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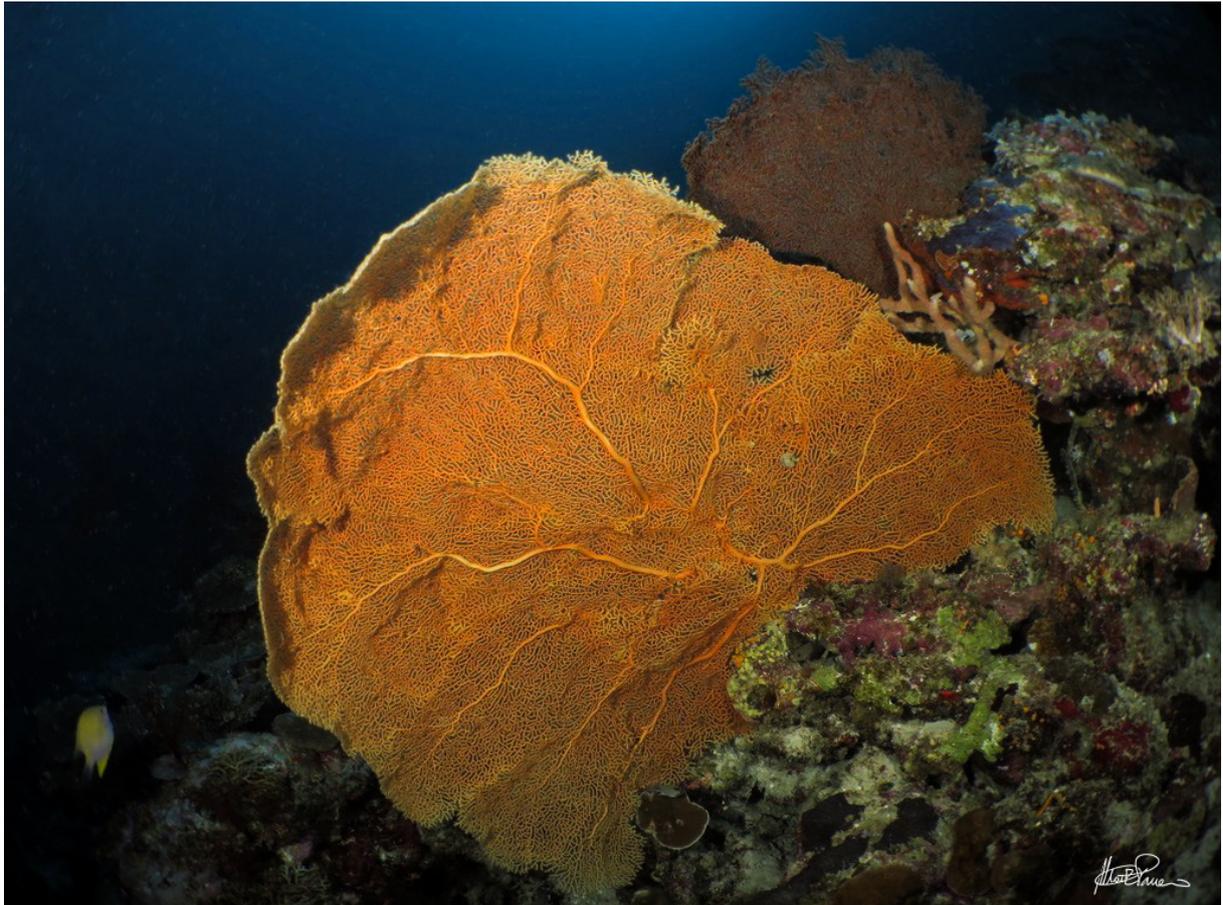
*Gorgonian spatial distributions, ecological  
interactions with fish assemblages and  
responses to their decline in health*



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August 2022

Master of Philosophy (Marine Ecology)  
ARC Centre of Excellence for Coral Reef Studies  
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*I dedicate this thesis to Umberto Panero and Donatella Barisan- my family in Italy whom I love unconditionally and who have supported me throughout my life.*

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## Abstract

Ecological engineers are important drivers in several ecosystems, including on coral reefs, as they can support large communities of organisms such as fish and invertebrate species that coexist with them. While scleractinian corals have received extensive research attention focussing on their spatial patterns, ecological relationships with other organisms, and effects of stressors, for other benthic structures, like gorgonians, research is still limited. Gorgonians (Cnidaria: Anthozoa) belong to the same group as soft corals, Octocorallia, and, as autogenic engineers, support a large variety of fish and invertebrate species through their own physical structure. Gorgonians are characterized by a wide range of growth forms, from simple like single strand whips, candelabrum growth forms to complex like bushy, fan, and branched structures. These structures provide habitats, shelters and feeding sites for many fish species. However, due to the increasing level of disturbances, caused by both natural and anthropogenic stressors, gorgonians have been dramatically impacted by habitat loss. Given the limited literature available on these topics, in this study I aimed to: (1) present a general introduction about gorgonians and their role as ecosystem engineers; (2) quantify spatial patterns of distribution and abundance of gorgonians across the depth gradient and to evaluate the effects of environmental factors such as current speed and benthic habitat structure on these spatial patterns; (3) to evaluate the influence of three gorgonian growth forms (branched, candelabrum, fan) on associated fish communities, including both mobile and resident fish assemblages; (4) to assess the effects of sea fan declining health on associated fish fauna. This study was conducted around the fringing reefs of the four islands (Orpheus Is., Pelorus Is., Curacao Is., and Fantome Is.) of the Palm Island Group, part of the central inshore area of the Great Barrier Reef, Australia.

Chapter 2 assessed the spatial patterns of abundance and distribution of gorgonians across depth and the influence of biophysical factors such as current speed and habitat cover on them. I used stereo video transects at 3 depths (15, 10, 5m) across 16 locations to assess the spatial patterns of gorgonian distribution and abundance across the depth gradient and locations, current meters at each depth to detect current speeds, and % of benthic habitat substrates was quantified. A total of 23 genera and 8 families of gorgonians were recorded. Gorgonian abundance and genera richness were increasing across the depth gradient, with 15m and 10m depth showing respectively values 3 times and twice higher than at 5m. Current speed and benthic habitat substrates had a positive effect on abundance and richness,

especially in deeper areas showing faster current speeds. At a community level, different gorgonian genera were inhabiting distinct depths, with the majority of the genera being azoozanthellate, hence explaining the relative patterns of abundance. *Ctenocella*, and *Dichotella*, respectively candelabrum and branched gorgonians were detected in deeper areas (15m), whereas whips (*Junceella*) and fans (*Annella*) were more prevalent at 10m. Overall, current speed was recorded as one of the main environmental drivers of communities at 15 and 10m, while % benthic substrata was different across depths, 15m and 10m seemed to be composed mainly of turf rock and macroalgae, while shallower areas 5m were dominated by hard corals (branching and massive), soft corals, and sand.

Chapter 3 investigated the influence of gorgonian growth forms on associated mobile and resident fish assemblages. I selected three gorgonian growth forms, branched, candelabrum, and fan. I used stationary videos, GoPro cameras mounted on a 30cm stand, and recorded 45 videos (n=15 videos per growth form), each one 30min in length. I counted and identified resident gobies on each gorgonian to genus level by conducting *in situ* visual surveys. While in the field, % habitat cover, topographic complexity (around 1m<sup>2</sup>) of each gorgonian, holdfast, and surface area were recorded. Results showed that gorgonian growth forms have an effect on abundance and species richness of associated mobile fish with higher values around more complex morphologies like fans and branched gorgonians, compared to candelabrum ones. No significant results were recorded for resident gobies abundance and richness across the three growth forms. At a community level, different growth forms attract different fish species, especially candelabrum structures that appeared to attract fish species not often detected around fans and branched gorgonians. Interestingly, the cleaner wrasse *Labroides dimidiatus*, was one of the species detected around all three growth forms. A distinctive pattern in community structure was found for resident gobies, with the genus *Pleurosicya* recorded exclusively on fans, while *Bryaninops* on both branched and candelabrum structures. Another factor that may have influenced fish communities around different growth forms was topographic complexity. Complex topography was usually recorded around fan and branched structures, where more fish species were recorded, whereas simple topographic complexity was usually recorded around candelabrum gorgonians.

Chapter 4 examined the influence of gorgonian declining health on associated fish communities. I deployed stationary videos, GoPro cameras on a 30cm stand (same methodology as chapter 2) in front of 50 individual sea fans for 30 min each. Sea fans were ranked in 5 health categories, based on the % live tissue left on their structures, 1, being the

healthiest (80-100%), to 5, the most-unhealthy (19-0%). I managed to show that sea fans are showing different states of health across the reefs across the fringing reefs of the Palm Islands, with 24% of the overall sea fan availability were unhealthy/dead, category 5 (0-19%), whereas category 1 (80-100%) showed only 20% availability. Sea fan declining health causes some effect on associated fish assemblages. In particular only abundance of mobile fish was influence by the state of health, with category 1 (80-100%) sea fans attracting the largest amount of fish. A clear decreasing pattern for resident gobies was shown, from category 1 to category 5, with no gobies present on dead sea fan skeletons. At a community level, again, sea fans' state of health had an effect on fish assemblages, with the healthiest gorgonians attracting more fish species than the other groups.

Overall, this study provides comprehensive data on the ecological importance of gorgonians on coral reefs, and, in particular, it is one of the pioneer studies that investigates gorgonians' spatial patterns, their ecological importance, and state of health on the Great Barrier Reef. Important baseline data are provided, useful for raising future hypotheses about the role of gorgonians on coral reefs. Further research can be suggested, perhaps improving the taxonomic knowledge, which could enable more species-specific studies on the ecological interactions between gorgonians and the associated organisms. A fruitful research path may be represented by the study of the causes of disturbances of gorgonian declining health, and in particular the understanding of how persistent this state of health is and whether it is increasing over time.

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## Chapter 1: General Introduction

The study of ecologically important species provides insights into the processes that structure ecosystems and determine how they respond to environmental change. A primary focus has been on *ecosystem engineers* or ‘organisms that directly or indirectly control resource availability to the surrounding communities through their own physical structures, hence causing biotic and abiotic changes of the environment’ (Jones et al. 1994, 1997). Ecosystem engineers can modulate resource availability for other species either directly, through their physical structure (autogenic engineers, e.g. trees, kelp forests, coral reefs), or indirectly, through biotic interactions (allogenic engineers, e.g. beavers, sea urchins, crown-of-thorns) (Jones et al. 1994; Crain and Bertness 2006). Allogenic engineers are critically important in all ecosystems, and patterns in their distribution and variation in their physical structure can have a major influence on the diversity and composition of the mobile animal assemblages they support (Jones et al. 1994; 1997; Romero et al. 2015; Ponge 2021). As a consequence, the global loss of biogenic habitat-forming species is a major cause of declining biodiversity. To fully understand the significance of any group of habitat-forming ecological engineers, it is important that we quantify their patterns of distribution, determine how animals are influenced by differences in habitat structure and how they respond to declining habitat health. Research on ecosystem engineers and their protection has been recognized as a top conservation priority (Crain and Bartness, 2006), but many potentially important groups have yet to be examined.

Coral reefs are some of the most diverse and productive marine ecosystems on the planet, where the primary ecological engineers, the reef-building scleractinian corals, support a large variety of fish and invertebrate species (Hoegh-Guldberg 1999; Wild et al. 2011). Numerous coral reef fishes depend on coral reef habitat for food, shelter, settlement sites and living space (Bell and Galzin 1984; Jones et al. 2004; Wilson et al. 2008; Kovalenko et al. 2012). Scleractinian corals vary in distribution and species composition along gradients of depth, exposure and current speed (Dai 1993; Goh and Chou 1993; Reskiwati et al. 2022), which has direct consequences for the distribution of the reef fish species they support. Different coral species and growth forms have a major influence on reef fish community composition (Komyakova et al. 2013), with high coral diversity and complexity promoting reef fish biodiversity (Bell and Galzin 1984; Kovalenko et al. 2012; Holbrook et al 2015). Over the last few decades, declining coral cover and complexity have been reported around the globe as a

result of multiple anthropogenic stressors, including climate change, crown-of-thorns outbreaks, disease and declining water quality (Hoegh-Guldberg 1999; Pandolfi et al. 2003; Coker et al. 2014; Hughes et al. 2017). Coral reef degradation has been directly linked to declining reef fish biodiversity and community structure (Jones et al. 2004; Feary et al. 2007; Coker et al. 2014). This has prompted increasing interest in other structurally complex, habitat forming taxa on coral reefs that can provide food and shelter for fishes, including sponges (Voultsiadou et al. 2010) and soft corals (Epstein and Kingsford 2019). However, the distributions of alternative ecological engineers, their ability to support reef fishes and withstand environmental change are poorly understood.

Gorgonians (Anthozoa, Subclass: Octocorallia, Order: Alcyonacea) have been recognized as another distinct group of autogenic engineers on coral reefs, with tree-like 3-dimensional structures that potentially enhance the biodiversity of invertebrates and fishes (Fabricius and Alderslade 2001; Buhl-Mortensen et al. 2010; Bullimore et al. 2013). Their skeletal structure has an internal axis made of gorgonin, a proteinaceous material, which confers flexibility to their structures and enables to hold an upright position that can extend several meters into the water column (Leversee 1976; Fabricius and Alderslade, 2001). They come in a variety of growth forms, including single strand sea whips, bushy and branched structures, and large sea fans (Fabricius and Alderslade 2001), all of which may support different fish assemblages. Large sea fans are one of the most photographed features of coral reefs, not only for their unique structure, but also because of the biodiversity of the fishes often associated with them. Some small fishes, such as the pygmy sea horse (*Hippocampus bargibanti*), live in a specialized association with sea fans of the genus (*Muricella*) (Smith et al. 2012; De Brauwer et al. 2020), while numerous other fishes are attracted to them as shelter sites (Chen et al. 1995; Goh et al. 1999).

While gorgonians are distributed over a wide range, from temperate to tropical latitudes, there have been relatively few studies that have examined their patterns of distribution, their ecological roles as fish habitat, or their susceptibility to anthropogenic impacts and the consequences for the fishes associated with them. The vulnerability of gorgonians to increasing anthropogenic stressors has become more evident in the last few decades, including physical damage from bottom trawling and long line fishing (Watling 2005; Bhagirathan et al. 2014), diseases such as *Aspergillosis* (Zuluaga-Montero and Sabat 2012) or other mass mortality events (Cerrano et al. 2005). Gorgonians are also directly exploited as

part of the aquarium trade and some, such as the red coral (*Corallium rubrum*), are collected and sold as ornaments or jewellery (Fabricious and Alderslade, 2001). The consequences of these impacts for local reef fish biodiversity have received extremely little attention.

The distribution and abundance of gorgonians are likely to be the same strong environmental gradients that influence scleractinian corals, such as depth and exposure. However, due to the presence of both zooxanthellate and azooxanthellate modes of nutrition in gorgonians (Muzik and Wainwright 1977; Rowley 2018), they are found over a broad depth range, from shallow to mesophotic areas (Goh et al. 1997, 1999; Bridge et al. 2012). Few studies have addressed the factors affecting spatial distributions of gorgonians, but substratum type, current flow, wave action, temperature and light penetration have all been implicated, especially in relation to depth distributions (Bayer 1961; Lasker and Coffroth 1983; Brown 1984; Goh and Chou 1994). Higher current strength may favor gorgonians as they depend on water flow for nutrition (Sponaugle 1991), however, different growth forms of gorgonians may respond to environmental gradients in different ways (Rowley et al. 2015). To date, most of the literature on factors affecting gorgonian distributions comes from studies in the Caribbean (Kinzie and Robert 1973; García-Parrado and Alcolado 1996; Quintanilla et al. 2018) and a few studies in Indonesia, Fiji, and Singapore (Muzik and Wainwright 1977; Goh et al. 1997; Rowley et al. 2015). Gorgonians have received very little attention throughout most of the Indo Pacific and on the Great Barrier Reef. They are often under-represented in general coral reef benthic cover surveys as, because of their tree-like growth form, they can occupy only a small proportion of the substratum. Unless studies focus specifically on factors affecting their distribution and numerical abundance, they are likely to remain neglected in coral reef monitoring programs.

Very few studies have addressed the role of gorgonians as a habitat of significance for coral reef fishes. There are many anecdotal observations of fishes aggregating around gorgonians, where they may acquire a range of resources such as food, shelter, settlement or breeding sites. However, the degree to which there are fishes that depend exclusively on gorgonians or have a preference for gorgonians over other habitat-forming species has not been evaluated. There are clearly a few highly specialised fishes such as the pygmy sea horse, *Hippocampus bargibanti*, which is only found on one genus of fan (Smith et al. 2012; De Brauwer et al. 2020). There are several other cryptobenthic fishes, such as some goby species from the genera *Bryaninops* and *Pleurosicya* that are strongly associated with certain growth forms of

gorgonians such as sea whips (Chen et al. 1995; Sih and Chouw 2009). Other fish, such as batfish and groupers, have been observed using the gorgonians as shelters, the former using the aggregation of single strand whips (*Junceella*) as shelter, and the latter using the candelabrum (*Ctenocella*) to ambush its prey. However, the fish assemblages associated with different gorgonian growth forms have yet to be quantitatively assessed. Fish communities may be influenced by a range of structural attributes of gorgonians, such as the number of branches (De Clippele et al. 2015) and surface area (Cúrdia et al. 2015), as has been observed for invertebrates associated with gorgonians, but these factors have not been addressed for fishes.

Gorgonians are vulnerable to the same anthropogenic stressors that are devastating coral reefs around the globe, but the current state of the health of different gorgonians has seldom been investigated and the impact of declining health on fishes has received virtually no attention. On temperate reefs, an alarming decrease in gorgonian populations in the shallower areas of the Mediterranean Sea have been documented, prompting the introduction of conservation strategies to protect these organisms (Valisano et al. 2015). A few investigations in the Caribbean have examined how *Gorgonia ventalina* was severely impacted by a fungal disease (*Aspergillosis*) caused by *Aspergillus sydowii* (Nagelkerken et al. 1997; Sánchez et al. 1997; Toledo-Hernández et al. 2007). Gorgonians are vulnerable to anthropogenic stressors such as bottom trawling and long-line fishing, which can be extremely destructive, especially on growth forms like sea fans (Scinto et al. 2008; Bhagirathan et al. 2014). There are many anecdotal observations of the declining health of sea fans through loss of live tissue, eventually resulting in dead skeletal structures, but the causes are often unknown. Such changes are likely to dramatically impact highly specialized fishes, which are usually the first to disappear through loss of habitat (Munday et al. 1997; Munday 2004). The effects on more mobile fishes may be less dramatic, but they may be impacted as the quality of the shelter gorgonians provide gradually declines as they lose their fine branching structure. The effects of declining gorgonian condition on fishes can be readily addressed by quantifying any differences in assemblage structure on gorgonians in different stages of declining health, but to date, there have been no studies of this kind.

The aim of this thesis was to assess the role of gorgonians as ecological engineers by addressing three broad questions: (1) What are the spatial patterns in gorgonian distribution and abundance, and what roles do current speed and habitat availability play in explaining

these patterns? (2) How do the fish communities associated with gorgonians vary among the different growth forms, including branching, candelabrum and fan structures? (3) What is the extent of damage to sea fans and how do fish communities respond to different stages of declining health? This is the first study of its kind for the Great Barrier Reef, and focusses on the Palm Islands, a coastal island group in the central region, where gorgonians can be extremely abundant. Each broad question is addressed in a different chapter, where there is a number of more specific objectives.

Chapter 2 evaluated the spatial patterns of abundance and distribution of gorgonian genera at 16 locations of the reefs of the Palm Island Group, and at each location, quantified abundance at three depths (5, 10, 15m). The effects of two biophysical factors, current speed and benthic habitat structure, on gorgonian distribution, abundance, and genera richness were investigated. In addition, changes in the structure of gorgonian assemblages along the depth gradient, in terms of generic composition and growth forms, were investigated.

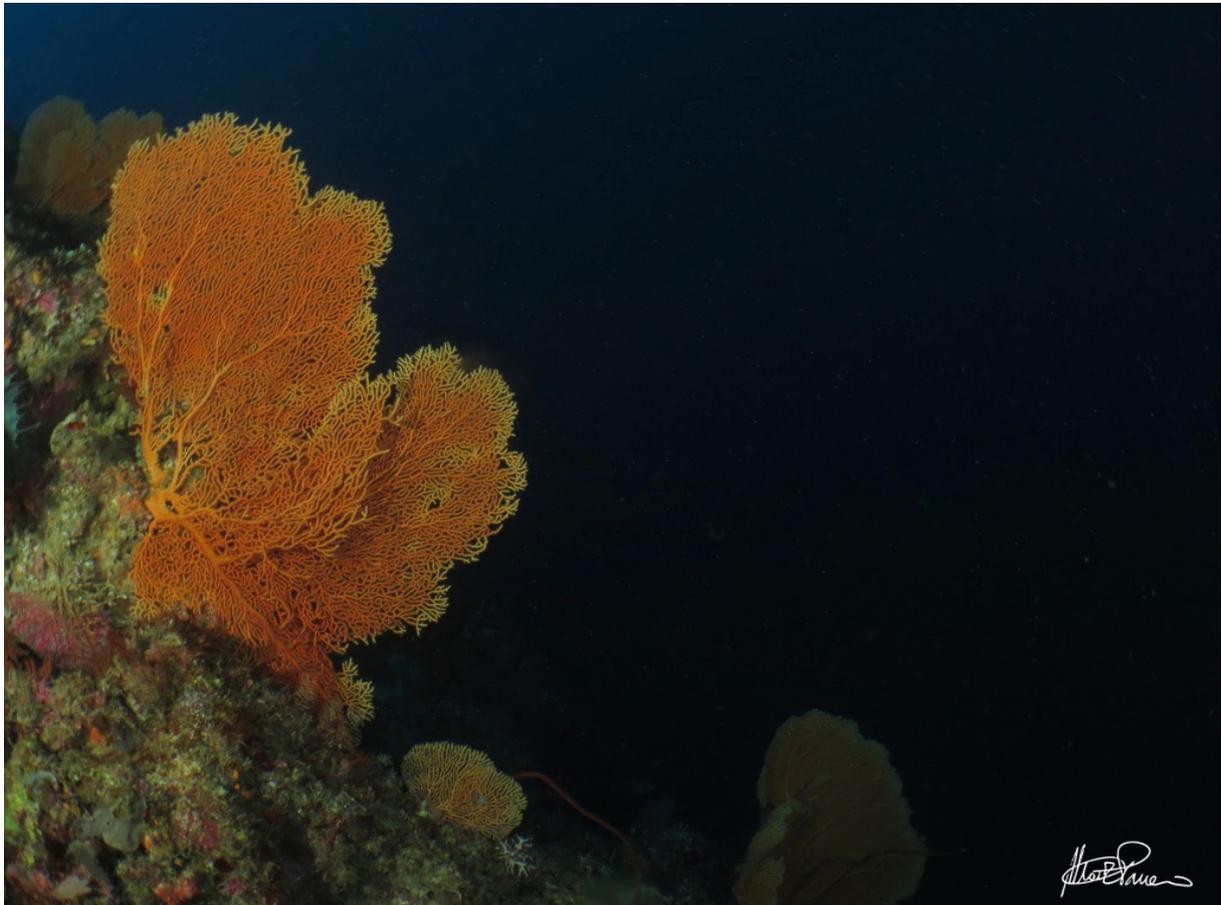
Chapter 3 focused on the influence of different gorgonian growth forms on the structure of fish assemblages that were associated with them, in terms of abundance, species richness and species composition. It compares three structurally different growth forms (branched, candelabrum and fans), distinguishing larger mobile fishes and small resident gobies. The fishes associated with gorgonians were compared to their overall abundance on the reef, to determine which species are attracted to gorgonians. Habitat structure around gorgonians was also quantified, to assess its likely role as an additional factor affecting reef fish assemblages.

Chapter 4 investigated the extent of sea fan damage at the Palm Islands by classifying all individuals into 5 different stages of declining health. Sea fans exhibited levels of health ranging from individuals exhibiting no observable damage, to those that were just dead gorgonian skeletons with no live tissue left. To examine the likely consequences for fishes, changes in the fish assemblages associated with individual gorgonians in different health stages were quantified, both for larger mobile fishes and small resident gobies.

In the general conclusions (Chapter 5), I summarize the main findings of the thesis and evaluate the role of gorgonians as ecological engineers and the significance of declining health. I suggest future research paths to undertake in order to better understand different aspects of gorgonian ecology and their significance to fishes. The preliminary findings of this thesis suggest that gorgonians require urgent conservation attention, including studies on

longer-term trends in gorgonian health and developing effective measures to reverse these trends.

## Chapter 2: Roles of depth, current speed and habitat structure in shaping gorgonian assemblages on inshore coral reefs



Gorgonian sea fan (genus: *Annella*) residing in the deeper area of a slope on the Great Barrier Reef, Australia.

## 2.1 Abstract

Gorgonians are a diverse and conspicuous component of coral reef ecosystems, providing habitat structure that supports unique assemblages of fishes and invertebrates. Evaluating their overall importance as ecological engineers requires an understanding of their spatial patterns of distribution, abundance and community structure, and the biophysical factors that drive these patterns. However, while these drivers have been well studied for scleractinian corals and other habitat-forming taxa, for gorgonians they are poorly understood. In this study, I quantified the abundance, genera richness, and assemblage structure of gorgonian assemblages using video surveys at three depths (5, 10 and 15 m) at 16 locations at the Palm Islands, an inshore island group in the central Great Barrier Reef. The potential role of water currents in driving gorgonian spatial patterns was assessed by deploying *in situ* current meters at each location and depth, and the potential role of habitat structure was assessed by quantifying benthic cover. Gorgonian abundance and genera richness consistently increased with depth, although the magnitude of the depth effect varied among locations. Abundance and genera richness were both positively related to current speed. Abundance increased with an increase in the percent cover of rubble and declined with increasing cover of hard corals. The structure of gorgonian assemblages also varied among depths, with whip (*Junceella*, *Viminella*) and fan (*Acanthogorgia*, *Anthogorgia*, *Annella*) growth forms being dominant at depths of 5 and 10 m, and branching (*Dichotella*, *Icilogorgia*) and candelabrum (*Ctenocella*) forms being dominant at 15 m. The shallow gorgonian assemblage was associated with high coral cover, while the deeper assemblage was associated with high current speeds, and high percent cover of rubble, turf and/or macroalgae. This study highlighted that the abundance, diversity and structure of gorgonian assemblages on coral reefs is likely determined by a range of biophysical factors linked to depth. Further work is required to isolate the primary drivers of these depth related effects and evaluate their relative importance.

**Keywords:** Alcyonacea, Ecosystem Engineers, Current, Depth, Benthic Substrata, Community Ecology

## 2.2 Introduction

Coral reefs are among the most biodiverse ecosystems on the planet, providing numerous social and economic benefits for human communities (Hoegh-Guldberg 2011; Hughes et al. 2017; Woodhead et al. 2019). The roles of different taxa in coral reef habitats will depend on their abundance, spatial distributions, and community structure. Understanding the physical and biological drivers of the spatial patterns of key habitat-forming organisms on coral reefs is essential to evaluate their significance to reef ecosystems as a whole (Bellwood et al. 2019). Naturally, most attention has been given to scleractinian corals, as they are the building blocks of coral reefs, and in recent years, widespread declines have been reported as a result of multiple stressors (Pandolfi et al. 2003; Bellwood et al. 2019; Williams et al. 2019). Scleractinian corals are important ecosystem engineers, supporting many other reef-associated species such as fishes and invertebrates (Jones et al. 1994, 1997; Graham and Nash 2013). However, there are numerous other habitat-forming benthic organisms on coral reefs, including soft corals, sponges and gorgonians, which also promote habitat diversity and spatial heterogeneity (Sponaugle 1991; Evans et al. 2011; Abeytia et al. 2013). These organisms can dominate the substratum on some coral reefs, contribute to the complex, three dimensional structure of reef habitats, and also support a broad range of unique fish and invertebrate species (Dinesen 1983; Jones et al. 1997; Diaz and Rützler 2001; Buhl-Mortensen et al. 2010; Grinyó et al. 2016). However, despite the potential importance of these taxa as ecosystem engineers, their spatial patterns in abundance, genera richness, and community structure, and the physical and biological drivers of these patterns have received much less attention (Dinesen 1983).

Gorgonians (Order Alcyonacea) are part of the Octocorallia subclass of the Anthozoa (which includes sea anemones, scleractinian corals, and soft corals), and are made up of three suborders: Calcaxonia, Holaxonia, Scleraxonia (Fabricius and Alderslade 2001). They are a conspicuous and diverse component of coral reef habitats, with growth forms to rival hard corals in structural diversity, including candelabrum, fan, whip, branched, and bushy growth forms (Fabricius and Alderslade 2001). Their complex structures create a diverse range of microhabitats that provide resources for a large variety of fish and invertebrate species (Graham and Nash 2013). There have, however, been few studies on the spatial patterns of abundance, genera richness, and structure of gorgonian assemblages, especially in the Indo-Pacific (but see Rowley 2018; Kupfner Johnson and Hallock 2020). The biology and morphology of gorgonians can provide clues as to which environmental factors determine

their abundance and distribution, and how this is likely to vary among species (Al-Marayati and Edmunds 2018). Gorgonians are passive suspension feeders, extracting nutrients from the water column, and therefore water motion, current speed, and water turbidity can have significant impacts on their feeding strategies (Muzik and Wainwright 1977; Chang-Feng and Ming-Chao 1993). Unlike scleractinian corals, there are zooxanthellate or azooxanthellate species among gorgonians (Rowley 2018). Unlike zooxanthellate gorgonian species, azooxanthellate species are not restricted to shallow depths where there is sufficient light availability for photosynthesis, and they can be found in deeper or more turbid areas (Kinzie 1973; Goh and Chou 1994; Fabricius and McCorry 2006). Gorgonians of different growth forms can adapt to the particular hydrodynamic regimes in the areas they occupy. For instance, gorgonians with a fan morphology are flexible and can orient themselves perpendicular to the water flow, which can enhance, not only their feeding outcomes, but also their ability to minimize hydrodynamic forces (Leversee 1976; Lin et al. 2002; Rodríguez-Lanetty et al. 2003).

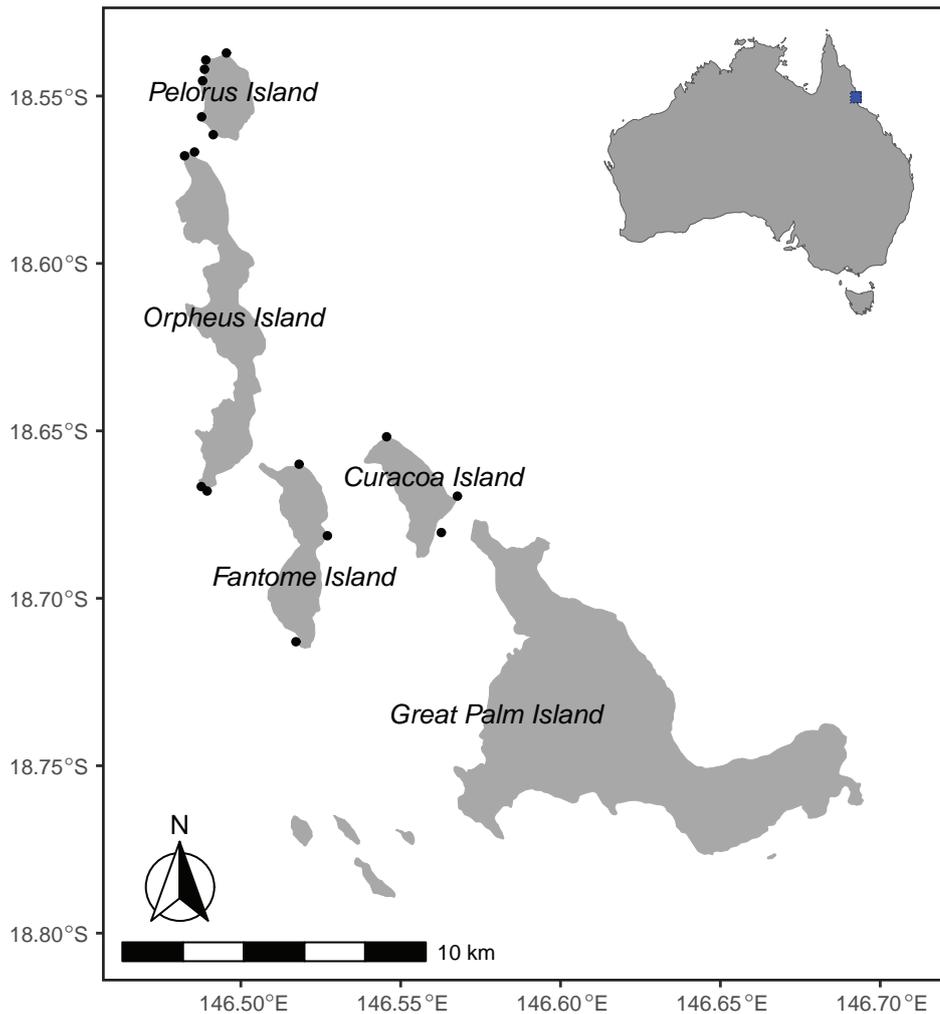
The abundance, genera richness, and community structure of gorgonians are therefore likely to vary among locations and along depth gradients (Goh and Chou 1994; Sánchez et al. 1997; Fabricius and McCorry 2006; Rowley 2018). Rowley (2018) showed that richness of azooxanthellate gorgonians increased with depth, while zooxanthellate forms showed the inverse pattern (Rowley 2018). Quintanilla et al. (2019) found higher abundances of larger gorgonian species, including the gorgonian fan, *Gorgonia ventalina*, at deeper depths, where there was less water motion (Quintanilla et al. 2019). Interestingly, in Singapore, high abundances of gorgonians were observed in shallow, turbid water where there was a lower abundance of competitors such as scleractinian corals, and greater availability of suitable substrata (Goh and Chou 1994). In the Caribbean, gorgonians are most abundant on the shallow reef crest, where there is high cover of scleractinian corals (Bayer 1961). In Venezuela, fans were more common at shallower depths, whereas tree-like morphologies were more common at greater depths, with a consistent depth-related pattern across the gradient (Rodríguez-Lanetty et al. 2003). Water movement is likely to play an important role in determining the distribution and abundance of gorgonians, with faster currents increasing feeding and growth rates. However, the ability to withstand high currents may vary among growth forms. For example, in the Caribbean, a study conducted at two reef habitats, lagoonal reefs and fore-reef terraces, showed that gorgonians were found mainly on shallow fore-reef terraces which had greater hydrodynamic energy (Sánchez et al. 1997). Clearly, the roles of

current speed and habitat structure in driving ecological patterns in gorgonians are complex and require further investigation.

This study evaluated spatial variation in the abundance, genera richness and assemblage structure of gorgonians among depths and locations at the Palm Islands on the central Great Barrier Reef. In addition, current speed and habitat structure were quantified to assess their potential roles in driving these spatial patterns. Gorgonians were surveyed using video surveys conducted on SCUBA at 3 depths (5, 10 and 15 m) at each of 16 fringing reef locations around the islands. Current speed was quantified by deploying in-situ current meters at the same 3 depths at all locations, and benthic cover was estimated using the same video surveys in order to evaluate the effects of habitat structure. The following questions were addressed: (1) How does gorgonian abundance and genera richness vary among depths and locations? (2) Are gorgonian abundance and genera richness positively related to average current speed? (3) How are gorgonian abundance and richness related to benthic habitat cover? (4) How does gorgonian assemblage structure vary along the depth gradient, and does the relative abundance of azooxanthellate and zooxanthellate genera, and the different growth forms, vary with depth? (5) What is the role of current speed and habitat structure in explaining spatial variation in the structure of gorgonian assemblages? I hypothesised that depth would be an important factor in explaining gorgonian distribution, but that it may not influence all gorgonian morphologies in the same way. I also hypothesised that current speed and benthic habitat structure would be two important drivers of abundance and community structure, as they are likely to be significant factors affecting gorgonian attachment and growth.

### **2.3 Methods**

This study was carried out in the Palm Islands on the central Great Barrier Reef (GBR), Australia, based at Orpheus Island Research Station (-18.7345°S, 146.5794°E). This group of inshore islands comprises 16 islands with extensive areas of fringing reef. To explore the extent of spatial variation in gorgonian abundance, genera richness and composition, surveys were carried out at 16 locations spread across four of the larger islands, including Orpheus, Pelorus, Fantome, and Curacoa (Fig 2.1).



**Figure 2.1** Study locations (1-16) of gorgonian surveys at four islands, Orpheus Is. (Goolboddi), Pelorus Is. (Yanooa), Fantome Is. (Eumilli), and Curacao Is. (Noogoo), in the Palm Island group on the central Great Barrier Reef

### Gorgonian surveys and video analysis

At each location, surveys were conducted by laying out four replicate 30m belt transects along the reef contour at each of three depths (5, 10, and 15 m), summing to a total of 192 transects. Gorgonian abundance was quantified by diver-based surveys using a stereo Diver-Operated Video (DOV) system (SeaGis, Australia). Our DOV method followed the recommendations of Goteze et al. (2019), with two GoPro Hero 5 cameras set to 1080p resolution and 60fps wide setting. Video surveys were chosen as they facilitate accurate identification after surveys have been conducted, provide a permanent record and allow for rapid data collection within a limited timeframe. I used EventMeasure software (SeaGis,

Australia) to measure a 2.5m field of view either side of each transect which provided a known belt width of 5m. Videos were then played back in a standard mediaplayer (QuickTime Player). All gorgonian colonies within each transect were identified to genus level (as per Fabricius and Alderslade 2001) and their growth forms recorded, providing estimates of abundance and genera richness per 150m<sup>2</sup>. To properly ID gorgonians to genus level, using videos, preliminary observations in the field were carried out. Overall, the level of certainty in gorgonian identification can be estimated to approximately 90-95%. Sea whips were often found in large clumps and were difficult to count individually, therefore estimates of their abundance were approximate.

### **Environmental variables: current speeds and habitat substrata**

To quantify current speeds at different locations and depths, I deployed Marotte HS Drag-Tilt Current Meters (Marine Geophysics Laboratory, James Cook University, Australia) at the same 3 depths that were surveyed at each location for a period of 6 days. Current meters were tethered to a weight in an upright position to ensure free movement of the instrument. All instruments were calibrated prior to deployment and set to record current speed (m s<sup>-1</sup>) and direction (degrees from North) every 10 seconds. After deployment, data were processed using the specialist software Marotte HS Config (Marine Geophysics Laboratory, James Cook University). Current speeds were averaged over the 6-day period. Surveys were conducted during late autumn 2021.

Benthic habitat surveys were carried out using a random point count method, with 300 points per video transect. Each video transect was stopped at 60 random times, and in each frame, the benthic organism or substratum beneath each of 5 random points was recorded. Benthic organisms and substrata were placed into the following categories: sand stable (not rippled), sand mobile (rippled), rubble, turf rock, macroalgae, sponges, soft corals, and hard corals of branching, encrusting and massive morphologies.

### **Statistical analysis**

All statistical analyses were performed using RStudio (Version 1.4.1717, R Core Team 2022). Generalized linear models (GLM) were used to test for differences in mean abundance and genera richness among locations and depths, and the interaction between location and depth.

Both abundance and richness models used a negative binomial error family with log link and were fitted in the “MASS” package (Venables and Ripley, 2002). Adjusted Tukey tests were used to identify pairwise differences between depth bands using the package “emmeans” (Russell et al. 2022).

To investigate the effect of current speed on gorgonian abundance and richness, I used Generalized linear mixed models (GLMM) with location as a random factor and current speed as a fixed factor. Models for abundance and richness were fitted with a negative binomial error family and log link. I also used GLMMs to test the effect of the percentage cover of each benthic substratum on gorgonian abundance. Each of these models used a negative binomial error family with log link and was structured with the percentage cover of each benthic organism/substratum as a fixed factor, and location as a random factor. All GLMMs were constructed using the package “glmmTMB” (Bolker 2019) which reports coefficient estimates with 95% confidence intervals. Marginal and conditional  $R^2$  values for GLMMs were calculated using the `r.squaredGLMM` function of the “MuMIn” package (Barton 2020). Marginal  $R^2$  provides the variance explained only by the fixed effects and conditional  $R^2$  provides the variance explained by the entire model. For all models, hypothesis tests of fixed effects were calculated as Type II Wald Chi-square tests conducted using the ‘`anova`’ function from the package “car”. The goodness of fit for all models was assessed using the “DHARMA” package (Hartig 2021).

As assemblages may be affected by the simultaneous effects of environmental variables, a multivariate approach was used to assess the interactions between them. First, to visualise differences in gorgonian assemblage structure I performed Non-metric multidimensional scaling (NMDS) using the function `metaMDS`, part of the “vegan” package (Oksanen 2020). Data were square-root transformed, followed by a Wisconsin double standardization and fit on a Bray-Curtis distance matrix. Fitted correlation vector scores for genera and current speed were extracted using the function ‘`envfit`’ and genera with the strongest correlations (pearsons  $r < 0.001$ ) plotted as a biplot using “`ggplot2`” (Wickham 2016). To then assess the role of depth in driving assemblage differences, I conducted permutational analysis of variance (PERMANOVA) using the `adonis2` function in the “vegan” package. PERMANOVA was run on 999 permutations and a Bray-Curtis distance matrix. An analysis of multivariate homogeneity (PERMDISP) was carried out using the ‘`betadisper`’ function to assess within group dispersion (Anderson and Walsh 2013).

Finally, to assess relationships among benthic organisms/substrata and gorgonian assemblage structure, I performed a distance-based redundancy analysis (db-RDA) on a Bray-Curtis distance matrix of square root transformed data. I used the functions ‘dbrda’ and ‘envfit’, part of the “vegan” package. Only significant ( $p < 0.05$ ) environmental variables were plotted as a vector biplot with the dbRDA axes (Paliy and Shankar 2016).

## 2.4 Results

### General patterns

In the surveys, I recorded 4,610 gorgonian individuals, belonging to the suborders Calcaxonia, Holaxonia and Scleraxonia. This included 8 families and 23 genera (Table 2.1). The majority were azooanthellate forms, except for *Hiksonella*, *Isis*, and *Pteronisis*. The genera included branching (9 genera), fan (7 genera), bushy (4 genera), whip (2 genera) and candelabrum (1 genus) growth forms (Fig. 2.2). In terms of relative abundance of the different genera, the fauna was dominated by two whip genera (*Junceella* and *Viminella*), two branching genera (*Dichotella* and *Ellisella*) and the candelabrum genera (*Ctenocella*), all belonging to the family Elisellidae (Fig. 2.2, Table 2.1). The other genera recorded were relatively rare.

**Table 2.1** Summary of the gorgonian genera recorded in this study. Gorgonians are categorised as zooxanthellate (Z) and azooxanthellate (AZ). Five growth forms are distinguished: branched (Br), bushy (B), fan (F), candelabrum (C), and whip (W)

Taxon	Z/AZ	Growth forms
SUBORDER: Scleraxonian		
FAMILY: Anthothelidae (Broch, 1916)		
<i>Icilogorgia</i> (Duchassaing, 1870)	AZ	Br
FAMILY: Melithaeidae (Gray, 1870)		
<i>Meliatheia</i> (Milne Edwards & Haime, 1857)	AZ	F
<i>Mopsella</i> (Gray, 1857)	AZ	Br
FAMILY: Subergorgiidae (Gray, 1859)		
Subergorgia (Gray, 1857)	AZ	Br
<i>Annella</i> (Gray, 1858)	AZ	F
Suborder: Holaxonians		

## FAMILY: Gorgoniidae (Lamouroux, 1812)

<i>Villogorgia</i> (Duchassaing and Michelotti, 1860)	AZ	F
<i>Hiksonella</i> (Nutting, 1910)	Z	B
<i>Pseudopterogorgia</i> (Kükenthal, 1909)	AZ	Br

## FAMILY: Acanthogorgiidae (Gray, 1859)

<i>Acanthogorgia</i> (Gray, 1857)	AZ	F
<i>Anthogorgia</i> (Verril, 1868)	AZ	F
<i>Muricella</i> (Verril, 1869)	AZ	F

## FAMILY: Plexauridae (Gray, 1859)

<i>Astrogorgia</i> (Verril, 1868)	AZ	Br
<i>Echinogorgia</i> (Kölliker, 1865)	AZ	B
<i>Euplexaura</i> (Verril, 1869)	AZ	F
<i>Paraplexaura</i> (Kükenthal, 1909)	AZ	Br
<i>Menella</i> (Gray, 1870)	AZ	Br

## SUBORDER: Calcaxonians

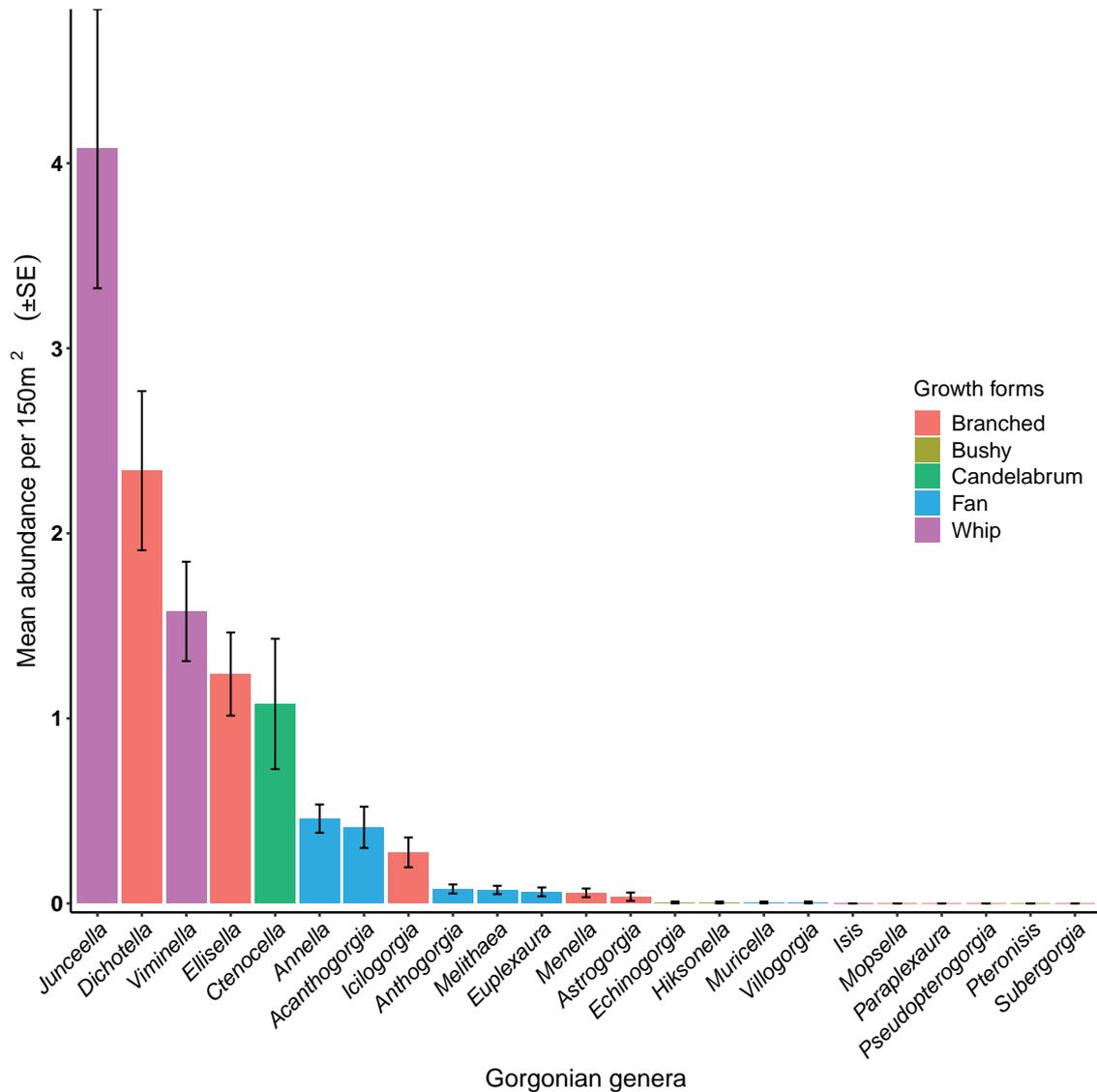
## FAMILY: Ellisellidae (Gray, 1859)

<i>Ctenocella</i> (Valenciennes, 1855)	AZ	C
<i>Dichotella</i> (Gray, 1870)	AZ	Br
<i>Ellisella</i> (Gray, 1858)	AZ	Br
<i>Junceella</i> (Valenciennes, 1855)	AZ	W
<i>Viminella</i> (Gray, 1870)	AZ	W

## FAMILY: Isididae (Lamouroux, 1812)

<i>Isis</i> (Linnaeus, 1758)	Z	B
<i>Pteronisis</i> (Alderslade, 1998)	Z	B

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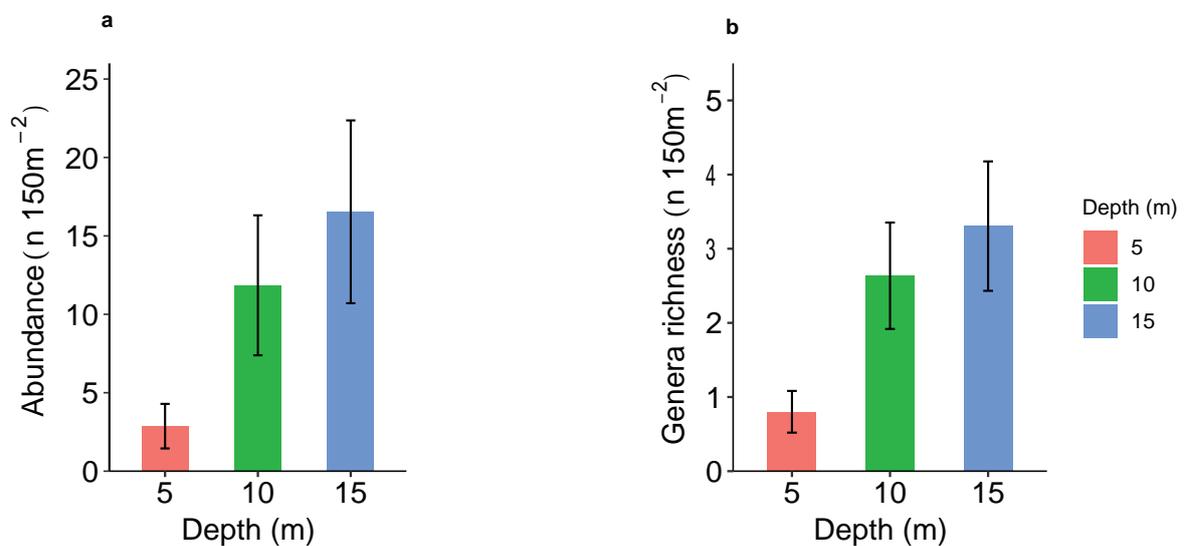
**Figure 2.2** Mean abundance of 23 gorgonian genera colour-coded by their growth forms: branched, bushy, fan, candelabrum, and whip

### How does gorgonian abundance and genera richness vary among depths and locations?

There were significant differences in the abundance (pooled across all genera) of gorgonians among depths (*GLM*,  $\chi^2 = 109.72$ ,  $df = 2$ ,  $p < 0.05$ ) and among locations (*GLM*,  $\chi^2 = 178.43$ ,  $df = 15$ ,  $p < 0.05$ ). Abundance generally increased with increasing depth, with numbers at 15 m about 5 times higher than at 5 m (Fig. 2.3a). However, the increase in abundance with depth was not consistent among locations, as indicated by a significant interaction between depth and location (*GLM*,  $\chi^2 = 194.62$ ,  $df = 30$ ,  $p < 0.05$ ). Pairwise comparisons between

depths found that abundance at 5m was significantly different to that at 10m and 15m, but did not differ between 10m and 15m (Table 2.2a).

Genera richness also varied among depths ( $GLM, \chi^2 = 119.363, df = 2, p < 0.05$ ) and among locations ( $GLM, \chi^2 = 85.769, df = 15, p < 0.05$ ), with richness increasing with increasing depth (Fig. 2.2b). This increase in richness with depth was not consistent among locations ( $GLM, \chi^2 = 76.548, df = 30, p < 0.05$ ), but on average, genera richness at 15 m was three times higher than at 5 m (Fig. 2.3b). Pairwise comparisons showed significant differences in genera richness among all depths (Table 2.2b).



**Figure 2.3** Mean gorgonian abundance **a** and genera richness **b** at each of the three depths. Error bars are 95% confidence intervals

**Table 2.2** Results of pairwise comparisons of (a) gorgonian abundance and (b) gorgonian richness between depths. LCL and UCL are the lower and upper 95% confidence limits respectively

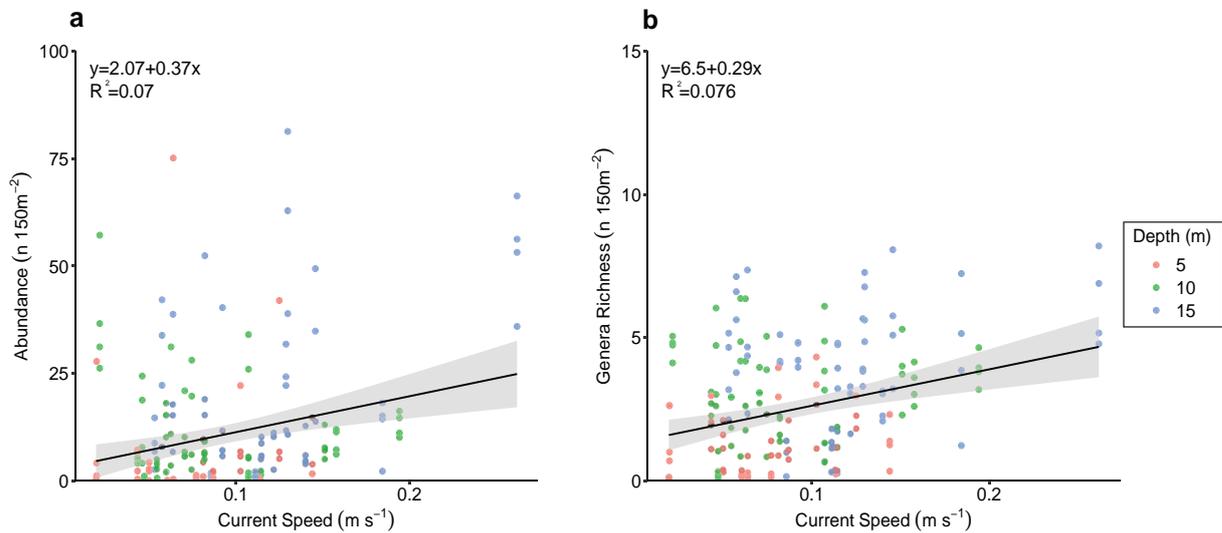
	<i>Depth</i>	<i>Contrast</i>	<i>SE</i>	<i>df</i>	<i>LCL</i>	<i>UCL</i>
	<i>Contrast</i>	<i>Estimate</i>				
<i>a) Mean abundance</i>	5 - 10	-8.98	1.95	190	-13.58	-4.386
	5 - 15	-13.67	2.63	190	-19.89	-7.446
	10 - 15	-4.68	2.19	190	-9.87	0.499
	5 - 10	-1.83	0.309	190	-2.56	-1.1043

<i>b)</i> Mean genera	5 - 15	-2.50	0.380	190	-3.40	-1.6060
richness	10 - 15	-0.67	0.304	190	-1.39	-0.0489

### Are gorgonian abundance and genera richness positively related to average current speed?

There was a significant relationship between the pooled abundance of gorgonians and average current speed (*GLMM*,  $\chi^2 = 4.7419$ ,  $df = 1$ ,  $p = .02$ ). With an increase in current speed of  $0.153\text{ms}^{-1}$  (95% CI 0.03- 0.71), abundance of gorgonians doubled (Fig. 2.4a). Although significant, the relationship was relatively weak, explaining 6.8 % of the variation in gorgonian abundance ( $R^2_{\text{marginal}} = 0.07$ ). There were a range of current speeds at all depths, but the fastest current speeds recorded at each location were usually at 15m.

There was a significant, positive relationship between genera richness and current speed (*GLMM*,  $\chi^2 = 3.9185$ ,  $df = 1$ ,  $p = .04$ ). To double the number of gorgonian genera, current speed would increase by  $0.33\text{ms}^{-1}$  (95% CI 0.00-0.58) (Fig. 2.4b). Again, the relationship was weak, explaining 7.6 % of the variation in genera richness ( $R^2_{\text{marginal}} = 0.076$ ). The *GLMM* indicated a statistically significant effect of current speed on genera richness.

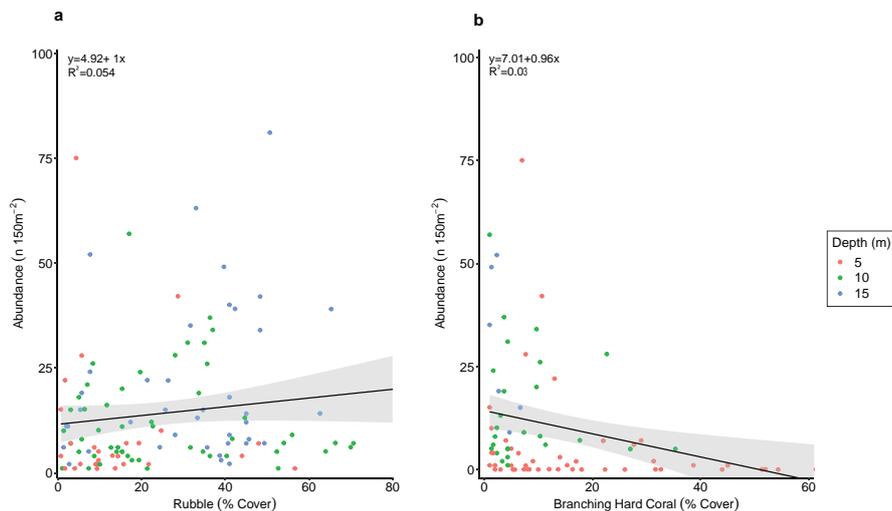


**Figure 2.4** Relationships between gorgonian abundance **a** and current speed, and genera richness and current speed **b**, with 95% confidence interval from *GLMM*s. Colours indicate the three depths surveyed (5, 10, 15 m). Points have been jittered.

## How are gorgonian abundance and richness related to benthic habitat cover?

The effects of benthic organisms or substrata on gorgonian abundance varied, with some positive and some negative trends detected (Fig. 2.5). The percent cover of rubble was a significant positive predictor of abundance (*GLMM*,  $\chi^2 = 5.82$ ,  $df = 1$ ,  $p = .02$ ), with a 4.92 increase in gorgonian abundance every 1 percent increase in cover of rubble (95% CI 1.00-1.03) (Fig. 2.5a). As with current speed, the relationship was weak, explaining just 5.4 % of the variation in gorgonian abundance. There was a significant negative relationship between gorgonian abundance and branching hard coral cover (*GLMM*,  $\chi^2 = 8.2768$ ,  $df = 1$ ,  $p = 0.004$ ) (Fig. 2.5b). Gorgonian abundance halved with an increase of 1.92 percent cover of branching hard coral (Fig 2.5b). This relationship, although significant, was weak, with percent cover of branching coral explaining just 3 % of the variation in gorgonian abundance respectively. There were no other significant relationships between gorgonian abundance and any of the other benthic organisms or substrata.

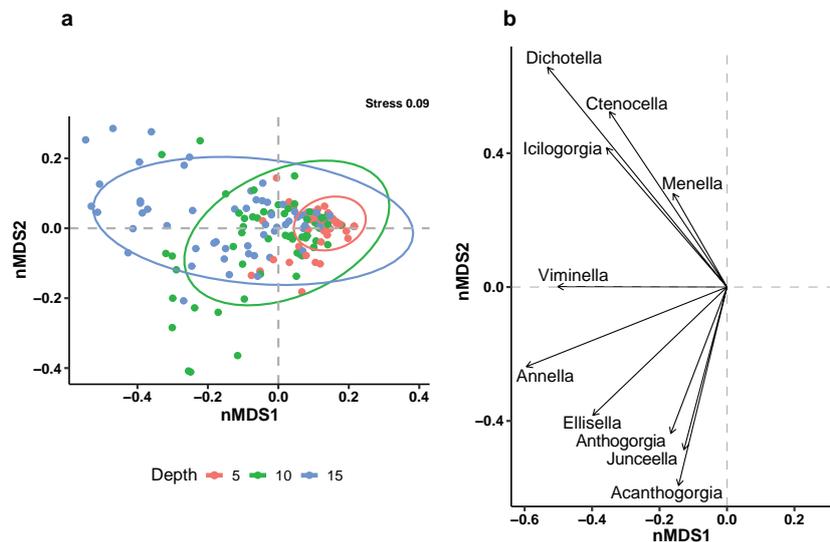
There was a significant negative relationship between gorgonian genera richness and branching hard coral cover (*GLMM*,  $\chi^2 = 7.6302$ ,  $df = 1$ ,  $p = 0.005$ ), with genera richness halving with an increase of 1.96 percent cover of branching hard coral. There were no significant relationships between gorgonian richness and any of the other benthic organisms or substrata.



**Figure 2.5** Relationships between gorgonian abundance and the percent cover of rubble **a**, branching hard corals **b**, with gorgonian abundance pooled across the 3 depths, with 95% confidence interval from GLMMs

### How does gorgonian assemblage structure vary along the depth gradient?

The PERMANOVA showed that assemblage structure varied significantly among the three depths ( $R^2=0.45$ , pseudo-F = 21,  $p = 0.001$ ; *betadisper*, pseudo-F = 27.201,  $p = 0.001$ ) (Table 2.3). The NMDS shows that the assemblage structure of gorgonian genera at 5m is distinct from that at 10 and 15m, which reflects the very low genera richness and absence of many genera at this depth. The NMDS also shows a gradual transition in genera composition from 10 to 15m (Fig. 2.6a). Nine of the 23 genera recorded were responsible for explaining the depth patterns in assemblage structure (Fig. 2.6b). All of these gorgonian genera were azooxanthellate (Table 2.1). However, there was a transition from a dominance of whip (*Junceella*, *Viminella*) and fan (*Acanthogorgia*, *Anthogorgia*, *Annella*) growth forms at 10m to branching (*Dichotella*, *Icilogorgia*) and candelabrum (*Ctenocella*) growth forms at 15m.



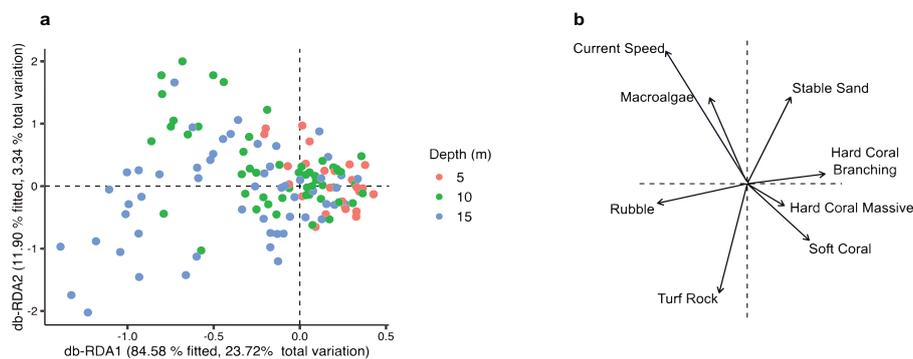
**Figure 2.6** Nonmetric multidimensional scaling (NMDS) plot **a** showing gorgonian assemblage structure across three depths (5, 10, and 15 m). Points represent gorgonians, grouped by community structures across depths using circles. NMDS plot **b** with arrows showing the nine most common genera of gorgonians across the assemblage structure, including only genera with  $p < 0.002$

**Table 2.3** Results of PERMANOVA examining differences in gorgonian assemblage structure among depths. Tests are based on Bray-Curtis dissimilarity distances and 999 permutations

Source	Df	Sums Sq	Mean Sq	Pseudo-F	Pr (>F)
Depth	2	0.20226	0.101131	27.201	0.001***
Residuals	189	0.70269	0.003718		

## What is the role of current speed and habitat structure in explaining spatial variation in the structure of gorgonian assemblages?

The distance-based redundancy analysis found that current speed and the benthic organisms/substrata explained 28.05 % of variation in gorgonian community structure, which clearly varied along the depth gradient (permutation test, pseudo-F = 9.91,  $p = 0.001$ , 999 permutations) (Fig. 2.7). Current speed and all of the benthic organisms/substrata had significant effects in the constrained ordination, with the exception of mobile sand and sponges (Table 2.4). The first axis of the db-RDA accounted for 84.58% of fitted variation (23.72% of the total variation) and strongly correlated with branching hard coral (Fig. 2.7b). This reflects high coral cover and low gorgonian abundance in shallow water. Vector overlays show that greater depths (10 and 15 m) were associated with higher percent cover of rubble, turf rock, and macroalgae. High macroalgal cover was also associated with higher current speed. Both of these habitat variables, turf rock and macroalgae, were more aligned with the second axis of the db-RDA which explained 11.90% of fitted variation 3.34% of total variation.



**Figure 2.7** Distance-based redundancy analysis (db-RDA) plot of the of benthic organisms/substrata across gorgonian assemblage structure at the three depths (5, 10, 15m) **a**, and significant benthic habitat variables correlated with each axis **b**, with length of the vectors

**Table 2.4** Significance of environmental constraints for db-RDA. Significant p values (<0.05) are in bold

<b>Environmental Gradient</b>	<b>Sum of squares</b>	<b>F</b>	<b>P</b>
Stable Sand	0.053	5.41	<b>0.007</b>
Mobile Sand	0.014	1.47	0.189
Rubble	0.105	10.68	<b>0.001</b>
Turf Rock	0.036	3.64	<b>0.026</b>
Soft Coral	0.067	6.76	<b>0.005</b>
Macroalgae	0.031	3.14	<b>0.037</b>
Branching hard coral	0.156	15.88	<b>0.001</b>
Massive and Encrusting Hard Coral	0.162	16.46	<b>0.001</b>
Sponges	0.023	2.35	0.099
Current Speed	0.047	4.77	<b>0.009</b>

## 2.5 Discussion

This study showed that gorgonians are a diverse component of the benthic communities on fringing reefs of the Palm Island Group, Great Barrier Reef. I recorded a total of 8 families and 23 genera, however the gorgonian assemblage was numerically dominated by 5 genera from the family Elisellidae, which made up 43 % of the total abundance of gorgonians. There was a decline in the abundance and genera richness of gorgonians with increasing depth, and a change in the structure of gorgonian assemblages with depth. These patterns were consistent across locations, despite considerable variation in abundance, species richness and community structure among locations. The depth-related patterns in assemblage structure were evident at the level of growth form, with whip (*Junceella*, *Viminella*) and fan (*Acanthogorgia*, *Anthogorgia*, *Annella*) growth forms in shallow water being replaced by branching (*Dichotella*, *Icilogorgia*) and candelabrum (*Ctenocella*) growth forms at greater depths. In terms of drivers, the abundance and genera richness of gorgonians were positively related to current speed, and the depth-related change in assemblage structure was also linked to faster currents in deeper water. Benthic habitat structure was also important, with

gorgonian abundance being positively related to the percent cover of rubble, and negatively related to branching hard coral cover. Gorgonian communities were depauperate in shallow water, where branching hard coral cover was high, and they were more diverse in deeper water where the percent cover of turf, rubble and macroalgal cover was high. Relationships with all of these drivers were generally weak and it is likely that gorgonian assemblages at the Palm Islands are influenced by a large range of biophysical factors that favour different growth forms at different depths. Other biophysical that may have influenced these distribution patterns could be changes over time due to disturbance events such as cyclones, as well as the availability of a short depth gradient around the islands. Further work at the species level will be required to evaluate the relative importance of these factors.

### **Depth-related patterns in gorgonian assemblages**

Most benthic organisms on coral reefs exhibit distinct patterns in abundance, diversity and community structure along depth gradients, and gorgonians are clearly no exception (Rowley 2018). My study showed gorgonian abundance and genera richness increased with depth over a relatively small depth range (5-15m). Similar patterns have been previously described for Indonesia (Rowley 2018) and in the Southern Mexican Pacific coast (Abeytia et al. 2013), with a substantial increase in abundance with depth. In Singapore, gorgonian genera richness was higher in deep water (~25m), where light availability was low, however gorgonian richness was also high in relatively shallow areas (~10m) where there were low abundances of competitors (e.g. hard corals and sponges) and low light availability due to high turbidity, usually typical of deeper areas (Goh and Chou 1994).

Depth-related patterns in gorgonian abundance, diversity and community structure may be linked to a range of biophysical factors, including reduced light and wave action, decreasing temperatures and changes in habitat structure (Dahlgren 1989; Yoshioka and Yoshioka 1989; Rowley et al. 2015). A study conducted in Indonesia by Rowley (2018) showed that azoozanthellate gorgonians had higher abundances and diversity in deeper areas where there is lower light. In contrast, this study showed that while the abundance of most gorgonian genera increased with depth at the Palm Islands, the gorgonian assemblages at all depths were dominated by azoozanthellate genera. Waters surrounding the Palm Islands are characterized by high turbidity, which may explain the dominance of azoozanthellate gorgonians even in shallow water. A previous study conducted in Hong Kong, where sediment and turbidity were

high, and water quality low, showed that the octocoral community was mainly composed of azooxanthellate taxa (Fabricius and McCorry 2006). Clearly, azooxanthellate gorgonians can be resistant to high turbidity and low light availability. In contrast, Caribbean gorgonians are primarily zooxanthellate, residing in clear shallow waters. A laboratory study by Kinzie (1973) investigated the ability of Caribbean gorgonians to withstand low light, by placing zooxanthellate and azooxanthellate gorgonians in a dark aquarium for 83 days. Most of the zooxanthellate forms died, presumably due to low light, which may explain their absence in deep water.

This study shows that changes in community structure along a depth gradient are likely linked to changes in the performance of different growth forms at different depths. Genera with whip and fan growth forms were more prevalent at 5 and 10 m, while branched, bushy and candelabrum growth forms dominated at 15 m. It has been suggested previously that deep water may be a refuge for genera that are less tolerant to physical disturbance (Costantini et al. 2016). Gorgonian colonies in shallow water are more susceptible to breakage due to higher wave action (West et al. 1993). Morphological features of gorgonians can also alter the intake of light, with different light quantity captured through the bushy and branching structures than fans (Rodríguez-Lanetty et al. 2003; Rowley et al. 2015). At the Palm Islands, the overall gorgonian fauna presented 9 genera with branching growth forms (*Dichotella*, *Ellisella*, *Icilogorgia*, *Menella*, *Astrogorgia*, *Mopsella*, *Paraplexaura*, *Pseudopterogorgia*, *Subergorgia*) and 7 with fan growth forms (*Annella*, *Acanthogorgia*, *Anthogorgia*, *Meliathaea*, *Euplexaura*, *Muricella*, *Villogorgia*). The Caribbean gorgonian fan, *Gorgonia ventalina*, resides in shallow water and its structure is presumed to help to capture light (Baker et al. 2015). Our study shows that gorgonians with tree-like morphologies, such as candelabrum and branched, can live in areas with relatively high current flows, which is consistent with the findings of other studies (Sánchez et al. 1997; Rodríguez-Lanetty et al. 2003). Ultimately, the prevalence of whips and fans at 5 - 10 m, and complex branching, bushy and candelabrum forms at 15 m, requires further investigation.

### **The role of current speed**

At the Palm islands, gorgonian abundance, genera richness and community structure were all related to current speed, with the majority of species being more abundant in areas where there are stronger currents. Gorgonians can adapt to different current speeds, but usually

prefer high current areas, which tend to bring a higher abundance of food (Chang-Feng and Ming-Chao 1993; Muzik and Wainwright 1977; Quintanilla et al. 2019). Gorgonians are filter feeders, passively capturing particles with their polyps (Sponaugle 1991). A study conducted in Fiji showed how sea fans can adapt to high flow velocities due to their skeletal structures being strong and flexible, allowing them to orient themselves to the current direction in order to maximise entrapment of food particles from the water column (Muzik and Wainwright 1977; Rodríguez-Lanetty et al. 2003). A lab study on the fan shaped *Leptogorgia virgulata* established that perpendicular oriented fans could gain more nutrients in the water column in a high current flow area (Leversee 1976). However, if current speed is too high, gorgonians may stop feeding and retract their polyps, whereas at low flows, feeding rates appear to be lower, and more energy is required to keep polyps open to gain nutrients (Muzik and Wainwright 1977). Gorgonians therefore have optimum flow requirements in order to feed efficiently (Leversee 1976; Yoshioka and Yoshioka 1989). We suspect that differences among genera in current speed requirements and tolerance to strong currents is a major determinant of the depth-related trends in gorgonian community structure at the Palm islands.

### **The importance of benthic habitat structure**

My study also confirms that benthic habitat structure can play an important role in shaping gorgonian assemblages (Dahlgren 1989; Sánchez et al. 1997). I found overall abundance was positively related to the percent cover of rubble, but negatively related to the percent cover of branching hard coral. Almost all of the benthic organisms/substrates explained spatial variation in assemblage structure to some degree, which likely represents genera-specific responses to the availability of preferred habitat. Low gorgonian genera richness in shallow water was associated with higher hard and soft coral cover, while greater genera richness in deeper water was associated with higher rubble, turf rock and/or macroalgal cover, each of which may favour different growth forms. Despite the shallow coral reef habitat having higher structural complexity, with branching hard corals and a wide variety of soft corals, there was lower gorgonian abundance and genera richness, which may be due to higher competition for space.

Habitat structure has been shown to be important in other investigations into gorgonian distributions, but the factors that are important vary among studies. Topographic complexity plays a critical role in shaping many ecological patterns on coral reefs and strong positive

relationships have been found between topographic complexity and gorgonian abundance and diversity (Al-Marayati and Edmunds 2018). Similarly, but in contrast with our findings, areas in the Caribbean show a high abundance of gorgonians in complex habitats dominated by branching hard corals and other benthic structure-forming organisms like sponges (Sánchez et al. 1997; Steiner et al. 2018). Clearly numerous benthic organisms contribute to the overall complexity of a given habitat, yet some may negatively influence gorgonian communities as a result of direct ecological interactions rather than beneficially provide complex habitat structure. Sponges for example, increase habitat complexity on coral reefs (Maldonado et al 2015) but are also known to negatively influence the distribution of gorgonians through competition for settlement space and allelopathic overgrowth (Dahlgren 1989; Slattery and Lesser 2021). Low complexity habitats with greater proportions of solid substrata are therefore preferred habitat types for some octocorals (Sánchez et al. 1997; Steiner et al. 2018), where bare areas of substrate may facilitate settlement and growth as there is low abundance of such competitors (Goh and Chou 1994). Gorgonian assemblages also follow spatial patterns corresponding to changes in benthic habitat zonation which are not always directly related to the absolute complexity of the habitat (Goldberg 1973, Kinzie 1973, Dahlgren 1989). In Western Australia, a cross shelf-gradient and resulting differences in benthic habitat composition between inshore versus offshore locations was a stronger driver of octocoral community composition than habitat complexity per-se (Bryce et al. 2018).

### **Ecological importance and further work**

My study adds to a diverse range of patterns in the distribution and abundance of gorgonians, and suggests we are not yet at a stage where general conclusions can be made. Nevertheless, I provide important baseline information at the genus level on the spatial distribution of gorgonians at the Palm islands, and have generated a number of hypotheses concerning the roles of current speed and habitat structure in explaining depth distributions. Given that multiple biophysical factors appear to be involved and are likely to vary in their importance among species, further work clearly needs to be done on this often-neglected group. Species level taxonomy is currently uncertain and will need to be resolved for patterns to be described at this level. The depth patterns are likely linked to a host of physical (light, wave action, current speed, substratum stability, topography) and biological factors (food availability, competing species), all of which must be investigated further. The tolerance of different growth forms to different depths and current speeds is likely to become an interesting future

research field, given the changing environmental conditions occurring on coral reefs. There will also be implications for understanding threats to gorgonian communities and the most effective conservation strategies. Whether the greater diversity in deeper water will provide a refuge from shallow water disturbances is clearly going to be an important question in future studies. However, the Palm Islands are exposed to high coastal turbidity and have experienced significant reef degradation at all depths. Understanding the impacts of this degradation on gorgonians and finding effective ways to mitigate these impacts are going to be critical issues over the coming decades.

### **Chapter 3: Fish assemblages associated with different growth forms of gorgonians on a coral reef**



A cryptobenthic goby residing and camouflaging on the branches of a gorgonian sea fan around the fringing reefs of the Palm Island Group, inshore central Great Barrier Reef.

### 3.1 Abstract

Ecosystem engineers are complex habitat-forming organisms that support a high biodiversity of mobile animals. On coral reefs, the role of scleractinian corals as important ecosystem engineers is well-known, with different growth forms supporting unique assemblages of reef fishes. However, the significance of other complex and structurally diverse benthic organisms like gorgonians has received much less attention. This study evaluated the influence of 3 different gorgonian growth forms (branched, candelabrum, and fan) on the abundance, species richness, and community structure of reef fishes. Larger fish associated with gorgonians were quantified from 30min stationary video recordings, with 15 replicate recordings of different individual gorgonians of each growth form. All small gobies resident on each gorgonian were quantified to the genus level from *in situ* visual surveys. The abundances of reef fishes in the general area surrounding gorgonians were quantified using five 1-minute timed swims to determine which species were attracted to or avoid gorgonians. Topographic complexity and percent cover of the benthic habitat around each gorgonian colony was quantified to assess potential role in explaining differences in fish communities among growth forms. Total abundance and species richness of the larger, more mobile species both differed significantly among the three gorgonian morphologies, with fans having the highest total fish abundance and species richness, and the candelabrum morphology having the lowest. The abundance and genera richness of resident gobies did not differ significantly among gorgonian morphologies. For larger fishes, candelabrum growth forms supported the most distinct fish assemblages, compared with fans and branched gorgonians. Resident gobies of the genus *Pleurosicya* were recorded exclusively on fans, while *Bryaninops* was found exclusively on both branched and candelabrum structures. Of the 15 most common larger fish species, 8 species, including the cleaner wrasse *Labroides dimidiatus*, appeared to be attracted by gorgonians, while other fishes appeared to avoid them. The differences in fish assemblages among gorgonian growth forms may have also been explained by benthic habitat structure surrounding gorgonians, with fans and branched growth forms attached to sites of high topographic complexity. This study suggests that gorgonians play a unique role as ecological engineers, with several fish species either attracted to or dependent on different gorgonian growth forms.

**Keywords:** Alcyonacea, Growth forms, Habitat association, Reef fish, Complexity

### 3.2 Introduction

Ecological engineers are important organisms that create, change, and maintain biogenic habitats and so have a disproportionate effect on biodiversity in all ecosystems (Jones et al. 1997). The most significant of these are autogenic engineers or structurally complex, sedentary species that provide habitat and essential resources to a wide range species (e.g. forests, grasslands, kelp beds, coral reefs). For example, the structural diversity of different forest habitats is known to have a major influence on animal communities, including insects, birds and mammals (MacArthur and MacArthur 1961; Wright and Jones 2006; Parker et al. 2007; Bartel et al. 2010). In marine environments, kelp forests, mangroves, seagrasses and biogenic reefs created by bivalves can support a large variety of vertebrates, invertebrates, and microorganisms through the provision of physical structure for settlement, shelter or ameliorating environmental stress (Jones et al. 1997; Kristensen 2008; Meadows et al. 2012; Steneck and Johnson 2013; Shelamoff et al. 2019; Ponge 2021). Marine animal diversity is often related to the variety of habitat forming species, with different ecosystem engineers supporting different animal assemblages (Bates and Dewreede 2007; Parker et al. 2007; Gustafsson and Boström 2011). The significance and importance of protecting ecological engineers is widely appreciated as deforestation and other drivers of biogenic habitat loss have become major causes of declining biodiversity on land and in the sea (Lugo et al. 1993; Symes et al. 2015). Key to this is understanding how different forms of autogenic engineers that vary in their structure and complexity impact on the animal assemblages they support.

Coral reefs are one of the most structurally complex biogenic habitats on earth and numerous studies have indicated this complexity plays a major role in sustaining high diversity in coral reef ecosystems (Roberts et al. 1987; Connell and Jones, 1991; Wilson et al. 2008; Gratwicke and Speight 2005). Here, the primary allogenic ecosystem engineers are scleractinian or reef-building corals. Analogous to trees, their calcium carbonate skeletons create a complex physical framework used by a large variety of reef-associated fish and invertebrate species (Wild et al. 2011). Different growth forms of hard corals, including massive, foliaceous and branching corals of different types are known to support different and diverse invertebrate and fish species (Stella et al. 2011; Komyakova et al. 2018). Declining coral cover, particularly of branching growth forms is leading to a major decline in coral reef fish biodiversity (Munday 2004; Feary et al. 2007). However, despite the obvious importance of scleractinian corals, there are numerous other benthic taxa that also contribute to the overall habitat complexity of

coral reefs and support animal biodiversity, including sponges (Voultsiadou et al. 2010) and soft corals (Epstein and Kingsford 2019). Recently, there is growing evidence to suggest that gorgonians can also function as important autogenic ecosystem engineers on coral reefs and can enhance biodiversity at the local scale (Rossi et al. 2017; Kupfner Johnson and Hallock 2020; Slattery and Lesser 2021).

Gorgonians are octocorals in the Order Alcyonacea, and are a diverse and often visually striking group of benthic organisms on coral reefs. They exhibit varied morphologies and individual colonies are often large and create extensive complex, three-dimensional structures on the reef. Gorgonian growth forms include elongated sea whips, large fans, bushy, branching and tree-like shapes (Fabricius and Alderslade 2001; Bullimore et al. 2013; Santavy et al. 2013). This wide variety of growth forms creates physical habitat for other reef taxa, potentially enhancing local biodiversity through the provision of shelter and feeding sites (Ponti et al. 2014; McLean and Yoshioka 2008; Buhl-Mortensen et al. 2010). However, to date few studies have quantified differences in the coral reef fishes associated with different growth forms of gorgonians. Many large mobile reef fish species can be readily observed taking shelter among the branches of sea fans and other gorgonians (Sih and Chouw, 2009; Cúrdia et al. 2015; Limviriyakul et al. 2020), but the degree to which they are specifically attracted to or depend on gorgonians is unknown. Gorgonian attributes, such as surface area, height, width are all potential drivers of the composition of fish communities that are associated with them (Goh et al. 1999; Carvalho et al. 2014; Cúrdia et al. 2015). Some small fishes, such as the pygmy seahorses, *H. bargibanti*, and *H. denise*, live in specialised relationships with just one or two sea fan species (Lourie and Randall 2003; Baine et al. 2008). Many cryptobenthic gobies appear to be associated only with gorgonians, including *Bryaninops*, *Pleurosicya*, *Phyllogobius*, *Luposicya* and *Lobulogobius* (Larson 2002). Many species appear to be associated with particular growth forms. For example, the sea whip goby *Bryaninops yongei*, which is only associated with a species of black coral sea whip, *Cirripathes anguina* (Munday et al 2002). A congener, *B. loki* has been recorded on different gorgonian genera and structures such as *Ctenocella* (candelabrum), *Junceella* (whip), *Ellisella* (whip), *Subergorgia* (fan), and black coral whips (Chen et al. 1995). Another species, the whip coral goby, *Bryaninops amplus*, appears to prefer the complex branching structure of *Dichotella gemmacea* (Sih and Chouw 2009). Evaluating the role of gorgonians as ecological engineers requires an understanding of how different growth forms impact on a

wide range of fish species, from mobile species that temporarily shelter in their branches, to smaller species that live in obligate relationships with particular gorgonian genera.

The aim of this study was to undertake a preliminary assessment of the role of gorgonians as ecological engineers by quantifying differences in reef fish assemblages associated with three distinct gorgonian growth forms (branched, candelabrum, and fan) on coral reefs at the Palm Islands, central Great Barrier Reef (GBR). The relative abundance of fish associated with gorgonians was compared to the overall abundance of fishes to determine which species are attracted to gorgonians. Because different gorgonian growth forms may be found in different microhabitats, this was assessed to examine whether habitat structure may also be important in explaining differences among gorgonian growth forms. The following specific questions were addressed:

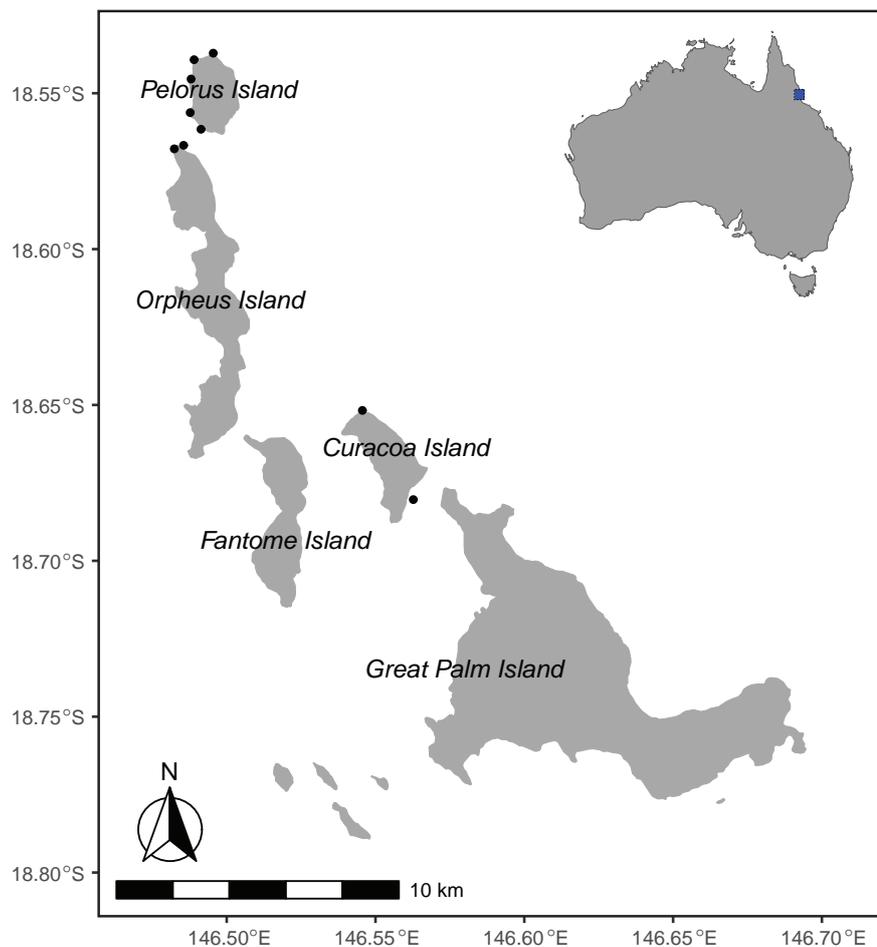
1. Does the abundance, species richness and community structure of larger mobile fishes and resident gobies differ among the three gorgonian morphologies?
2. How does the relative abundance of mobile fishes associated with gorgonians differ from the overall relative abundance of fishes on the reef? i.e. which species appear to be attracted to gorgonians?
3. Is the mobile fish assemblage associated with different gorgonian growth forms also likely to be influenced by gorgonian surface area, the topographic complexity and composition of the surrounding benthic habitat?

I hypothesised that each of the three gorgonian growth forms would vary in terms of the abundance and species richness of fish assemblages associated with them, and support distinct fish communities as a product of their varied architectural complexity. I expected these differences to be greatest for small resident goby species, that tend to be highly specialised in terms of habitat use. I also hypothesized that fans would support a high number of fish species, given their fine branching structure and their position high in the water column. In contrast, gorgonians of candelabrum morphology were not expected to support as many fish species due to their simple structure, and because they tend to occur in sandy habitats with strong currents.

### **3.3 Methods**

#### **Study location and sampling design**

This study was carried out in the Palm Islands, a group of inshore islands on the central Great Barrier Reef (GBR), based at Orpheus Island Research Station (-18.7345°S, 146.5794°E). I conducted surveys at 9 locations around 3 of the islands, with 2 survey locations at Orpheus Island, 5 at Pelorus Island, and 2 at Curacao Island (Fig. 3.1). A total of 45 gorgonian colonies were surveyed, 15 of each of three growth forms, branching, candelabrum and fans (as described by Fabricious and Alderslade, 2001) were selected randomly within a depth band of 6m to 14m across the 9 locations. Each colony was identified to genus level.



**Figure 3.1** Map of the Palm Islands showing the locations surveyed, two at Orpheus Is (Goolboddi), 5 at Pelorus Is (Yanooa), and 2 at Curacao Is (Noogoo)

### **Fish assemblages associated with gorgonians**

To estimate overall abundance, species richness and species composition of the larger mobile reef fishes using gorgonians, stationary videos were recorded directly in front of each colony

for 30 minutes. GoPro cameras (Hero 7, 8, and 9) set to 1080p resolution and 60fps wide setting, were mounted on a 30cm high stand, attached to a dive weight. Each camera was placed at a distance that would allow a full view of the colony. Once each camera was deployed, divers immediately left the area to allow the fish community to resettle and avoid disturbance during the survey.

The fish assemblages were quantified from the videos by recording all fish individuals that were seen in the immediate vicinity of the gorgonian or that swam past close to the colony in the 30min period. Fish were identified to species level. To reduce the influence of diver disturbance on fish counts the first 30 seconds of footage was excluded from the analysis. Care was taken not to count individuals repeatedly re-entering the field of view.

After each video recording, *in situ* visual surveys of each gorgonian colony were performed using a head torch to record the abundance of resident gobies. Resident gobies were identified to genus level and where possible, close-up pictures were taken to further verify their identity.

### **Mobile fish abundance**

To compare the relative abundance of fish using gorgonians to the relative abundance of fishes in the reef habitat around each gorgonian colony, fish abundance was estimated from five 1-minute random timed swims at each of the 9 locations where gorgonians were surveyed. The timed swims were recorded using a GoPro camera set to 1080p resolution and 60fps wide setting to ensure a wide enough field of view, 1.8m wide (screen resolution 1920x1080). All fish within the field of view were identified to species and recorded.

### **Gorgonian size and habitat structure**

After each video survey, the height, from the lowest to the highest point, and the width of each individual gorgonian was measured to the nearest cm, and the surface area of each colony was estimated from the height and width of each colony. Each surface area was estimated by timing height and width, given the irregularities of each growth form.

The benthic substratum that each colony was attached to, the holdfast, (i.e. rock, sand, rubble, hard coral encrusting) was recorded. The benthic habitat in a 1m<sup>2</sup> area around each gorgonian colony was characterised by estimating topographic complexity on four-point scale (low,

medium, complex, and very complex) and the percent cover of rock, sand, rubble, gorgonians, soft corals and hard coral in the same 1m<sup>2</sup> area was estimated by placing 5 random points on the first frame in each video and identifying the different substrate beneath each point. Reef aspect was recorded, how inclined the reef slope was, from 1 to 5, 1 being a wall to 5 being the least steep slope.

### **Data analysis**

All statistical analyses were performed using RStudio (Version 1.4.1717, R Core Team 2022). Generalized Linear Mixed Models (GLMMs) were used to test whether the abundance and species richness of mobile fish differed among the three gorgonian morphologies. These models had morphology as a fixed factor and colony number as a random factor, and used a negative binomial error function with a log link. To test if the abundance and genera richness of resident gobies differed among the three gorgonian morphologies I used a GLMM, with morphology as a fixed factor and colony number as a random factor (field ID for each individual colony), using a Poisson function. For each of these four models, a hypothesis test for the factor morphology was performed using a Type II Wald Chi-square test using the ‘anova’ function from the library “car”. GLMMs were performed using the library “glmmTMB” (Bolker 2019) and fit assessed using the DHARMA library (Hartig 2021). For each of the four models, pairwise comparisons based on adjusted Tukey tests were conducted using ‘emmeans’ (Russell et al .2022).

To visualise the differences in fish community structure between gorgonian morphologies I performed Non-metric Multi-dimensional Scaling (NMDS) using the function metaMDS, part of the “vegan” library (Oksanen 2020). Fish abundance data were square-root transformed, followed by a Wisconsin double standardization and fit on a Bray-Curtis distance matrix. Wisconsin double standardization, a vector transformation, was used to standardize the values of abundance by species maximum, and then by the sample total, and multiplied by 100 (Noy-Meir et al.1975). Using the function ‘envfit’, I plotted the fish species with the strongest correlations (pearsons  $r < 0.05$ ) as a biplot in ggplot2 (Wickham 2011). In order to quantify the effect of different gorgonian morphologies on fish species, at an assemblage level, a permutational analysis of variance (PERMANOVA) using the adonis2 function was performed (Oksanen 2020). The PERMANOVA was run on 999 permutations and Bray-Curtis distance matrix. An analysis of multivariate homogeneity (PERMDISP) was

carried out using the 'betadisper' function to assess within group dispersion (Anderson and Walsh 2013).

To compare fish communities associated with gorgonians to those found on the surrounding areas of reef, I calculated the mean abundance of each fish species recorded across the 45 gorgonian colonies (pooled across the 3 morphologies) and per 1-minute timed swim on the surrounding areas of reef (averaged across all replicate timed swims at each of the 9 locations). The 15 most abundant species found on gorgonians were selected and their relative abundances on gorgonians and on the surrounding areas of reef were compared.

To test the effects of the other environmental variables on reef fish community structure, I performed a distance-based Redundancy Analysis (db-RDA) on a Bray-Curtis distance matrix of square root transformed fish abundance data. The other environmental variables included gorgonian colony area, topographic complexity of the benthic habitat in the 1m<sup>2</sup> area around each gorgonian, percent cover of benthic substrata, gorgonian colony area, and reef aspect. The functions 'dbrda' and 'envfit', both part of the Vegan library, were used to plot the vectors of the environmental constrains tested, with length of the arrows indicating the nature and strength of the relationship. I plotted only significant environmental variables ( $p < 0.05$ ) as vectors or scaled correlation with the dbRDA axes (Paliy and Shankar 2016).

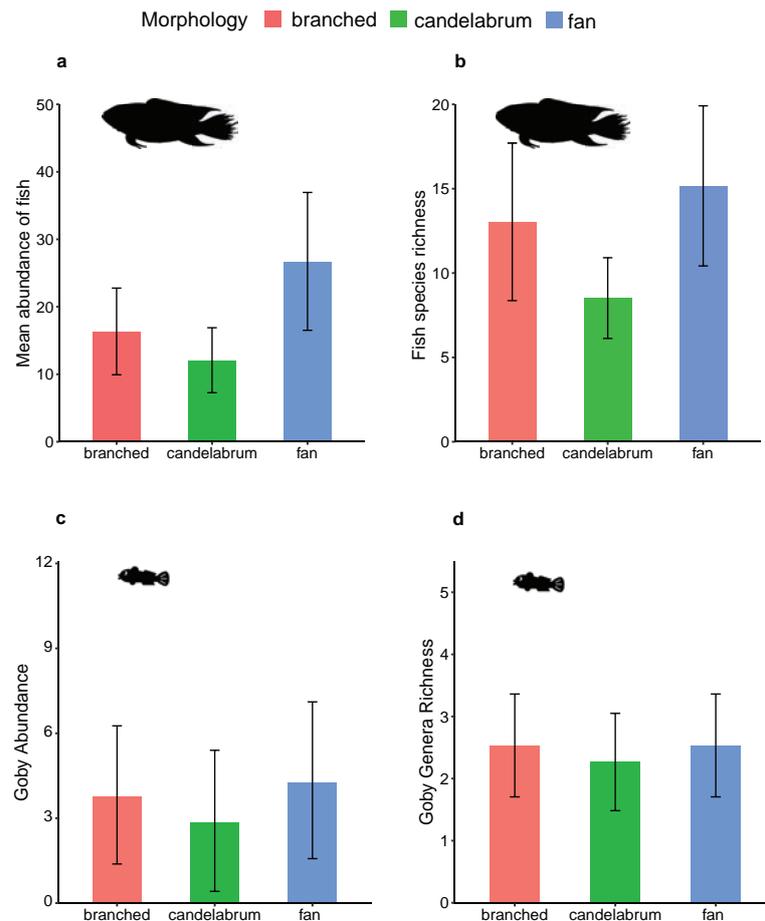
### 3.4 Results

#### **Do the abundance, species richness and community structure of mobile fishes and resident gobies differ among the three gorgonian morphologies?**

Gorgonian morphology was a significant predictor of mobile fish abundance (*GLMM*,  $\chi^2 = 8.65$ ,  $df = 2$ ,  $p = 0.01$ ), which was highest on fans (~26 individuals per colony) and lowest on candelabrum forms, which on average supported less than half the number of fishes (~12 individuals per colony) (Fig. 3.2a). Pairwise comparisons found significant differences in fish abundance between fan and candelabrum morphologies, and between fan and branched growth forms, but not between branched and candelabrum forms (Table 1a). The species richness of mobile fish also varied significantly among morphologies (*GLMM*,  $\chi^2 = 10.42$ ,  $df = 2$ ,  $p = 0.005$ ) (Fig. 3.2b). The highest average species richness was recorded on fan colonies (~15) which had roughly twice the number of species compared to candelabrum structures (~8

species). Pairwise comparisons showed significant differences in the average fish species richness across all morphologies (Table 3.1b).

Gorgonian morphology was not a significant predictor of resident goby abundance ( $GLMM, \chi^2 = 1.48, df = 2, p = 0.47$ ) (Fig 3.2c) or genera richness ( $GLMM, \chi^2 = 0.69, df = 2, p=0.7$ ) (Fig. 3.2d). The abundance and species richness of resident gobies was generally low, with an average of 3 individuals and 1 genus per colony.

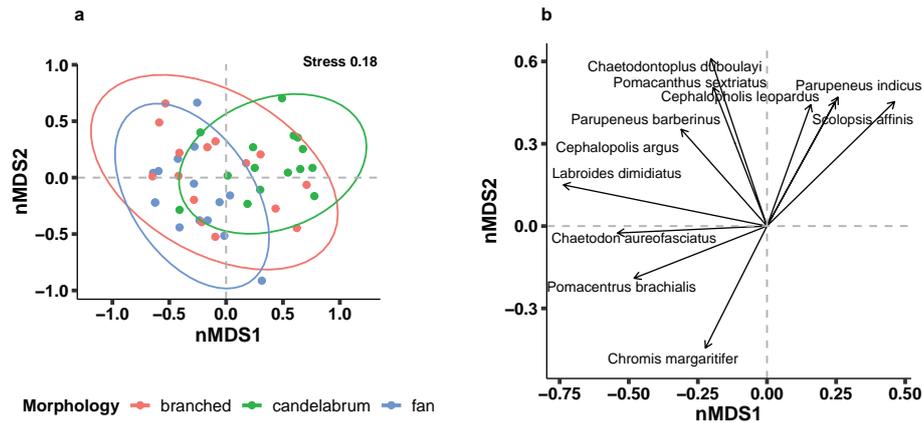


**Figure 3.2** Mean abundance of **a** mobile fish and **b** mobile fish species richness for each gorgonian morphology **c** resident goby genera **d** goby genera richness across three gorgonian morphotypes: branched, candelabrum, fan. Error bars are 95 % confidence intervals

**Table 3.1** Pairwise differences in (a) fish mean abundance and (b) fish species richness

	<i>Morphology</i>	<i>Contrast</i>	<i>SE</i>	<i>df</i>	<i>LCL</i>	<i>UCL</i>
	<i>Contrast</i>	<i>Estimate</i>				
<b>a) Fish mean abundance</b>	Branched-candelabrum	4.26	3.97	43	-5.38	13.91
	Branched-fan	-10.39	5.98	43	-24.89	4.12
	Candelabrum-fan	-14.65	5.60	43	-28.23	-1.07
<b>b) Mean fish species richness</b>	Branched-candelabrum	4.52	2.28	43	-1.02	10.053
	Branched-fan	-2.13	2.33	43	-7.78	3.520
	Candelabrum-fan	-6.56	2.35	43	-12.35	-0.952

PERMANOVA showed that gorgonian morphology has a significant effect on the community structure of mobile fish ( $R^2=0.13$ , *adonis*,  $F=3.19$ ,  $p=0.001$ ) (Table 3.2). However, there were significant differences in the multivariate spread among gorgonian morphologies (*betadisper*,  $F=3.40$ ,  $p=0.029$ ), therefore the significant PERMANOVA result should be interpreted with caution. The NMDS plot shows some overlap among all three morphologies, but fish communities associated with candelabrum growth forms were the most distinct (Fig. 3.3a). Of the 158 species of fish recorded that were considered associated with gorgonians, the cleaner wrasse, *Labroides dimidiatus*, *Chaetodon aurofasciatus*, *Pomacentrus branchialis*, and *Chromis margaritifer* were among the most common on all three growth forms. *Scolopsis affinis* and *Parupeneus indicus* were more often detected around candelabrum structures (Fig. 3.3b). *L. dimidiatus* was observed cleaning other fish species in the fan colonies more often than in the branched and candelabrum gorgonians. Two grouper species, *Cephalopholis argus* and *Cephalopholis leopardus*, and two angelfish species, *Chetodontoplus duboulayi* and *Pomacanthus sextriatus*, were commonly found around branched and fan gorgonians.

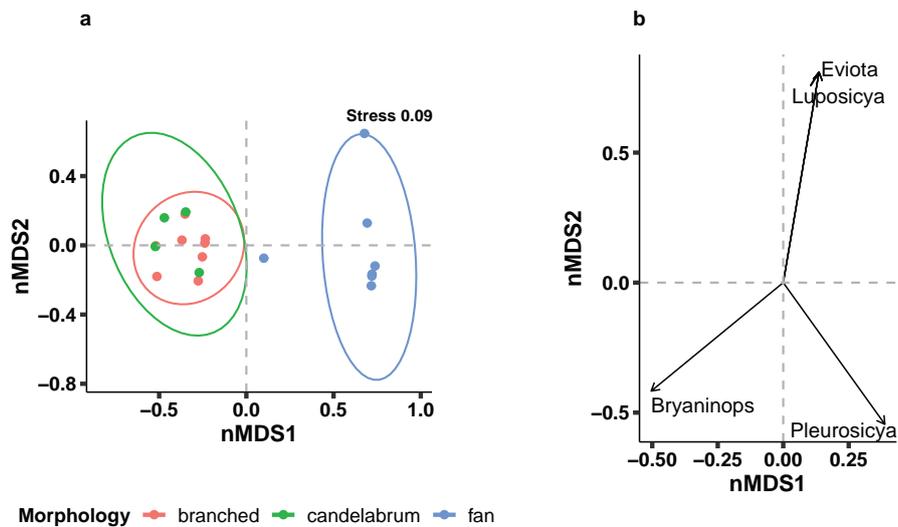


**Figure 3.3** a NMDS community structure of mobile fish across three morphologies and b arrows represent the most common species in the community (sum > 30)

**Table 3.2** PERMANOVA results of differences in mobile fish assemblage structure across three gorgonian morphologies. Tests are based on Bray-Curtis dissimilarity distances and 999 permutations

Source	Df	Sums Sq	R <sup>2</sup>	Pseudo-F	Pr (>F)
Morphology	2	0.40219	0.132209	3.1962	0.001***
Residuals	42	2.64252	0.86791		

PERMANOVA showed that the composition of goby genera also varied among gorgonian morphologies (19.4%, *adonis*,  $F = 1.9266$ ,  $p = 0.178$ ) (Table 3.3). However, as with the mobile fish species, there were significant differences in multivariate spread among gorgonian morphologies (*betadisper*,  $F = 29.338$ ,  $p = 0.001$ ). The NMDS shows that the composition of goby genera on candelabrum gorgonians was different to that on branching and fan morphologies, with branching and fan morphologies being similar in goby assemblage composition (Fig. 3.4a). There were four goby genera (*Eviota*, *Luposicya*, *Pleurosicya*, and *Bryaninops*) observed living on gorgonians. The genera *Eviota* and *Pleurosicya* were found exclusively on gorgonian fans, with *Eviota* most commonly seen on the holdfasts of the fans, and *Pleurosicya* around the upper part of the fans, always in the live tissue. The genus *Bryaninops* was present on branched and candelabrum gorgonians, but not on fans (Fig. 3.4b). The genus *Luposicya* was very rare, and found only on the fan structured gorgonians. Only two out of four goby genera recorded in my study were driving the differences in the NMDS (*Pleurosicya*, *Bryaninops*).



**Figure 3.4 a** Nonmetric multidimensional scaling (NMDS) plot showing goby genera assemblage across the different gorgonian structures (branched, candelabrum, fan). Each point is a gorgonian colony with at least 1 resident goby. Circles group gorgonians by different morphologies; **b** Arrows displaying the 4 goby genera within the gorgonian assemblage structure

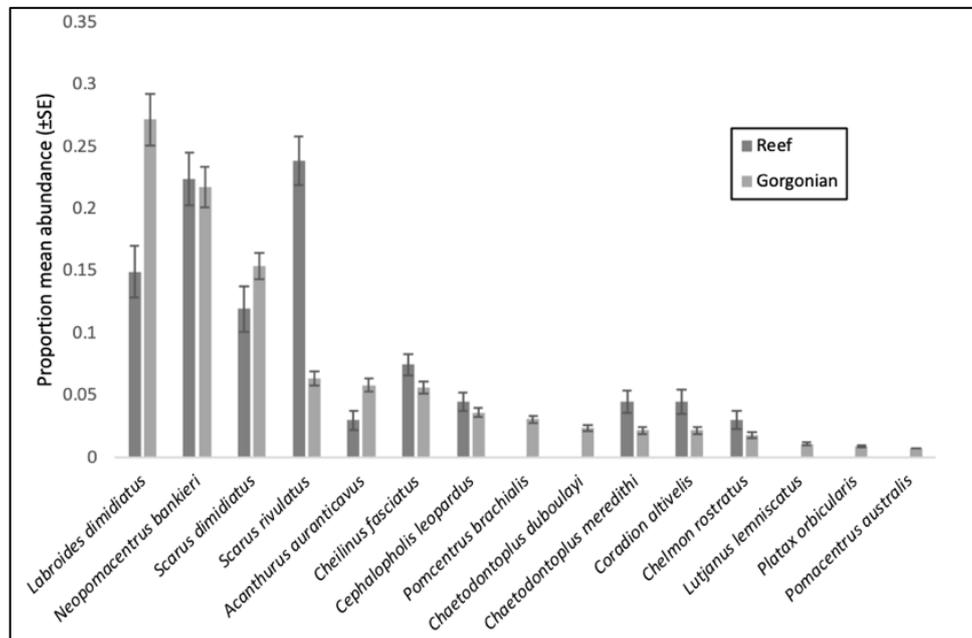
**Table 3.3** PERMANOVA results testing differences in goby assemblage structure among morphologies, only considering colonies where gobies were present. Tests are based on Bray-Curtis dissimilarity distances and 999 permutations

Source	Df	Sums Sq	Mean Sq	Pseudo-F	Pr (>F)
Morphology	2	3.3203	1.66016	29.338	0.001 ***
Residuals	16	0.9054	0.5659		

### How does the relative abundance of fishes associated with gorgonians compare with their relative abundance on the surrounding reef?

The relative abundance of the 15 most common fishes associated with gorgonians differed from their relative abundance on the surrounding reefs, with about 8 species found in higher numbers on gorgonians (Fig. 3.5). The most abundant species associated with gorgonians, the cleaner wrasse, *Labroides dimidiatus*, appeared to be attracted to gorgonians as it accounted for 27.1% of the individuals on gorgonians, but only 14.9% of individuals on the reef. High numbers of *Neopomacentrus bankieri* around gorgonians appeared to just reflect their high abundance on the reef, while *Scarus rivulatus* appeared to avoid gorgonians. Several species

found associated with gorgonians in low numbers were too rare on the reef to appear in the abundance counts, so are likely to be attracted to gorgonians.

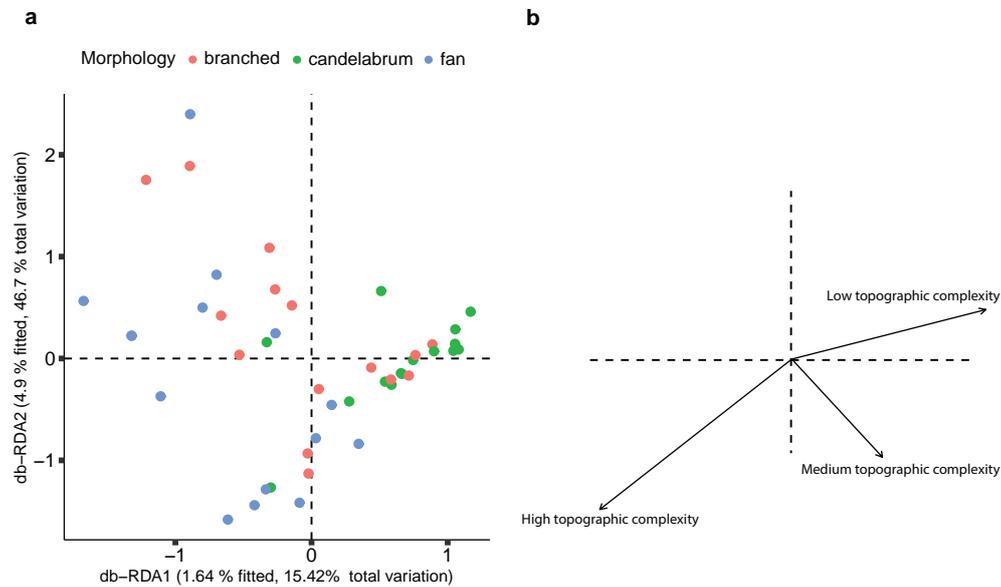


**Figure 3.5** Relative abundance of 15 most common fish species found in association with gorgonian colonies, on gorgonians and on the surrounding area of reef.

### What factors other than growth form may explain these patterns e.g. topography, surface area and habitat substrata?

The topographic complexity in the 1m<sup>2</sup> area around each gorgonian colony was a significant predictor of the assemblage structure of mobile fish (Table 3.5, Fig. 3.6a). High topographic complexity was associated with gorgonian fans, whereas medium and low topographic complexity was associated with candelabrum and branched gorgonians. Topography explained 4.1% ( $\text{adj}R^2 = 0.041$ ) of the variation in the assemblage structure of mobile fish among gorgonian morphologies, and was the only variable that was significant in the db-RDA (permutation test, pseudo-F = 1.62,  $p = 0.002$ , 999 permutations) (Table 3.5). Axis 1 of the db-RDA, explained 1.64% of the variation (15.42% total), and was strongly correlated with very complex topography of the substrate (Fig. 3.6b). Axis 2 of the db-RDA explained 4.9% of the variation (46.7% total variation). None of the other environmental variables (Table 3.5) included in the db-RDA had a significant influence on the variation in mobile fish community structure among gorgonian morphologies. Candelabrum gorgonians did not support large

numbers of fish or large numbers of fish species, because of their locations and very simple structures, usually subjected to high water flows and adverse habitat conditions.



**Figure 3.6** Distance-based redundancy analysis (db-RDA) plot showing **a** the relationship between topographic complexity and fish communities across gorgonian growth forms (branched, candelabrum, fan) **b** Vector biplot indicating the strength and direction of the relationship relative to the ordination. Only vectors with significant correlation coefficients at the 0.05 level are displayed.

**Table 3.4** Environmental variables used in the Distance-based redundancy analysis (db-RDA). Significant variables are shown in bold

<b>Environmental Constraint</b>	<b>Sum of squares</b>	<b>Pseudo - F</b>	<b>P</b>
Holdfast	0.25868	1.3062	0.126
Topography	0.37220	1.8795	<b>0.003</b>
Reef aspect	0.22887	0.8668	0.698
Colony Surface Area	0.06657	1.0084	0.404
% Rock	0.07098	1.0753	0.359
% Sand	0.06929	1.0497	0.386
% Gorgonians	0.04342	0.6577	0.813
% Soft Coral	0.05778	0.8752	0.577
% Rubble	0.04468	0.6769	0.836

% Hard Coral	0.04819	0.7300	0.717
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### 3.5 Discussion

This study has shown that the different gorgonian growth forms appear to support different abundances and species richness of the larger mobile fishes. As predicted, fans and branched gorgonians had higher abundances and species richness of mobile fish species compared to the simpler candelabrum forms. Unexpectedly, resident gobies did not show any significant differences in abundance and richness among the three selected growth forms, but both the numbers of individuals and genera were low. Differences were also observed at the community-level, with the most distinct assemblages associated with candelabrum gorgonians. However, the heterogeneity of the three morphologies can predict differences in the overall communities of fish observed. The goby communities on the different growth forms were distinct, with the genus *Pleurosicya* found only on gorgonian fans, and the genus *Bryaninops* found only on branched and candelabrum growth forms. For the most abundant mobile fishes using gorgonians, more than half appeared to be attracted to gorgonians, with a disproportionate representation on gorgonians compared to their relative abundance on the reef. Although fans appeared to be the most important habitats for fishes, the topographic complexity of the 1m<sup>2</sup> area around each gorgonian fan was the only environmental variable measured that explained a significant percentage of the variation in mobile fish community structure among gorgonian morphs. Although fans and branched gorgonians appeared to be the most important habitats for fishes, this effect could have also been explained by habitat structure, as these growth forms were found in areas with high topographic complexity, while candelabrum gorgonians, which had low abundance and species richness of mobile fishes, were found in areas with low topographic complexity. Overall, it appears that gorgonians are a significant biogenic habitat on coastal reefs at the Palm Islands, with both large and small resident fishes clearly responding to the different growth forms and their immediate habitats.

#### **Differences in mobile fish abundance and species richness among gorgonian morphologies**

This study showed that gorgonians with the more complex growth forms, like fan and branched gorgonians, attracted higher abundances and species richness of mobile fish, than the simpler candelabrum growth form. The abundance and genera richness of resident gobies,

however, did not differ among growth forms, but their numbers were low. This is consistent with other studies, where gorgonian morphological attributes such as surface area, fractal dimension for complexity, and the % covered by epibionts, have been considered important drivers, both for abundance and taxonomic richness of invertebrates (Cúrdia et al. 2015). It supports a large number of studies that have shown that greater morphological complexity of corals in general can enhance fish abundance and richness (Gratwicke and Speight 2005; Graham and Nash 2013). Overall, the higher the 'architectural complexity', the higher the diversity of fishes, most likely due to the higher diversity of shelter and feeding sites. A study on temperate gorgonians has shown that species with a complex morphological structure (e.g. *L. lusitanica*) or a large round structure (e.g. *E.gazella*) attracted a larger biodiversity of organisms (Carvalho et al. 2014). The size of gorgonian colonies is also likely to be important, with a larger the surface area associated with a higher abundance and diversity (Carvalho et al. 2014). However, while other studies have demonstrated the importance of gorgonian size in driving abundance and richness of associates, in this study the three morphologies were characterized by very distinct size ranges, with size of fans (usually large) being the only one explaining the pattern demonstrated by previous studies (as per Carvalho et al. 2014).

### **Differences in fish community structure among gorgonians growth forms**

In this study, there were differences in mobile fish community structure among gorgonian growth forms, with similar communities on fan and branched gorgonians, and a more distinct fish assemblage on candelabrum gorgonians. A potential cause of these patterns may be the variability of growth forms, which can lead to different fish communities around them. Although mobile reef fishes are generally associated with substrata providing shelter, some fish species can show high versatility, hence able to occupy a wide variety of habitats across the reef (Coker et al. 2015). This appeared to be the case for many fish species using gorgonians. For instance, species such as *Chaetodontoplus duboulayi*, *Pomacanthus sextriatus*, *Cephalopolis argus*, and *C. leopardus* were commonly found on all three growth forms. Similarly, the cleaner wrasse, *Labroides dimidiatus*, was recorded on all three gorgonian morphotypes. It appeared to be preferentially establishing cleaning stations around gorgonians, especially fans, which has not been previously documented. In the Caribbean groups of Octocorals have been associated with a large diversity of fish as they provide high

and wide field of views. Therefore, growth form may not be the driver of fish-gorgonian associations, but rather the any higher structure on the reef, like gorgonians, may indicate their use as cleaning stations by a large variety of fish. Additionally, gorgonians can also be found in groups, which may drive more fish to use them as cleaning stations, given the availability of shelter. In my study, some fish species such as *Parupeneus indicus* and *Scolopsis affinis* were found around branched and, more often, observed around candelabrum structures. Planktivorous damselfish were commonly found associated with all three growth forms, including *Neopomacentrus bankieri*, *Chromis margaritifer* and *Pomacentrus brachialis*, and appeared to be indiscriminate in their choice of shelter sites. However, food availability may represent a factor driving the abundance of planktivorous damselfish around these structures, due to strong currents and high topographic complexity. Some fish species attracted to gorgonians, such as the butterflyfish *Chaetodon aureofasciatus* may be generalist coral feeders that occasionally consume gorgonians (Pratchett, 2005a). Fish species such as *Scolopsis bilineata* and *Parupeneus indicus* were almost exclusively associated with candelabrum gorgonians. They were observed swimming around in the sand-dominated habitats where candelabrum gorgonian structures where often the only biogenic habitat providing shelter.

Although the abundance and genera richness of resident gobies did not differ among gorgonian growth forms, there were obvious differences in the assemblage structure. Two genera, *Eviota* and *Pleurosicya* were found exclusively on fans, with *Eviota* being almost always found on the holdfast of the fans and *Pleurosicya* usually found on the gorgonian upper body structure, covered in live tissue. Interestingly, the genera *Eviota* and *Pleurosicya* were sharing the same habitat, but were using different part of the fans. *Eviota*, often recorded on the holdfast of the colony, was mostly likely using gorgonians as temporary shelter, while *Pleurosicya* was clearly dependent on fans. The genus *Bryaninops* was found in both branched and candelabrum growth forms, and was never found on gorgonian fans.

The *Bryaninops*, and *Pleurosicya* species recorded here are clearly gorgonian specialists that are living in obligate association with gorgonians. These genera are almost always habitat specialists of some sort. A study conducted in the Red Sea showed that *Bryaninops* was associated with some *Acropora* sp, *Millepora* sp, and *Cirripathes* sp, and *Pleurosicya*, in much more limited numbers, with some massive scleractinian corals and *Acropora* species (Herle 2007). The genus *Bryaninops* has previously been shown to prefer more complex branched structures like *Dichotella* sp., than linear ones such as sea whips, *Junceella* sp. (Sih

and Chouw 2009). Further work is needed to examine these relationships at the species level, both for the fishes and the gorgonians, as levels of specialization may be higher than can be resolved by focussing on genera.

### **Fish communities on gorgonians vs on surrounding areas of reef**

The comparison of the relative abundance of mobile fish species on gorgonians and on the reef clearly suggested that more than half the species are specifically aggregating around gorgonians. This included *Labroides dimidiatus*, *Scarus dimidiatus*, *Acanthurus auranticavus*, *Pomacentrus brachialis*, *Chaetodontoplus duboulayi*, *Lutjanus lemniscatus*, *Platax orbicularis*, and *Pomacentrus australis*. These species appear to be associating with gorgonians for different reasons, including cleaning stations (*L. dimidiatus*), preferred shelters (*Cephalopolis leopardus*) and perhaps food (*Chaetodontoplus duboulayi*). Some of the higher numbers may result from fishes attracted to the cleaning station, rather than the gorgonian itself. Interestingly, the cleaner wrasse *Labroides dimidiatus* was present among the three morphotypes due to the large concentration of fish abundance and diversity, its 'fish species clients', around the colonies (Tebbich et al. 2002). Regardless of the gorgonian shape, *L. dimidiatus* was using gorgonians as aggregations of biodiversity to perform its functions. The planktivore, *Neopomacentrus bankieri* showed similar relative abundance around gorgonians and on the reef, and appears to be attracted to any complex structure. Other species appeared to be avoiding gorgonians (e.g. *Scarus rivulatus*, *Cephalopolis leopardus*, *Cheilinus fasciatus*, *Chaetodontoplus meredithi*, *Coradion altivelis* and *Chelmon rostratus*). Currently, not enough is known of the habitat preferences or diets of these species to explain this pattern.

### **The influence of other habitat factors**

The degree of topographic complexity around the colonies, as well as the structure of the surrounding benthic habitat, can be related to the abundance and diversity of fish attracted by different gorgonian morphologies (Sih and Chouw 2009). In this study, high topographic complexity was recorded around fan and branched gorgonians, whereas candelabrum gorgonians were usually located in areas of low topographic complexity, usually flat, sandy areas. This provides a potential alternative or additional explanation for why mobile reef fish

assemblages differed among the growth forms. There are many studies which have found that topographic complexity can promote reef fish diversity (Roberts et al. 1987; Gratwicke and Speight 2005; Richardson et al. 2017). It is likely that the vertical reach of fans is simply adding to the 3-D complexity of the reef, allowing shelter-seeking fishes such as small planktivores, to feed further up in the water column (Rilov et al. 2007).

### **Conclusions and further research**

This study has provided a preliminary assessment of the significance of gorgonians as ecosystem engineers on coral reefs and is the first of its kind for the Great Barrier Reef. This study is preliminary as it gives an overview of the role of gorgonians on coral reefs, by providing evaluations of fish-gorgonian associations. Overall, the assumptions that gorgonians may represent cleaning stations as well as important ecosystem engineers for coral reefs are met. However, this study shows some limitations such as the short time span in which it took place, hence the limited knowledge on how fish may use gorgonians in different times of the day. Some gorgonians clearly stand out on coral reefs, with large fans sometimes the most conspicuous structures reaching into the water column, acting as biodiversity hotspots for reef fishes and associated fauna (Carvalho et al. 2014). Fishes were generally responding to the different gorgonian growth forms, both in terms of abundance, species richness and composition. Further work is needed to understand what attracts different species to different growth forms, as the overall knowledge of the ecological relationships between fish and gorgonians is extremely limited. This is going to require improvements in the taxonomic knowledge of gorgonians, as these findings may obscure important patterns evident at the species-level. The finding that the cleaner wrasse is preferentially using gorgonians as cleaning stations warrant further investigation, as it is not known whether fish are attracted to the gorgonians themselves or the cleaning stations. Gorgonians may be ideal locations used as cleaning stations due to their shapes, forms and elevation high-up in the water column, which may enable more fish to reach the area. In the Caribbean, gorgonians were documented to be ideal cleaning stations, providing areas for fish to be protected from other predators (Rilov et al. 2007).

This study provides a baseline for understanding how fish communities may respond to the loss of ecological engineers on coral reefs. The effect of declining hard coral cover due to a range of environmental stressors, including increasing temperatures, acidification, long-term

effects of climate change is well known (Hoegh-Guldberg 1999; Hughes et al. 2017). However, how fish will respond to the loss of alternative habitat structures, such as soft corals and gorgonians, is unknown. My work indicates the kinds of species that may be detrimentally affected by the declining health of gorgonians, including not just resident gorgonians specialists, but many larger mobile fishes that are associated with them. Whether most of these fishes will decline or find alternative habitats requires further investigation. Overall, further research on gorgonians used as cleaning stations may be needed, especially understanding whether these colonies in the Indo Pacific area have the same roles on the reef as in the Caribbean. Potential differences may be found, given the extreme high abundance of these octocorals in the Caribbean areas. Understanding the use of gorgonians by fish in different times of the day may be useful to evaluate the role of these organisms once it gets dark, and whether they can be refuges for fish. I would predict many species will be adversely affected and strongly advocate long-term monitoring of the health of gorgonians and changes in the abundance of the gorgonian-associated fishes highlighted in this study.

## Chapter 4: Declining health of gorgonian sea fans and its influence on associated fish communities



A sea fan (genus: *Annella*) showing live tissue loss (~ 75% left) on the reefs of the Palm Island Group, Great Barrier Reef.

#### 4.1 Abstract

The global decline in the health of coral reefs has been widely documented, with decreasing coral cover having a negative impact on reef fish biodiversity. Fishes associated with individual coral colonies change on a local scale as they transition from healthy living corals, through partial damage, to dead overgrown skeletons. However, little is known about the health status of other habitat-forming species such as gorgonians and how their declining health effects fish assemblages. In this study, I quantified levels of damage to gorgonian sea fans on fringing reefs at the Palm Islands (central GBR) and evaluated the effects of increasing damage on fish abundance, species richness and assemblage composition. Sea fan health was surveyed at 16 locations, with 4 replicate stereo video transects along 10m and 15m depth contours at each location. All individual sea fans observed were classified into five health categories (C1-5), based on 20% increments in the percentage of live tissue left, with category C1 being the healthiest (80-100% tissue) and C5 being the most-unhealthy (0-19% tissue). The responses of fish assemblages to declining health were quantified using 30-min recordings from stationary GoPro cameras, with 10 replicate recordings of gorgonians in each health category. Across the 16 locations, only 20% of sea fans were in the healthiest category (C1) and almost a quarter (24%) were severely damaged (C5), with the rest in different stages of declining health. Generalized Linear Mixed Models (GLMMs) results showed that health categories were significant predictors of the overall abundance for larger mobile fish and small resident gobies (Teleostei: Gobiidae). The abundance of gobies decreased progressively with increasing damage, reaching complete goby absence on sea fans in C5. The healthiest gorgonians (C1) had the most distinct structure of larger, more mobile fish assemblages, with *Halichoeres melanurus* and *Platax teira* more common than on unhealthy gorgonians. This paper provides the first evidence that sea fan damage is having a negative effect on local fish assemblages, with potential larger scale effects a cause for concern.

**Keywords:** Alcyonacea, Marine Fish, Degradation, Anthropogenic Stressors, Great Barrier Reef

## 4.2 Introduction

The degradation and eventual loss of biogenic habitats represents one of the major causes of declining biodiversity in most ecosystems (Duncan and Blackburn 2007; Hanski 2011; Munstermann et al. 2022). This is particularly true for coral reefs, where there is evidence of declining coral cover around the globe due to multiple anthropogenic effects, including ocean warming and associated bleaching, eutrophication and sedimentation, and overharvesting of grazers (Hughes et al. 2003, 2017; Pandolfi et al. 2003; Sandin et al. 2008; Bellwood et al. 2019). Given that a large proportion of coral reef fish are dependent on corals for food, shelter or recruitment sites, coral loss is having a major negative impact on reef fish biodiversity and community structure (Jones et al. 2004; Munday 2004; Pratchett 2005b; Graham et al 2008; Wilson et al. 2008; Pratchett et al 2011). These effects have been observed at the scale of individual coral colonies, with many small fish species sensitive to early stages of declining health such as moderate bleaching, while others can survive until coral colonies are completely dead (Feary et al. 2007; Bonin et al. 2009; Stuart-Smith et al. 2018; Robinson et al. 2019; Magel et al. 2020). Short-term effects of coral death on corallivores and small coral specialists, can be followed by longer-term effects on generalist species that are adversely affected by declining topographic complexity (Wilson et al. 2010; Graham et al. 2011; Pratchett et al. 2013). Understanding the extent of the threat to fish biodiversity is a two-stage process, the first step being to quantify the extent of the reduction in the health or habitat-forming species, and the second step establishing at what stage in declining habitat-health do fish start exhibiting negative responses. Until now, the focus has been on scleractinian corals, and the extent of damage to other habitat-forming taxa and the impacts on fish assemblages are poorly understood.

Gorgonians (Anthozoa, Octocorallia) are another diverse group of habitat-forming organisms on coral reefs, potentially playing an important role as ecosystem engineers (Dinesen 1983; Jones et al. 1994; Rossi et al. 2017). While not as dominant as scleractinian corals, the complex 3D structure of many gorgonians support unique combinations of fish species, including many species that are gorgonian specialists that are not found on other reef substrata (Chen et al. 1995; Baine et al. 2008; Sih and Chouw 2009; Smith et al. 2012) (see also Chapter 3). However, there is growing evidence that similar anthropogenic stresses adversely affecting corals are also having negative impacts on gorgonians (Cerrano et al. 2000; Munro and Munro 2003). Increasing terrestrial run-off, pollution and sedimentation loads appear to be causes of declining gorgonian abundance (Amaral and Jablonski 2005; Fabricius 2005).

Gorgonians have also been impacted by coral diseases, such as *Aspergillosis* on *Gorgonia ventalina* in the Caribbean, which has caused dramatic population declines (Williams and Bunkley-Williams 2000; Zuluaga-Montero and Sabat 2012). Increasing water temperature appears to be causing the spread of diseases among many octocoral species, altering the composition of the benthic community (Lasker and Coffroth 1983; Cerrano et al. 2000). On coral reefs in the Bahamas, gorgonians were observed to lose zoozanthellae due to thermal stress, followed by an outbreak of *Vibrio* that caused tissue necrosis (Harmelin and Marinopoulos 1994; Nagelkerken et al. 1997; Lasker 2005). An ‘octocoral bleaching event’ was documented in Puerto Rico, where a large % of each gorgonian showed loss of colour, the same way the bleaching occurs for hard corals (Prada et al. 2010). Despite these isolated examples, the extent of damage to the whole gorgonian assemblages and the impacts of declining gorgonian health on fishes have not been investigated.

Large sea fans are some of the most conspicuous arborescent structures on coral reefs (Muzik and Wainwright 1977; Bayer et al. 1983). They support a variety of large mobile reef fishes sheltering in their branches and some small specialised species that have an obligate association with fans (Chen et al. 1995; Baine et al. 2008; Smith et al. 2012). There is increasing anecdotal evidence that sea fans are under stress, with individuals in some locations in various stages of decline (Harvell and Suchanek 1987; Sandoval-sierra et al. 2016; Edmunds 2020). Once healthy sea fans that are almost 100% living tissue can end up as just dead skeletons, with just the remnant of thick branches remaining on the reef. The causes of this damage are not always apparent, but it can be predicted to severely impact on small specialised fish species and perhaps also the larger shelter-dependent species. However, there have been few quantitative studies on the extent of damage, specifically for sea fans, and no studies that have examined the stages at which declining sea fan health impacts on fish assemblages.

The aim of this study was to provide the first assessment of the full extent of damage to a sea fan assemblage and quantify the stage at which declining health impacts on fish assemblages. The study focussed on the inshore Palm Island Group (central GBR), where significant damage to sea fan was observed in a general study on their distribution and abundance (Chapter 2). The following specific questions will be addressed:

1. How prevalent is the damage on sea fans? That is, what proportion of the population is healthy and how many can be observed in different stages of declining health?

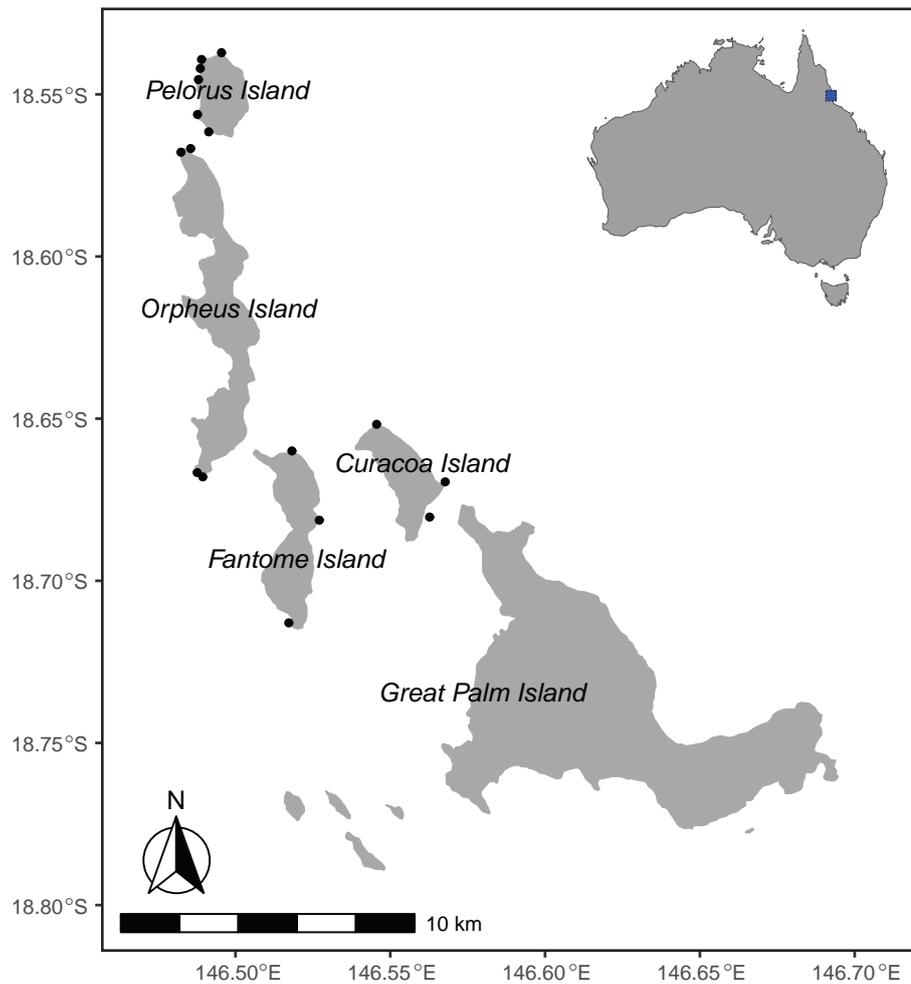
2. How does sea fan health affect the abundance and richness of fish assemblages, including both larger mobile fishes and small resident gobies? At what stage of declining health are fishes first affected?
3. How does sea fan health affect the assemblage structure of mobile fishes? That is, what fish species decline and what species increase in response to declining health?

I predicted sea fans to be present in a wide range of stages of health, from completely healthy individuals to dead skeletons, with no live tissue. I hypothesised that fish abundance and species richness would decline in relation to declining sea fan health, but with stronger and earlier responses in small specialised gobies. In addition, I hypothesized most larger reef fish species would respond negatively to sea fan damage, but some fish species may be attracted to resources provided by dead gorgonian surfaces.

## **4.3 Methods**

### **Study area and survey design**

This study took place in the Palm Islands on the central Great Barrier Reef (GBR), Australia (18.7345°S, 146.5794°E). Gorgonian health surveys and stereo video observations of fishes were conducted at 16 locations around four islands: Orpheus Is., Pelorus Is., Fantome Is., and Curacoa Is. (Fig. 4.1).



**Figure 4.1** Sixteen study locations at the Palm islands (central Great Barrier Reef) for surveys of gorgonian health, including 4 locations at Orpheus Is. (Goolboddi), 6 at Pelorus Is. (Yanooa), 3 at Fantome Is. (Eumilli), and 3 at Curacao Is.

### Survey of gorgonian health

To quantify the health of gorgonian fans, diver-operated 30m stereo-video transects were recorded at the 10m and 15m depth contours at the 16 locations, with 4 replicate transects at each depth (i.e. a total of 128 transects. Stereo-video methods followed the standard procedures outlined in Goetze et al. (2019)). The diver-operated stereo-video system (SVS) (SeaGis, Pty) comprised 2 GoPro cameras (Hero 5) set at 1080p resolution and 60fps wide, which allowed a known field of view to be measured during video analyses (2.5m each side of the transect). For all individual sea fans observed, the percentage of live tissue present on the skeleton was visually estimated and then placed into 1 of 5 health categories based on

20% increments in tissue loss (Table 4.1). Category 1 (C1), the healthiest colonies, were those with 80-100% live tissue present. Category 5 (C5), the least healthy, had 0-19% of live tissue remaining.

**Table 4.1** Gorgonian health categories (C1-5), 1 being the healthiest, 5 the most unhealthy

<b>Health category</b>	<b>% live tissue on each sea fan</b>
C1	80-100%
C2	60-79%
C3	40-59%
C4	20-39%
C5	0-19%

### **Effects of gorgonian health on fish**

To quantify fish communities associated with gorgonian fans in different health categories, 10 gorgonians in each of the five health categories were selected randomly within a depth band of 6m to 14m across, with variable numbers from the 16 locations. Stationary videos using GoPro cameras (Hero 7, 8, and 9), set to 1080p resolution and 60fps wide were recorded for 30 minutes of each colony. The cameras were mounted on a 30cm stand on a dive weight and placed directly in front of each colony at a distance, approximately 50cm-1m, depending on the size of the colony, that ensured the whole structure of the colony was captured. Once each camera was deployed, divers would leave the area to avoid disturbing the fish communities during the survey.

The 50 stationary videos were also played back continuously in the same standard media player (Quicktime). All fish immediately around, on or passing the gorgonian colony were counted and identified to species level, including resident gobies and larger more mobile species moving in and out of the area surrounding the sea fan. Care was taken not to repeat the count the larger fish re-entering the screen multiple times. To minimize the influence of diver disturbance on fish counts the first 30 seconds of each video was excluded from the analysis. For large schools of fish estimates were made of the total number of individuals.

## Data analyses

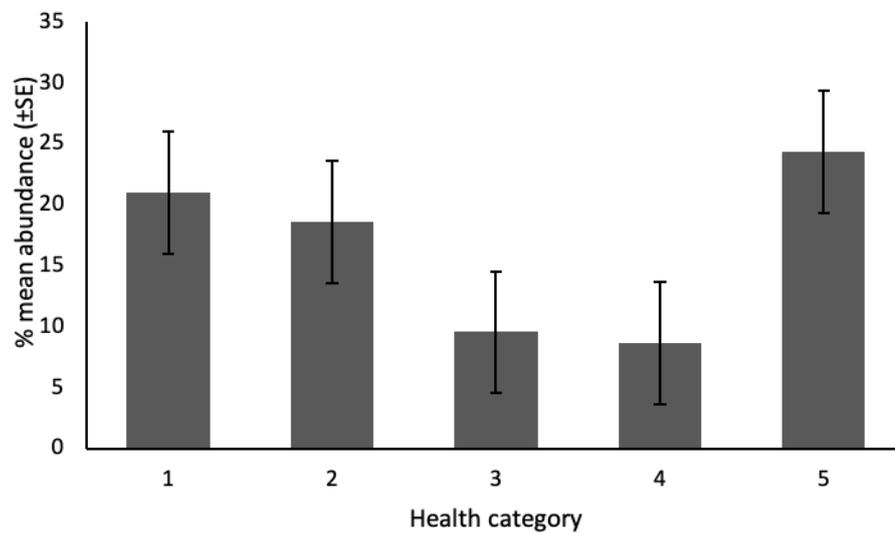
To quantify the proportion of colonies in each health category, mean percentage of gorgonians in each category per transect was calculated using the data obtained from the 30m video transects. For fish assemblages, statistical analysis was carried out using RStudio (Version 1.4.1717, R Core Team 2022) and graphics were generated using the package ‘ggplot2’ (Wickham 2011) and ggvegan (Simpson 2019). To test the differences in mean abundance and species richness between sea fan health categories for stereo video transects a Generalized Linear Mixed Model (GLMM) was conducted, using location as a random factor and testing the fixed factor hypothesis (health categories) by using a Type II Wald Chi-square test using the ‘anova’ function from the library “car”. Analyses were run separately for larger mobile fishes and small resident gobies. In all models, health category (1-5) was modelled as a fixed effect and individual gorgonian ID as the random effect. Abundance and richness of mobile fish species were modelled against a negative binomial distribution and goby genera abundance and richness modelled against zero-inflated Poisson distributions (log link). Additionally, pairwise comparisons amongst combinations of health categories were explored using planned contrasts and adjusted Tukey’s tests in the package ‘emmeans’ (Russell 2021). These comparisons were carried out to test the differences among health categories. Model validations included checks of fit by residuals and dispersion, carried out using the DHARMA package (Harting 2021). GLMMs were performed using the glmmTMB package to estimate maximum likelihood among health categories (Brooks et al. 2017).

Non-metric multidimensional scaling (NMDS) using the function metaMDS, part of the “vegan” library (Oksanen 2020) was used to visualise differences in fish assemblage structure in relation to sea fan health categories. The ordination was performed on square-root transformed data, followed by a Wisconsin double standardization and fit on a Bray-Curtis distance matrix. Fitted correlation vector scores for fish species were extracted using the function ‘envfit’ and fish species with the strongest correlations (Pearsons  $r < 0.5$ ) plotted as a biplot using “ggplot2” (Wickham 2016). No multivariate analysis was conducted for resident gobies since not enough data was available for a NMDS analysis.

## 4.4 Results

### How prevalent is the damage on sea fans?

The gorgonian health survey showed that only 20% of individuals were in the healthiest category (C1) (Fig. 4.2). The highest proportion of sea fan colonies surveyed (24%) were in the unhealthiest C5, with 8 individuals observed that were completely dead. The lowest proportion (9%) were in C4 (Fig. 4.2). There were significant differences in the mean abundance of sea fans in each health category across the 16 locations (*GLMM*,  $\chi^2 = 21.505$ ,  $df = 4$ ,  $p < 0.05$ ). Pairwise comparisons between health categories showed significant differences between health category 1 and 4 (Table 4.2).



**Figure 4.2** Mean percent abundance of sea fans in the 5 different health categories at the 16 locations ( $n = 16$ ) around 4 islands of the Palm Island Group, Australia. Health categories are based on 20% increments in the percentage of live tissue left on the sea fan structure: 1 (100-80%), 2 (79-60%), 3 (59-40%), 4 (39-20%), 5 (19-0%)

**Table 4.2** Pairwise differences mean abundance of sea fans at the 5 health categories (1-5). LCL and UCL are the lower and upper 95% confidence limits. Significant contrasts are indicated in bold.

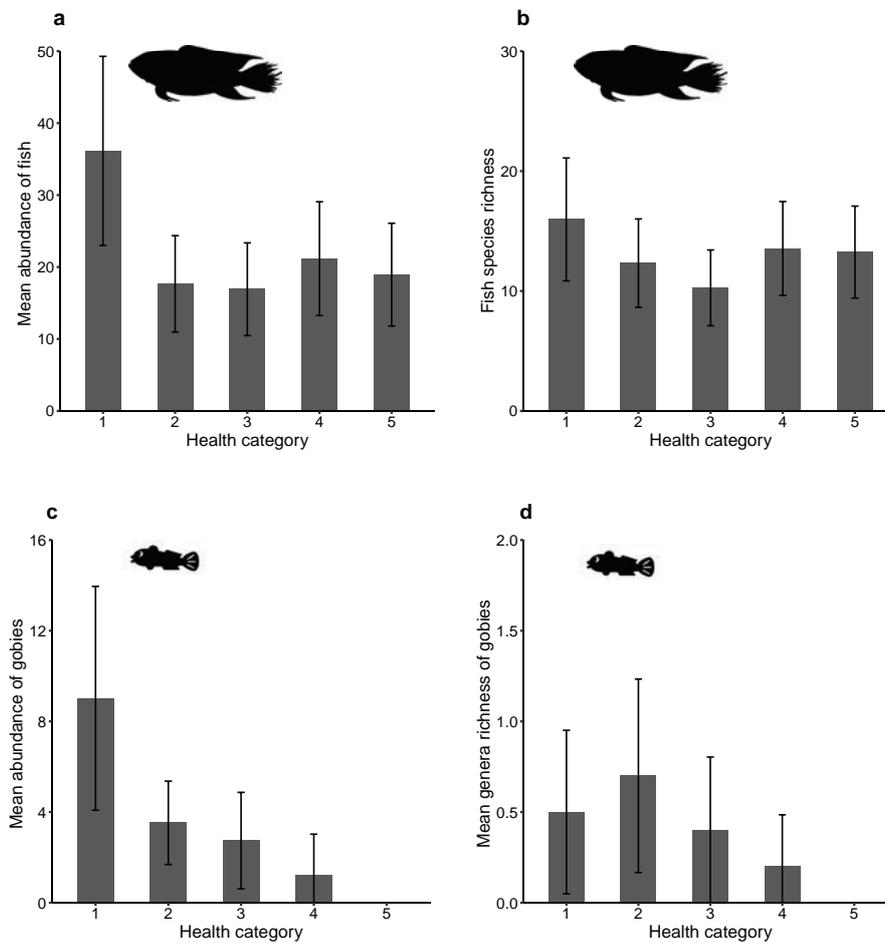
Health Categories Contrasts	Contrast Estimate	SE	df	LCL	UCL
1-2	1.37	1.55	78	-2.96	5.69
1-3	3.14	1.44	78	-0.88	7.16
1-4	4.56	1.44	78	<b>0.53</b>	<b>8.59</b>
1-5	0.98	1.64	78	-3.62	5.57
2-3	1.77	1.20	78	-1.58	5.13
2-4	3.19	1.16	78	-0.05	6.44
2-5	-0.39	1.48	78	-4.52	3.73
3-4	1.42	0.81	78	-0.84	3.68
3-5	-2.17	1.31	78	-5.83	1.50
4-5	-3.59	1.27	78	-7.12	-0.05

### How do different health categories of sea fans influence the abundance and species richness of fishes?

A total of 128 fish species were recorded across all gorgonian colonies in the stationary videos. Gorgonian health category was a significant predictor of the mean abundance of mobile fish (*GLMM*,  $\chi^2 = 11.43$ ,  $df = 4$ ,  $p = 0.02$ ). The healthiest category (C1) recorded more than double the mean abundance of fishes (~36 individuals per colony), compared to the other health categories (Fig. 4.3a). However, pairwise comparisons between health categories (C1-5) could not detect which levels differed from one another (Table 4.3). There was no significant effect of sea fan health on the species richness of mobile fishes (*GLMM*,  $\chi^2 = 5.07$ ,  $df = 4$ ,  $p = 0.27$ ) (Fig. 4.3b).

For goby communities, fan health was significant predictor of goby mean abundance (*GLMM*,  $\chi^2 = 12.6$ ,  $df = 4$ ,  $p = 0.01$ ), with the highest mean goby abundance (~9 individual gobies) found on sea fans in the healthiest category (C1). Goby abundance declined in relation to declining sea fan health, with no gobies were found on gorgonians in C5 (Fig. 4.3c). Sea fan health was not a significant predictor of goby genera richness across health

categories 1-4 ( $GLMM, \chi^2 = 2.66, df = 4, p = 0.61$ ), but no species were present on fans in the unhealthiest category (Fig. 4.3d).



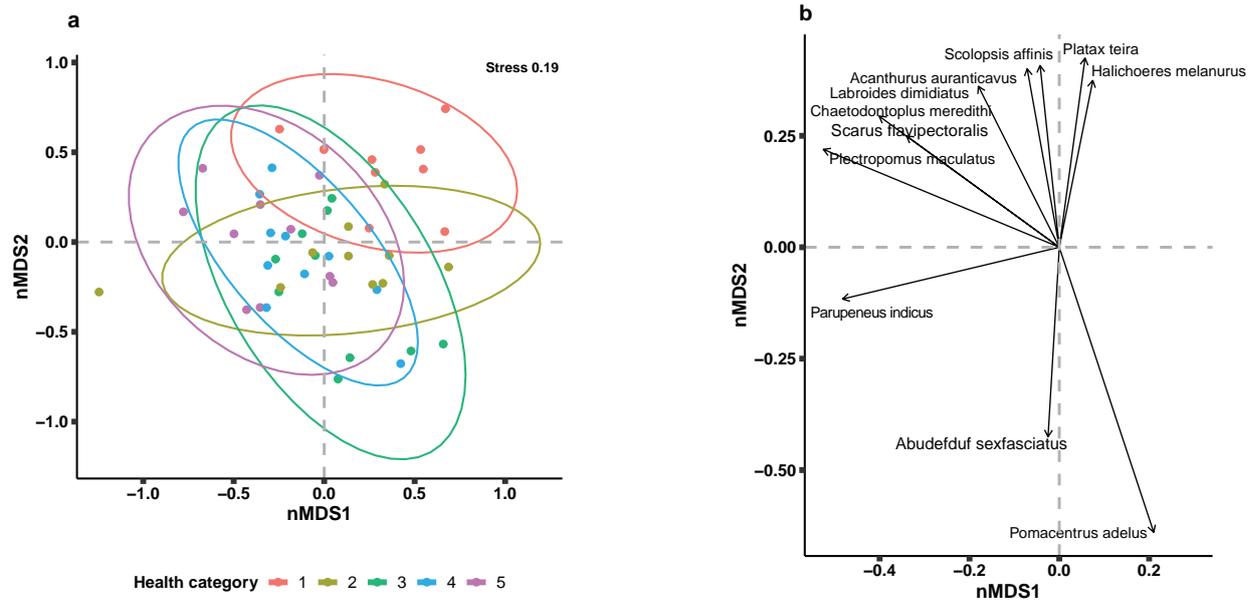
**Figure 4.3** Mean abundance of **a** mobile fish and **b** fish species richness around different gorgonian health categories. Mean abundance of **c** resident gobies and **d** goby genera richness. Error bars 95% confidence intervals.

**Table 4.3** Pairwise differences in fish mean abundance (contrast estimate) between 5 health categories (1-5). LCL and UCL are the lower and upper 95% confidence limits respectively.

Mobile fish mean abundance					
Health category contrasts	Contrast estimate	SE	df	LCL	UCL
1-2	18.48	7.33	48	-2.29	39.26
1-3	19.23	7.27	48	-1.38	39.85
1-4	14.97	7.62	48	-6.62	36.58
1-5	17.20	7.43	48	-3.86	38.27
2-3	0.74	4.61	48	-12.34	13.84
2-4	-3.50	5.15	48	-18.10	11.09
2-5	-1.28	4.86	48	-15.07	12.51
3-4	-4.25	5.06	48	-18.62	10.11
3-5	-2.02	4.78	48	-15.58	11.52
4-5	2.22	5.30	48	-12.78	17.24

### How do different health categories of sea fans influence the structure of mobile fish assemblages?

Multivariate analyses of the mobile fish community found that fan health had a significant effect on fish community composition (PERMANOVA  $\text{adj}R^2=0.209$ , *adonis*, pseudo-F= 1.6488,  $p=0.001$ ; *betadisper*, pseudo-F = 0.6235,  $p = 0.64$ ) (Table 4.4). Communities in all five health categories showed some degree of overlap, but communities on fans in C1 were the most distinct (Fig 4.4a). Of the fish species most strongly correlated with the NMDS ordination, the batfish *Platax teira*, and the wrasse *Halichoeres melanurus* were more aligned with the healthiest sea fans (C1) (Fig. 4.4b). The damselfish, *Pomacentrus adelus*, showed a clear alignment with fans in health C2. The goatfish, *Parupeneus indicus*, appeared to be characteristic of assemblages in the two unhealthiest categories (C4, C5). Other species such as, *Scarus flavipectoralis*, *Chaetodontoplus meredithi*, *Labroides dimidiatus*, *Plectropomus maculatus*, *Acanthurus auranticavus* and *Scolopsis affinis* were found on sea fans in all health categories (Fig. 4.4b).



**Figure 4.4** NMDS plot representing **a** community structure of mobile fish around the 5 categories (1-5) of sea fans, **b** arrows represent the fish species with the strongest correlation with the NMDS axes in the community ( $p < 0.02$ )

**Table 4.4** Results of PERMANOVA: differences in fish species assemblage structure across 5 health categories. Tests are based on Bray-Curtis dissimilarity distances and 999 permutations

Source	Df	Sums Sq	Mean Sq	Pseudo - F	Pr (>F)
Health categories	4	0.01841	0.0046032	0.6235	0.657
Residuals	45	0.33223	0.0073828		

#### 4.5 Discussion

This study found that gorgonians exhibited a wide range of health condition at the Palm Island Group, with only 20% of individuals in the healthiest category. Almost a quarter (24%) were in the unhealthy category (C5), with less than 20% of live tissue remaining and it was not uncommon to find them completely dead. The different health categories were significant predictors of abundance of mobile fish assemblages, with the healthiest sea fans (C1) showing the highest abundance of mobile fish. Resident gobies declined in abundance in relation to sea fan health, with no individuals at all on sea fans in the unhealthiest category (C5). While there were no effects of sea fan health on fish species richness, there were subtle differences

in fish assemblage structure, with the batfish *Platax teira* and the wrasse *Halichoeres melanurus* associated with healthy gorgonians, and the goatfish (*Parupeneus indicus*) associated more often with unhealthy individuals. Many large reef fish, such as *Chaetodontoplus meredithi* and the parrotfish *Scarus flavipectoralis*, were often seen sheltering or feeding in the branches of almost completely dead sea fans. Overall, there are clear signs that sea fans are under stress at the Palm island and the local-scale impact on fishes is cause for concern.

### **The extent of declining sea fan health**

The wide range of health conditions of sea fans at the Palm Islands suggests that they are under stress, with a quarter in very poor condition. At this stage, the causes of live tissue loss and whether this is normal or part of a long-term decline are unknown. There is no specific information on stresses impacting on sea fan health at the Palm Islands, but inshore reefs of the GBR are known to be subject to multiple anthropogenic disturbances, most notably, nutrient enrichment and high sediment loads from terrestrial run-off and river discharge (Wenger et al. 2015). This is known to be detrimental to large and fragile organisms like sea fans and other gorgonians (Fabricius 2005; Rowley et al. 2015). The majority of damaged sea fans observed in this study were covered with a thin layer of fine sediment, and further work is needed to establish the sediment-source and whether or not it is instrumental in leading to tissue loss.

The results described here are consistent with other studies on the status of gorgonians, with declines in abundance documented in Colombia (Sanchez et al. 2014), Indonesia (Scinto et al. 2008) and in the Caribbean (Zuluaga-Montero and Sabat 2012). In the Caribbean, populations of *Gorgonia ventalina* has been severely affected by a disease namely aspergillosis, caused by *Aspergillus sydowii* (Toledo-Hernández et al. 2007). To date, only one record of that disease has been recorded for the Indo Pacific, for the gorgonian genus *Annella* in the Andaman Sea (Phongpaichit et al. 2006). The health of *Briareum asbestinum* was negatively affected by a disease during an El Niño event (Harvell et al 2001), as well as the genus *Plexaura* was severely disturbed by abnormal changes in temperature (Lasker 2005). Declining sea fan health in the Caribbean has been attributed to the negative effects of epibionts or fish grazing on gorgonians (Kinzie, 1973). There is very limited research on gorgonian declines in the Indo Pacific area, but high gorgonian mortality as a result of caprellid amphipod outbreaks

have been recorded in North Sulawesi, Indonesia (Scinto et al. 2008). It is not clear whether disease or these other factors have contributed to the state of sea fans at the Palm Islands, but all warrant investigation.

### **Effects of gorgonian health on fish abundance and species richness**

Sea fans in different stages of declining health clearly had a negative impact on abundance of the larger mobile fish associated with gorgonians. Mobile fish abundance was highest around the healthiest sea fans (C1) and lowest around those in the lowest health category (C5). The abundance of resident gobies progressively declined from healthy to unhealthy sea fans, and were completely absent on sea fans with less than 20% live tissue remaining (C5). While the species richness of mobile reef fishes did not decline, the loss of small fish species on severely damaged gorgonians could be problematic, especially if this is part of a long-term trend. Small, highly specialised cryptobenthic gobies are well-known to decline when their primary habitat declines and they can go locally extinct (Munday et al. 1997, 2004; Doll et al. 2021). This has not specifically been reported for gorgonians, but the genera *Pleurosicya* and *Bryaninops* have species that live in obligate association with gorgonians (Chen et al. 1995; Sih and Chouw 2009; see Chapter 3). Elsewhere, other cryptobenthic fish such as the pygmy seahorse (*Hippocampus bargibanti*), which has evolved to be extremely specialised on sea fans (*Muricella plectana*, *M. paraplectana*), is already in a critical vulnerability state (De Brauwert et al. 2020). Sea fan degradation is clearly a serious extinction risk for these kinds of species.

### **Effects of gorgonian health on the local structure of mobile fish assemblages**

The different stages of sea fan health had observable effects on the structure of fish assemblages, with the healthiest sea fans being the most distinct. Healthy sea fans appeared to be more characterised by the batfish *Platax teira* and the wrasse *Halichoeres melanurus*, while the goatfish (*Parupeneus indicus*) was associated with unhealthy individuals. Other species appeared more characteristic of sea fans in intermediate stages of tissue loss. For example, *Pomacentrus adelus*, was most abundant in gorgonians in health category (C2). There were clearly several species that were not all that influenced by gorgonian tissue loss, and some that may preferentially be associated with damaged gorgonians. *A. sexfasciatus*, an

omnivorous planktivore, was recorded feeding on dead sea fan branches (C5), perhaps covered in various types of detritus deposited on the dead branches of the structure (e.g. small dead invertebrates). The piscivorous grouper, *Plectropomus maculatus*, was often observed using the fans to ambush its prey, without discrimination for the % of live tissue cover. Other species such as the herbivore, *Scarus flavipectoralis*, was often seen feeding in the dead branches of sea fans. Hence, to some degree, having sea fans in different stages of health may promote fish diversity on a scale larger than individual fans. However, the species-specific responses to damage, and the longer-term implications of further declines in health require further investigation. Understanding the dependence of fish with these structures can explain the effects of their health decline on the fish populations. Even if mobile fish only use gorgonians as cleaning stations the decline in health of these colonies can produce a decrease in architectural complexity on the reef, hence reducing the availability of structures to congregate for a large variety of species. Sea fans with only or less than 20% of tissue left are usually just small branches, hence the overall fan-like structure can cause a loss of complexity, therefore reducing the availability of protection for fish.

### **Conclusions and further research**

This was the first study to address the association between sea fan health and fish assemblages. The results indicate that this relationship warrants further investigation, as gorgonians do not appear to be in a perfect state of health at the Palm Islands, with approximately a quarter of the population in extremely low condition (<20% live tissue remaining). Fish assemblages, particularly resident gobies, are clearly being negatively impacted on unhealthy gorgonians, although having gorgonians in a wide range of health conditions may be normal and even promote fish diversity. Further work is needed to determine whether the low health condition is part of a long-term trend related to increasing anthropogenic pressures or is to some extent the natural condition. Sea fans are clearly being influenced by processes leading to tissue loss, and the roles of sedimentation, disease and other factors require investigation. I suggest comparative studies of gorgonian health between inshore vs. off-shore locations to better understand any terrestrial influence on gorgonian condition. Fishes are clearly responding to low sea fan health, but whether or not this represents a local extinction risk for some small, specialised species will also need to be evaluated. Overall, this study provides important information on the state of health of sea

fans, however the observational nature and the restricted time frame of this research may represent some limitations to this study. Further research avenues focusing on comprising other environmental factor in the study such as topography, and different locations may be key to better understand the effects of gorgonian health decline on associated fish populations. The present study provides a base-line for the current status of gorgonian health for inshore reefs on the GBR and how it is impacting on reef fishes. It clearly suggests that long-term monitoring of gorgonians and the fishes they support are warranted as part of a complete understanding of the status of the Great Barrier Reef and developing the best management strategies for protecting important habitat-forming species.

## Chapter 5: General discussion

Understanding the structure of ecological communities and the processes and interactions that create them is a fundamental concept in ecology. Whilst many biotic interactions are defined as direct trophic pathways or competition, some species link both trophic and physical aspects of the community, exerting significant influence over the distribution of other species. This concept of some species as ecosystem engineers has been widely studied for terrestrial systems (Jones et al. 1994; 1997), but research identifying engineers in marine systems is still lacking. Coral reefs, particularly scleractinian corals, key habitat forming taxa, are facing an uncertain future in the light of global anthropogenic climate change. Therefore, identifying other species which have significant impacts upon the physical structure of the habitat and coral reef communities may be important for maximising conservation outcomes and maintaining the overall ecosystem function.

In this thesis I demonstrated that gorgonians play an important role in shaping reef fish community structure as autogenic ecosystem engineers. Gorgonians directly provide habitat through their physical structure and their relative abundance in the ecosystem significantly affects the biodiversity of both highly specialised and more generalist reef fishes. The distribution of gorgonians, however, is governed by several important environmental factors.

In **chapter 2** I found that depth, current speed and the surrounding benthic substrata were important determinants of gorgonian abundance and genera richness. Despite depth was an important driver, other environmental factors may be explaining the spatial patterns of distribution of gorgonians. The overall relative abundance of gorgonian genera across depth was also closely related to their growth forms, with distinct genera and morphologies residing at different depths. The variety of growth forms exhibited by gorgonians generated interesting questions about potential differences in their roles as engineers. Colony size, shape and branch morphology affects the nature of physical habitat provision and therefore also which species might interact with the colony.

I tested this in **chapter 3** and found that three distinct gorgonian growth forms (branched, candelabrum, fan) attracted different mobile fish and resident goby assemblages. In particular, the latter discriminating among morphologies, with the genus *Pleurosicya* exclusively found on fans, and *Bryaninops* only on branched and candelabrum structures. Branched and fan

morphologies attracted similar fish communities, whereas candelabrum gorgonians attracted different fish species, probably due to their simple structures, and to the sand-dominated habitats in which they are often found.

Lastly, in **chapter 4**, I investigated the effects of sea fan health on associated fish communities. Sea fans in poor physical health, with 0-19% live tissue on their structures, had the lowest mobile and resident fish abundance. For habitat specialist resident gobies, declining fan health was detrimental and these fishes completely disappeared from the most-unhealthy gorgonian hosts. Across my study sites, sea fans displayed variable health states around the reefs of the Palm Island Group. This suggests that there is further research required to understand the environmental drivers of gorgonian health states and the broader effects of reef fish biodiversity on the inshore reefs of the Great Barrier Reef.

The results of this thesis contribute to the understanding and recognition of gorgonians as an important component of coral reef ecosystem structure. Like scleractinian corals they are engineering species that provide resources to both highly specialised and generalist reef fishes. However, unlike hard corals, they remain a relatively understudied group. Although surveys specifically assessing habitat complexity and benthic diversity on coral reefs do generally include gorgonian colonies in sampling methods, the results of these surveys all too often combine multiple non-scleractinian taxa into ambiguous “other” groupings. To accurately quantify the significance of gorgonians as ecosystem engineers in coral reef systems, this important group needs to be examined in their own right and, more specifically, included in survey and monitoring methodologies.

As global tropical coral reefs are in a constant process of degradation as a result of anthropogenic climate change and associated stressors, detailed knowledge of other reef taxa that contribute to overall ecosystem structure and function will be essential for effective conservation actions. Most studies of ecosystem engineers show that these organisms have a positive effect on species diversity in the community (Wright and Jones, 2006). Recently, there has been an increasing focus on engineering species and their potential to facilitate elements of ecosystem restoration (Byers et al 2006). Whilst single-species approaches to conservation and, indeed, restoration activities in general, are controversial, understanding which species could contribute most to ecosystem recovery following disturbance may prove critical to future management considerations and biodiversity trajectories. Although data on the effect of elevated ocean temperatures on gorgonians and their algal symbionts are scarce,

some recent studies suggest that gorgonian corals exhibit markedly higher tolerance to thermal stress compared to many scleractinian species (Goulet et al. 2017). Shifts from scleractinian dominated reef systems to soft and gorgonian coral-dominated reefs (Caribbean) are becoming more evident in recent decades. Clearly, this may represent a change in the benthic community structure, however, long term and large spatial scale effects on fish communities are still unknown. Results from this thesis suggest that if gorgonians can persist in elevated seawater temperatures, they may continue to support high levels of fish diversity as hard coral habitats are lost. Although these fish communities will likely differ from those supported by hard coral habitats, studying the role of gorgonians in changing reef systems will be vital to understand future patterns in marine biodiversity.

This said, gorgonians are clearly not immune to many forms of natural and anthropogenic stressors. This was highlighted by the variable health states of gorgonians surveyed around the Palm Islands. A key finding of this thesis was that the effects of declining gorgonian health can be detrimental to associated fish communities. The cause of tissue loss on colonies in my thesis are unknown, hence further work on GBR gorgonian communities is warranted to identify drivers of declining gorgonian health in the region. Even if gorgonians are relatively resilient to thermal anomalies, there are a multitude of other stressors like declining water quality and high sedimentation loads which are likely negatively affecting colony health. One interesting consideration is the persistence of dead gorgonian colonies on the reef as abiotic physical structures and whether they are still able to provide a habitat to associated fauna, including fish and invertebrates. Further research is needed to understand the use that fish do of dead gorgonian skeletons, whether they can still represent useful structures that can be used by mobile fish.

Responses of gorgonian communities to environmental change will vary at both local and larger spatial scales. Like most coral reef taxa, gradients in multiple biophysical factors (e.g. temperature, light, salinity, wave action, exposure) are key determinants of gorgonian distribution patterns. This thesis found that gorgonian communities in the Palm Islands are shaped by depth, current speed and other dominant types of surrounding benthic substrata. These depth-related patterns can be influenced also by the availability of food, which may vary depending on the turbidity levels in the area. Given that the Palm Islands are in an inshore area of the GBR, these distribution patterns of gorgonians across depths may be influenced by the high level of turbidity present. The effect of depth has always been a prominent environmental factor in coral reef ecology, however, it is now a hotly debated topic

for its potential role in buffering the effects of thermal stress and serving as a “refugia” for some reef taxa (Bongaerts et al. 2017). Gorgonians are known to span considerable depth ranges and are often the dominant taxa contributing to habitat complexity in deeper, mesophotic coral ecosystems (Benayahu et al. 2019). High colony density and large individual colonies have been recorded at 70m in locations off Vaitogi, Tutuila, American Samoa (Montgomery et al. 2019). Also, shallow water gorgonians tend to be more abundant in deeper areas, such as in the WMNP (Tukang Besi Islands), Indonesia, where a clear depth-related pattern for azoozanthellate gorgonians was observed (Rowley 2018). The study of gorgonian size distributions across depth may reveal further interesting population dynamics of these slow-growing and long-lived group of organisms. Several aspects of gorgonian life history strategies are still poorly understood. Particularly, it is unknown how old these structures can be, their annual growth rates and whether their growth rates differ between morphologies and species. Understanding the age and annual growth rates of these organisms could be helpful to better evaluate their resilience to disturbances and their longevity for the associated fauna to use them as habitats. The specialist nature of some gorgonian-fish associations further highlights the importance of gorgonians in maintaining coral reef diversity. Perhaps the most well-known and charismatic example of these specialist relationships is the pygmy seahorse (*Hippocampus bargibanti* and *H. denise*) with the fans *Muricella plectana* and *M. paraplectana*. Results from this thesis demonstrated that some goby genera were exclusively found on certain gorgonian morphologies. Whilst a molecular revolution is currently underway in scleractinian coral taxonomy, gorgonian lineages and taxonomic resolution has received limited research attention. Improvements in the taxonomic knowledge of gorgonians will not only clarify fundamental evolutionary patterns but are also likely required to better understand and identify obscure, species-specific associations with fish and other reef taxa.

In summary, this thesis has captured multiple aspects of the current ecological status of gorgonians in the Palm Islands, an inshore region of the Great Barrier Reef. Relative to other benthic reef taxa, gorgonians remain understudied. The chapters in this thesis represent some of the only gorgonian-focused research in the region to date, particularly regarding fish-habitat associations. Globally, there is a surge of interest in maintaining and conserving marine ecosystems and a broad range of strategies have been employed to achieve these conservation goals. It is however, evident that the success of holistic conservation measures

will require consideration of all ecosystem engineers or species whose actions have “significant impacts” upon the physical structure of their habitats.



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## Appendix A

**Table 1-** Summary of locations (1-16) across the Palm Island Group. For each location, depth bands, latitude and longitude, and average current speed ( $\text{m s}^{-1}$ ) per depth were recorded.

Location*	Depth			
	(meters)	Latitude	Longitude	Average current speed ( $\text{m s}^{-1}$ )
1	15	-18.537151	146.495449	0.06
	10			0.05
	5			0.06
2	15	-18.539208	146.489122	0.05
	10			0.06
	5			0.10
3	15	-18.668024	146.489465	0.14
	10			0.11
	5			0.02
4	15	-18.669458	146.567672	0.08
	10			0.04
	5			0.06
5	15	-18.561587	146.491371	0.18
	10			0.16
	5			0.08
6	15	-18.566632	146.485521	0.13
	10			0.19
	5			0.12
7	15	-18.556155	146.487752	0.11

	10			0.07
	5			0.14
8	15	-18.542017	146.488616	0.11
	10			0.11
	5			0.04
9	15	-18.712956	146.517208	0.09
	10			0.07
	5			0.06
10	15	-18.6812677	146.5270923	0.09
	10			0.05
	5			0.09
11	15	-18.6599120	146.5182695	0.12
	10			0.08
	5			0.11
12	15	-18.651770	146.545556	0.26
	10			0.15
	5			0.08
13	15	-18.567906	146.482413	0.13
	10			0.06
	5			0.05
14	15	-18.545447	146.487961	0.06
	10			0.02
	5			0.02
15	15	-18.680315	146.56266	0.15
	10			0.11

	5			0.11
16	15	-18.666617	146.487588	0.11
	10			0.05
	5			0.05