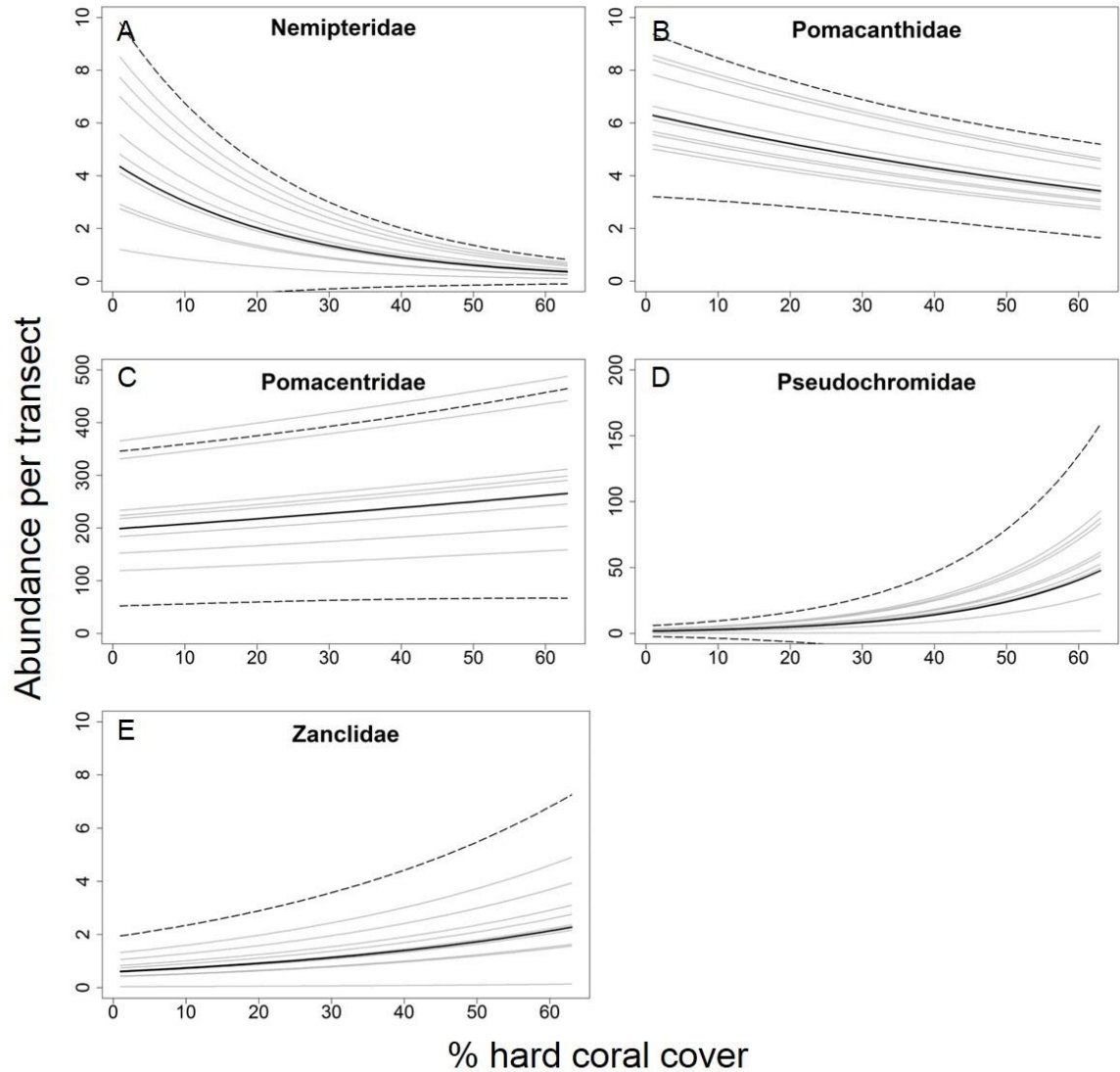


Figure 13: Zero-inflated negative binomial generalized linear mixed effect models fitted to the relationship between fish families' abundance and hard coral cover for each year separately (solid grey lines) and mean of all years (solid black line) and confidence intervals of the mean (dashed black lines): A) Nemipteridae, B) Pomacanthidae, C) Pomacentridae, D) Pseudochromidae, E) Zanclidae.

Of the 13 fish families, 8 had >1% fish community abundance contribution. Subsequently, within the each family with >1% abundance contribution, a number of fish species with statistically significant hard coral cover – abundance relationship were identified by the zero-inflated GLMMs (Table 9). For Acanthuridae, *Ctenochaetus striatus* was the species with the most notable change in abundance, with a highly negative relationship with increasing coral cover (Figure 14A). Both species of Anthiinae considered experienced strong positive

relationships with increasing coral cover (Figure 14B). Within Chaetodontidae family, a large number of species with significant hard coral cover – abundance was identified, all of which had a positive relationship with increasing coral cover (Figure 14C). Although the model identified 3 species, only *Odonus niger* seemed to experience a notable (positive) change in abundance with increasing coral cover, for Balistidae family (Figure 14D). Labridae species had a mixed response, with 3 positive and 3 negative relationships, with increasing coral cover (Figure 15A). Two out of 3 Pomacanthidae species demonstrated negative hard coral cover – abundance relationships (Figure 15B). The majority positive response of Pomacentridae species (5 out of 7) to increasing coral cover was observed (Figure 15C). Finally, the only species of Pseudochromidae family considered, *Pictichromis paccagnellae*, increased strongly with the growing hard coral cover (Figure 15D).

Table 9: Summary of zero-inflated negative binomial generalized linear mixed effect model showing the effect of hard coral cover and year on fish abundance. The table shows the best-selected model indicating parameter means with standard errors for fixed effects (FEM), and variance terms with standard deviation for random effects (REV). Hard coral cover is fixed effects and Year represents random effects. Significance codes: '**' 0.001 '***' 0.01 '**' 0.05.**

Selected model: fish abundance ~ hard coral + random (year)											
FAMILY/Species		FEM±(SE)	z statistic	P	REV±(SE)	FAMILY/Species		FEM±(SE)	z statistic	P	REV±(SE)
ACANTHURIDAE						LABRIDAE					
<i>C. striatus</i>	intercept	3.25(0.24)	13.58	***	0.47(0.69)	<i>H. hortulanus</i>	intercept	0.98(0.36)	2.71	**	1.07(1.04)
	hard coral	-0.03(0)	-7.2	***			hard coral	-0.02(0.01)	-2.79	**	
<i>Z. scopas</i>	intercept	2.11(0.17)	12.48	***	0.17(0.42)	<i>H. prosopeion</i>	intercept	-1.07(0.61)	-1.75	0.08	2.2(1.48)
	hard coral	-0.01(0)	-2.18	*			hard coral	0.04(0.01)	3.87	***	
<i>N. vlamingii</i>	intercept	-0.93(0.62)	-1.5	0.13	1.85(1.36)	<i>H. melapterus</i>	intercept	0.65(0.42)	1.55	0.12	1.21(1.1)
	hard coral	0.04(0.01)	2.51	*			hard coral	-0.02(0.01)	-1.96	*	
ANTHINAE						<i>C. fasciatus</i>	intercept	-0.99(0.44)	-2.25	*	1.31(1.15)
<i>P. squamipinnis</i>	intercept	-4.43(1.25)	-3.55	***	4.34(2.08)		hard coral	0.02(0.01)	3.28	**	
	hard coral	0.16(0.03)	4.95	***		<i>C. chlorourus</i>	intercept	-0.87(0.53)	-1.64	0.1	1.81(1.35)
<i>P. tuka</i>	intercept	-0.59(1.42)	-0.42	0.68	0.53(0.73)		hard coral	-0.03(0.01)	-2.74	**	
	hard coral	0.1(0.03)	3.23	**		<i>T. amblycephalum</i>	intercept	-0.3(1.19)	-0.25	0.8	12.28(3.5)
BALISTIDAE							hard coral	0.03(0.01)	3.17	**	
<i>O. niger</i>	intercept	2.31(0.47)	4.94	***	0(0)	POMACANTHIDAE					
	hard coral	0.03(0.01)	2.22	*		<i>C. vroliki</i>	intercept	1(0.27)	3.76	***	0.52(0.72)
<i>M. niger</i>	intercept	-3.49(1)	-3.48	***	3.87(1.97)		hard coral	-0.02(0.01)	-3.71	***	
	hard coral	0.05(0.02)	2.27	*		<i>P. diacanthus</i>	intercept	-0.15(0.32)	-0.47	0.64	0.69(0.83)
<i>M. vidua</i>	intercept	-1.68(0.6)	-2.8	**	2.39(1.55)		hard coral	0.02(0.01)	2.87	**	
	hard coral	0.04(0.01)	4.34	***		<i>C. tibicen</i>	intercept	1.04(0.24)	4.3	***	0.08(0.28)
CHAEDONTIDAE							hard coral	-0.03(0.01)	-3.47	***	
<i>F. flavissimus</i>	intercept	0.37(0.31)	1.18	0.24	0.76(0.87)	POMACENTRIDAE					
	hard coral	0.01(0)	3.02	**		<i>P. vaiuli</i>	intercept	2.59(0.44)	5.84	***	1.64(1.28)
<i>C. lunulatus</i>	intercept	-0.21(0.35)	-0.59	0.56	0.96(0.98)		hard coral	-0.03(0.01)	-3.87	***	
	hard coral	0.02(0.01)	3.42	***		<i>C. amboinensis</i>	intercept	1.57(0.48)	3.27	**	1.36(1.17)
<i>C. baronessa</i>	intercept	-0.34(0.3)	-1.15	0.25	0.52(0.72)		hard coral	0.04(0.01)	3.84	***	
	hard coral	0.02(0.01)	2.88	**		<i>D. reticulatus</i>	intercept	3.14(0.68)	4.6	***	4.59(2.14)
<i>H. varius</i>	intercept	-0.21(0.31)	-0.66	0.51	0.57(0.76)		hard coral	-0.02(0.01)	-2.81	**	
	hard coral	0.01(0.01)	2.5	*		<i>P. lepidogenys</i>	intercept	2.15(0.2)	10.79	***	0.01(0.09)
<i>C. punctatofasciatus</i>	intercept	-0.57(0.36)	-1.6	0.11	0.02(0.15)		hard coral	0.01(0.01)	2.34	*	
	hard coral	0.03(0.01)	4.36	***		<i>C. analis</i>	intercept	0.84(0.82)	1.02	0.3	1.38(1.18)
<i>H. chrysostomus</i>	intercept	-0.88(0.36)	-2.42	*	0.1(0.31)		hard coral	0.05(0.02)	2.58	**	
	hard coral	0.03(0.01)	3.59	***		<i>C. lepidolepis</i>	intercept	-0.77(0.68)	-1.13	0.26	2.86(1.69)
<i>C. meyeri</i>	intercept	-2.24(0.57)	-3.97	***	0.18(0.42)		hard coral	0.05(0.01)	3.51	***	
	hard coral	0.05(0.01)	4.61	***		<i>C. retrofasciata</i>	intercept	0.05(0.92)	0.05	0.96	2.62(1.62)
PSEUDOCHEMIDAE							hard coral	0.04(0.02)	1.97	*	
<i>P. paccagnellae</i>	intercept	1.86(0.53)	3.47	***	2.19(1.48)						
	hard coral	0.03(0.01)	2.94	**							

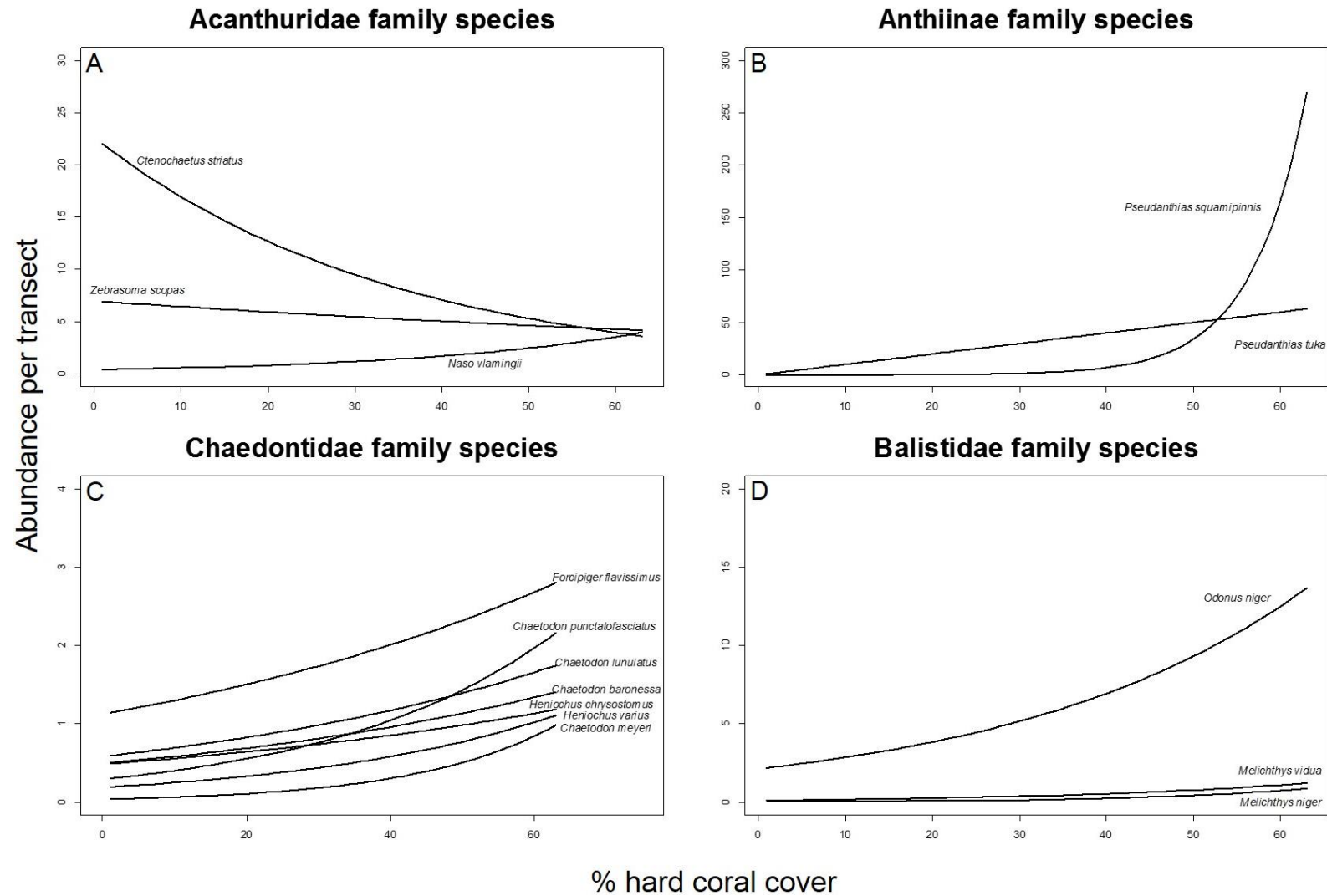


Figure 14: Statistically significant zero-inflated negative binomial generalized linear mixed effect models for the relationship between species' abundance and hard coral cover for each year separately (solid grey lines) and mean of all years (solid black line) with the mean confidence intervals (dashed black lines): A) Acanthuridae, B) Anthiinae, C) Balistidae, D) Chaetodontidae.

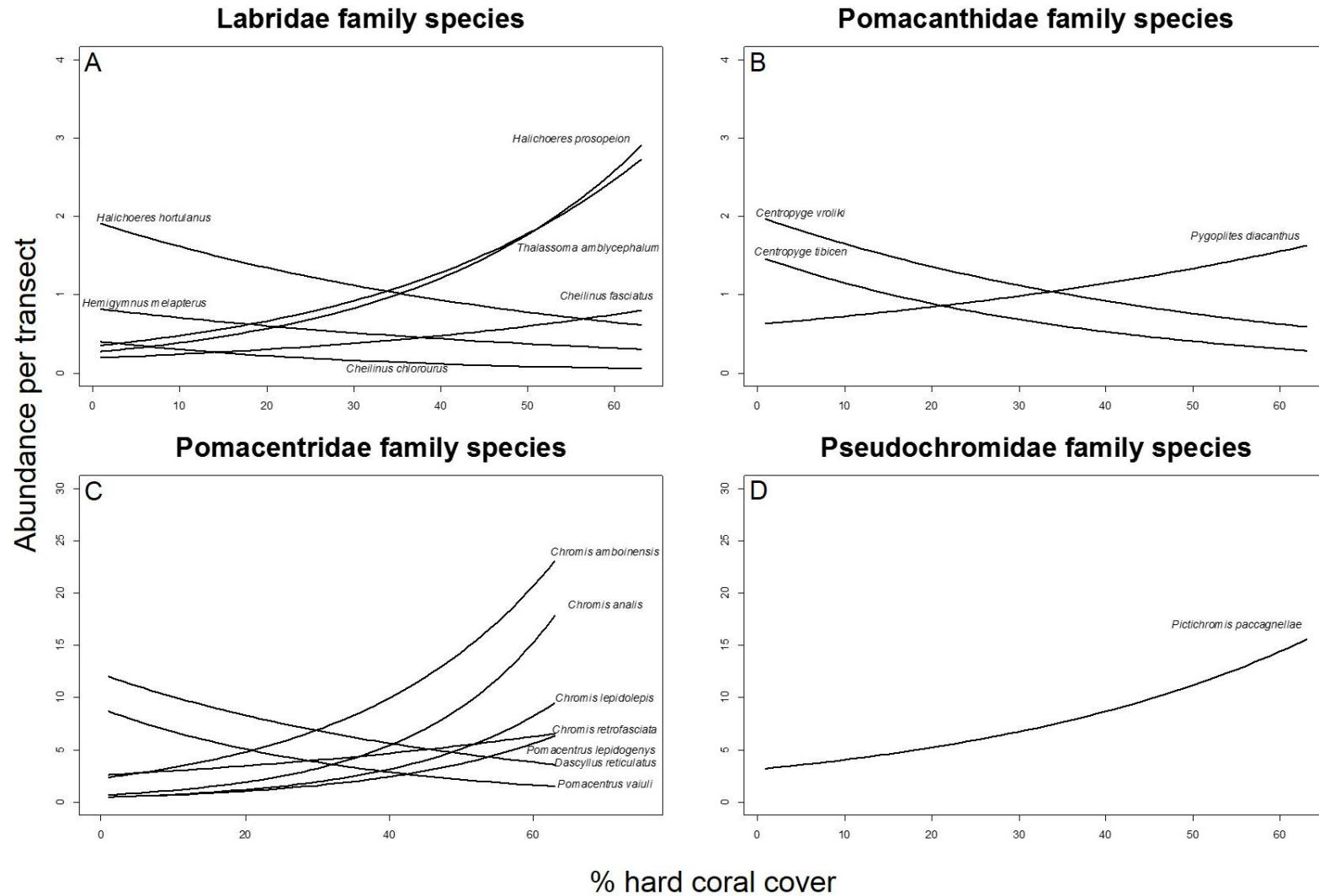


Figure 15: Statistically significant zero-inflated negative binomial generalized linear mixed effect models for the relationship between species' abundance and hard coral cover for each year separately (solid grey lines) and mean of all years (solid black line) with the mean confidence intervals (dashed black lines): A) Labridae, B) Pomacanthidae, C) Pomacentridae, D) Pseudochromidae.

Out of 5 feeding guilds considered, herbivorous was the only guild to show no statistically significant relationship with hard coral cover, identified by GLMMs (Table 10). All 4 feeding guilds with statistically significant relationships experienced a negative effect of increasing hard coral cover on their abundance (Figure 16).

Table 10: Summary of zero-inflated negative binomial generalized linear mixed effect model showing the effect of hard coral cover and year on fish feeding guild abundance. The table shows the best-selected model indicating parameter means with standard errors for fixed effects mean (FEM), and variance terms with standard deviation for random effects variance (REV). Hard coral cover is fixed effects and Year represents random effects. Significance codes: '**' 0.001 '***' 0.01 '**' 0.05.**

Selected model: fish abundance ~ hard coral + random (year)					
Feeding guild		FEM ± (SE)	z statistic	P	REV ± (SE)
Carnivorous	intercept	4.78(0.13)	34.39	***	-6.22(1.02)
	hard coral	0.005(0.002)	2.1	*	
Coralivorous	intercept	2.3(0.12)	17.93	***	-6.15(3.4)
	hard coral	0.01(0.003)	4.17	***	
Omnivorous	intercept	3.76(0.14)	26.65	***	-4.06(0.4)
	hard coral	0.01(0.003)	4.38	***	
Planktivorous	intercept	4.51(0.16)	27.83	***	-5.6(0.78)
	hard coral	0.01(0.003)	3.79	***	

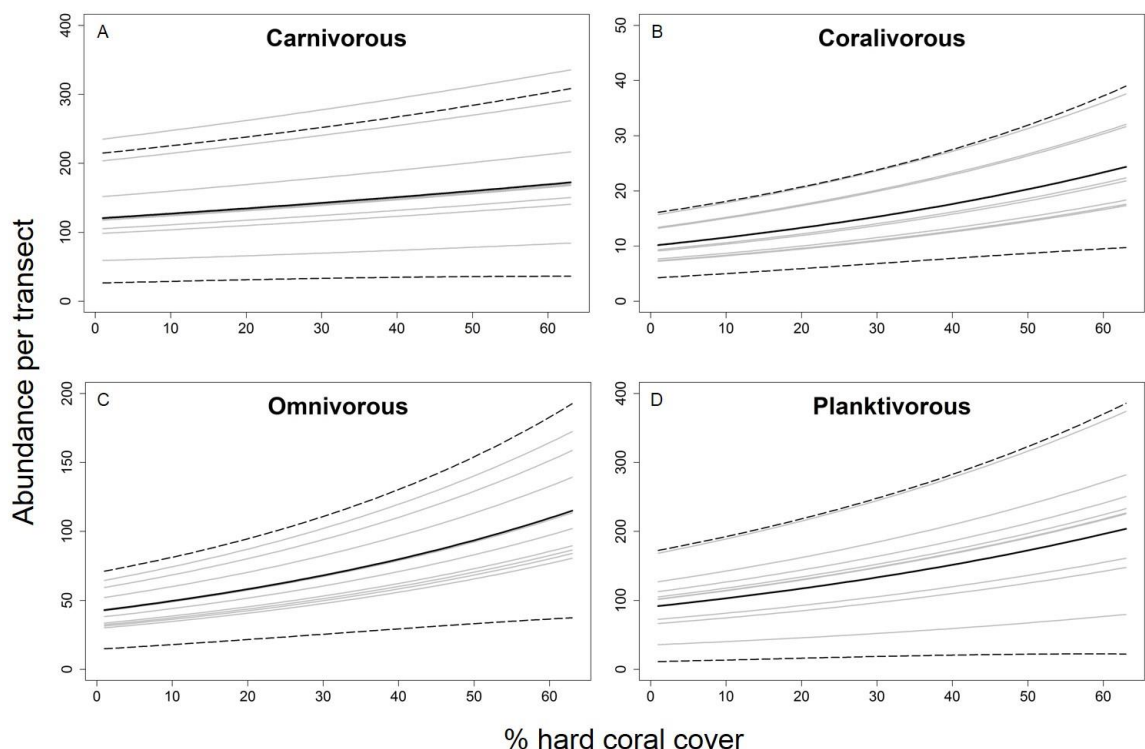


Figure 16: Zero-inflated negative binomial generalized linear mixed effect models fitted to the relationship between fish feeding guilds' abundance and hard coral cover for each year separately (solid grey lines) and mean of all years (solid black line) and confidence intervals of the mean (dashed black lines): A) Carnivorous, B) Coralivorous, C) Omnivorous, D) Planktivorous.

2.4 Discussion

With habitat change resulting from decreasing hard coral cover, a strong decreasing trend in mean fish abundance, at the fish community level, over the entire course of the monitoring period was observed. The trajectory of fish community change coincided highly with prominent events of decrease in hard coral. The outcome was transition of the fish community to a community distinctly different in abundance and species composition to that from the start of the monitoring. A number of similar studies have also identified coral cover as the main driver of change of coral fish communities (Booth and Beretta, 2002; Jones *et al.*, 2004), while others did not (Roberts and Ormond, 1987; Friedlander *et al.*, 2003; Lecchini *et al.*, 2003; Chittaro, 2004; Walker, Jordan and Spieler, 2009). Many of the studies which identified no changes, however, explored habitat – fish associations at different initial hard coral covers and at smaller magnitudes of change, compared to the cover decline of almost 70%, over a period of 11 years, observed in this study.

Although, there are no reports in the literature of any mass bleaching events for the study area immediately prior, during or after the monitoring, OISST data demonstrated a large number of temperature peaks, exceeding coral bleaching threshold, while ERSST data confirmed occurrence of DHMs in 2002, 2005 and 2006, which could have contributed to the reduction in hard coral cover observed. Even if no direct bleaching occurs, regular increases in temperature can weaken corals by reducing their growth rates and reproductive potential, and leave them more vulnerable to disease (Burke *et al.*, 2011). The change in habitat however, could have also been coupled with and further exacerbated by other important factors and driven by multiple mechanisms. Illegal use of cyanide and explosives in fishing has been reported to significantly contribute to reef destruction throughout Indonesia (Allen and Werner, 2002). Bomb fishing, causing physical destruction of coral,

was identified as one of the most prevalent fishing practices used within the WNP (Clifton, Unsworth and Smith, 2010). With high density of the population present, coupled with their dependency on the reef for food, it is likely that the physical damage to the habitat produced would have been considerable. A number of personal observations of the blast fishing damage to the coral, as well as hearings of explosions in the close proximity, were made throughout the monitoring period. Finally, fast coral disease progression rates and high tissue mortality rates for coral diseases have also been reported on many of the sites sampled in the park (Haapkylä *et al.*, 2009).

While the alteration of the habitat had a strong effect on the fish community abundance, the effect on the fish community richness was more subtle, with large variation observed in the data. Nonetheless, the effect was identical – with a decrease in hard coral cover the number of species also decreased. In accordance with these results, several studies also found positive relationship between coral cover and fish species richness, whereas others identified no correlation between the two (Bell and Galzin, 1984; Sano, Shimizu and Nose, 1984). Interestingly, there are also authors which argue that a small decline in hard coral cover can produce an increase in species richness, but only at initially high coverage, and that further coral loss of >20% results in a subsequent decline in species richness of fish communities (Wilson *et al.*, 2006). The total number of species and family level assemblage composition (213 species, 34 families) identified over the course of the monitoring period in the WNP of South-east Sulawesi were closely comparable to those observed in the areas of North Sulawesi, where a total number of 264 species belonging to 36 families were reported between 2005 and 2007 (Ferse, 2008). In other localities around Indonesia, such as around Pari Island, Togean Islands and Weh Islands, similar numbers of species present were also reported (Allen and Werner, 2002; Madduppa *et al.*, 2012). It is however worth noting that the numbers reported in the geographically neighbouring studies were observed over variable

time and spatial scales. The number of species identified in this study was markedly higher than in tropical shallow reef ecosystems reported from other areas of the world (e.g. Gladfelter, Ogden and Gladfelter, 1980; Khalaf and Kochzius, 2002). The area of the South-east Sulawesi, in which the monitoring took place, is characterised by highly complex and complete tropical ecosystems, formed between coral reefs and mangrove swamps and seagrass habitats found in close proximity (Unsworth *et al.*, 2009). As a result, in addition to being set within a highly biodiverse region, the fish biodiversity likely benefited from associations with mangrove and seagrass habitats, both known to make significant contributions in fish numbers to the adjacent reefs, and increase their biodiversity (Robertson and Duke, 1987; Blaber *et al.*, 1992; Unsworth *et al.*, 2008).

For fish families, Anthiinae and Pseudochromidae showed a strongly positive abundance relationship with coral cover, resulting in large decreases in their numbers over the course of the monitoring period, in conjunction with the change in habitat. At species level, positive relationships with hard coral cover of all the species considered within these families were also observed. Most Anthiinae and Pseudochromidae live close to the substratum and due to their small size rely on the coral structural matrix for shelter. Their decline in abundance observed in this study could be attributed to the loss of habitat caused by bomb fishing, resulting in direct structural collapse of the reef matrix. Decrease in abundance was also seen for Pomacentridae, another family of small-bodied coral dwellers, as well as for a number of species within the family. Prior to 2006, the most dominant species were exclusively made up of the members of small bodied, coral habitat – reliant fish families, and although the dominance between some of these species changed over years, they were subsequently generally replaced by species of the same family. After 2006, loss of dominance of certain small bodied and their replacement by the species of other families was observed. In the study, this further confirms the argument of the reliance of these families on coral habitat,

since the shift in species dominance occurred at the point at which the benthic habitat experienced profound changes. Besides the essential habitat loss for small-bodied coral dwellers, reduction in hard coral can also cause reduction in food availability for coral feeding fish. Here, these fish were represented by a number of species within the Chaedontidae. A strong relationship between hard coral cover and fish abundance of this family, resulting in a decrease in fish numbers over the monitoring period due to the coral loss was observed. Even though not all members of the family are obligate coralivores, all species considered in the study had a positive relationship with hard coral. Concordant with these findings, there is a large body of evidence also confirming the positive correlation between the abundance of Chaedontidae and the amount of hard coral available (Roberts, Shepherd and Ormond, 1992; Chabanet and Letourneur, 1995). There is some evidence, however, that the hard coral cover is not always the most important limiting factor for the abundance of Chaedontidae and the effects could be species dependent (Fowler, 1990).

While this study demonstrated consistent declines as a result of changing habitat for the entire fish community abundance, as well as for a number of fish families and species, the abundance of certain fish families and species increased. Acanthuridae, Nemipteridae and Pomacanthidae represented the most prominent examples. Within Acanthuridae, *C. striatus* expressed a strong positive relationship with decreasing hard coral cover. Most members of this family (including *C. striatus*) are herbivorous/detritivorous, feeding on surface film of algae covering abiotic substrate and loose sediment (Krone *et al.*, 2008). Reduction in coral cover was accompanied by an increase in abiotic cover, thereby increasing the food availability for these fish. Subsequently, the rise in the abundance of Acanthuridae, can be explained by the reduction in live coral and a resulting increase in abiotic cover, observed here. Furthermore, although the overall species composition did not change dramatically, abundance contribution of the species pointed to a shift in dominance over years, with the

appearance of *C. striatus* in 2006 and a decrease in dominance of previously higher ranked Pomacentridae members. The period of the shift in species dominance corresponds to that of large decreases in hard coral cover and increases in abiotic cover, resulting in the shift in abundance of certain species. Increase in Acanthuridae species, following reduction in hard coral cover, has also been reported in previous studies (e.g. Lindahl *et al.* 2001), however there also are those which failed to detect the relationship (Hart and Russ, 1996; Sano, 2004), as well as studies which reported a decrease in Acanthuridae abundance (Wilson *et al.*, 2006). Fishes of Pomacanthidae and Nemipteridae also experienced increases in numbers, for entire families, and a number of individual species considered within Pomacanthidae. Species belonging to these families are commonly highly mobile invertebrate and small benthic fish feeders which, as a result, do not depend strongly on live coral, for food or habitat (Russell, 1990; Nelson, 2006). Furthermore, they may also benefit from increases in abiotic cover, primarily rubble and turf, housing many larval fish and invertebrates. Accordingly, as the findings suggest, the change in habitat composition did not have a negative effect on the species of this family and their numbers increased following decrease in coral cover.

The abundance of Carnivorous, Coralivorous, Omnivorous and Planktivorous feeding guilds demonstrated positive relationship with hard coral cover. Herbivorous feeding guild, however, had no statistically significant relationship with changing coral cover. This, most certainly at least in part, could have been attributed to the specific species composition of this particular guild. The feeding guild was predominately made up of species belonging to Acanthuridae and Pomacentridae families. While Acanthuridae had strong negative relationship, Pomacentridae had positive relationship with hard coral cover and as a consequence, most likely resulted in failure to detect a relationship when both were put together. These findings were further supported by analyses of the species composition

similarity and those of family dominance change through time. During the initial years of monitoring, characterised by high hard coral cover, Pomacentridae species were overall amongst the most prominent in terms of species composition and family dominance. In the final years of study, in which hard coral cover was much lower, Acanthuridae were established and significantly characterised species composition and family assemblage. However, despite no statistically significant relationship observed between herbivores and hard coral cover, the analysis of the feeding guilds dominance identified the herbivorous guild as the one most responsible for change in dominance through time. While the composition of the fish feeding guilds was dominated by the planktivorous guild throughout, a strong and ubiquitous presence of the herbivorous feeding guild was evidenced post 2005.

In conclusion, while this chapter does not investigate the specific principles of how different parts of the habitat are used on a small scale or across different marine ecosystems, it unarguably demonstrates how important the overall habitat is in structuring the associated fish community. As the results demonstrated, this is mainly due to the fish dependency on the habitat for shelter and food. At the current rate of loss and degradation of this essential habitat, recovery of fish stocks is unlikely and further fish declines are expected. In turn, the fisheries which provide food security, livelihoods and well-being to thousands of people within the WNP, are seriously threatened. Consequently, threats to these reefs do not only endanger ecosystems and marine species, but also directly threaten the adjacent communities which depend on the essential ecosystem services provided by them. The relative importance of the reefs is further emphasised by the fact that many people within the WNP live in poverty and have very limited or no capacity to adapt to the effects of reef degradation. According to this, a much more effective conservation and sustainable use of coral reef resources may be the only option to overcome the loss of ecosystem services provided by the reefs of the WNP.

2.5 Supplementary material

2.5.1 Most abundant species (copyright FishBase)



Amblyglyphidodon curacao
(Staghorn damselfish)



Amblyglyphidodon leucogaster
(Yellowbelly damselfish)



Caesio cuning
(Redbelly yellowtail)



Caesio teres
(Yellow and blueback fusilier)



Chromis amboinensis
(Ambon chromis)



Chromis analis
(Yellow chromis)



Chromis ternatensis
(Ternate chromis)



Chromis viridis
(Blue green damselfish)



Chrysiptera cyanea
(Blue devil)



Ctenochaetus striatus
(Lined bristletooth)



Dascyllus reticulatus
(Reticulate dascyllus)



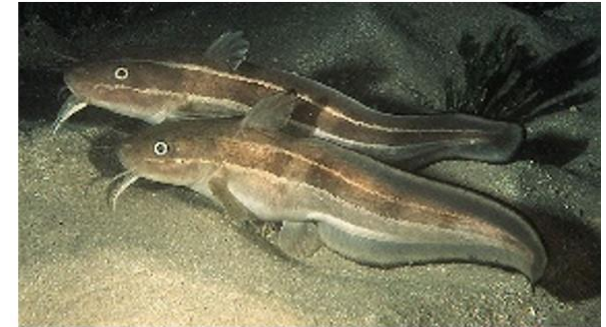
Neoglyphidodon nigroris
(Black and gold chromis)



Odonus niger
(Red-toothed triggerfish)



Pictichromis paccagnellae
(Royal dottyback)



Plotosus lineatus
(Striped eel catfish)



Pomacentrus brachialis
(Charcoal damsel)



Pomacentrus moluccensis
(Lemon damsel)



Pomacentrus vaiuli
(Ocellate damselfish)



Pseudanthias huchtii
(Threadfin anthias)



Pseudanthias squamipinnis
(The sea goldie)



Pseudanthias tuka
(Bartlett's Anthias)



Pterocaesio tile
(Dark-banded fusilier)



Thalassoma amblycephalum
(Bluntheaded wrasse)



Zebrasoma scopas
(Brown tang)

3 Chapter 3: Fish habitat use within and across tropical and temperate reefs

3.1 Introduction

Previously, the effects of changing reef habitat on the entire reef – associated fish community were discussed in a tropical ecosystem (Chapter 2). The current chapter focused on a number of fish species, commonly occurring in these tropical ecosystems, to examine the effect of behavioural variation in habitat use through niche partitioning. At the same time, the effect of behavioural variation in niche partitioning was also observed for a number of species from a temperate ecosystem. The mechanisms of fish habitat use were subsequently compared within, as well as across the ecosystems studied. As a result, this chapter increases the understanding of the role the habitat plays in niche partitioning processes responsible for sculpturing fish communities.

The species' niche can be described as an n-dimensional hyperspace partitioned into environmental and trophic (resource) components, representing the ecosystem (Hutchinson, 1957). The fundamental niche is defined as the space resulting from the combination of physiological and behavioural characteristics in the absence of competition, when the species potentially occupies the space along all the axes of the ecosystem (Begon, Harper and Townsend, 2006). The presence of physiologically intolerable environmental conditions, dominant competitors and predation pressure, along the ecosystem axes, prevents the species to fully exploit the entire ecosystem, so the constrained space actually occupied by the species under these effects represents the realised niche (Hutchinson, 1957; Whittaker, Levin and Root, 1973; Devictor *et al.*, 2010). As a result of many different simultaneous interactions shaping and defining its size, realised niche space is n-dimensional. In order to measure any dimension of the realised niche, an interaction of the

specific acting agents needs to be considered. Empirical studies encompassing *in situ* niche measurements are extremely scarce and the relative roles of the interactions which shape species' realised niches, other than those based on species' phenotypic traits, remain poorly understood (Hooper *et al.*, 2005; Tingley *et al.*, 2014).

How habitat influences the distribution of organisms is of central importance to ecology (Nanami *et al.*, 2005), with a number of studies reporting species-specific habitat associations (Jones, 1991). To date however, in order to understand communities and ecosystems, studies generally do not take into account the organisms' evolutionary history for evaluating the species' ecosystem function and subsequently quantifying the species' niches (Petchey and Gaston, 2006; Villéger, Novack-Gottshall and Mouillot, 2011). In 2014, Bellwood and Brandl pioneered a study, by measuring *in situ*, part of the realised niche of herbivorous fish species on a tropical marine coral reef (Brandl and Bellwood, 2014). The niche sizes of the species studied were calculated and were subsequently used to infer the degrees of the redundancy and complementarity between the species.

To describe a realised niche, currently most interest is based around the measurement of the niche space, delineated by a number of individuals with the most extreme positions within the sample, represented by the total area of the convex hull (TA) encompassing the data points (Jackson *et al.*, 2011; Brandl and Bellwood, 2014). The niche sizes obtained using this method are generally characterised by a smaller number of divergent individuals within the population and thus measuring the TA takes into consideration individual variability within a species. More recently, a different method based on the measurement of the standard ellipses (SEA) has been proposed. While SEA provide ecologically relevant information about the individual, population or community they represent (Bearhop *et al.*, 2004), the SEA metric has only been discussed for the calculations of the isotopic niche overlaps

(Jackson *et al.*, 2011; Syväranta *et al.*, 2013). The use of SEA has been argued mainly because this method may not be as strongly influenced by the sample size as the convex hull method. The SEA essentially represents the niche mean values of the community in question (Jackson *et al.*, 2011). Ecologically speaking this method does not emphasise the importance of the within-species individual variability and likely represents the niche space delimited by the most frequent and abundant traits characterising the individuals sampled. As such, the SEA niche measurement method is representative of the niche of the majority of the individuals within the population, but not of the few divergent individuals.

Using individual based, continuous behavioural data, estimations were made of realised niches sizes, the niche overlaps and the interactions between the TA and SEA metrics, for the most commonly occurring species of the fish families representative of distinct feeding guilds within a tropical coral- and temperate algal- dominated reef habitat. Patterns of fish habitat partitioning were observed and compared for species, within each and across different ecosystems, as a function of the space occupied at any given moment, while considering behaviour traits, based on what the fish do while moving, as well as the total time dedicated to each habitat occupancy and related behaviour. By carrying out the continuous individual behavioural observation, documenting all behavioural units and habitats used, a new way of assessing realised niches of species in the habitats studied is offered. Firstly, realised niche overlaps were compared by measuring the TA of each species, but as an alternative, a metric based on SEA was also used. Subsequently an attempt was made to give a comprehensive comparison of the differences in the realised niche sizes between the two metrics used. In order to address the issue of the adequate sample size encountered in ecological studies, an alternative sample size correction was presented for the both metrics and the pros and cons of using either was discussed. The following hypotheses were tested: i) the time budget for occurrence in a specific habitat and expressing

certain behaviour associated with a substrate type will be distinct for fish species within and across ecosystems; ii) realised niche sizes will differ between species and ecosystems; iii) the optimum sample size for measuring the realised niche will be independent of the ecosystem studied but dependent on the measurement metric used.

3.2 Materials and methods

Field-based observations were conducted using behavioural time budgets to measure part of the realised niche and their overlaps and subsequently test for sample size dependency for a number of fish species on tropical coral- and temperate algal-dominated rocky reefs.

3.2.1 Sampling habitats and species

The sampling took place on the coral reefs around Curieuse and Praslin islands in the Seychelles in the Indian Ocean and on the algal-covered rocky reefs off the western coast of Mallorca island in the Western Mediterranean Sea, in April and June of 2015, respectively (Figure 17). In both locations 8 different sites were sampled, each separated by a minimum distance of 500m (Table 11)

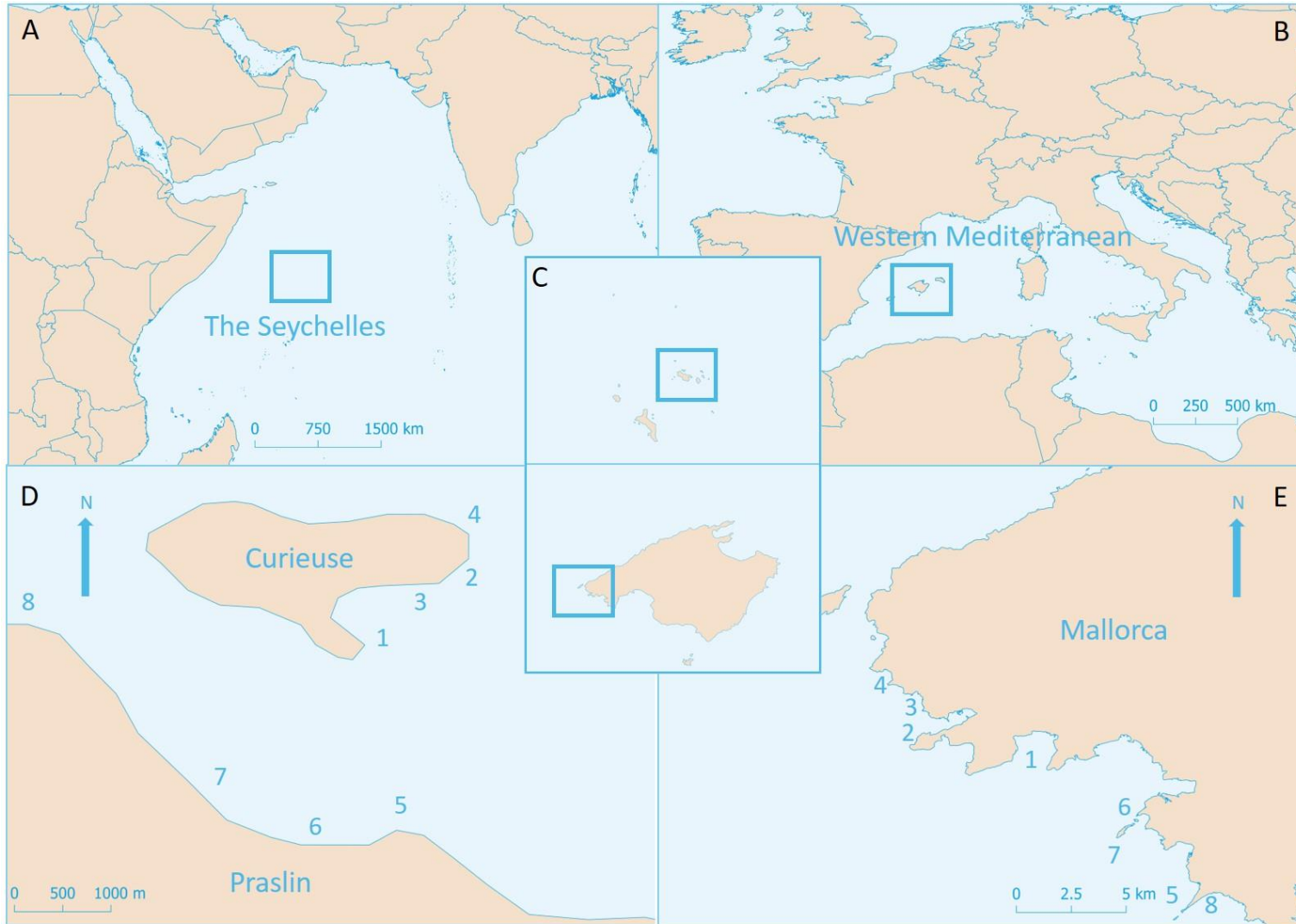


Figure 17: Sampling locations. Boxed areas represent A) The Seychelles, B) Western Mediterranean, C) Curieuse and Praslin islands' and western coast of Mallorca sampling area; D) Seychelles sampling sites and E) Mallorca sampling sites.

Table 11: Sampling sites' geographic coordinate locations.

Site N°	Seychelles	Latitude	Longitude	Mallorca	Latitude	Longitude
1	Baie Laraie	4°17.19'	55°43.56'	Cala Egos	39°33.12'	2°22.06'
2	East Bay	4°16.55'	55°44.3'	Cala Llamp	39°31.7'	2°23.29'
3	Home Reef	4°17.3'	55°44.14'	Es Basc	39°35.92'	2°21.29'
4	Point Rouge	4°16.4'	55°44.37'	Es Guix	39°31.41'	2°25.29'
5	PS1	4°18.22'	55°44.8'	Es Total	39°33.32'	2°21.62'
6	PS3	4°18.31'	55°43.43'	Malgrats Este	39°30.05'	2°27.2'
7	PS4	4°18.17'	55°43.8'	Malgrats Oeste	39°29.92'	2°27.1'
8	PS6	4°17.21'	55°42.14'	Rafaubeitx	39°28.32'	2°29.44'

On the coral reefs, the data collection was conducted between 1m and 12.5m, while on the algal-covered rocky reefs the sampling depth was between 1m and 15m. At each site the fish community and the habitat composition were assessed by underwater visual census (Harmelin-Vivien *et al.*, 1985; English, Wilkinson and Baker, 1997). All the fish sighted within 2.5m to each side and 5m above the 30m transect were recoded and identified to species level. The sampling was conducted between 09:00 and 14:00h, excluding the high activity periods of early morning and late afternoon, thus reducing variability in fish densities due to diurnal influence on behaviour (Colton and Alevizon, 1981; Harmelin-Vivien *et al.*, 1985). The continuous Line Intercept Transect technique was used to assess the benthic community along the same 30m transects used for fish surveys (English, Wilkinson and Baker, 1997). The area intercepting the transect tape was classified according to the benthic category and the percentage cover of each category was then calculated by dividing by the total transect length and multiplying by hundred. The cover was estimated for the same number of benthic categories in each location; algae, branching, massive and dead coral, rock, rubble and sand for the Seychelles and *Posidonia oceanica*, erect, filamentous and turf algae, rock, rubble and sand for Mallorca.

Based on the data from the visual censuses, the most abundant fish families were subsequently identified. Whenever logistically possible, the most commonly occurring

species within the families from different feeding guilds were used for the behavioural sampling. The following coral reef species were selected in the Indian Ocean: *Pomacentrus caeruleus* (planktivore), *Ctenochaetus striatus* (detritivore), *Hemigymnus melapterus* (macro-invertebrate feeder), *Chaetodon trifasciatus* (coralivore). As the Mediterranean study species *Symphodus tinca* (macro-invertebrate feeder), *Coris julis* (micro-invertebrate feeder), *Sarpa salpa* (herbivore) and *Diplodus vulgaris* (omnivore) were selected. All observations were carried out on adult individuals with full adult marking and of an adult size. In a case in which the fish exhibited a detectable response to the observer, the data was discarded.

3.2.2 Behaviour

The optimum sampling time was determined by initial, continuous, 30 minute observations of 4 individuals of each species. The total number of behaviours the individual demonstrated during this period was recorded in order to subsequently plot the cumulative number of observed behaviours by the time and species (Lehner, 1979). The total observation time was broken down into accumulating five minute periods (Martin and Bateson, 1993). Subsequently, the optimum observation time was determined by identifying the five minute period in which $\geq 80\%$ of all behaviour types were displayed and beyond which few new behaviours were seen for each additional unit of time spent observing.

A randomly selected individual of the study species was followed underwater and all its behaviour was continuously recorded. By using the continuous recording sampling method, it was possible to document a complete account of all behaviour units of interest; occurrence, duration and sequences of events (Lehner, 1979). A catalogue of behaviours observed was made and each behaviour was assigned a short abbreviation in order to make recording the data easier (Brockmann, 1994). The following behaviours were identified; intraspecific (a)

and interspecific aggression (b), advertising (ad), cleaning (c), diffused feeding (df), focused feeding (f), water column feeding (wc), hovering (h), searching (s), roaming (rm) and rubbing (rb). Diffused and focused feeding were defined by a number of bites taken from the substrate – $df \leq 2$, $ff \geq 3$. Advertising (ad) and searching (s) behaviours were observed only in Mediterranean fish species and were not seen in any of the Seychelles' species sampled. In addition, the duration (in seconds), of each behaviour expressed was measured. Finally, the habitat in which each of the behaviours occurred was characterised and recorded. The habitat was assigned the surface orientation (Figure 18), as well as the substratum type. With the exception of the dead coral category found only on the coral reef sites, the abiotic substrata (r: rock, rub: rubble, s: sand) were the same for the both locations. The biotic substrata types included macro-algae (alg) and two broad coral categories - branching (b) and massive (m) for the Indian Ocean coral reefs and seagrass (p) and algal morphotypes (et: erect, fl: filamentous, tf: turf) for the Mediterranean algal-covered rocky reefs. For the Mediterranean reefs, seagrass and algal categories were represented by: p – *Pocedonia oceanica*, et – *Cystoseira spp.*, fl – *Dictyota spp.* and tf – *Corallinaceae spp.*

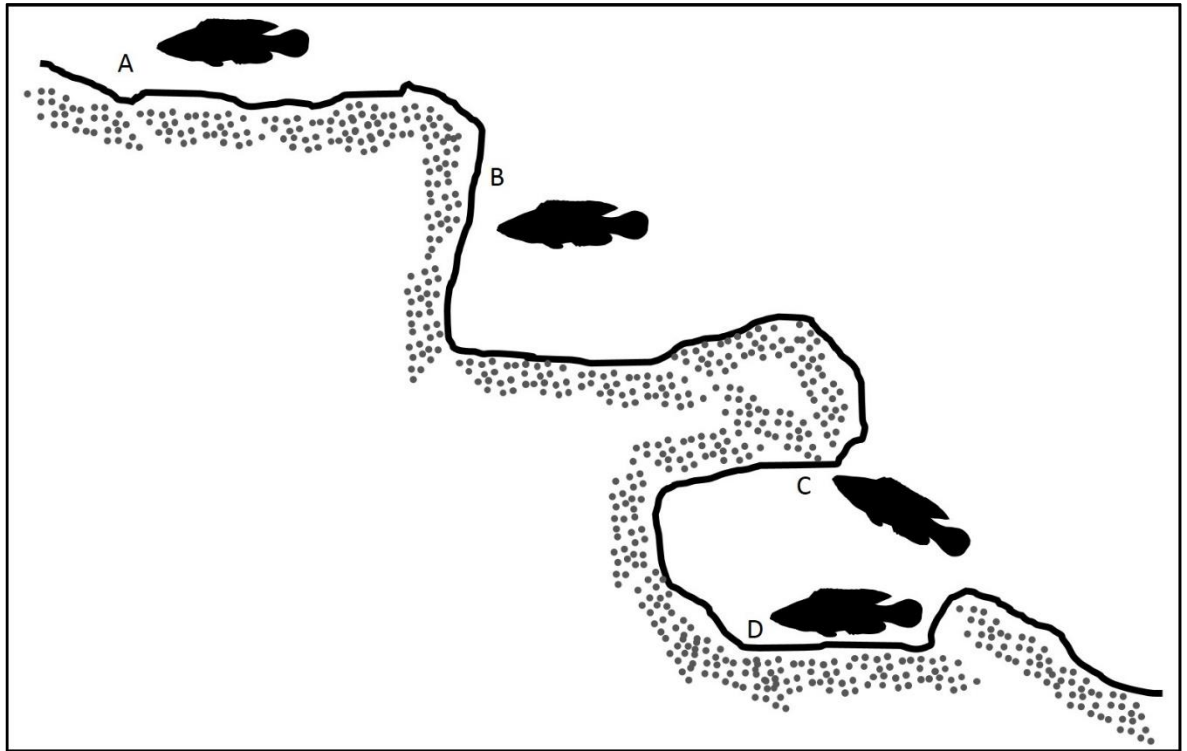


Figure 18: Habitat surface orientation, A: open horizontal, B: open vertical, C: underside or D: concealed.

3.2.3 Convex Hull and Standard Ellipse Area

To assess a realised niche (thereafter RN) of species, a niche space can be created using the behavioural observations made on individuals (Brandl and Bellwood, 2014). The time each behaviour was expressed during the sampling period, the surface position and the substratum type were recorded. Subsequently, a data matrix structure was created with the top row containing labels of all possible combinations of the behaviour, surface position and the substratum type and the main column containing individual fish IDs. The matrix was then populated with each individual's total time contribution to the corresponding combination of behaviour, surface position and substratum type, observed during the 10 minute sampling period.

A principal co-ordinate analysis (PCoA) was performed on the data from the matrix using PrCoord program in CANOCO 4.56 (ter Braak and Smilauer, 2002). Principal co-ordinate analysis can be used to represent patterns from pairwise distance measures and is designed

to function with multiple distance metrics (Brandl and Bellwood, 2014). The data was imported into the PrCoord, log transformed ($\log(y+1)$), with the Euclidian distance used as the distance measure in the calculation. As a result, a data file containing sample coordinates on all PCoA axes with positive eigenvalues was created. Based on the relative importance of the time for each of the combinations in the initial dataset, the eigenvalues of the PCoA analysis represented the position of the individuals in the space from which individual coordinates were extracted (Laliberté and Legendre, 2010). Using the individual coordinates, a species' niche size can be calculated that encompasses all individuals of a species within a given ecosystem (Brandl and Bellwood, 2014).

To work out the species' RNs and the niche overlaps between species, termed the realised niche overlap, representing redundancy or complementarity, two different metrics were used, the Total Area of the Convex Hull (TA) and the Standard Ellipse Area (SEA). The TA is delimited by the individuals within the species of a given sample with the most extreme positions. The SEA calculation method has previously been used for the comparison of the isotopic niche sizes among and within communities (Jackson *et al.*, 2011). The SEA describing some data x and y is underpinned by its associated covariance matrix

$$\left(\Sigma = \begin{bmatrix} \sigma_x^2 & cov(x, y) \\ cov(y, x) & \sigma_y^2 \end{bmatrix} \right)$$

which defines its shape and size, and the means of the x and y that define its location. The eigenvalues (λ) and eigenvectors (v) of Σ then give the lengths of the semi-major axis $a = \lambda_1^{-1}$ and the semi-minor axis $b = \lambda_2^{-1}$, and the angle of the a with the x axis $\theta = \sin^{-1}(v_{12})$. The Standard Ellipse Area is then given by $SEA = \pi ab$ and can be plotted as such.

To display the PCoA results, the file produced by PrCoord was used as the species data file in the CANOCO principal component analysis (PCA) method, with scaling of scores focused on inter-sample distance, no post-transformation of species scores and centring by the species only. The output with the values for the axes 1 and 2 was subsequently used to carry out a number of tasks: plot TAs and SEAs for each species individually, calculate the overlap between the TAs of species, calculate the overlap between the SEAs of species, as well as compare the differences in the percentage overlaps between TAs and SEAs for each species. All the tasks were performed in R software (R Development Core Team, 2015) using the package Stable Isotope Analysis in R (SIAR) (Parnell *et al.*, 2010).

3.2.4 Sample size dependency

The TA and SEA dependency to sample size was tested, as different sample size can change the distribution of time spent in each behaviour. To account for this, and thus investigate the possible change in the values of the TA and SEA of each species, depending on the number of individuals sampled, 1000 resamplings for each sampling size ranging from 10 to 90 individuals were simulated by adding Poisson noise to the behavioural time series. For each empirical sampling the average number of behaviours was calculated and the probability of obtaining 1, 2, 3, 4, ... k behaviours for each individual was estimated. Subsequently the time spent in each behaviour was randomly distributed, accounting for the distribution of time in each behaviour observed in the empirical sampling. All the simulations were performed in Octave software version 4.2.0 (Eaton *et al.*, 2017).

3.3 Results

3.3.1 Habitat

High degree of variability in habitat composition was observed at the Seychelles sites. The branching coral cover ranged from 49.4% at PS4 to 2.3% at Point Rouge, the site which also had the lowest cover of massive coral cover of 9.3%, while Baie Laraie had the highest massive coral cover with 48.2%. The highest % of the rock cover was observed at PS1 (45.2%), Point Rouge (36.7%) and PS6 (36.3%). Home Reef (45.1%) and Point Rouge (42.1%) had the highest cover of rubble, while the remaining two abiotic categories (sand and dead coral) had relatively low presence at all sites. The cover of algae at PS3 was 40.3%, but it was relatively low at the remaining sites. The total number of fish and fish species richness per 100m² ranged between 497.8 individuals and 35.6 species at Point Rouge to 2043.3 individuals and 48.9 species at PS4. In Mallorca on the other hand, the benthic habitat of the sites at which the sampling took place, was overall characterised by algal cover, of which the erect algal morphotype was the most dominant at all sites and ranged from a minimum of 42.6% at Malgrats Oeste, to the maximum of 66.1% of the total benthic cover at Rafaubeitx. The abundance of fish, as well as fish species richness per 100 m², were however much lower than those of the Seychelles sites and ranged from 186.7 individuals at Es Guix and 12.2 species at Cala Egos to 640 individuals and 22.2 species at Es Total (Table 12).

Table 12: Sampling site habitat characteristics including percent \pm SE of benthic cover composition and fish abundance ($A \pm SE$) and fish species richness ($S \pm SE$), per 100m², for Seychelles and Mallorca.

Seychelles	Benthic Community (% cover)							Fish Community	
Site	Branching	Massive	Rubble	Rock	Sand	Algae	DC	A	S
Baie Laraie	7.2 \pm 1.6	48.2 \pm 8.1	22.6 \pm 3.7	3.7 \pm 0.4	10.7 \pm 6.2	7.3 \pm 4	0.3 \pm 0.3	634.4 \pm 0.4	38.9 \pm 2.6
East Bay	20.6 \pm 3.6	27.1 \pm 3.8	24.1 \pm 6.2	4.7 \pm 2.5	16.1 \pm 4.9	5.9 \pm 1.4	1.6 \pm 0.6	1208.9 \pm 1	44.4 \pm 1.6
Home Reef	3.9 \pm 1.1	24.6 \pm 9.1	45.1 \pm 8.8	5.8 \pm 1.4	3.3 \pm 0.7	14.2 \pm 5.6	3.1 \pm 2.3	1398.9 \pm 1.3	38.9 \pm 3.5
Point Rouge	2.3 \pm 1.2	9.3 \pm 1.3	42.1 \pm 13	36.7 \pm 10.5	9 \pm 2.6	1.7 \pm 1.3	0 \pm 0	497.8 \pm 0.6	35.6 \pm 4.6
PS1	22.4 \pm 1.9	12.3 \pm 4	12.2 \pm 4.1	45.2 \pm 2.8	2.6 \pm 1.5	0 \pm 0	5.3 \pm 2	694.4 \pm 0.5	45.6 \pm 1.7
PS3	16.6 \pm 5.8	17.4 \pm 2.6	15.1 \pm 8	4 \pm 1.7	0.2 \pm 0.2	40.3 \pm 14.8	6.3 \pm 3.2	2043.3 \pm 3.8	42.2 \pm 4.6
PS4	49.4 \pm 1.4	19.2 \pm 3.8	22 \pm 2	4.2 \pm 2	2.1 \pm 0.4	1.3 \pm 1.2	1.7 \pm 0.5	1433.3 \pm 1	48.9 \pm 2.4
PS6	20.8 \pm 2.2	11.3 \pm 1.1	23.8 \pm 5.3	36.3 \pm 4.3	0 \pm 0	3.7 \pm 0.9	4.1 \pm 1.5	918.9 \pm 0.7	46.7 \pm 0.6
Mallorca	Benthic Community (% cover)							Fish Community	
Station	Erect	Filament	Turf	Posidonia	Rubble	Rock	Sand	A	S
Cala Egos	43.6 \pm 8.8	8.2 \pm 2.2	25.9 \pm 1.9	5 \pm 2.2	14.1 \pm 6	3.1 \pm 1.6	0.2 \pm 0.2	280 \pm 0.4	12.2 \pm 0.7
Cala Llamp	64.8 \pm 2.2	11.5 \pm 1.6	12.5 \pm 2.5	9.3 \pm 2.9	1.8 \pm 1.3	0 \pm 0	0 \pm 0	557.8 \pm 0.5	17.8 \pm 0.3
Es Basc	51.5 \pm 7.7	8.1 \pm 2.4	18.4 \pm 5.9	6.7 \pm 4.1	1.1 \pm 0.6	3.6 \pm 2	10.6 \pm 9.3	221.1 \pm 0.2	18.9 \pm 0.4
Es Guix	49.8 \pm 3.5	17.3 \pm 1.8	31.5 \pm 1.8	0 \pm 0	1.3 \pm 1.1	0 \pm 0	0 \pm 0	186.7 \pm 0.2	14.4 \pm 0.4
Es Total	56.4 \pm 6.2	6.1 \pm 1.2	29.7 \pm 5.3	3.1 \pm 1.7	0.7 \pm 0.4	3.9 \pm 1.2	0 \pm 0	640 \pm 0.6	22.2 \pm 0.6
Malgrats Este	42.6 \pm 3.7	1 \pm 0.4	33.7 \pm 8.3	0 \pm 0	6.8 \pm 3.6	16 \pm 2.7	0 \pm 0	283.3 \pm 0.3	20 \pm 0.9
Malgrats Oeste	62 \pm 4.6	18.5 \pm 3.9	9.7 \pm 2	6.5 \pm 3	2.1 \pm 1.1	1.2 \pm 1.2	0 \pm 0	454.4 \pm 0.5	16.7 \pm 0.6
Rafaubeitx	66.1 \pm 5.9	8.1 \pm 2.7	17.9 \pm 3.7	0 \pm 0	4.2 \pm 2.3	1.5 \pm 0.9	2.3 \pm 2.3	484.4 \pm 1.1	20 \pm 0.5

3.3.2 Behaviour

The total number of fish behaviours observed for the given period varied between individuals and species, however all species required two five minute periods to express $\geq 80\%$ of all the behaviour types (Figure 19 and Figure 20). According to this, 10 minutes was determined to be the adequate observation time.

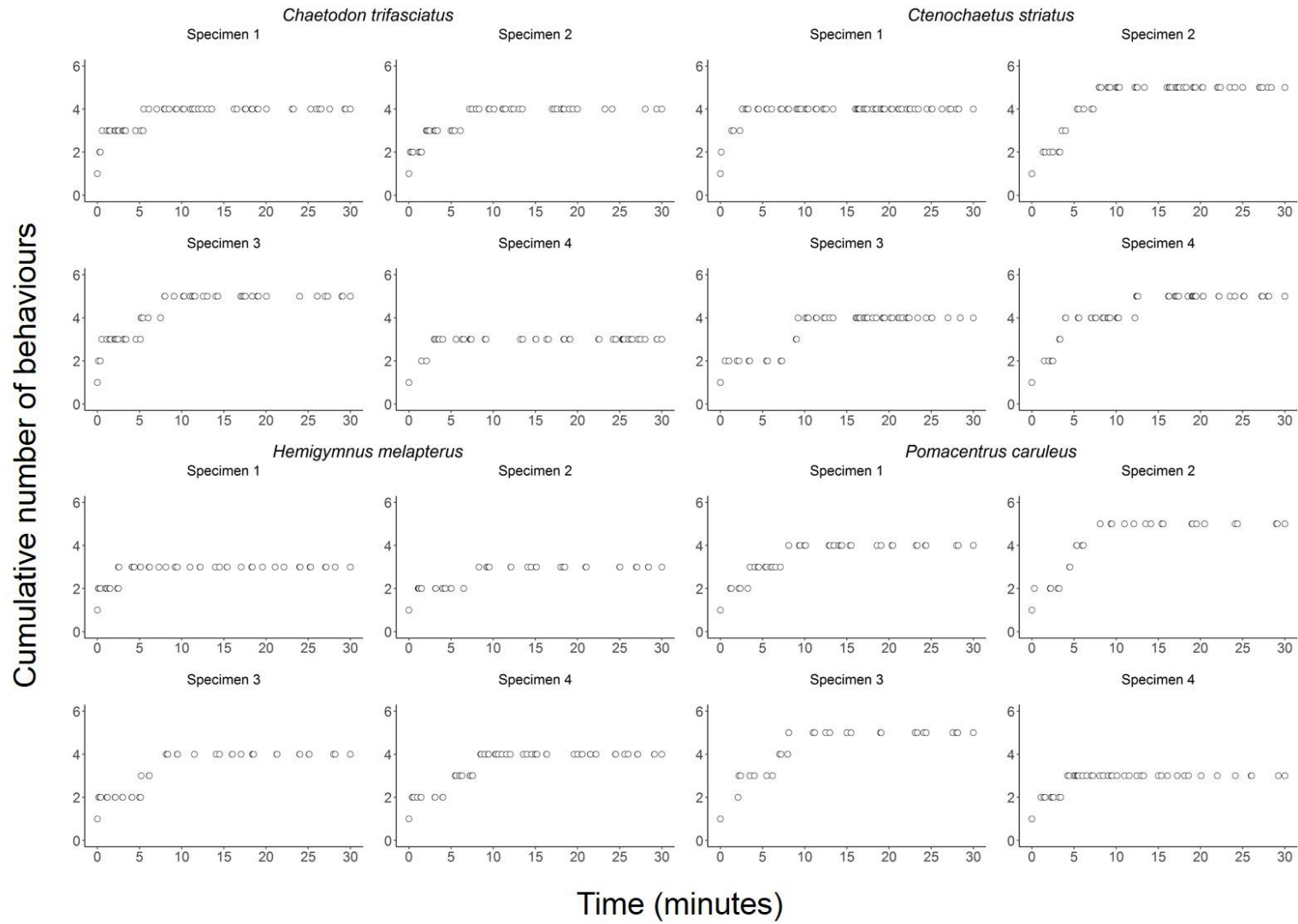


Figure 19: Behavioural time budget in Seychelles, representing continual behavioural traits accumulated over time for all individuals (n=16) of each species sampled.

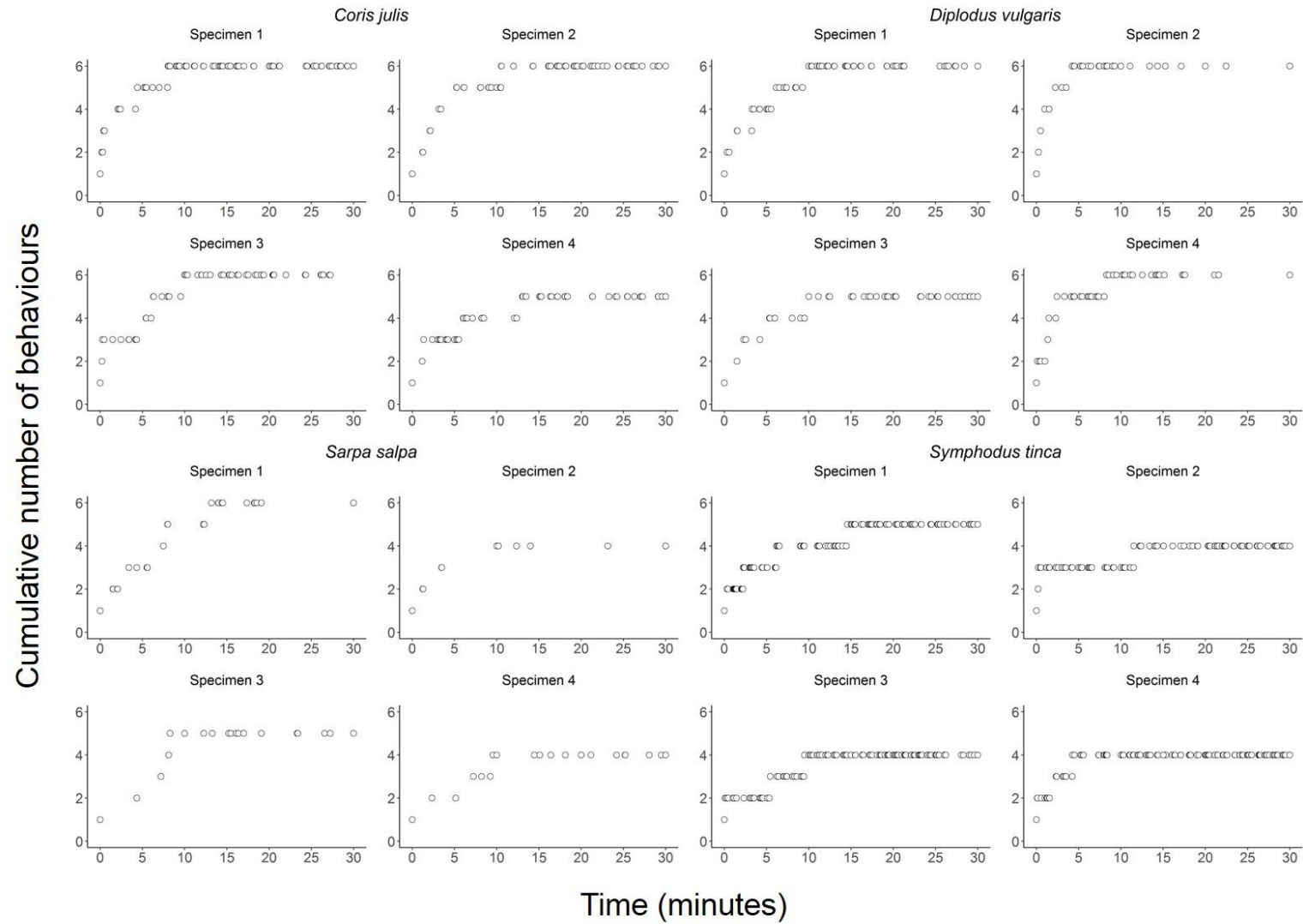


Figure 20: Behavioural time budget in Mallorca, representing continual behavioural traits accumulated over time for all individuals (n=16) of each species sampled.

Overall, for the 178 individuals sampled in the Indian Ocean a total of 2651 changes in behaviour were recorded, while a total of 9815 were observed for the 328 individuals sampled in the Mediterranean. The numbers of individuals sampled were evenly distributed in each location along all the species studied (Table 13).

Table 13: Total number of individuals sampled per species and their distribution across sites for Seychelles and Mallorca.

Seychelles					
Site	Species				
	<i>C.trifasciatus</i>	<i>C.striatus</i>	<i>H.melapterus</i>	<i>P.caruleus</i>	Total/site
Baie Laraie	5	5	5	5	20
East Bay	7	5	5	6	23
Home Reef	6	5	5	7	23
Point Rouge	6	7	5	7	25
Praslin 1	5	5	5	5	20
Praslin 3	8	5	5	7	25
Praslin 4	5	5	5	5	20
Praslin 6	7	5	5	5	22
Total/species	49	42	40	47	178
Mallorca					
Site	Species				
	<i>C.julis</i>	<i>D.vulgaris</i>	<i>S.salpa</i>	<i>S.tinca</i>	Total/site
Cala Egos	10	10	10	10	40
Cala Llamp	9	10	10	10	39
Es Basc	10	9	10	10	39
Es Guix	10	10	10	10	40
Es Total	10	10	10	11	41
Malgrats Este	10	10	10	10	40
Malgrats Oeste	13	12	12	13	50
Rafaubeitx	10	11	9	9	39
Total/species	82	82	81	83	328

The observational data for all species sampled in the Seychelles demonstrated a preference for the horizontal open space, with three out of four species also spending a proportion of the time associated with open vertical areas, which in the case of *C. trifasciatus* was the highest with 23% (Figure 21). *P. caruleus* was the species spending most time concealed (12%) but their behaviour was mainly concentrated on water column feeding (83.9%). The behaviours of *H. melapterus* were mainly concentrated on roaming (68.9%) and on diffused

feeding for *C. trifasciatus* (65%). The latter species also demonstrated roaming and focussed feeding behaviours. *C. striatus* distributed their time between roaming (31.7%), focussed (23.8%) and diffused feeding (23.3%). For the feeding locations, *C. striatus* demonstrated the preference for rock, dead coral and rubble (52.3%, 20.6% and 17.8%, respectively), *C. trifasciatus* fed mainly within branching (62.2%) and massive coral (23.6%), while *H. melapterus* spent most of the time feeding within the sand habitat (48.7%). The water column feeding of the *P. caruleus* occurred mainly over the branching coral (45.8%) and rubble substrates (34.7%).

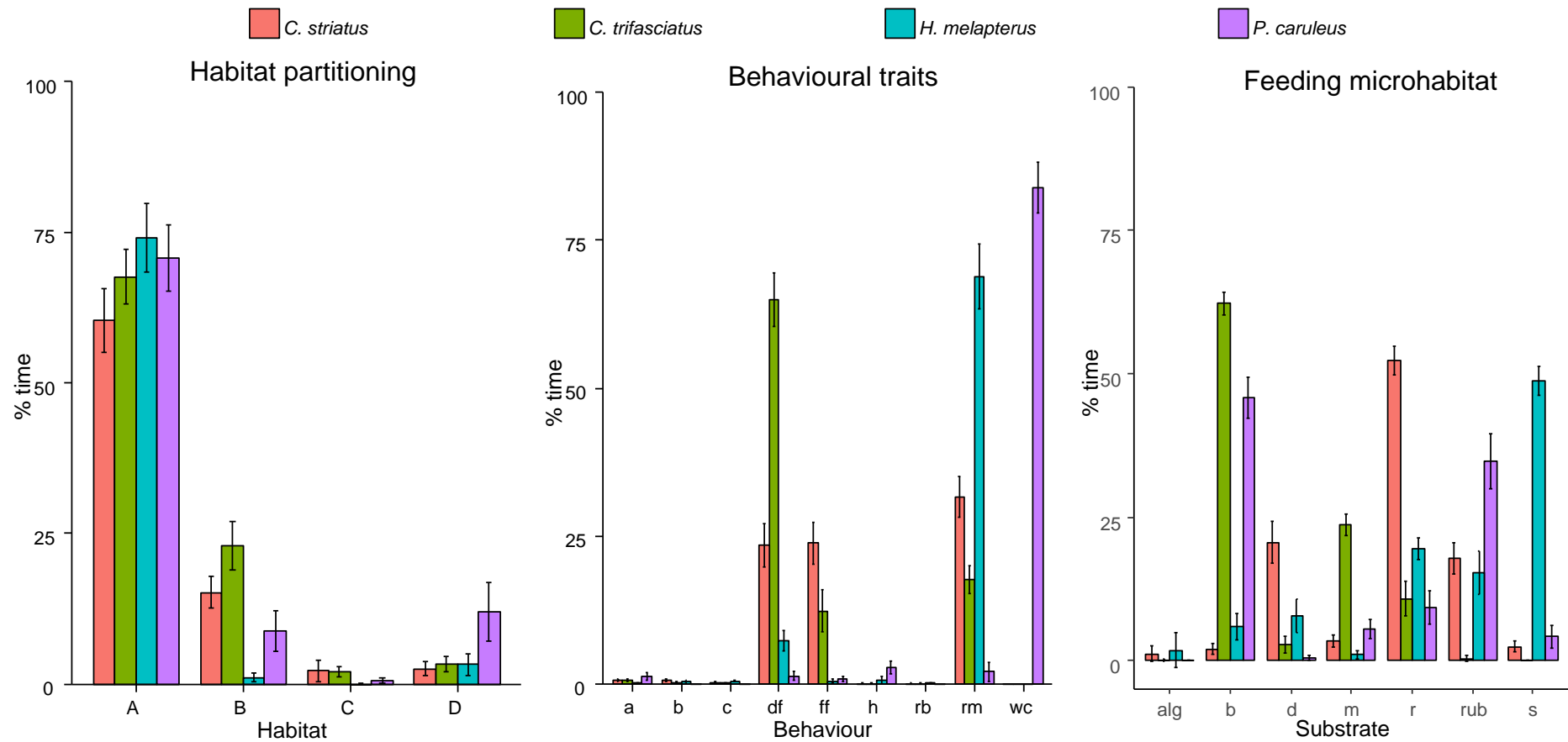


Figure 21: Graphic representation of the time spent for each species in the Seychelles according to: Habitat partitioning patterns (A=open horizontal, B=open vertical, C=underside, D=concealed); behavioural traits (a=intraspecific aggression, b=interspecific aggression, c=cleaning, df=diffused feeding, ff=focused feeding, h=hovering, rb=rubbing, rm=roaming and wc=water column feeding); feeding habitat preferences (alg=algal, b=branching, d=dead and m=massive coral morphotypes, r=rock, rub=rubble, s=sand). Error bars show Standard Error of the Mean.

In Mallorca, the observational data across all species revealed a majority preference for the horizontal open space, which in the case of *S. salpa* was as high as 89.7% of the total observational time spent (Figure 22). The remaining three species demonstrated a small preference for open vertical areas spending on average 20% of the total time interacting with this surface type. The dominant behaviour for all four species was roaming. *D. vulgaris* demonstrated hovering (17.1%), a behavioural characteristic that was unique to this species, as well as searching (13.3%), also demonstrated by *C. julis* (29.5%). With regards to the feeding modes, *S. salpa* was the only species to express the preference for focused (23.2%), rather than diffused feeding (10.1%). For the feeding habitats, turf and erect tree-like algal morphotypes were the preferential morphotypes chosen by all species. *D. vulgaris* (21.2%) and to some extent *C. julis* (17%) also demonstrated feeding within filamentous algae morphotype. While no other species spent any notable time feeding within Posidonia beds, *S. salpa* spent 31.4% of the total feeding time within this habitat.

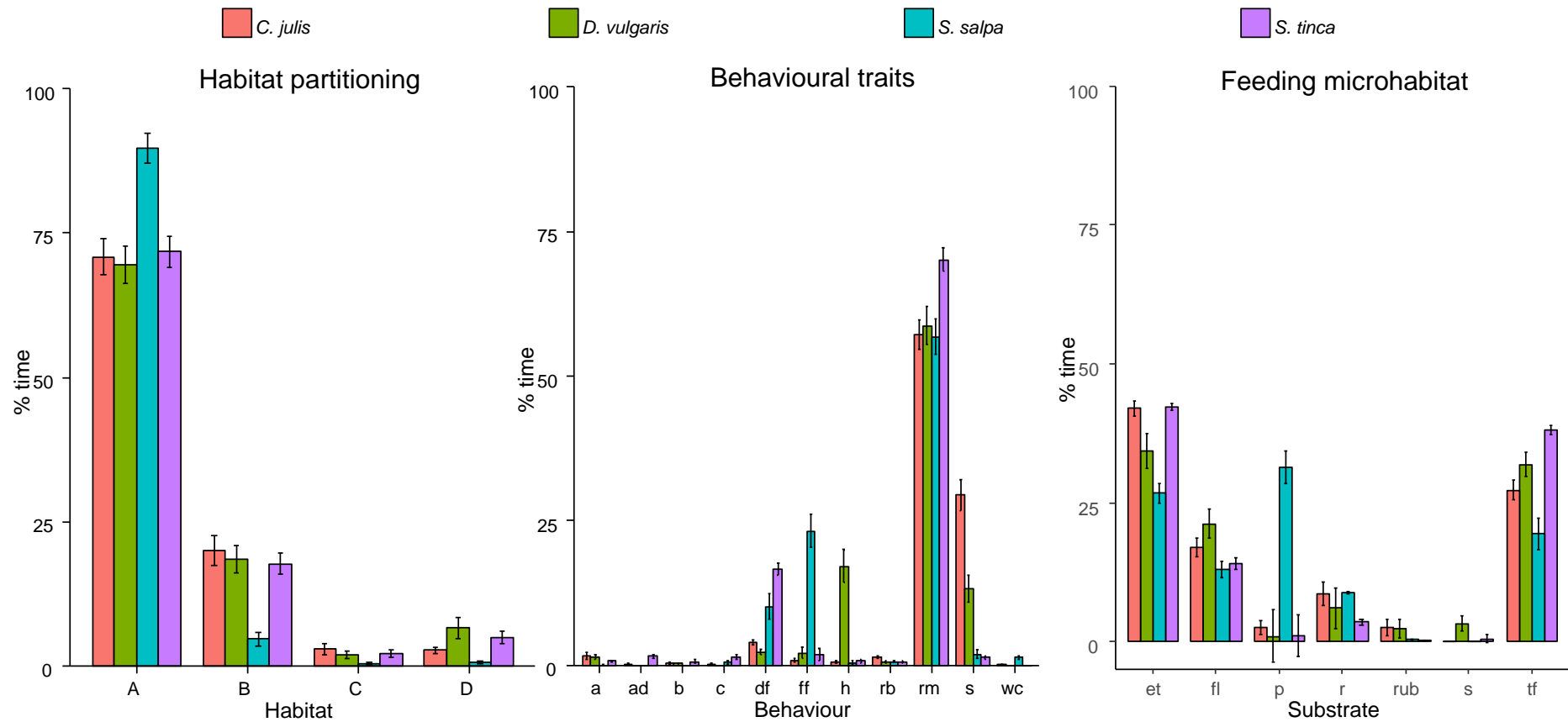


Figure 22: Graphic representation of the time spent for each species in Mallorca according to: Habitat partitioning patterns (A=open, horizontal, B=open, vertical, C=underside, D=concealed); comparison of behavioural traits (a=intraspecific aggression, ad=advertising, b=interspecific aggression, c=cleaning, df=diffused feeding, ff=focused feeding, h=hovering, rb=rubbing, rm=roaming, s=searching and wc=water column feeding); feeding habitat preferences (et=erect treelike and fl=filamentous algal morphotypes, p=Posidonia, r=rock, rub=rubble, s=sand, tf=turf algae). Error bars show Standard Error of the Mean.

3.3.3 Convex Hull and Standard Ellipse Area

Clear differences in the size of the RN surface areas were observed between those expressed by TA and those expressed by SEA, for all species, both in the Seychelles and Mallorca (Table 14). Subsequently, the degree of the RN overlap between species also revealed great differences in the amount of overlap, depending on whether it was considered for the TAs' overlap or the SEAs' overlap.

Table 14: The values of the surface areas of the realised niches represented by Convex Hulls and Ellipses for the Seychelles' and Mallorcan species.

Species	Convex Hull	Ellipse
Seychelles		
<i>C. trifasciatus</i>	0.51	0.17
<i>C. striatus</i>	0.92	0.34
<i>H. melapterus</i>	0.7	0.25
<i>P. caruleus</i>	0.07	0.01
Mallorca		
<i>C. julis</i>	0.87	0.28
<i>D. vulgaris</i>	0.93	0.28
<i>S. salpa</i>	1	0.26
<i>S. tinca</i>	0.77	0.23

For the Seychelles' species, the highest degree of overlap of the RN was observed between *H. melapterus* and *C. striatus* (Figure 23 and Table 15). The TA overlap was 95.5%, while the SEA overlap was 79.2%. On the other hand *C. striatus* RN overlapped 69% and 57.2% for the TA and the SEA respectively, with the RN of the *H. melapterus*. With the exception of a very small TA RN overlap of *C. trifasciatus* (1.5%), neither of the other two species overlapped with *P. caruleus*. Conversely, *P. caruleus* demonstrated TA RN overlap of 10.5% and 0.5% with *C. trifasciatus* and *C. striatus* respectively, however no SEA RN overlap was evidenced for this species. A large difference in the degree of overlap between TA and SEA RN was observed between *C. trifasciatus* and *C. striatus* (54.6% VS 5.2%) and *C. striatus* and *C. trifasciatus* (30.1% VS 2.6%), as well as between the RNs of *C.*

trifasciatus and *H. melapterus* (55.4% VS 11.4%) and *H. melapterus* and *C. trifasciatus* (40.5% VS 7.8%).

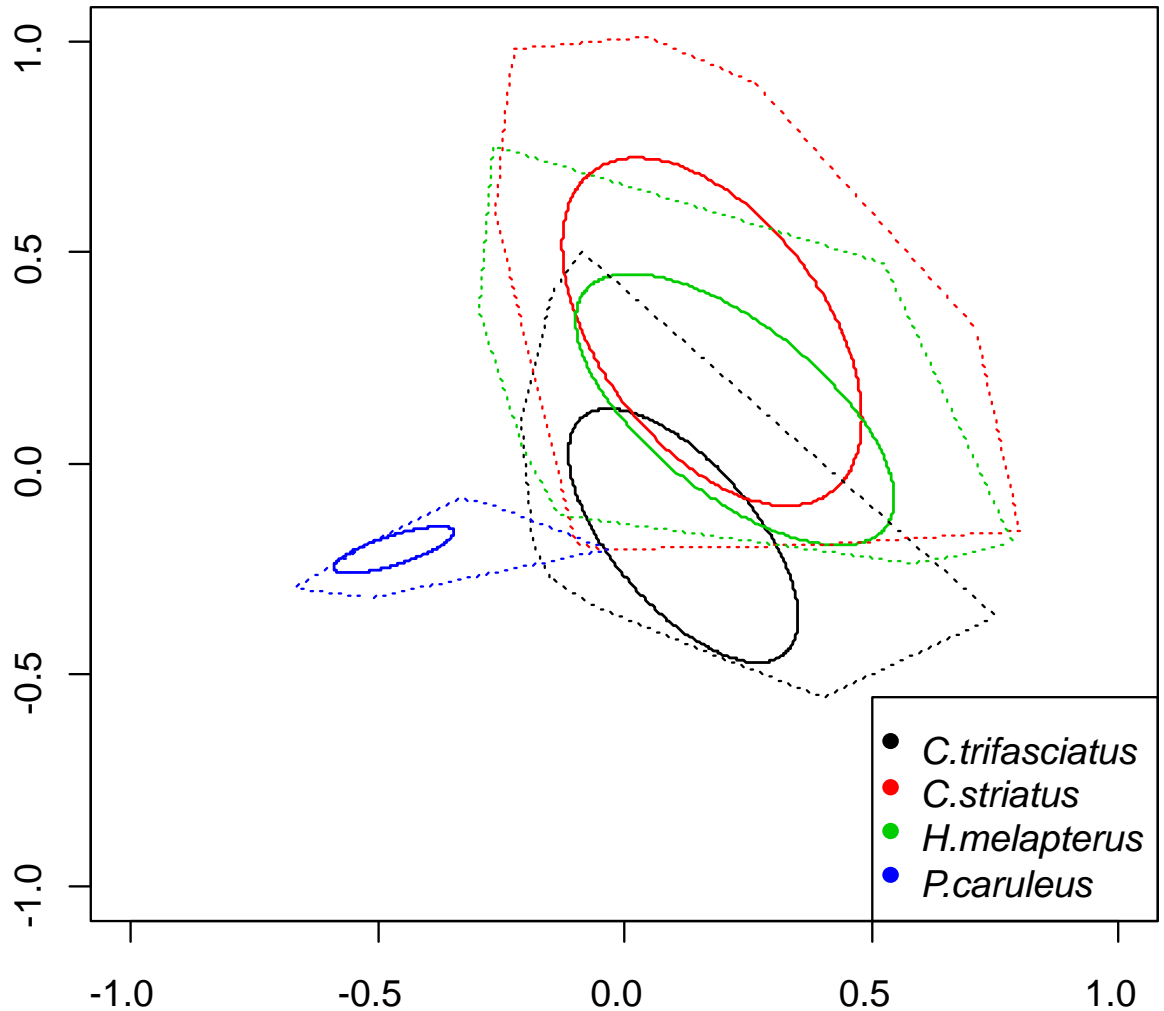


Figure 23: Graphic representation of the realised niches of Seychelles species. Convex hulls (dotted lines) are plotted around and encompass the most extreme values, while the ellipses (continuous lines) represent statistically most likely niche distribution of the species.

Table 15: Calculations of the realised niche overlap between species based on convex hulls and ellipses in the Seychelles, expressed in % of the total area of the four species analysed. Ct: *C. trifasciatus*; Cs: *C. striatus*; Hm: *H. melapterus*; Pc: *P. caruleus*.

Seychelles										
Convex Hulls	Ct	Cs	Hm	Pc	Ellipses	Ct	Cs	Hm	Pc	
		54.6	55.4	1.5	Ct		5.2	11.4	0.0	
	Cs	30.1		69.0	0.0	Cs		2.6	57.2	0.0
	Hm	40.5	91.5		0.0	Hm		7.8	79.2	0.0
	Pc	10.5	0.5	0.0		Pc		0.0	0.0	0.0

In Mallorca, the species demonstrated a larger degree of RN overlap overall, both for TA and SEA, compared to that of the Seychelles' species, although the same pattern was observed; the RN overlap of the TA was greater between all species, than that of the SEA (Figure 24 and Table 16). The highest degree of overlap was observed between the RN of *C. julis* with the RN of *D. vulgaris*. The TA overlap was 91.9%, while the SEA RN overlap was 73.6%; *D. vulgaris* RN overlapped 86.1% and 73.3% for the TA and the SEA respectively, with the RN of the *C. julis*. A large degree of overlap was also seen between the RNs of *S. tinca* with *C. julis* with 85.3% for the TA and 65.8% for the SEA and *S. tinca* with *D. vulgaris*, 84.2% for the TA and 59% for the SEA. On the other hand, the RN overlap of two species, *C. julis* and *D. vulgaris* with *S. tinca* expressed high TA overlap values (75.3% and 69.6%, respectively), while the SEA overlap values indicated a medium degree of RN overlap for the same species (53.6% and 47.9%, respectively). The most pronounced differences between the TA and SEA niche overlap were observed in the remaining combinations of overlaps, respectively; *S. salpa* and *D. vulgaris* (75.9% VS 13.1%) and *D. vulgaris* and *S. salpa* (81.9% VS 12.2%), *S. salpa* and *C. julis* (64.4% VS 1.5%) and *C. julis* and *S. salpa* (74.3% VS 1.4%). Finally, despite indicating a large – medium RN overlap by the TA (65% and 49.8%, respectively), no RN overlap was indicated by the SEA, between the RNs of *S. tinca* and *S. salpa*, nor between *S. salpa* and *S. tinca*.

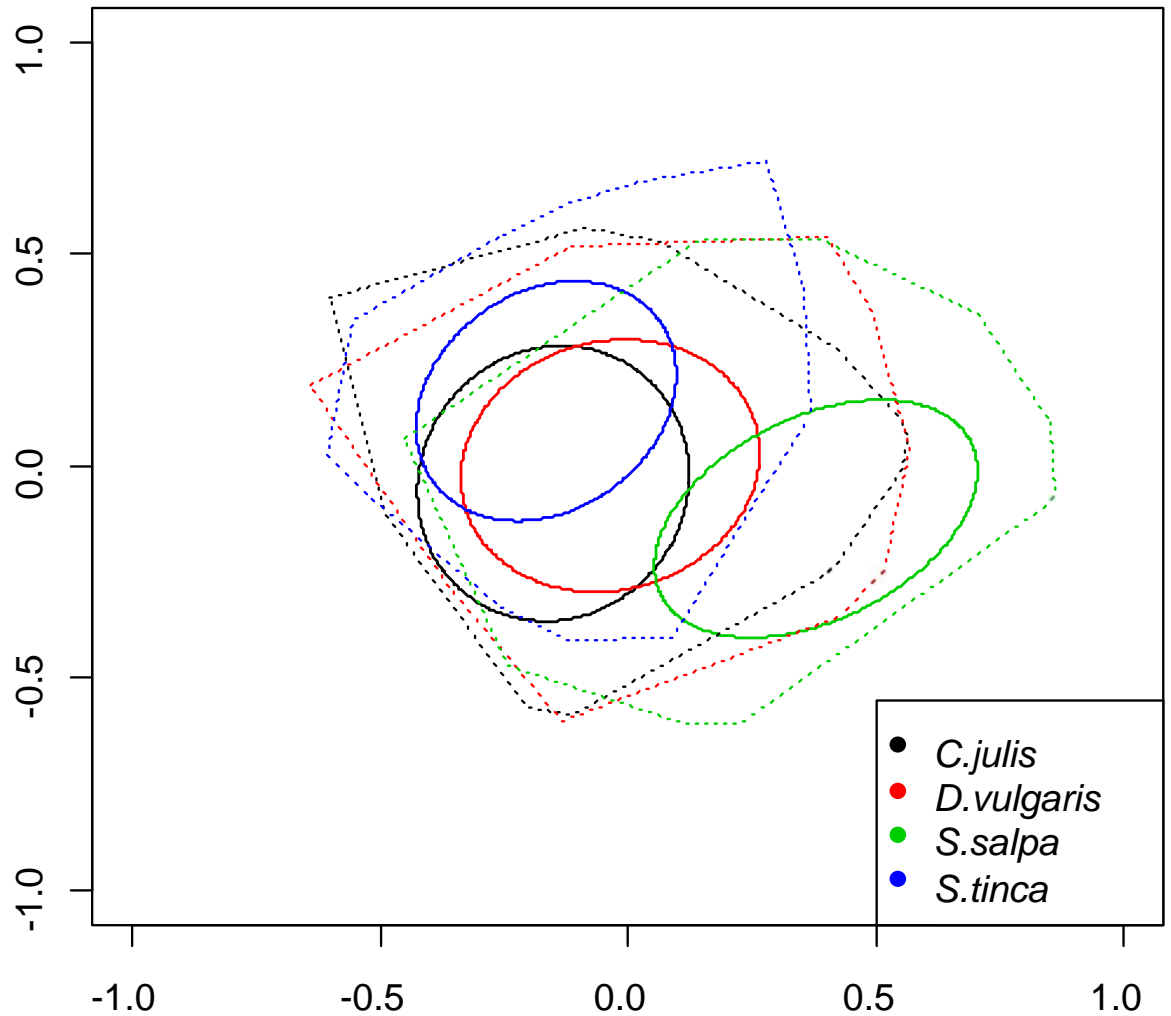


Figure 24: Graphic representation of the realised niches of Mallorca species. Convex hulls (dotted lines) are plotted around and encompass the most extreme values, while the ellipses (continuous lines) represent statistically most likely niche distribution of the species.

Table 16: Calculations of the realised niche overlap between species based on convex hulls and ellipses in Mallorca, expressed in % of the total area of the four species analysed. Cj: Coris julis, Dv: Diplodus vulgaris, Ss: Salpa salpa, St: Simphodus tinca.

Mallorca									
Convex Hulls	Cj	Dv	Ss	St	Ellipses	Cj	Dv	Ss	St
Cj		91.9	74.3	75.3	Cj		73.6	1.4	53.6
Dv	86.1		81.9	69.6	Dv	73.3		12.2	47.9
Ss	64.4	75.9		49.8	Ss	1.5	13.1		0.0
St	85.3	84.2	65.0		St	65.8	59.0	0.0	

3.3.4 Sample size dependency

By simulating different sample sizes, the change in values of the TA and SEA and thus, their dependency to the sample size was observed. The simulated values followed similar patterns

for all species in the Seychelles and Mallorca (Figure 25 and Figure 26). The variability for both TA and SEA reduced with the increasing sample size. For the maximum number of samples simulated, the variation was however always smaller for the SEA than the TA (in many cases the variation for the SEA was reduced to zero). For the Seychelles, the model predicted higher values for both, TA and SEA, compared to the observed values from the data, however the overestimate in the case of the SEA was in comparison much smaller. For Mallorca, the resamplings also predicted higher values of the TA than those observed empirically, however the SEA values estimated by the model were very proximate to the SEA empirical values of the species. Finally, with the increasing sample number the TA values increased, eventually tailing off, while the SA values generally remained unaffected after a very small number of samples, for both Seychelles and Mallorca.

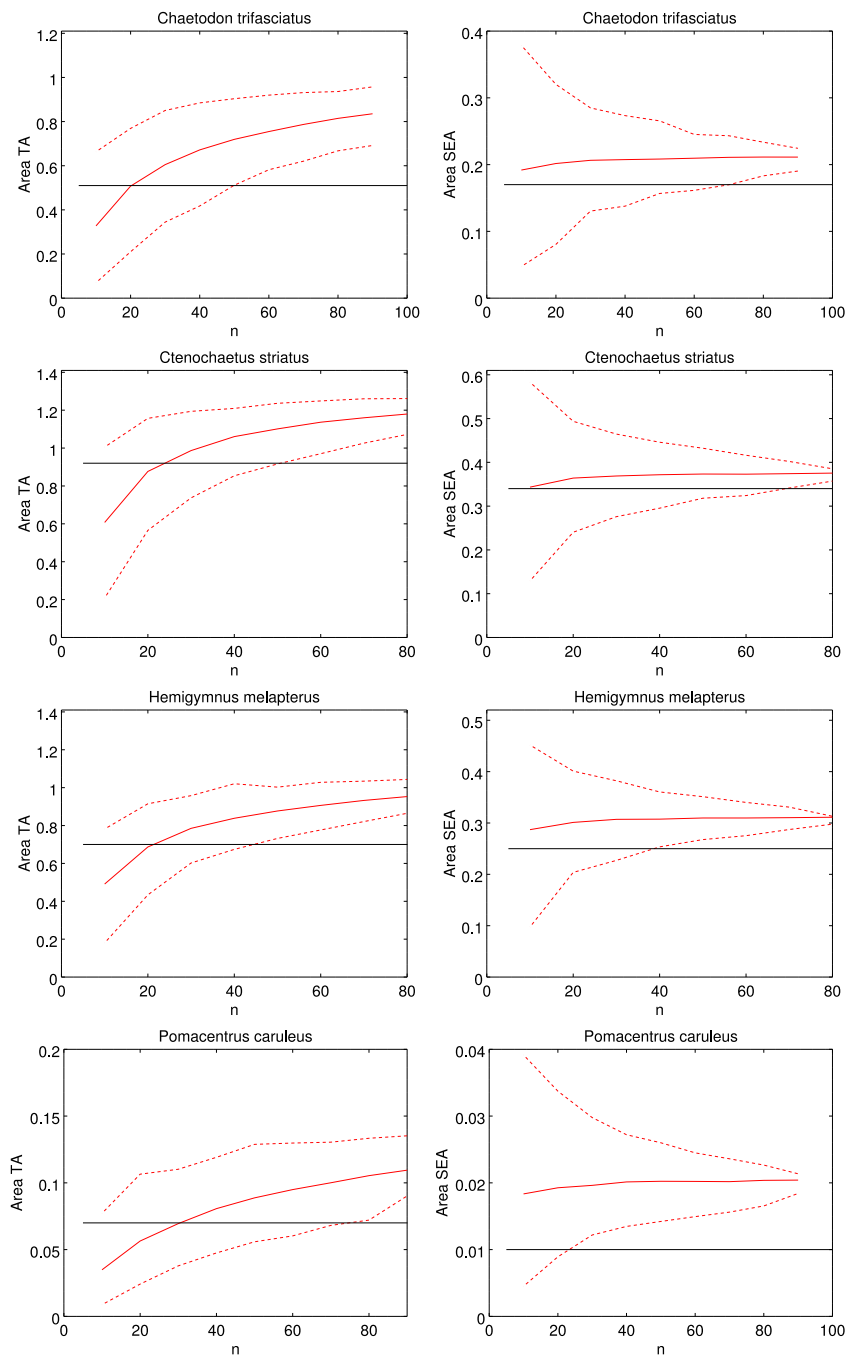


Figure 25: Realised niche size modelling using increasing sample size for TA (left column) and SEA (right column) for the Seychelles species. The solid black line indicates the observed total niche area for each metric calculated from the observation data. The solid red line represents the mean TA (left column) and mean SEA value (right column) calculated for 1000 random selections of individuals with increasing sample size ($n+5$). The red dotted lines represent the lower and the upper confidence intervals (0.05% and 99.5%) for the niche area estimates after each 1000 resamplings with increasing sample size.

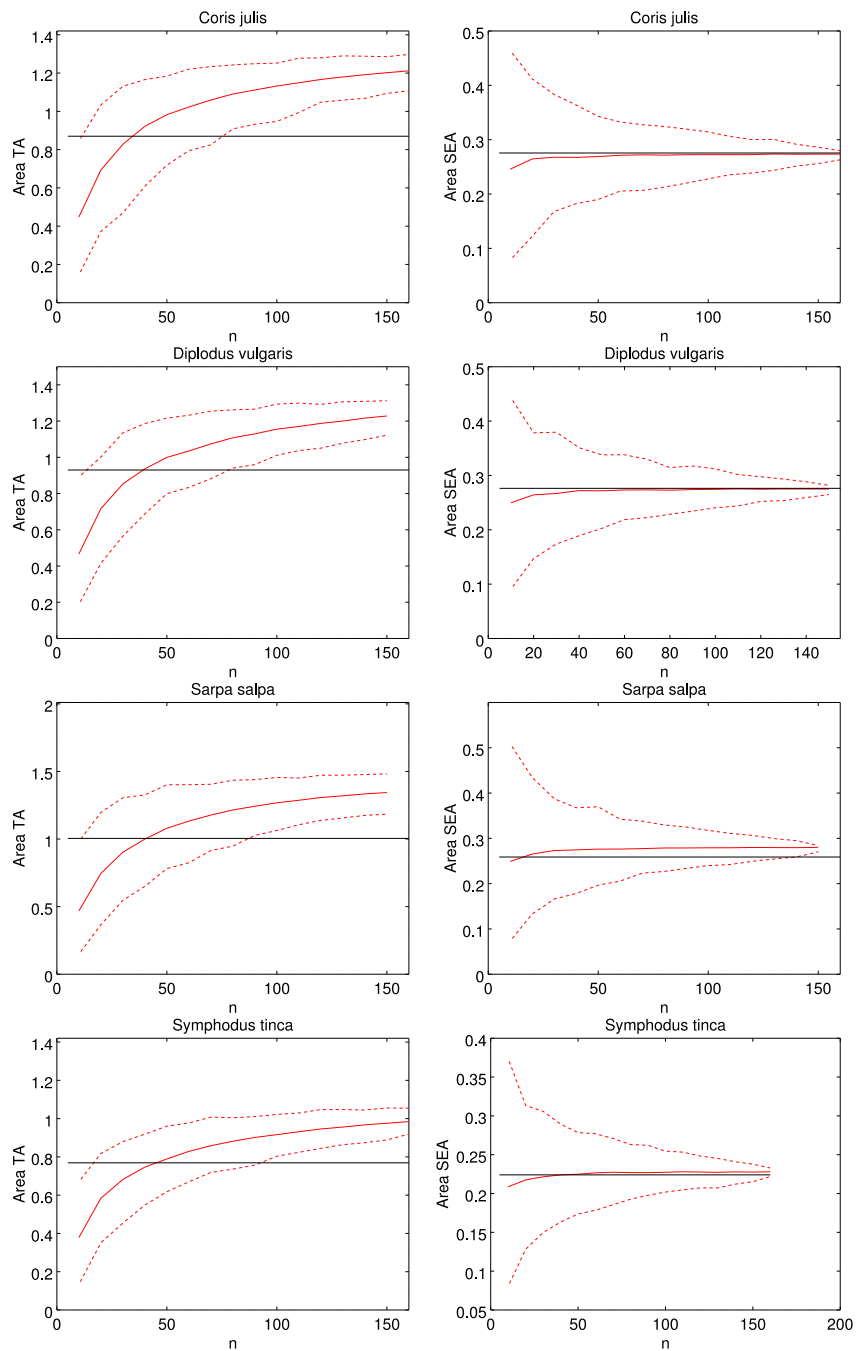


Figure 26: Realised niche size modelling using increasing sample size for TA (left column) and SEA (right column) for Mallorca species. The solid black line indicates the observed total niche area for each metric calculated from the observation data. The solid red line represents the mean TA (left column) and mean SEA value (right column) calculated for 1000 random selections of individuals with increasing sample size (n+5). The red dotted lines represent the lower and the upper confidence intervals (0.05% and 99.5%) for the niche area estimates after each 1000 resamplings with increasing sample size.

3.4 Discussion

In order to describe the habitat use, fish behaviours were sampled and species' RN sizes measured. The species sampled were representative of the most abundant families present in two coastal marine environments, a coral-dominated tropical and an algal-dominated temperate ecosystems. The assessment of the RNs of the species was carried out by the means of a new continuous field observations method, based on the time contribution of each behaviour to the habitats of interest.

Species from both systems displayed highly similar habitat surface orientation preferences, spending the majority of their time in open spaces. Regardless of the ecosystem considered, behavioural patterns of the species studied were uniformly comparable. All species invested their time mainly into movement and feeding, rather than direct interaction with others. The main differences between the two ecosystems were observed for the species' partitioning of the feeding habitat. Individually, Seychelles' species selected between either coral or abiotic habitat. One species (*C. trifasciatus*) fed mainly within the coral and two others (*C. striatus* and *H. melapterus*) fed almost exclusively within the abiotic habitat. One species, *P. caruleus*, used a mixture of both habitats, however since this species is planktivorous, the benthic habitat choice during feeding can be attributed to other factors, such as protection from predation, rather than food derivation from the substrate itself. In Mallorca, the feeding occurred predominantly in the algal part of the habitat for all species. With the exception of *S. salpa*, which also displayed interest for *P. oceanica* habitat, the feeding time was distributed between a number of algal habitats. It is noteworthy however that the ratios of relative habitat availability were different in each ecosystem, with a significantly larger algal availability in the temperate, than coral availability in the tropical ecosystem.

The vast majority of the current literature using empirical data, attempting to quantify RNs and their overlaps, relied on a single methodology of considering the two-dimensional representation of the feeding niche of the species, in which data points correspond to individual diets expressed as paired isotopic coordinates (Syväranta *et al.*, 2013). Much like isotope analysis studies, this study observed the extreme values representing those individuals with higher differences in their trophic behaviour or habitat preferences, as the ones determining the RN size. In the stable isotope studies it is uncommon to have sample sizes larger than 15-20 individuals within a given population (Syväranta *et al.*, 2013), which may result in significant underestimations of the true population niche size if only the TAs are measured. This is because the TA is likely to be highly sensitive to the number of observations (Worton, 1995; Jackson *et al.*, 2011). It is logical to think that the chance of discovering additional individuals lying outside the current niche would increase by increasing the sampling effort. Thus, if the sample size is larger, the niche would likely increase, assuming that the individuals are not identical and a variation within the population exists. In this case, while a number of individuals would be found outside and would subsequently increase the initial niche size, a large number of others would likely fall within a smaller niche area. Consequently, using this method for measuring niche sizes emphasises the importance of the few, while not equally considering that of the majority, which can be interpreted as not entirely representative of the largest part of the population. Studying populations with less variation can as a result, in theory, give more precise niche size estimates using this method, however it is difficult to know what the real ranges are at the population level if only a small number of individuals have been analysed (Syväranta *et al.*, 2013). The TA method would thus give more accurate measurement of the niche size by sampling more individuals from the given population. The comparison of the results of niche sizes from populations with unequal samples using the TA measurements can be inaccurate

if the number of the individuals sampled determines the niche size. Despite some of the shortcomings mentioned, this method considers the information on intraspecific variation which is important when describing a niche of a population (Bolnick *et al.*, 2003). To address the problem of the sample size the SEA was also calculated, obtaining alternative niche measurements (Jackson *et al.*, 2011; Syväranta *et al.*, 2013).

Independently of the measurement metric used in this study, the high degree of the RN overlap was observed only between *H. melapterus* and *C. striatus* in the Seychelles and *C. julis* and *D. vulgaris* in Mallorca. The sizes of the RNs, as well as the overlaps between species, were always larger for the TA than those calculated using SEA, and the differences were of many magnitudes, for a number of species. Thus, using the same data, but calculating the niche sizes via different metrics, somewhat contradictory results were obtained, providing evidence for high degree of redundancy (large niche overlap), while also discovering extensive complementarity among species (small niche overlap), in both geographical areas studied. The results using the TA method in this case indicated that the species studied delivered their function over a wide range of microhabitats, with high variance among individuals and consequently large niche sizes, leading to high degree of overlapping and extensive redundancy (except, perhaps not to such extent, in the case of *P. caruleus*). On the other hand, in the Seychelles, the niche sizes calculated using the SEA method were at least half the size of those calculated using the convex hull method, while in Mallorca, they were over three times smaller for each species. These findings suggest a much more restricted habitat utilisation patterns leading to less niche overlapping and a higher degree of complementarity. As a consequence, in order to understand the habitat use through niche partitioning, subsequently influencing fish communities, it is extremely important that informed and thus adequate ecological parameters are considered.

Despite the obvious statistical implications of using different measurement metrics, the ecological consequences of using one or the other are likely to be extremely important. Informed use of the appropriate RN measurement metric in ecology should be based on the ecologically desirable outcome of the study, and not just the statistical significance of the results. For example, the priority of a study can be to ensure the persistence of the genetic diversity often captured by the behavioural variability of the population, while the aim of a rapid population assessment study can be to only identify the most frequent and dominant behaviours characterising the population. In this case, the TA metric would be preferred in the former, while the use of SEA metric would be better for the latter. This is of course coupled with a number of trade-offs reflected in the logistical possibilities and other limitations, which also need to be considered. The sufficient sample number required for each method, being one of the limitations, has already been discussed in the context of the isotopic niches (Jackson *et al.*, 2011; Syväranta *et al.*, 2013). By simulating different sample sizes, this study demonstrates that the accuracy of each method for the measurement of the RN, based on the time contribution of behaviours to the habitats, is influenced by the number of the samples considered. For both, Seychelles and Mallorca, the TA model predicted higher values than those empirically observed, thus perhaps indicating an insufficient sample number of this study to accurately measure the TA values. The model made a better prediction for the SEA values, although not as accurate in the Seychelles as in Mallorca, where the predictions were almost identical to the observed values. Since the number of samples taken in the Seychelles was lower than that in Mallorca, the findings indicate that, even though the SEA values were a good approximation, in order to obtain entirely accurate SEA niche values, a larger sample size was required for the Seychelles. Regardless of the species sampled, the model predicted TA and SEA values tailed off and the variability reduced for both metrics with the increased sample size, in the Seychelles and Mallorca.

This suggests that if a sufficient sample size is eventually considered each method will accurately measure the RN. One method will produce the niche size taking into consideration individual variation, while the other will likely be characterised by the niche size defined by the most frequent and common behaviours found among the species. In view of the evidence, conducting studies on the RN overlap based on just one and completely disregarding the other method is potentially ecologically dangerous, if the data, like in this case, can simultaneously be interpreted as indicating redundancy, as well as complementarity of the same species. While the studies reviewing the use of the same methodologies in the isotopic niche calculations ultimately suggest the use of the SEA over the TA, recommendation here cannot be as straight forward. The TA metrics have been recently successfully used for the calculation of the RN in the marine environment (Brandl and Bellwood, 2014), while this study is the first to calculate them using also the SEA. Based on the findings, it is evident that both methods provide ecologically relevant information about the species and community they represent and as such should be considered in future studies alike and not only in the stable isotope studies. Contrary to the stable isotope studies however, in an ideal scenario, and for the complete transparency of the findings, it is recommended to represent the RNs using both methods with statistically sufficient sample numbers, followed by the study-specific argument of giving one or the other method more importance based on the ecological questions the study aims to answer.

In conclusion, this chapter observed and compared patterns of habitat use of certain fish species within and across tropical and temperate ecosystems, characterised by different local biodiversity and habitat features dominated by distinct biological ecosystem engineers. Comparing the mechanisms of fish habitat use within and across different ecosystems increases the understanding of the role the habitat plays in niche partitioning processes responsible for shaping fish communities. Subsequently, in order to build upon this

understanding, in addition to the knowledge of how habitats are used by fish, discovering the mechanisms driving selection or avoidance of particular habitats is essential.

4 Chapter 4: Fish habitat selection and avoidance on a temperate reef as a model ecosystem

4.1 Introduction

In the previous chapter (Chapter 3), by focusing on certain species in different systems, the research field expanded to habitat – fish associations across ecosystems. Thus, by selecting a number of model species from coral – dominated tropical and algal – dominated temperate reef ecosystems, fish habitat use mechanisms were observed and compared within the ecosystem and between them. Informed by the findings, advocating potentially uniform patterns in habitat partitioning across different ecosystems, this chapter investigated behaviour of a fish species from temperate reef ecosystem, chosen as the model system, to look at how fish use these habitats in terms of selection or avoidance.

In the Mediterranean Sea, the model system chosen, seagrass meadows, erect macroalgae forests covering rocky reefs and shallow heterogeneous mixed bottoms composed of sand, gravel, pebbles and rocks constitute the most important habitats for juvenile fish development (Garcia-Rubies and Macpherson, 1995; Harmelin-Vivien, Harmelin and Lebourleux, 1995; Moranta *et al.*, 2006). Seagrass meadows are formed by a number of seagrass species, however *Posidonia oceanica* is the most dominant in the region (Larkum, Orth and Duarte, 2006). Within sublittoral habitats of the Mediterranean macroalgae forests that form on rocky substrata are dominated by Fucales, mainly of the genus *Cystoseira* (Ballesteros *et al.*, 1998). Seagrass meadows and the macroalgae forests are highly structurally complex and are considered key ecosystem engineers (Coleman and Williams, 2002).

Although one of the most heavily researched seas, studies on the use of olfactory system in habitat selection of the Mediterranean fish species are scarce. Furthermore, at present, very

little is known about the ecology of Mediterranean juvenile fishes, despite their importance in the maintenance of system biodiversity and productivity (Halpern, Gaines & Warner 2005). Essential habitats for juveniles are not accurately defined and factors influencing their selection within the Mediterranean are poorly understood (but see studies by Guidetti 2000; Cheminée *et al.*, 2013).

By deploying the flume-based design, which over the past two decades has been highly popular in habitat selection studies (Atema *et al.*, 2002; Coppock *et al.*, 2013; Dixson *et al.*, 2008; Gerlach *et al.*, 2007 and references therein), an attempt was made to determine the effects of chemical cues on habitat selection or avoidance, in juvenile *Symphodus ocellatus*, an abundant fish species resident within the Mediterranean. To date however, in order to test for habitat selection, the flume methodology studies exclusively rely on the amount of the time spent in the specific water mass representative of the habitat and use it as the single indicator of the preference (*e.g.* Coppock *et al.*, 2013; Dixson *et al.*, 2011, 2008; Munday *et al.*, 2009). As a result, an effort was also made to demonstrate that the responses of fish in the flume experiments can be more complex than just the difference in time of the occupancy between the two water masses and that perhaps, the somewhat simplistic belief that the habitat selection behaviour can be described using a single indicator is not entirely true. Thus, the behavioural response triggered by the detection of a particular cue, in addition to the time spent in each water mass, was also examined by analysing the mean and variance of speed of the individual fish movements, a complimentary approach previously not considered in the flume experiments. The following hypotheses were tested in the study: i) juvenile fish will display a preference for habitat containing chemical cues from conspecifics, as well as seagrass and macroalgae, when compared to odourless habitat; ii) fish will avoid habitat containing predatory chemical cues; iii) the speed of response will be greater in juvenile fish exposed to water containing predator cues compared to algal and

seagrass habitat cues or conspecific cues, since the movement of fish was expected to be greater under stressful conditions. Finally, a more sophisticated Bayesian statistical method was used to calculate both, proportion of time spent in the water masses representative of specific habitats, as well as to analyse the behavioural response of each individual within the specific water mass. The statistical approach was coupled with the development of the rigorous novel protocol for habitat selection behavioural analyses using exclusively publicly available apparatus and software, all described within.

4.2 Materials and methods

4.2.1 Study species

Wild type juveniles of the Ocellated wrasse (*Symphodus ocellatus* (Linnaeus, 1758)), between 1.4 cm and 3.6 cm standard length, were used in the experiments (Figure 27). This species is ubiquitously found in the Mediterranean and demonstrates a strong association with algal-covered rocky, as well as *P. oceanica* seagrass habitats, throughout both juvenile and adult life stages (Cheminée *et al.* 2013 and references therein). The male builds, maintains and guards a nest made of algae in which several females lay their eggs (Whitehead *et al.*, 1986). Newly hatched larvae have a pelagic larval stage of 9 – 11 days, after which they settle on rocky bottoms covered with algae and *P. oceanica* beds, at a length of approximately 8 mm, where they remain permanently (Raventós and Macpherson, 2001; Crec'hiriou and Lenfant, 2015). Test individuals were caught while SCUBA diving using hand-held nets, transported to the laboratory and acclimatised for a minimum of 24 hours. The fish were held in 90 litre, open circulation holding tanks at a stocking density of approximately 30 individuals per tank. The water supplying the tanks was sand – filtered and UV – sterilised seawater.

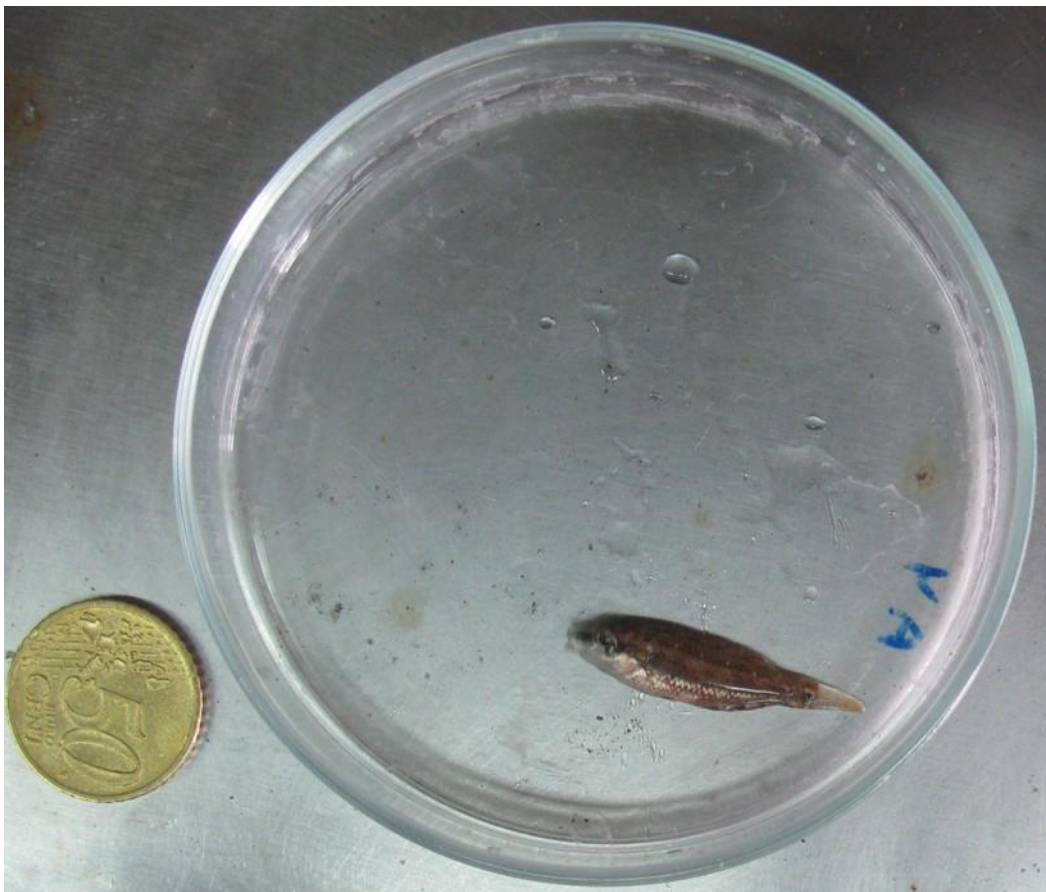


Figure 27: A specimen of the study species, juvenile *Symphodus ocellatus* (photo by A Gouraguine).

4.2.2 Experimental procedure and video image processing

The responses of juvenile *S. ocellatus* to olfactory cues representative of distinct habitats were tested using a two-current choice-flume methodology (Gerlach *et al.*, 2007). In order to reduce any possible turbulence and ensure even water flow, a set of sponges were placed directly at the water entrance into the flume. Further sponges were placed at the entrance of the choice channel (stopping the fish entering one side and remaining there for the duration of the experiment), as well as the exit, thus creating a rectangular choice arena measuring 25 cm in length and 16 cm in width. A switch was developed and used in each of the individual fish experiments to quickly change the side to which the water was delivered to the flume, thus significantly reducing the bias associated with the possible lack of experiencing of the both water masses by the individual fish. The water was fed to the flume by pumps at

constant flow, which was regulated and maintained at 0.5 l min^{-1} , through deployment of two flow meters (Figure 28). In order to eliminate possible water mixing between flows, caused by differences in water density due to different temperatures between the water masses, the temperature of both treatment and control water used was measured at the start of each trial.

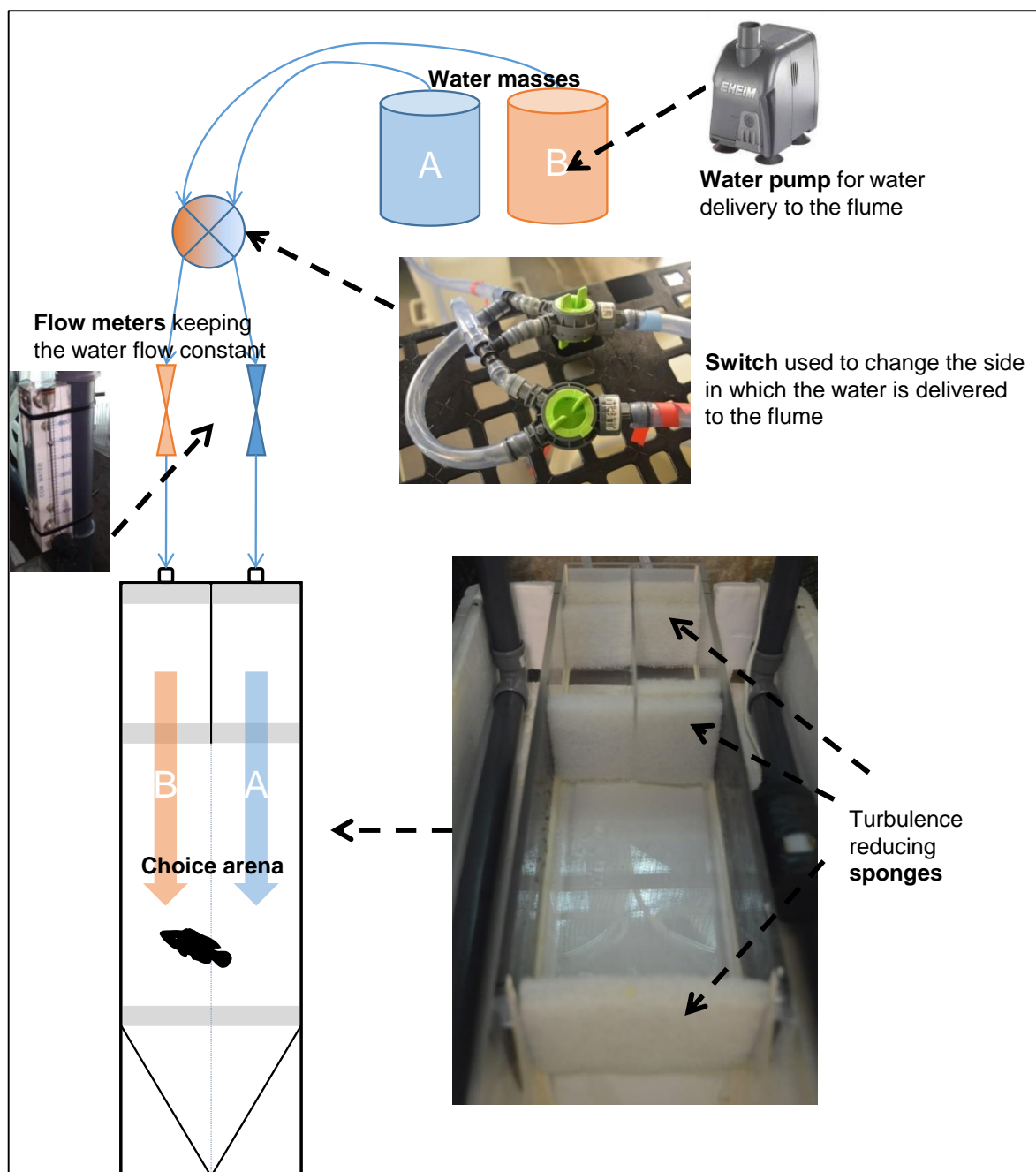


Figure 28: Two-channel choice-flume experimental design.

The fish were released at the downstream end of the flume in the choice arena. They were able to swim within the arena and freely choose between water flowing from the two distinct sources. Fluorescein dye tests were conducted each morning at the start of the water change, prior to individual trials being carried out, to ensure that the two flow channels exhibited distinct and parallel water flow, with no visible turbulence (please follow the link for a video showing an example test conducted prior to the commencement of the experiment - <https://www.youtube.com/watch?v=oQZnm7WWqRM>). The fish were given 1 minute to acclimatise to the two water flows, after which the movement of the fish within the test arena was recorded for 5 minutes. Thereafter, the side of the water sources was swapped over and a further 1 minute rest period was allowed, immediately followed by a further 5 minute recording period. This process eliminated potential bias associated with side preferences of the test arena that were not associated with the water source. The entire movement sequence of the individual within the choice arena was recorded using a GoPro HERO 3 camera (GoPro, Colorado, USA), mounted to a PVC structure directly above the choice flume (Figure 29 and Figure 30A). Following experimentation 5 minute test videos were converted to image stacks using VirtualDub (v.1.10.4) software. The information on the individual's position was obtained for each second through subsampling the original framing rate. The two-dimensional swimming behaviour was tracked from the images with ImageJ software, using the Mtrack2 plugin (Abràmoff, Magalhães and Ram, 2004). Prior to tracking, arena coordinates were set for each fish individually and consequently, accurate positions of the fish movement were ensured despite any possible movements of the camera over the course of the experiments. The tracks of the fish and the arena coordinates were imported into R software (R Development Core Team, 2015) in order to i) visually assess the quality of the data and ii) obtain the time spent (as number of s) and speed (in cm s^{-1}) of fish in each water

mass (Figure 30B). Once tested, fish were weighed to the nearest 0.01 g and their length was determined to the nearest 0.1 mm.

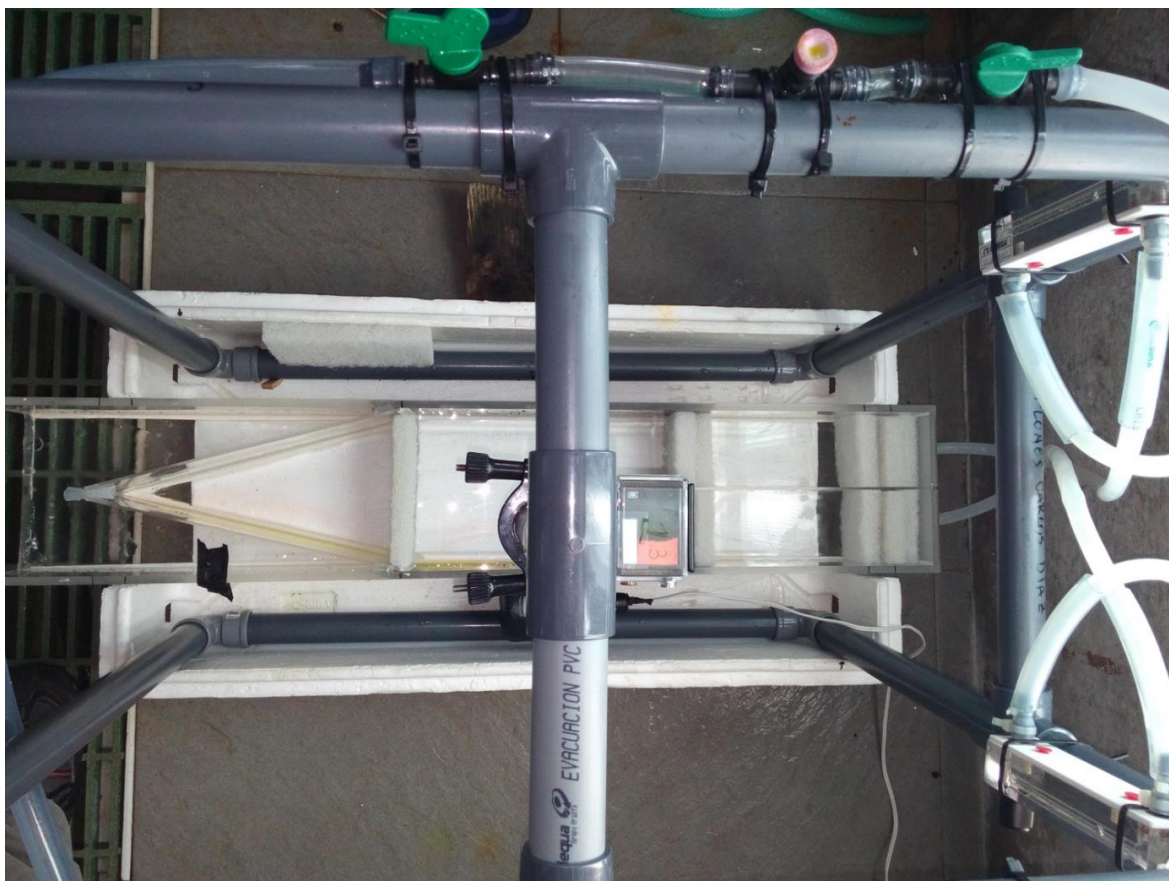


Figure 29: Two-channel choice-flume used in the study(photo by A Gouraguine).

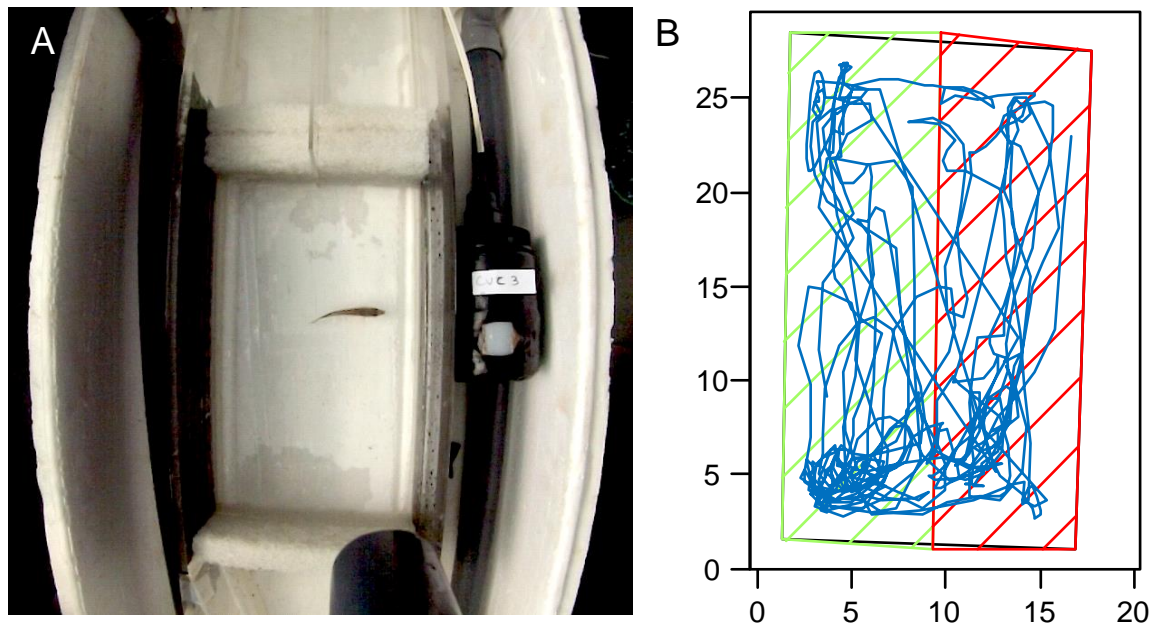


Figure 30: A) sample image representing a single frame extracted from a video, showing an individual fish within the choice arena, B) example of an individual fish movement track within the choice arena, extracted using the Mtrack2 plugin in ImageJ software, and subsequently imported and computed in R software.

4.2.3 Olfactory habitat choice tests

In total, five experimental pairwise trials were conducted: (1) the control water (sand – filtered and UV – sterilised seawater) was supplied to the both sides of the flume simultaneously to ensure there were no preferences to either side of the choice flume; in the subsequent experimental trials the control water was compared to sand – filtered and UV – sterilised seawater aerated for 24 hours under ambient conditions and infused with (2) seagrass and (3) algal covered rocky reef habitat water, both obtained by soaking 2.5 kg (wet weight) of *P. oceanica* and *Cystoseira* per 100 l of the control water, (4) conspecifics water obtained by harbouring thirty *S. ocellatus* individuals per 100 l of control water, (5) predator water obtained by harbouring four individuals of the local natural predator the Painted comber (*Serranus scriba* (Linnaeus, 1758)) (Whitehead *et al.*, 1986) per 100 l of control water.

The flume was thoroughly rinsed with the control water between all experimental procedures. For each pairwise comparison 30 fish were individually tested. Each fish was used only once to avoid pseudo-replication. Fish which did not swim actively and thus did not experience both water masses were omitted from the analysis (3% of all the fish sampled). All experiments were conducted in a separate room in the laboratory with minimal disturbance from the outside environment. The experiments were conducted during daylight hours between 09:00 and 17:00 h.

4.2.4 Statistical analysis

Bayesian statistical approaches were used to calculate habitat preference (time within each water mass), and to investigate the behavioural response (the mean of speed and variance of speed) of fish in each of the water masses within the trials (control vs. treatment habitat), as well as between the treatment water masses of the trials (treatment vs. treatment habitat). The mean speed was expected to change due to the presence of chemical habitat cues that the individual fish could detect. The variance was expected to inform about the existence of rapid and accelerated changes in movements, as a response of passing through different habitats. The same methodology was used to calculate the mean and variance of the speeds within and between experimental trials, however the comparison between trials only considered the movements within the treatment habitat water mass and excluded those in the control water mass.

For the analysis of the water mass preference only, the input data used the count of frames the fish i was at a given side (C_i) in a given number of frames (N_i). The count C_i was assumed to come from a binomial distribution:

$$C_i \sim \text{Binomial}(p_i, N_i)$$

Between-fish variability was accounted for assuming that the (logit-transformed) probability for a given fish (p_i) was normally distributed around the average value (P_j) of the treatment j (each experiment):

$$\text{Logit}(p_i) \sim \text{Normal}(\text{Logit}(P_j), \sigma)$$

Flat priors (normally distributed priors with zero variance and 10^{-6} tolerance) were assumed for $\text{Logit}(P_j)$.

A sensitivity analysis was performed in order to ensure temporal independence between successive observations (i.e., the same analysis was carried out taking one frame per second and one frame each five seconds).

Preliminary histograms of speed distribution of the fish in a given water mass strongly suggested a gamma distribution. Accordingly, the speed at a given moment (t) of the fish i ($S_{t,i}$) when it is inside a given water mass (either at control or treatment water) is given by:

$$S_{t,i,\text{water}} \sim \text{Gamma}(\text{shape}_{i,\text{water}}, \text{rate}_{i,\text{water}})$$

where *shape* and *rate* are the two parameters of the gamma distribution. The mean and variance of the distribution are related with *shape* and *rate* by closed expressions:

$$\text{shape}_{i,\text{water}} = (\text{mean}_{i,\text{water}}/\text{sd}_{i,\text{water}})^2$$

$$\text{rate}_{i,\text{water}} = (\text{mean}_{i,\text{water}}/\text{sd}_{i,\text{water}})^2$$

Means ($mean_{i,j,water}$) and standard deviation ($sd_{i,j,water}$) of each fish (i) were normally distributed around a treatment (j) average ($MEAN_{j,water}$ and $SD_{j,water}$) for dealing with fish specific responses to the same treatment so that

$$mean_{i,j,water} \sim Normal (MEAN_{j,water}, \sigma M_{j,water}$$

$$sd_{i,j,water} \sim Normal (SD_{j,water}, \sigma M_{j,water}$$

Flat priors were assumed for $MEAN_{j,water}$ and $SD_{j,water}$. In order to facilitate between-treatment comparisons, treatment-related effects were expressed as control minus treatment differences:

$$\Delta MEAN_j = MEAN_{j,control} - MEAN_{j,treatment}$$

$$\Delta SD_j = SD_{j,control} - SD_{j,treatment}$$

The Bayesian approach used has a number of application advantages in complex hierarchical models with temporal and spatial autocorrelation (Lunn *et al.*, 2000). Within- and between-treatment comparisons were conducted by comparing the treatment means of each parameter using Bayesian Credibility Intervals (2.5% and 97.5%). Unlike the p-value, the Bayesian posterior distributions assume that there is a given probability that the parameter of interest lies within the interval (Ellison, 2004). The model was implemented in R and run using the R2jags library (Horne *et al.*, 2007) which uses JAGS (Just another Gibbs sampler) to perform Markov Chain Monte Carlo (MCMC) for sampling probability distributions of model parameters.

4.3 Results

The flume trials conducted resulted in no statistically significant fish selection preference or avoidance, in terms of the time spent, for any of the water masses tested (Figure 31).

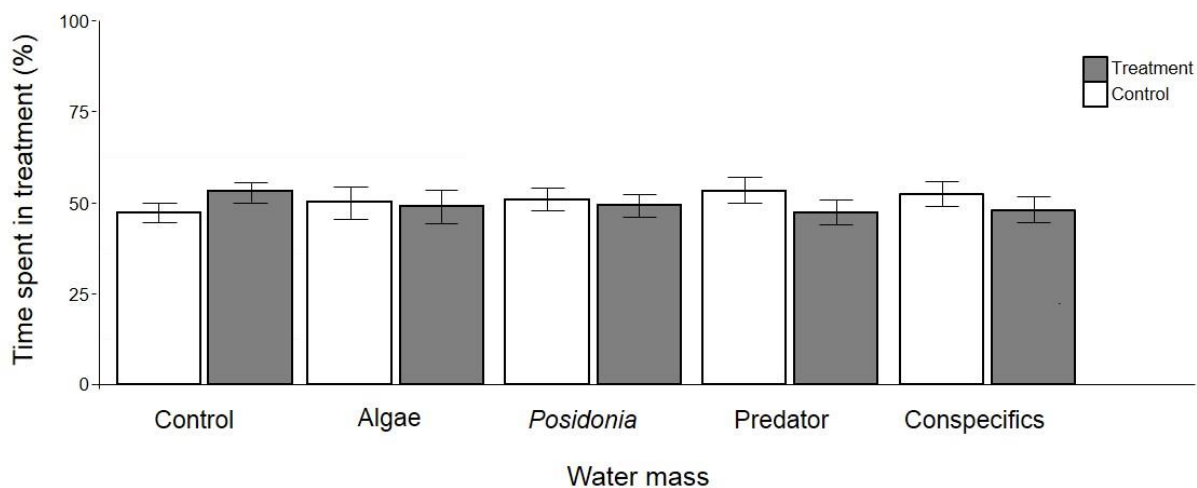


Figure 31: Olfactory response of *S. ocellatus* showing % time spent and standard error of the mean (vertical bars) in control and treatment water masses of each trials.

The temporal independence between successive observations was confirmed by the sensitivity analysis carried out, which demonstrated that the percentage of time spent in each water mass in different trials was not different from a random distribution in any of the trials (Table 17).

Table 17: Bayesian Credibility Intervals (BIC) (median and 95%) of the sensitivity analysis performed in order to prevent errors due to autocorrelation of the position in the immediate following second and the actual position (performed every 1 and 5 seconds). A median value (50%) of 0.5 means no preference for being in any of the water masses; median values >0.5 indicate preference for the control water mass, while median values of <0.5 indicate preference for the treatment.

		<i>Bayesian Credibility Intervals</i>			
		n	2.50%	50%	97.50%
1 second	Control vs Control	23	0.47	0.53	0.6
	Algae vs Control	25	0.46	0.52	0.58
	Predator vs Control	29	0.5	0.56	0.62
	<i>P. oceanica</i> vs Control	24	0.48	0.52	0.57
	Conspec. vs Control	24	0.47	0.54	0.6
5 seconds	Control vs Control	23	0.49	0.55	0.6
	Algae vs Control	25	0.46	0.53	0.59
	Predator vs Control	29	0.5	0.56	0.62
	<i>P. oceanica</i> vs Control	24	0.48	0.52	0.57
	Conspec. vs Control	24	0.47	0.54	0.6

The results did however demonstrate differences of speed and variance of speed in control and treatment water masses within the trials. In the predator and algae trials faster movement of the fish tested was evidenced, as well as higher number of the fast movement bursts in the treatment water masses. In contrast, fish tested in the *P. oceanica* trial moved more slowly and experienced fewer fast movement bursts in the treatment water mass. No notable differences in speed or the number of burst speed movements were observed within the control and conspecific treatments (Figure 32, Table 18).

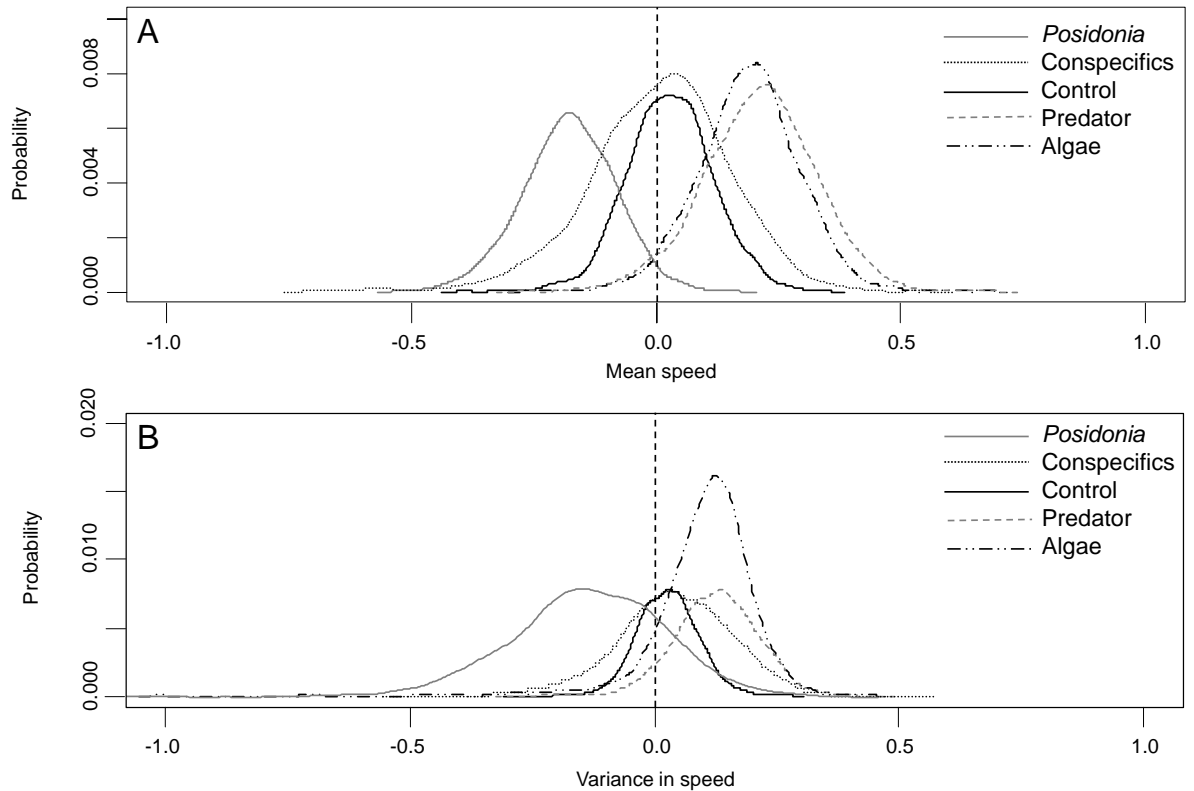


Figure 32: Within treatment movement analysis: A) Probability distributions of the differences between the fishes' means of the speed (the distribution displacement to the right means faster, while the displacement towards the left signifies slower movement within the treatment water mass), B) Probability distributions of the differences in the variance contained within the fishes' movements (the distribution displacement to the right means more, while the displacement towards the left signifies fewer burst speed movements within the treatment water mass).

Table 18: Bayesian Credibility Intervals (BCI) (median and 95%) for posterior distributions of the probabilities of having different mean speed and variance of speed in either water mass.

	Differences in mean speed				Differences in variance of speed		
	n	Bayesian Credibility Intervals			Bayesian Credibility Intervals		
		2.50%	50%	97.50%	2.50%	50%	97.50%
Control vs Control	23	-0.09	0.07	0.25	-0.1	0.02	0.14
Algae vs Control	25	-0.02	0.19	0.38	-0.11	0.11	0.26
Predator vs Control	29	-0.03	0.21	0.42	-0.04	0.13	0.28
<i>P. oceanica</i> vs Control	24	-0.34	-0.14	0.03	-0.46	-0.13	0.15
Conspec. vs Control	24	-0.25	0.06	0.3	-0.19	0.07	0.3

In addition, by disregarding the values within the control water masses and isolating only those from the treatment water masses, the analysis of movement between trial groups revealed differences in the fishes' mean speeds and variances of speed. Higher speeds were observed in algae, predator and *P. oceanica* trials treatment water masses, in comparison, medium velocity swimming was observed in the control trial, while the slowest swimming

occurred in the conspecifics trial treatment water mass. The highest number of burst speed movements was observed in the treatment water mass of predator trial, control, algae and *P. oceanica* experienced an intermediate number, while the treatment water mass of the conspecifics trial had fewest burst speed movements (Figure 33, Table 19).

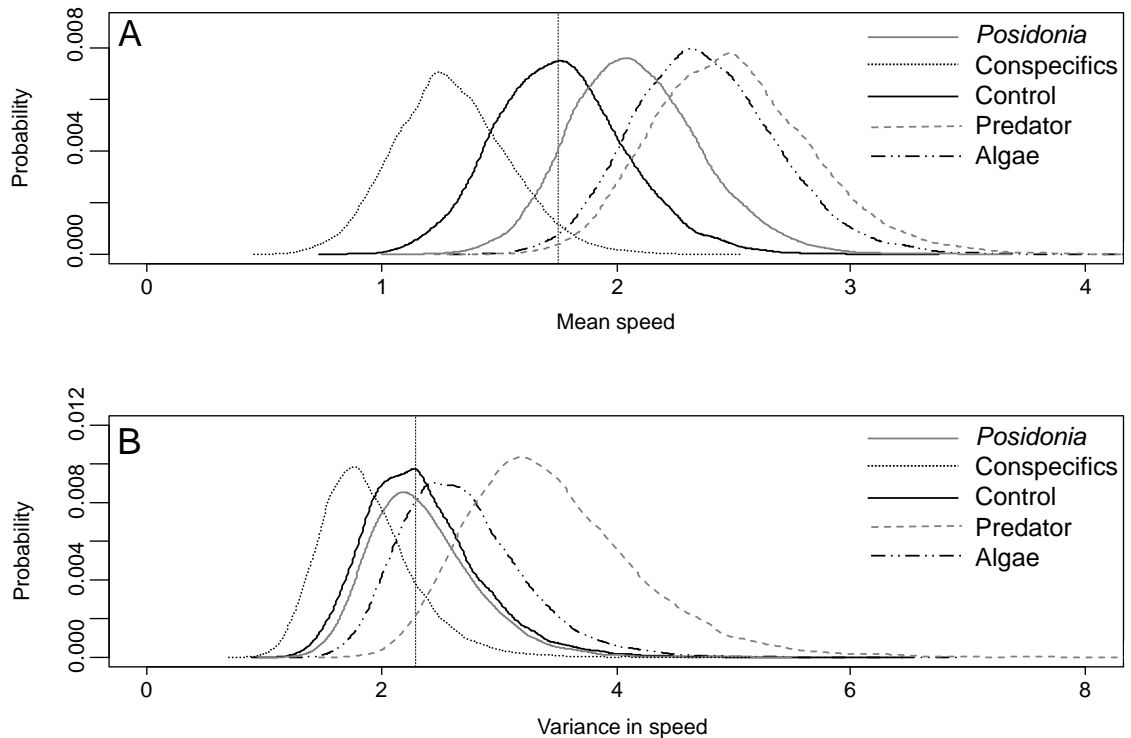


Figure 33: Between treatments movement comparison using the values isolated from the treatment water mass only in each experiment: A) Probability distributions of the comparison between the fishes' means of the speed (the distribution displacement to the right means faster, while the displacement towards the left signifies slower movement), B) Probability distributions of the comparison in the variance contained within the fishes' movements (the distribution displacement to the right means more, while the displacement towards the left signifies fewer burst speed movements). Vertical dashed lines represent the mean value of the control treatment mean speed and the control treatment variance of speed, respectively.

Table 19: Bayesian Credibility Intervals (BCI) (median and 95%) for posterior distributions of the probabilities of having different mean speed and variance of speed between treatment water masses (mean speed and variance of speed within the control water masses are not included, values isolated from the treatment water masses only).

	Differences in mean speed				Differences in variance of speed		
	<i>Bayesian Credibility Intervals</i>				<i>Bayesian Credibility Intervals</i>		
	n	2.50%	50%	97.50%	2.50%	50%	97.50%
Control	23	1.25	1.75	2.36	1.56	2.29	3.51
Algae	25	1.83	2.36	3.03	1.86	2.63	3.92
Predator	29	1.91	2.48	3.24	2.32	3.37	5.19
<i>P. oceanica</i>	24	1.59	2.07	2.69	1.63	2.3	3.43
Conspecifics	24	0.85	1.28	1.8	1.25	1.83	2.81

4.4 Discussion

Despite the lack of habitat preference through time spent in either water mass, the difference in speed and variance of speed expressed when the fish entered specific water masses demonstrated a capacity of detecting habitats via olfactory stimuli and responding by changes in behaviour i.e. movement patterns. Accordingly, it is likely that the olfactory treatment stimulus was detected and it triggered a behavioural response, it did not however cause directional movement away or towards the stimulus, explaining the lack of preference in time spent by the fish within a specific water mass and thus potential habitat. It is possible however that a stronger habitat preference in terms of the time spent in specific water masses may have been seen in larval fish of the same species rather than in already settled individuals. Previous studies have demonstrated that early life fish consider multiple, stepwise cue use for orientation from pelagic toward inshore habitats (Huijbers *et al.*, 2012). First, the long distance orientation from the pelagic zone toward the coastline is accomplished by the use of acoustic cues. Subsequently, when closer to the settlement habitat, the fish rely on olfactory cues in water plumes followed by the visual cues used for location and settlement to the specific benthic habitat. The olfactory system could thus play a secondary role in habitat detection and selection at the juvenile stage of the species examined. While the prevalence of a well-developed response to chemical cues in many

aquatic organisms has in part been attributed to the high turbidity of the areas inhabited (Mirza and Chivers, 2001), the importance of the visual sensory system has been demonstrated in areas of high water transparency (McCormick and Manassa, 2008). Shallow coastal areas of the Mediterranean Sea are typically characterised by high water clarity (Ballesteros and Zabala, 1993) which can give visual cues a more dominant sensory input in habitat selection/avoidance decisions for juveniles already settled within these habitats.

The comparison of speed and variance of speed within treatment trials demonstrated a capacity of change in behaviour to a complex array of olfactory stimuli, however there were no strong differences or clear ecological patterns observed in the movement within the control and treatment water masses of distinct trials. Once the habitat olfactory stimulus was detected and consequently the response triggered, the behaviour expressed could have prevailed for a period of time even if the fish moved into the presumably odourless habitat, which was confirmed by observing no differences in speed or the number of burst speed movements within the control trial containing identical water masses. Thus absolute speeds in individual trials both in treatment and control water would have been influenced by the olfactory stimulus tested. As a consequence, speeds were examined and subsequently large differences in speed in the treatment water masses between the trials were detected. These speed differences between treatment water masses of the trials were magnitudes greater compared to the differences within individual treatments and control trials. It was not possible to entirely eliminate the chance of presence of dissolved molecules within trial water masses, which could have somewhat altered the water density, however the base water used throughout the experiment was sand – filtered and UV – sterilised, which removed any initial suspended matter, resulting in an unlikely impairment of the laminar flow within the flume (Jutfelt *et al.*, 2016). Moreover, the control water and the experimental setup used were identical for all trials and were carefully managed throughout the experiment and thus,

these stark differences in absolute speeds between treatment trials were thought to have a behavioural response resulting from the effect of the treatment water rather than being connected to any external factor related to experimental procedures. It was therefore assumed that the speed differences observed in the treatment water could have been compared between treatment trials.

The observed increase in swimming speed in the predator trial experiment could have been the result of the behavioural alarm mechanism, suggesting that the juveniles have the capacity to recognise and react to detrimental habitats (Herbert and Steffensen, 2005). In addition to the increased speed, a higher number of burst speed movements was evidenced within the same trial. Most fish exhibit avoidance response through sudden, high-energy burst of unsteady swimming activity, consequently the burst speed is a trait correlated with greater survivorship (Domenici and Blake, 1997; Langerhans *et al.*, 2004). Previous studies have demonstrated that a rapid approach by the predator may trigger an early response in the prey allowing it to escape (Domenici and Blake, 1997). The juveniles tested displayed behaviour which is likely to be appropriate for potentially threatening habitat, characterised by the presence of predator signals: escaping with burst speed movements. Recognising and responding to potential threatening and other detrimental habitats is critical because this type of behavioural response occurs at the expense of other fitness-related behaviours and is energetically costly in itself (Frith and Blake, 1991; Lima, 1998; Meager *et al.*, 2011).

The faster movement in trials representative of algae and *P. oceanica* habitats could have been the consequence of activation of the food searching mechanism, further confirmed by the results of variance of speed, since the search for food, unlike for example the escape of predation, does not require frequent abrupt changes in speed. Prolonged periods of fast swimming may result in considerable expenditure, while swimming at lower speed results

in lower energy expenditure (Soofiani and Priede, 1985). Accordingly, the swimming speed could be a balance between decreased energy consumption at low speeds and increased energy gain when searching for food at higher speeds by encountering more prey. An optimum searching strategy could thus be to respond on detecting an odour and search at an increased swimming speed, as evidenced in the trials of algae and *P. oceanica*. Similar behaviour has also been demonstrated in Atlantic cod, which was able to detect a food odour source from a distance of several hundred meters and respond immediately to the odour plume by carrying out a rheotactic search at a moderately increased swimming speed (LØkkeborg, 1998).

On the other hand, in the case of the habitat characterised by the presence of conspecifics, since during much of the juvenile life stage *S. ocellatus* expresses shoaling behaviour (Cheminée *et al.*, 2013), it is possible that the presence of the olfactory cue had a calming effect on the individuals tested, thus resulting in slower movement and fewer burst speed movements. Shoaling can provide fish with a number of advantages, including reduced predator risk by using a number of anti-predator mechanisms, enhancements to foraging through social observation and increased foraging times, reduced energy expenditure by reducing drag and increasing lift around individuals swimming within the school and migration advantages, since the mean direction is likely to be a more accurate estimate of the correct destination than any individual's choice (Larkin and Walton, 1969; Pitcher, 1993). Accordingly, as a consequence of the information gained through detection of the odour in the conspecifics trial it is likely that the juveniles experienced somewhat safer habitat in comparison to the rest of the trials. Detection of the conspecifics olfactory cue and its behavioural response demonstrated in the trial could prove beneficial for future studies involving the species and can therefore be used for optimising the experimental conditions and procedures. When given no “olfactory incentive”, as seen in the case of the control water,

the fish were observed swimming at an intermediate speed and experiencing intermediate number of burst speed movements compared to the rest of the treatments, demonstrating that if no olfactory stimulus was present, no change in behaviour was triggered.

While the most likely interpretations were put forward, some of the findings of the study remain unclear. Further experiments which would include modified flume design, as well as testing additional fish species during different life stages are essential in order to conclusively interpret all the habitat selection behavioural responses. Even though the results presented within the study are not conclusive with respect to the reasons of the observed behaviours, they clearly show that habitat selection is a complex process. There are distinct differences in habitat selection/avoidance behaviours and the response to the water masses containing chemical cues characteristic of different habitats is not random.

In this chapter, habitat selection, in the context of the model system, was observed through detection of behavioural responses of the species studied. Occurrence of subtle and absence of strong behavioural habitat selection responses observed here however point to the complexity of the relationship between habitat and fish. In relation to the thesis, this chapter further reinforces the importance which the habitat and its properties have over the associated fish species.

5 Chapter 5: General discussion

Shallow water marine habitats are changing dramatically in response to environmental change. Their alteration in turn threatens fish communities relying on them for habitat provision. At present however, a much better understanding of the interaction between changing habitats and the associated fish communities is required. To address this key ecological topic, the principal aim of the thesis was examining, linking and comparing the mechanisms which underpin the habitat driven responses of reef fish, from entire communities down to species level, across tropical and temperate ecosystems. In this section, the findings from the data chapters were discussed in more detail with relevance to the thesis' main aim (see Table 20). Additionally, in ecological terms, the novelty of the findings of the individual chapters, their synthesis and potential for future research built upon were also discussed. Finally and importantly, the scope for broadly applicable conservational benefits stemming from this research was outlined.

Table 20: Data chapters' summary: questions addressed, overall results, their ecological significance and contribution to the knowledge.

	Chapter 2	Chapter 3	Chapter 4
Aim	The effect of changing habitat on the associated coral reef fish community	Patterns of fish habitat use and their comparison between species, within and across tropical and temperate reef habitats	Fish habitat selection using olfaction in a temperate model system
Result	Change in fish community structure, resulting from the fish dependency on the habitat for provision of shelter and food, followed by the functional change of the ecosystem	Variation in the size of the habitat used and its overlap between species within systems and uniform patterns in habitat use and comparable fish habitat size and overlap across systems	Detection of a range of subtle behavioural responses displayed during habitat selection or avoidance
Significance	Highlights the importance of the overall habitat in structuring the associated fish community and provides key ecological information about ecosystems following structural change and habitat loss	Argument for comparable mechanisms behind fish habitat use and interaction and uniform response of fish communities to habitat change across ecosystems	Highlights the extent of complexity of the mechanisms used in fish habitat selection and the ubiquitous importance of the habitat and its properties for the associated fish
Knowledge contribution	Essential information for understanding how the degradation of habitats influences functional diversity at community level and subsequent ecosystem function	Highlights the importance of the species' niche overlap calculations for predictions of functional redundancy in relation to changing habitats	Significance of the fish habitat selection mechanisms in quantification of habitat change, affecting the settlement processes responsible for functional diversity and ecosystem service provision

5.1 The effects of long-term habitat change on fish community composition

Long-term changes of the benthic habitat and their effects on the associated fish community were assessed in the Wakatobi National Park, located within the Coral Triangle, area renowned for being extremely biodiverse, yet currently severely threatened. Using this highly biodiverse ecosystem as the model system, it was demonstrated how important, in terms of shelter and food resources, the overall habitat is in structuring the associated fish community. Assessment of habitat – fish relationships using reef monitoring data encompassing multiple and consecutive years is rare for the Coral Triangle region,

highlighting the importance of the current study in understanding these biodiversity hotspots. At the same time, irrespective of the area they are established in, most long-term monitoring programmes are characterised by similar limitations, associated with the design and subsequent ecological interpretation of their results. Due to the general lack of funding associated with decades long projects, many coral reef monitoring programmes rely on inexpensive, but also inexperienced volunteer observers to carry out the surveys. By conducting extensive training prior to the surveys, a degree of care was taken to eliminate potential bias associated with inexperienced taxonomists in the monitoring programme from which the data was used for this thesis. Even so, it is highly probable that misidentification of certain species occurred, as well as discrepancies in fish counts, due to different personal survey criteria established by different observers. Furthermore, juvenile fish were not considered and consequently a proportion of ecologically important information associated with settlement and recruitment could have been lost (Wilson *et al.*, 2010). Despite the limitations and initial variability in the data, clear tendencies in the relationships between the change in habitat and fish were detected in this study. Relationships between habitat and individual fish species were tested for significance, thus allowing for exclusion of non-significant, often occasional species, and representation of all other species with statistically significant relationships. By grouping species into families the overall fish abundance observed was conserved, while overcoming an important shortcoming associated with the interpretation of the results influenced by possible erroneous identification of certain species. These analytical approaches enabled identification and discussion, with a high degree of confidence, of those fish which as a result of habitat change through decreasing hard coral availability experienced not only decrease, but also increases in abundance. Consequently, despite the commonly associated shortcomings discussed, this study gives useful suggestions on their data management and highlights the potential of the long-term

monitoring programs, based on the importance of the ecological information about habitat – fish relationships they facilitate.

5.2 Uniformity of habitat – fish relationship across different ecosystems

Outcomes of Chapter 2 demonstrated that, for the community and many fish families and species, there were clear changes that appeared to be driven by habitat alteration. However, examination at a much finer scale is necessary to know how alterations of certain habitats will affect species interactions with the habitat and not only the community composition and abundance. For this purpose, the Chapter 3 focused on measurement and comparison of individual species' niches within the habitat, thus examining how the fish use and interact with specific parts of the habitat. In order to test the generalised model, communities across systems characterised by different local biodiversity and habitat features, dominated by distinct biological ecosystem engineers, were investigated.

Owing to identical sampling techniques and uniformly applicable niche size estimation methodologies used, comparisons of the fish species niches and their overlaps were possible across the different ecosystems studied. As a result, the comparisons revealed that ecologically similar species of comparable feeding strategies and guilds, but that inhabit different ecosystems – detritivorous *C. striatus* and herbivorous *S. salpa* and macro invertebrate feeders *H. melapterus* and *S. tinca*, had very similar RN sizes, regardless of the niche measurement metric used, in their respective tropical and temperate ecosystem. On the other hand, the remaining species of the each ecosystem were ecologically different, characterised by distinct feeding strategies, and their RN sizes also differed. In the context of the thesis' research, discovery of uniform habitat – fish relationships indicates that mechanisms behind fish habitat use and interaction could indeed be similar within and across

other marine ecosystems, thus increasing the understanding of the role the habitat plays in niche partitioning processes responsible for sculpturing fish communities. Naturally, it is possible that the similarities and differences in niche sizes across the ecosystems were coincidental, however, there is a strong belief that had adequate additional species been compared, the same patterns would have been observed. For example, if *Chromis chromis* from temperate reef ecosystems were sampled, due to the already reported similarities in behaviour and microhabitat use of many Pomacentrids, independent of the geographic location, as well as the personal experience of the behaviour of the two species, a niche size comparable to that of the *P. caruleus* sampled in the tropics would have likely been observed (Medeiros, Souza and Ilarri, 2010). So, despite perhaps being ecologically bold in suggesting that habitat has highly similar effect on fish species from different ecosystems, resulting in directly comparable niche size of “similar” fish species across ecosystems, the empirical evidence provided could serve as a base for exploring this theory further. Subsequent efforts are necessary in order to find out, empirically, whether the size of realised niches of ecologically similar species are comparable across ecosystems, regardless of the habitat and biological diversity characterising them. Since the RNs of the common species and those representative of only two ecosystems were measured in this study, future sample sizes can be improved upon. As a result, to further explore the potentially interesting idea that the change in habitat will affect the associated fish community in the same way, regardless of the ecosystem type and location, further studies are encouraged, incorporating individual behavioural observations of additional study species and in different aquatic ecosystems.

5.3 Habitat selection

Following on from Chapter 3’s uniform patterns in habitat use across different ecosystems in Chapter 4, habitat selection, in the context of a single model system and species, was

investigated. By using stimulation by chemical cues, characteristic of specific habitats, a range of subtle habitat selection and avoidance responses were observed. As a result these findings further highlight the ubiquitous importance which the habitat and its properties have on the associated fish and the extent of the intricacy of the relationship.

Due to the number of benefits within the laboratory setting, most of the recently published studies have relied on two-current choice flume methodology for testing fish olfactory habitat selection (Jutfelt *et al.*, 2016). Within the marine environment, the majority of the olfactory habitat selection studies to date were conducted on the coral reef species, with the focus being heavily on the larval stage fish (e.g. Atema *et al.*, 2002; Gerlach *et al.*, 2007; Dixon *et al.*, 2010, 2011; Paris *et al.*, 2013). To date there are only two studies published on habitat selection using the two-current choice flumes in temperate marine fish, both conducted on larval fish (Radford *et al.*, 2012; Havel and Fuiman, 2015). In consequence, the use of olfactory cues in habitat selection of temperate fish is largely unknown for all life stages. Thus, by conducting the research on habitat selection within the thesis, the key ecological question of the importance of habitat on the associated fish was further addressed. This study is the first of its kind to report on the olfactory habitat selection of a temperate juvenile fish.

All of the two-current choice flume habitat selection studies conducted to date used the time spent in the specific water mass within the flume as the main proxy for olfactory habitat selection. In this study, a different olfactory response was evidenced demonstrating that the responses of fish in habitat selection are highly complex and that measuring only the differences in time of the occupancy between the water masses in olfactory habitat selection is not sufficient. Although the ability of detection of a specific habitat was evidenced, the results demonstrated that the olfaction was not actively used for selecting or avoiding a

habitat. The detection of an olfactory habitat stimulus resulted in a change of speed and variance of speed, a study aspect previously not explored by habitat selection flume studies. Thus, the analyses of speed could in future prove to be an important complementary tool for studying behavioural responses of fish in habitat selection and further contribute to our knowledge about the importance of habitat for the associated fish community.

5.4 Chapter synthesis

If the global concept of the thesis is considered, the topics studied within are crucial for understanding of the ecosystem functioning and its consequent service provision. The service provision depends on functional diversity, which in turn depends on the community composition controlled by the physical structure of the habitat, species interactions and settlement. This thesis has significantly contributed to the scientific knowledge of each of the factors responsible for driving the functional diversity of shallow water tropical and temperate reefs.

As the habitats are changing it is particularly important to understand how the degradation influences levels of functional diversity and redundancy. As seen in Chapter 2, despite examining a highly biodiverse system, which as the theory suggests should be capable of sustaining the loss of certain fish species without the loss of ecosystem function, the fish community changes were not redundant. Analyses at family and species level detected significance in the relationship between habitat change and habitat-dependent fish, as did the analyses of the change in species composition and dominance. A large-scale shift from habitat-dependent, small-bodied planktivorous species to larger-bodied Acanthurids was evidenced. The changes in the fish community species composition, associated with the degradation of the habitat, were thus not functionally redundant and most likely resulted in functional change of the ecosystem. On the other hand, the assessment of redundancy

through grouping species into feeding guilds failed to detect the relationship between the changing habitat and herbivores, the guild most commonly associated with functional change on coral reefs. Using the approach of grouping individual species into feeding guilds to assess the ecosystem resilience was thus proven to be inadequate and provided no additional information to that already gained by working on a much more resolute level, using fish families and species. When the fish trophic level is considered, all the resulting conclusions are based on their diet. What is not taken into account is how a trophic group would react to change other than that related to food. If separated into families and species, in addition to also being able to assess their dependency on habitat for food, many other ecologically important fish-habitat relationships are considered (e.g. the importance of habitat for shelter). Moreover, it could be argued that the trophic level approach could provide erroneous information leading to ecologically unsound conclusions. For example, it is unlikely that by grouping many of the Pomacentridae species and Caesionidae (2 most abundant families in the study) into planktivorous trophic guild would accurately predict the effect of habitat change on the guild and the subsequent effect on the ecosystem function. Apart from feeding on plankton these families are ecologically different. Amongst other differences, the most relevant in the context of the study is their association, or lack of, to the habitat. Pomacentridae are highly dependent on the habitat for refuge, while Caesionidae are not. By using the family level approach it was not only that the type of relationship of these families to habitat was empirically confirmed, but also that Pomacentridae had a positive relationship with the habitat, which was most likely due, but not limited to, their dependency on the habitat for shelter. Ideally, to accurately predict functional diversity and redundancy in relation to changing habitats, in addition to species-specific feeding habits and habitat requirements, information should also be considered for a number of other functional traits characterising the species, including behaviour, life

history, body form and size, etc. It is only then, that with some degree of confidence it can be postulated to what extent will the change in habitat result in functional change of the ecosystem. By empirically measuring the individual niches, the degree of redundancy between species can be calculated. In the Chapter 3, a large scale realised niche overlap was observed between several species, on both tropical and temperate reefs. As a result, the loss of some of these species could in theory be compensated by others. On the other hand, limited or no niche overlap was also seen for one of the species considered in each habitat. According to these results, the changes in fish community resulting from the change in habitat do not necessarily implicate functional changes but in order to assess the extent of the change it is necessary to empirically measure the redundancy and complementarity between species within the community. Finally, it is also very important to take into consideration and quantify how the habitat change may affect the fish settlement processes, as settlement is key to structuring the community and thus functional diversity and ecosystem services. For example, if the benthic habitat of a reef changes, the immediate and obvious result is the change of the physical structure but this also may result in the change of reef smell and its subsequent attraction for settlement. The results from Chapter 4 indeed demonstrate that it is likely that the reduction in macroalgal cover from a temperate reef can have effect on fish attraction to this habitat. Accordingly, the change in habitat, in addition to affecting fish community composition and species interactions, is likely to also alter functional diversity and resulting ecosystem services via reduced recruitment and habitat avoidance.

5.5 Conservational applications

All of the stressor-driven effects on the shallow tropical and temperate reef habitats highlighted throughout the thesis are likely to increase in the future i.e. global warming,

ocean acidification, habitat destruction, declining water quality, damaging fishing practices. For successful future management, the values of these habitats need to be better assessed in order to demonstrate real estimates of the ecosystem services that they provide. Better valuations of these services, in part provided by the evidence given within the thesis, can illustrate for communities and governments the significance of habitat loss and encourage their protection and restoration.

The extent and severity of local and global threats to the tropical coral reefs outlined within the thesis point to an urgent need for action to preserve the critically important ecosystem services that the reefs provide. As seen in the WNP example, people's high dependence on reefs for food and livelihood means that the degradation of the reefs will be severe for local populations, which in turn will also have wider implications for globally important fish stocks. Many reef nations socially and economically vulnerable, which is also coupled with high reef dependency and low adaptive capacity. These nations require national and local efforts to reduce reef dependence and build adaptive capacity, alongside reducing immediate threats to reefs. Identifying the needs of reef-dependent communities could reduce their vulnerability to future reef loss and emphasise the significance of sustainable reef use for poverty reduction and economic development. The ecosystem service provision of temperate reefs are also highly threatened and many opportunities for conservation of these habitats in key areas throughout the Mediterranean exist. Despite substantially lower immediate existential human dependence on these reefs, the loss of functional diversity caused by alteration in species interactions and settlement will have considerable consequences on many ecosystem services provided. Given the extent of the historical damage, for any reasonable ecosystem improvement, in addition to vigorous conservation, the management in many areas of the Mediterranean should also focus on restoration. Most algal-dominated reefs of the Mediterranean are found within the exclusive economic zones of individual

countries and thus the individual management of these countries must be strengthened to manage and protect these habitats.

As threats to shallow water coral- and algal-dominated habitats continue to grow the associated fish communities will continue to change. Interactions between habitat and fish will be further and more seriously threatened, resulting in less diverse communities and ecosystems that fail to be maintained. The thesis has shown that the alteration of habitats and the subsequent effect on fish communities can indeed have significant consequences for functional diversity and the ecosystem services that derive from these functions. Restoration and conservation efforts may be able to produce recovery of ecosystem functions through safeguarding the functional diversity of fish species. The purpose of currently established marine protected areas is mainly to ensure biodiversity, protect threatened species or critical habitats and increase fisheries production in neighbouring areas. More attention should be given to safeguarding the functional diversity of species that support ecological processes responsible for ecosystem provision. Further contributions to the knowledge of the functional aspects of species and their habitat interaction and requirements are necessary. This knowledge is key for conservation of the shallow water tropical and temperate reefs that will require a profound understanding of species functional features, their complementarity, and range of responses to habitat change.

In summary, the findings of this thesis added to our understanding of what shapes fish communities, how fish interact with their environment during habitat change and what potential mechanisms can drive such interactions. This detailed information is key to future conservation planning following habitat loss and structural change, which greatly threatens reefs around the world. Knowledge of the effects of habitat change on fish communities will ensure the survival and consequent ecosystem provision of these, and fragile ecosystems

alike. To finalise, in addition to the overall ecological significance of this thesis discussed throughout, a brief summary of potential specific management and conservational applications of the research, achieved by each of the data chapters, is given below:

- The long-term monitoring data proved itself to be extremely powerful in detecting the effect habitat change had on the associated fish community. Obtaining such data in sufficiently large areas and/or over long periods of time by an alternative scientific approach is otherwise unfeasible. Consequently, monitoring programs are critical for adequate management and conservation of ecosystems and all efforts should be made to increase their implementation.
- A body of empirical evidence was given to demonstrate comparable habitat use patterns of ecologically similar species between ecologically dissimilar ecosystems. The most obvious value of these findings to conservation is their potential to aid in development of a uniformly applicable management and conservation strategy for protecting seemingly different ecosystems.
- Using a single model species, a strong indication was given that behavioural response of organisms to different habitats can be more complex than previously thought. For future conservation it will be essential to integrate the findings to more adequately assess the effect of habitat alteration on the corresponding animal community.

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