Tropical Water Quality Hub

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Final Report

Recommendations to maintain functioning of the Great Barrier Reef

Kennedy Wolfe, Ken Anthony, Russell C. Babcock, Line Bay, David Bourne, Thea Bradford, Damien Burrows, Maria Byrne, Dione Deaker, Guillermo Diaz-Pulido, Pedro R. Frade, Manuel Gonzalez-Rivero, Andrew Hoey, Mia Hoogenboom, Mark McCormick, Juan-Carlos Ortiz, Tries Razak, Anthony J. Richardson, Hannah Sheppard-Brennand, Jessica Stella, Angus Thompson, Sue-Ann Watson, Nicole Webster, Donna Audas, Roger Beeden, Vicki Bonanno, Jesseca Carver, Karen Chong-Seng, Mel Cowlishaw, Jen Dryden, Michelle Dyer, Paul Groves, Dylan Horne, Neil Mattocks, Lauric Thiault, Jason Vains, David Wachenfeld, Damien Weekers, Genevieve Williams and Peter J. Mumby

THE UNIVERSITY OF QUEENSLAND
AUSTRALIA

Recommendations to maintain functioning of the Great Barrier Reef

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Cover photographs: Peter J. Mumby

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ACRONYMS

AIMS	Australian Institute of Marine Science
BMI	Benthic Mobile Invertebrate
CCA	Crustose Coralline Algae
CITES	Convention on International Trade in Endangered Species
CoTS	Crown-of-thorns starfish
CSIRO	Commonwealth Scientific and Industrial Research Organisation
DAF	Department of Agriculture and Fisheries
DoEE	Department of the Environment and Energy
EAM	Epilithic Algal Matrix
GBR	Great Barrier Reef
GBRMP	Great Barrier Reef Marine Park
GBRMPA	Great Barrier Reef Marine Park Authority
IUCN	International Union for Conservation of Nature
JCU	James Cook University
LTMP	Long-Term Monitoring Program
MMP	Marine Monitoring Program
NESP	National Environmental Science Programme
OUV	Outstanding Universal Value
RIMReP	Reef 2050 Integrated Monitoring and Reporting Program
RRAP	Reef Restoration and Adaptation Program
RRRC	Reef and Rainforest Research Centre Limited
TWQ	Tropical Water Quality
USYD	The University of Sydney
UQ	The University of Queensland
UNESCO	United Nations Educational, Scientific and Cultural Organisation

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EXECUTIVE SUMMARY

Coral reefs are among the most diverse ecosystems on Earth and provide immeasurable contributions to marine (and terrestrial) ecosystem processes, functions and services. Yet, coral reefs, including the world's largest – the Great Barrier Reef (GBR), Australia – are increasingly vulnerable to local (e.g. fisheries, water quality) and global (e.g. ocean warming, ocean acidification) stressors. Shifts in the processes that maintain reef functioning are already measurable on the GBR, including for habitat (e.g. reef growth) and production (e.g. fisheries) functions. Conservation of biodiversity has historically been the focus of ecosystem-based management on the GBR, but it is increasingly recognised that a subset of species can be particularly important. Ultimately, global protection of coral reefs depends on fast action towards a low-carbon economy, but this must be augmented with local action to prevent degradation of reef structure and functioning. Explicit identification and protection of key taxa that support positive interactions is imperative to conservation success, and in providing targeted information to safeguard species, biodiversity and functioning into the future.

The biology and ecology of GBR taxa are broadly understood but data on ecosystem functioning are largely weighted towards certain groups (i.e. corals and fishes). Though broad in scope, this is the first study to make a comprehensive assessment across a diverse range of taxonomic and functional groups on the GBR – from microbes to predatory fishes – to summarise reef functioning. Effort was focused on classical reef slope and reef crest habitats, as these are typically the most diverse, coral-rich ecosystems that support the greatest range of ecosystem services. This refined approach acknowledges the exclusion of other important reef biomes (e.g. mangroves, seagrass meadows, inter-reefal areas), but was employed to ensure a targeted research design with effective management outputs. Similarly, some taxa were not assessed (e.g. reptiles, mammals, seabirds) as these groups are often rare on the reef and/or already intensively addressed or protected.

While whole-ecosystem management is necessary to maintain the integrity of coral reefs, many of the attributes examined here, at the level of species, ecological processes and ecosystem functions, are of Outstanding Universal Value and contribute greatly to the GBR and its World Heritage property. The information presented provides a first step to inform holistic management aiming to preserve functionally important taxa and processes, and provides the opportunity to build out from the current framework to other important coral reef biomes (e.g. mangroves, seagrass meadows, inter-reefal areas) and values (e.g. social, cultural, economic).

A panel of GBR experts across a range of disciplines was established to aid project development and identify taxa that play critical roles on the GBR to expedite management of this system. Specifically, we assessed (1) which taxa drive processes that maintain a healthy reef, and address whether or not management is considered (2) a priority (i.e. *are they vulnerable?*) or (3) feasible (i.e. *can they be managed?*). This was augmented by input from a range of researchers and managers, and an extensive compilation of the literature. The project operated under these three main criteria (Figure ES1):

1- ***Process-based assessment:*** Evaluation of 70 taxonomic and functional groups common on the GBR based on their contributions to nine key ecosystem processes; primary production, herbivory, predation, nutrient cycling, symbiosis, calcification, bioerosion,

ecosystem engineering and recruitment facilitation. Each process was considered equally important to a functioning reef. Species groups were scored in terms of:
   a. the *magnitude* of their contribution to each process (*direct* and *indirect*),
   b. their level of functional *redundancy* regarding each process (greater importance placed upon unique or irreplaceable contributions; i.e. low redundancy),
   c. whether their contribution to each process was *dependent* on other species (greater importance being placed where dependency was low).

2- ***Vulnerability:*** Impacts of nine predominant threats facing each functional group; sedimentation, pollutants, eutrophication, ocean warming, ocean acidification, severe storms/cyclones, fisheries, population outbreaks and disease. Taxa were ranked based on their known and predicted vulnerabilities to each stressor, and recoverability, on the GBR.

3- ***Manageability:*** Comparison of each group based on their potential responsiveness to and feasibility of intervention, so that realistic and timely recommendations could be presented.

In a combined model, these three tiers of information were used to identify functionally important taxa that might warrant special protection. Scientific *certainty* was addressed (Figure ES1), used *post hoc* to weight our recommendations, particularly where certainty was comparatively low. High certainty solidified the merit of our recommendations, while scores that were uncertain were highlighted under precautionary principles so that functional groups that 'slipped through the cracks' in our ranking system due to data deficiencies were not overlooked. Thus, low-ranked taxa had the potential to be elevated in importance if certainty was low.

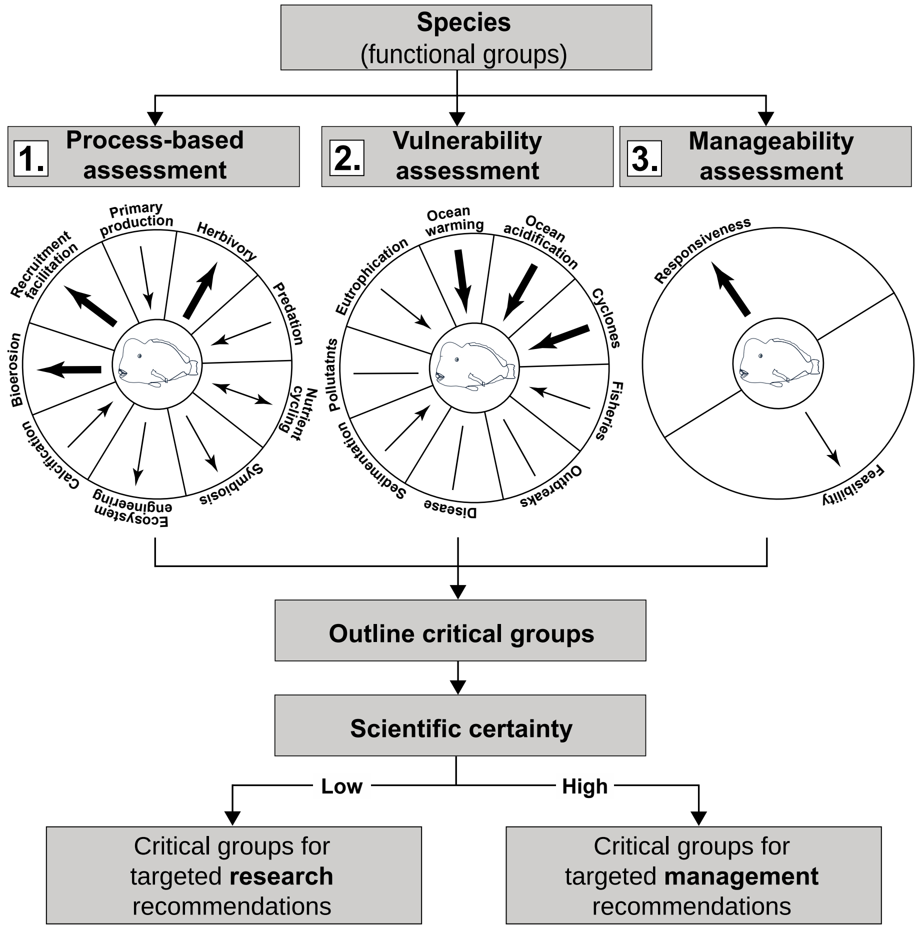

Figure ES1: Framework outlining the assessment criteria employed to identify key functional species for targeted management recommendations, based on their (1) functional importance (process-based assessment), (2) vulnerability, and (3) manageability on the GBR. Black arrows represent estimated data; i.e. high (bold) or low (thin) contributions; positive (outwards), negative (inwards) or neutral (line only) influences. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

We provide scientific consensus in support of:

(1) taxa of particular functional importance,
(2) taxa and processes of outstanding value and/or threat,
(3) recommendations for enhanced and targeted protection, and
(4) informed scenarios for knowledge gaps, future research and novel management.

Our process-based assessment outlined a diversity of key players (Figure ES2), including **branching and tabular corals**, **microorganisms**, **crustose coralline algae**, **turf algae**, **crown-of-thorns starfish** (and **triton snails**), and **herbivorous parrotfishes**. Past and present management schemes (e.g. zoning, GBRMPA Blueprint for Resilience) are commended for their efforts regarding many of these groups, and momentum should be maintained in education, conservation and monitoring initiatives for these key taxa.

We focused on highlighting functional groups that are currently underappreciated in their roles to guide development of novel management strategies and future research objectives. We highlight novel taxa (Figure ES2) including **chemoautotrophic microbes**, **cleaner wrasse**, **bivalves**, **coral-associated decapods**, and **detritivorous fishes**), which may benefit from specific consideration in management initiatives, including expanding current research and monitoring programs to effectively capture these groups to inform whole-system models. Many of these priority and novel taxa are distinct and identifiable, rendering themselves particularly attractive to future endeavours in education and citizen science, if not already captured.

We also broadcast groups where scientific certainty was particularly low (Figure ES2) including for **cryptic predators**, **deposit-feeding sea cucumbers**, **marine worms**, **cryptic sponges** and **crustaceans**, to encourage future research directions and management innovation for poorly described taxa and functions. For novel candidates and groups where certainty was particularly low, empirical data on their roles in ecosystem functioning and vulnerability to the growing number of stressors on coral reefs are imperative to ensure that functioning is adequately safeguarded at its highest degree.

Overall, while we suggest there is significant room to increase monitoring, and novel opportunities for management and science, we find that **current initiatives effectively capture key groups with benefits to reef function**.

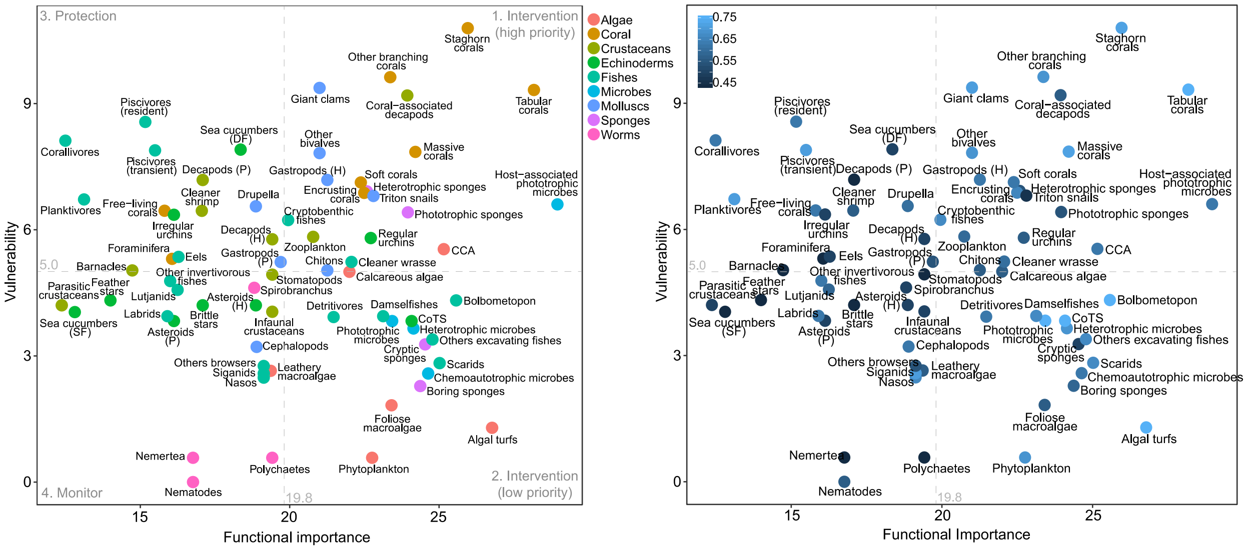

Figure ES2: Functional importance and vulnerability of 70 functional groups common on the GBR, coloured by phyla (left) and scientific certainty weighting (right); light blue = high certainty; dark blue = low certainty.

This project also identified critical knowledge gaps that currently limit our understanding of ecosystem functioning. Within the lifetime of this project, teams of researchers from within the scientific working group, and beyond, addressed these gaps. These are presented as five case studies that highlight species with pivotal roles, with recommendations case-by-case:

1- Invertivory on the GBR: a poorly understood link in the trophic chain – It is estimated that ~70% of fishes on the GBR feed predominantly on invertebrates, but data gaps remain regarding invertivory on benthic mobile invertebrates (BMIs). In a review of >550 studies, only 35 documented invertivorous fishes to incorporate BMIs in their diet on the GBR. This included 174 species from 20 families, a great diversity of ~10% of the total known number of fish species on the GBR. Targeted research is imperative to quantify predator-prey dynamics for invertivores on the GBR, including prey availability, trophic transfers from within the reef matrix and beyond, and their potential to mediate trophic cascades in degrading reef systems.

2- Calculating the carbonate budget for the GBR: coral cover and coralline growth – A total carbonate budget was calculated for the GBR from rates of carbonate production (reef growth) and bioerosion (reef destruction) using AIMS LTMP data spanning 2014–2018. Carbonate production was dominated by hard corals (~94%), with the remainder by CCA. *Acropora* exhibit the greatest calcification rates. A negative budget was calculated in the northern GBR, driven by low carbonate production rather than high bioerosion rates. The carbonate budget increased in the central GBR and was greatest in the south. Temporally, the GBR budget increased between 2014 and 2017, but declined thereafter, likely attributed to coral bleaching. Recommendations include (1) focused attention on key contributors to the carbonate budget (e.g. acroporids), and (2) improving our understanding of bioerosion processes, including spatial variability and quantifying rates for key contributors beyond the parrotfishes.

3- Microbial communities on the GBR: links to water quality parameters that indicate healthy reef systems – Pelagic microbial communities were characterised across the GBR to identify: a) how they are influenced by input of riverine floodwaters and plumes on inshore reefs, and b) how they change along inshore to offshore gradients. Pelagic microbial communities respond in a deterministic way to environmental fluctuations and drivers. Specifically, the Prochlorococcaceae:Synechococcaceae relative abundance ratio provides an indicator of the contribution of nutrient enrichment in GBR waters, which seems sensitive at spatial and temporal scales. Microbial community dynamics can be modeled to determine how ecosystem functions predict changes in reef health. Establishment of microbial baselines through a network of microbial observatories spanning key habitats along gradients on the GBR would enable a robust assessment of the microbial contribution to reef function and health.

4- Spatial patterns and functional impacts of recreational spearfishing on the GBR – While often considered negligible compared to other fishing practices, the highly selective method adopted by spearfishers (i.e. targetting large individuals) can result in specific ecological consequences. Surveys of spearfishers active on the GBR were used to assess spatial preferences and key target species among spearfishers from Bundaberg (south) to Cooktown (north). Piscivorous coral trout (*Plectropomus* spp.) were the preferred targets, but with interesting results for nominally herbivorous parrotfishes (*Chlorurus microrhinos*, *Scarus ghobban*) and invertivorous tuskfishes (*Choerodon* spp.). A demographic analysis of fishery impacts on key herbivores and tuskfishes would be desirable for the GBR.

5- Juvenile CoTS ‘in waiting’: the missing link in population and connectivity models – CoTS begin their benthic life stage as small herbivorous juveniles, with a shift in diet to become coral predators as they grow. Interestingly, juvenile CoTS can remain in the herbivorous stage for several years in aquaria, but this life stage is poorly characterised *in situ*. Juveniles were raised in aquaria on a range of algal diets for 4.5 months. Their ability to subsist on biofilm alone suggests that juvenile CoTS may be able to survive for extended periods of time in coral rubble habitats prior to the switch to coral food. This may create a time lag across the larval settlement–juvenile–outbreak CoTS life history, which is currently uncaptured in population models and size-age relationships. Early warning signals for outbreaks may exist in the benthos through juvenile reserves, but where these exist remains unknown.

1.0 INTRODUCTION

Coral reefs have changed profoundly over recent decades due to cumulative impacts from local (e.g. fisheries, water quality) and global (i.e. ocean warming) stressors. While continued exposure to extreme events could stimulate some level of adaptive capacity and resilience in surviving cohorts (Maynard et al. 2008, Hughes et al. 2019b), reef recovery and persistence will be variable at local and global scales (Guzman and Cortes 2007, Graham et al. 2011b, Glynn et al. 2015, Bento et al. 2016, Mumby et al. 2016, de Bakker et al. 2017, Mellin et al. 2019). It is estimated that up to 90% of coral reefs may disappear as soon as 2050 if global emissions are not curbed in line with improved local management strategies to resolve mounting pressures (Wilkinson 2006, Albright et al. 2016a, Schleussner et al. 2016, van Hooidonk et al. 2016, Harvey et al. 2018, Hughes et al. 2018a).

High biodiversity systems, like coral reefs, are suggested to have broader systemic resilience to environmental perturbation through increased trait diversity and functional redundancy (Boucher 1997, Bellwood et al. 2004, Hooper et al. 2005, Micheli and Halpern 2005, Ferrigno et al. 2016, McWilliam et al. 2018). Species-poor ecosystems may be particularly susceptible to collapse following the loss of just a few key species (Mumby et al. 2008). One of the foremost examples of this exists for Caribbean reefs, where loss of a predominant grazing herbivore (a diadematid sea urchin) resulted in undesirable algal growth and catastrophic, largely irreversible, phase shifts towards macroalgal and cyanobacterial reefs (Hughes 1994, Gardner et al. 2003, Mumby et al. 2006a, Brocke et al. 2015, de Bakker et al. 2017). Even in high diversity ecosystems, the loss of key species can result in ecological changes that impair critical functions and services, including resource use, fisheries productivity and carbonate accretion (McClanahan et al. 2002, Kennedy et al. 2013, Holbrook et al. 2015, Rogers et al. 2015, Mora et al. 2016, Harborne et al. 2017, Mumby 2017, Rogers et al. 2018a, Clements and Hay 2019).

Coral reefs are complex ecosystems with a great diversity of players including microbes, algae, corals, sponges, invertebrates and fishes (Reaka-Kudla 1997, Fisher et al. 2015). While high biodiversity is considered the hallmark of healthy and productive ecosystems, many studies highlight the critical importance of a small subset of species in maintaining ecosystem functioning through a range of positive interactions (Halpern et al. 2007, Naeem et al. 2012, Shaver and Silliman 2017, Renzi et al. 2019), their broad distributions and high abundances, or high degree of specialisation with limited functional redundancy (Bellwood et al. 2004, Hooper et al. 2005, Mouillot et al. 2013). Corals, for example, are major contributors to calcification and reef building, but some species contribute disproportionately to coral recovery and coverage (e.g. *Acropora*) (Johns et al. 2014, Ortiz et al. 2014, Ortiz et al. 2018), while others contribute more to rates of reef building in high sediment regions (e.g. *Turbinaria*) (Browne 2012, Morgan et al. 2016). Beyond corals, microbial organisms underpin many ecosystem processes (Glasl et al. 2018a), benthic invertebrates and cryptobenthic fishes are at the foundation of fisheries productivity (tertiary production) (Depczynski and Bellwood 2003, Kramer et al. 2015, Brandl et al. 2018, Brandl et al. 2019), planktivorous fishes partition their feeding activity into different reef zones (Hamner et al. 1988, Holzman et al. 2005, Motro et al. 2005, Yahel et al. 2005), some herbivorous fishes are more important in controlling fouling macroalgae (Bellwood et al. 2004, Mumby et al. 2006a, Hoey and Bellwood 2009, 2010b, Mumby et al. 2014, Loffler et al. 2015a), and so on. This means that biodiversity conservation, which is often based on broad scale habitat protection through marine reserves (Maynard et al. 2016, Mellin et al. 2016), could enhance effectiveness by augmenting its strategy to include specific provisions for key species (Halpern et al. 2007, Naeem et al. 2012, Shaver and Silliman 2017, Richards and Day 2018).

While a wealth of empirical data and literature compilations address ecosystem functioning on coral reefs, they are typically targeted at specific taxa, processes and/or stressors. What is lacking in this era of review science is a comparative assessment across the diverse range of taxonomic and functional groups of coral reef species to synthesise available knowledge to inform science and management. Given global degradation of many coral reefs, it is not only timely but imperative to ask whether or not key ecosystem functions – and the species that support them – are being adequately protected. To date, the paradigm in ecosystem restoration has been to reduce the negative effects of physical stress, human impacts and/or species interactions (e.g. invasions), but explicit recognition of positive species interactions is critical to conservation success (Halpern et al. 2007, Mumby and Steneck 2008, He et al. 2013, Shaver and Silliman 2017, Thomsen et al. 2018, Renzi et al. 2019, Zhang and Silliman 2019). Identifying and protecting species of particular functional importance is essential for the conservation of coral reefs, and in providing targeted information to safeguard species, biodiversity and functioning in a future ocean (McClanahan et al. 2014, Rogers et al. 2015, Richards and Day 2018).

Here we employed expert elicitation coupled with an extensive compilation of the literature to create a hierarchy of key coral reef taxa – from microbes to top predators – that support reef functioning. As a particularly data-rich system, our synthesis is focused on the Great Barrier Reef (GBR), Australia. We provide a framework to assess taxa based on their contributions to ecosystem functioning through a process-based assessment, and to examine their perceived vulnerability and manageability to improve the holistic management of GBR species, values and processes. Specifically, we assessed which taxa drive processes that maintain a healthy reef, and address whether or not management is considered a priority (i.e. *are they vulnerable?*) or feasible (i.e. *can they be managed?*). Elicitation results were used to guide compilations of the literature for key taxa outlined at various levels of ecosystem processes, functions and stressors, including combined total rankings. This includes case-specific compilations for key species (tabular corals, branching corals, microorganisms, crustose coralline algae (CCA), turf algae, herbivorous parrotfishes, crown-of-thorns starfish (CoTS)), and novel candidates (chemoautotrophic microbes, cleaner wrasse, bivalves, coral-associated decapods, detritivorous fishes).

Scientific certainty was addressed so that data-deficient groups were not overlooked in our analysis with the objective to highlight novel cases. We also present five case studies to address current gaps in knowledge that limit our understanding at various levels of ecosystem functioning on the GBR, including (1) invertivory, (2) the carbonate budget, (3) microbial links to water quality, (4) recreational spearfishing, and (5) the CoTS juvenile life stage. We conclude by outlining the desired outcomes for both science and management to support and protect key functional species on coral reefs, using a framework that can be expanded to guide future integrated and holistic management.

1.1 Ecosystem functioning on coral reefs

Ecosystem functioning refers to the range of natural processes and components that contribute to the production and exchange of energy and materials (Srivastava and Vellend 2005, Pacala and Kinzig 2013, Bellwood et al. 2019), sustain and fulfil life (Daily et al. 1997), and provide goods and services for human use (de Groot et al. 2002). Despite the diversity of interpretations in the literature, the overarching typology of ecosystem function considers the natural properties and processes that work to support an ecosystem, and their direct or indirect anthropogenic benefits (de Groot et al. 2002, Jax 2005, Srivastava and Vellend 2005, Farnsworth et al. 2017). In the marine environment, ecosystem functioning depends on interactive physical (e.g. waves, currents, sediment, light), chemical (e.g. nutrient cycling, ocean pH, salinity) and ecological (e.g. primary production, herbivory, predation, calcification) processes. While we recognise that physical and chemical processes are essential components of coral reefs, a species' contribution to ecosystem functioning is inextricably linked to its ability to perform ecological processes (Figure 1). To identify species – or functional groups of species – that are disproportionately important to the maintenance of coral reef functioning, this review focused on key ecological processes.

We examined species' contributions to a range of ecological process that scale up to support habitat (e.g. reef accretion) and production (e.g. fisheries) functions (Figure 1). Together, these form the foundations of coral reefs through (1) habitat provisioning and the stocks of energy and material (e.g. calcification, bioerosion), and (2) the production and fluxes of energy and materials across ecosystem networks (e.g. trophic transfers, photosynthesis, nutrient uptake) (de Groot et al. 2002, Srivastava and Vellend 2005, Kennedy et al. 2013, Harborne et al. 2017, Bellwood et al. 2019). These effectively incorporate the construction (and destruction) of the biogenic reef structure – the fundamental framework of coral reefs (Wild et al. 2011) – and trophic pathways and interactions across the food web (Figure 1). Habitat and production functions encapsulate the most important goods and services provided by coral reefs, scaling up to benefit coastal protection and fisheries production (Moberg and Folke 1999, Harborne et al. 2017). Many of these ecological process and functions are attributes of Outstanding Universal Value (OUV) and contribute to the values and integrity of coral reefs, including for the World Heritage property of the GBR (GBRMPA 2014c).

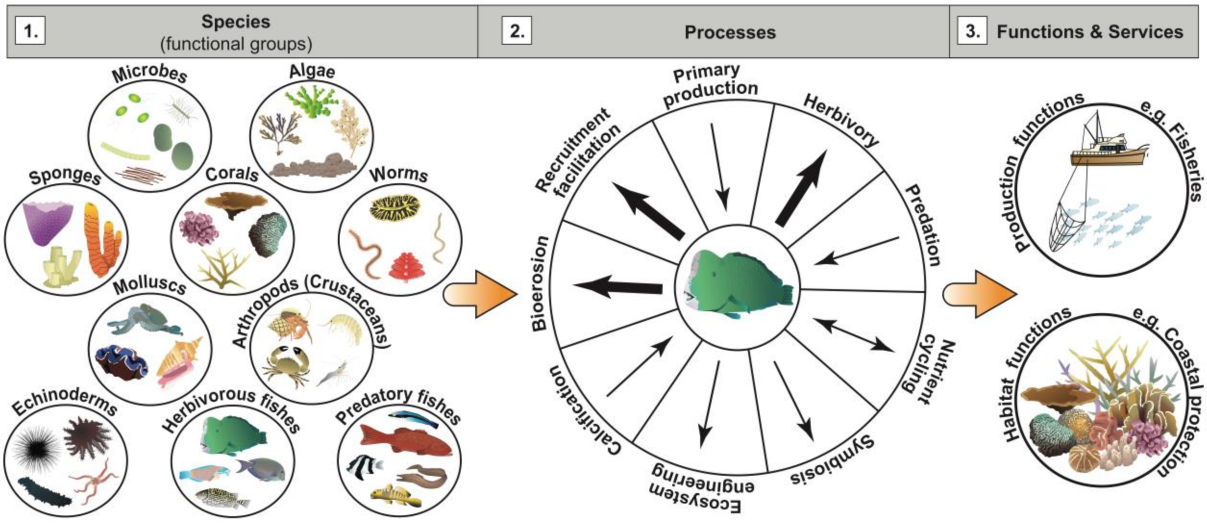

Figure 1: Conceptual diagram outlining levels of natural components in coral reef ecosystems; (1) individuals (functional groups), (2) their contributions to ecosystem processes, and (3) links to ecosystem functions and services. Black arrows represent estimated contributions to each process, i.e. high (bold) or low (thin) contributions; positive (outwards) or negative (inwards) influences. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

While a wealth of empirical data and literature reviews address ecosystem functioning on coral reefs, they are typically targeted at specific taxonomic groups, processes and/or stressors. What is lacking in this era of review-science is a comparative assessment across the diverse range of taxonomic and functional groups of coral reef species to synthesise available knowledge to inform science and management. It has never been more important to ask whether or not key ecosystem functions – and the species that support them – are being adequately protected. Identifying and protecting species of particular functional importance is essential to the conservation of coral reefs, and in providing targeted information to safeguard species, biodiversity and functioning in a future ocean (McClanahan et al. 2014, Rogers et al. 2015, Richards and Day 2018).

1.2 Threats challenging coral reef functioning

The biology and ecology of coral reef species are generally well understood, but information on reef ecosystem functioning is largely weighted towards hard (scleractinian) corals and reef fishes (Bellwood and Choat 1990, Bellwood et al. 2004, Munday et al. 2009b, Stuart-Smith et al. 2013, McClanahan et al. 2014, Pratchett et al. 2015, Bourne et al. 2016, Bellwood et al. 2017, Konow et al. 2017, Bierwagen et al. 2018, Brandl et al. 2018, McWilliam et al. 2018, Bellwood et al. 2019), overlooking many other species important to a functioning ecosystem. A growing number of studies provide comprehensive reviews of the significance of alternative groups to reef functioning, including for microorganisms (Mouchka et al. 2010, Charpy et al. 2012, Garren and Azam 2012b, Thompson et al. 2015, Hernandez-Agreda et al. 2017), sponges (Wulff 2006, Bell 2008, Maldonado et al. 2015, Pawlik et al. 2018), algae (McCook et al. 2001, Tribollet 2008, Nelson 2009, Connell et al. 2014), phyto- and zoo-plankton (McKinnon et al. 2007, Ferrier-Pages et al. 2011), echinoderms (Birkeland 1989, Pratchett et al. 2014, Purcell et al. 2016a), and coral-associated invertebrates (Castro 1976, Stella et al. 2011b).

Some also review specific ecological processes on coral reefs, such as bioerosion (Hutchings and Kiene 1986, Sammarco 1996, Tribollet 2008), calcification and carbonate accretion (Allemand et al. 2011, Tambutte et al. 2011, Bertucci et al. 2013, Kennedy et al. 2013), herbivory (Cvitanovic et al. 2007, Mumby 2009a, Bonaldo et al. 2014, Puk et al. 2016), foraging associations (Lukoschek and McCormick 2000), cleaning symbioses (Cote 2000, Vaughan et al. 2017), and certain modes of predation like corallivory (Cole et al. 2008, Rotjan and Lewis 2008, Konow et al. 2017, Rice et al. 2019). As coral reefs degrade, a growing body of literature also draws focus on the environmental stressors threatening biological processes and reef functioning, including climate change (Hoegh-Guldberg et al. 2007, Atkinson and Cuet 2008, Baker et al. 2008, Pratchett et al. 2008b, Przeslawski et al. 2008, Graham et al. 2011b, Harley et al. 2012, Andersson and Gledhill 2013, Munday et al. 2013b, Albright et al. 2016a, Anthony 2016, Hoey et al. 2016a, Camp et al. 2018a, Espinel-Velasco et al. 2018, Harvey et al. 2018), storms and cyclones (Harmelin-Vivien 1994), water quality (Fabricius 2005, McKinley and Johnston 2010, Brodie et al. 2012, Browne et al. 2012, Erftemeijer et al. 2012, Wear and Thurber 2015, Hairsine 2017), and stressors more generally (Wilkinson 1999, Brodie and Waterhouse 2012, Ban et al. 2014b, Uthicke et al. 2016, Harborne et al. 2017, Richards and Day 2018), but with the majority still focused on corals and fishes.

Due to a growing number of local and global stressors, irreversible shifts in the ecological processes that maintain coral reefs are already measurable, including for those that support habitat and production functions (De'ath et al. 2012, Cinner et al. 2016, Cinner et al. 2018, Hughes et al. 2018b, Richardson et al. 2018, Rogers et al. 2018a). Some examples include changes to processes that support: (1) calcification and bioerosion rates, which impacts reef community composition, reef accretion and the net carbonate budget (Silverman et al. 2012, De'ath et al. 2013, Dove et al. 2013, Silverman et al. 2014, DeCarlo et al. 2015, Albright et al. 2016b, Perry and Harborne 2016, Manzello et al. 2017, Schönberg et al. 2017, Albright et al. 2018, Cyronak et al. 2018); (2) herbivory and algal growth that results in phase shifts away from coral towards algal-dominated reefs (Ceccarelli et al. 2006, Hughes et al. 2007b, Mumby 2009b, Burkepile and Hay 2010, Cheal et al. 2010, Hoey and Bellwood 2011, Bellwood et al. 2012b, Adam et al. 2015a); (3) impaired recruitment opportunity and success, which limits reef growth and persistence across generations (Doropoulos et al. 2012b, Doropoulos and Diaz-Pulido 2013, Hughes et al. 2019a); and (4) antagonistic population outbreaks of predatory species with impacts on live coral cover (Endean 1982, Brodie and Waterhouse 2012, De'ath et al. 2012, Baird et al. 2013, Pratchett et al. 2014, Hoey et al. 2016b). Such shifts in coral reef ecosystems will continue to have serious repercussions on ecosystem resilience and recovery, and in how we shape current and future management practices (Knowlton 2012, Uthicke et al. 2016, van de Leemput et al. 2016, Osborne et al. 2017, Stuart-Smith et al. 2018). With this in mind, we provide a framework to rationalise priority species and processes that work to support coral reefs at their highest levels of functioning in a changing environment.

1.3 Setting the scene: The Great Barrier Reef

Comprised of ~3000 individual reefs, the GBR is possibly the most complex natural system in the world (Knowlton 2012, Day 2016). This coral reef ecosystem supports many high-value sectors, including trade, fisheries and tourism, estimated to provide ~AU$6 billion to the Australian economy, annually (McCook et al. 2010, Stoeckl et al. 2011, Brodie and Waterhouse

2012, Knowlton 2012, O'Mahoney et al. 2017). Due to its global and ecological significance, the GBR has been managed as a national Marine Park since 1975 (GBRMP Act 1975), and in 1981, became the first coral reef to be granted World Heritage status by the United Nations Educational, Scientific and Cultural Organisation (UNESCO). Management has since focused on resource use with a particular devotion to the preservation of biodiversity (McCook et al. 2010) to maintain its OUV. The GBR Rezoning Plan (2004), implemented in July 2004, increased the area of the Marine National Park (Green) Zone from <5% to 33% of the total GBRMP area, enhancing protection of reefs from activities including shipping, fisheries and recreation (Fernandes et al. 2005, Day 2016). This scheme continues to demonstrate significant contributions to the management of biodiversity, ecosystem resilience and socioeconomic values, and so the GBR is often hailed for its gold standard for reef management (McCook et al. 2010, Day 2016).

Given the size of the GBR, spatial confines in jurisdiction have created complexity to ecosystem-based management on the reef, particularly involving land-based riparian and coastal activities (e.g. water quality, riverine discharge, port development) (Brodie and Waterhouse 2012, Day 2016). In addition, parts of the World Heritage Area of the GBR fall outside the Marine Park, further complicating jurisdictional boundaries and management (GBRMPA 2014c). While biodiversity conservation has historically been considered pivotal to ecosystem-based management of the GBR through successes in marine park zoning (Fernandes et al. 2010, McCook et al. 2010, Day 2016), it is increasingly necessary to target management provisions towards key functional taxa to support ecosystem functioning and stability in a future ocean (Richards and Day 2018).

2.0 METHODOLOGY

2.1 Expert elicitation

Expert elicitation can provide valuable insight and information to inform science and decision-making, particularly when there are significant limitations and inconsistencies in scientific knowledge (Morgan et al. 2001, Knol et al. 2010, O'Leary et al. 2011, Polasky et al. 2011, Runge et al. 2011, Martin et al. 2012, Ban et al. 2014b, Morgan 2014, Rogers et al. 2015). As knowledge of reef functioning is largely weighted towards certain taxonomic and functional groups (e.g. corals and fishes; Bellwood et al. 2004, Stuart-Smith et al. 2013, Bellwood et al. 2017, Bierwagen et al. 2018, McWilliam et al. 2018, Bellwood et al. 2019), we employed expert elicitation to facilitate a comparative assessment of the functional roles of coral reef species across a diversity of taxa – from microbes to top predators.

Experts were selected from a literature search and using background knowledge of coral reef ecologists currently involved in research in the focal region, the GBR. Using a snowball approach, experts were invited to participate in the project ensuring a multidisciplinary assemblage was represented. A total of 18 experts were directly involved in project development and/or the elicitation process. This size pool is within the lower (n=3; Clemen and Winkler 1999) and upper (n=60; de Franca Doria et al. 2009) ranges for the expert elicitation process (Ban et al. 2014b).

2.2 Project and survey development

In a two-day workshop that convened our panel of GBR experts (Appendix 1), we identified 70 functionally and taxonomically distinct groups of marine species common on the GBR (Figure 2). Functional groups remained broadly defined, but were occasionally refined to individual species with explicit and well-documented roles (e.g. CoTS). Subsequent in-depth examination was intended for highly ranking groups at later stages of the project through targeted literature searches. Some taxa were excluded (e.g. marine reptiles, mammals, seabirds) as these groups are often rare on the GBR and/or already intensively addressed and managed (see: Stoeckl et al. 2010b, Birtles et al. 2014, GBRMPA 2014b, c, Richards and Day 2018, Risch et al. 2019). Many species within these taxa are of OUV and are critical to the way the World Heritage Convention is implemented on the GBR (GBRMPA 2014c), with key social and economic value, particularly regarding tourism (Stoeckl et al. 2010a, Stoeckl et al. 2010b). The exclusion of these species does not devalue their contributions to a functioning ecosystem (e.g. Savage 2019) or their necessity to be considered in context of social, cultural and economic values for holistic management (GBRMPA 2014a, c).

As the world's largest coral reef ecosystem, the GBR is an amalgamation of bioregions with their own, often unique, functional dynamics (McCook et al. 2010, Day 2016) and governance (Day 2002, Brodie and Waterhouse 2012, Morrison 2017). Due to the sheer size and diversity of the GBR, our expert panel chose to focus attention on the functioning of classical reef slope and reef crest habitats (Appendix 1), as these are typically the most diverse and coral-rich ecosystems that support the greatest range of services (Mumby et al. 2008, Harborne et al. 2017). This refined approach acknowledges the exclusion of other important and interconnected biomes of coral reefs (e.g. mangroves, seagrass meadows, inter-reefal areas) (GBRMPA 2004, 2014b, c, van de Koppel et al. 2015), including deep (or mesophotic) reefs (Bridge et al. 2012, Harris et al. 2013, Turner et al. 2017), but was employed to ensure a targeted research design to inform the holistic management of GBR species, values and processes. There is the opportunity to build on the current framework of biological functioning in future work to include other important coral reef biomes, and give greater consideration to social, cultural and economic values.

Figure 2: Taxonomic and functional groups considered in this assessment. Examples in parentheses. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/) and (Hutson et al. 2018). Note: (1) dinoflagellate Zooxanthellae are not considered part of the 'phytoplankton', (2) it is understood that foraminifera are not corals, (3) zooplankton includes groups outside of the Crustacea (e.g. larvaceans, chaetognaths, salps).

A methodology to assess functionally important species was developed by our scientific panel during the workshop (Appendix 1; Figure 3). Outcomes were used to construct annotated online surveys that operated under three main criteria:

1- **Functional importance**: a process-based assessment of species' contributions to ecosystem processes and functions.

Question: Who contributes most to ecosystem functioning on the GBR?

2- **Vulnerability**: an assessment of the sensitivity and exposure of species to current and near-future stressors, and their likely recoverability.

Question: What species are most vulnerable on the GBR, and do they require protection?

3- **Manageability**: an assessment of the probable effectiveness and feasibility of a management intervention in context of biological functioning.

Question: Is management feasible for important species?

Surveys to address these criteria were developed online using the Surveymonkey platform, which were open for several weeks (July–August 2018). Surveys were targeted at our expert panel, but responses remained anonymous. A low-range scoring system (e.g. none/low/high) was employed to reduce ambiguity in responses (see Tables 2, 5, 6), as qualitative words and broad scoring ranges are prone to subjectivity and uncertainty (Morgan et al. 2001, Morgan 2014). Space for comments and feedback was provided throughout the surveys (Appendix 2), which is outlined as a critical elicitation process to ensure expert knowledge is accurately captured and interpreted (Martin et al. 2012). A total of 16 survey responses were completed across our taxonomic and functional groups, with equal-weighted averages taken across expert responses. Group averages are simple, but can be effective in producing estimates of elicitation (Martin et al. 2012). Scores were checked and calibrated against the literature and empirical data (where possible) to reduce subjectivity and bias. Scoring criteria are explicitly outlined for each assessment (Figure 3; see Tables 2, 5, 6).

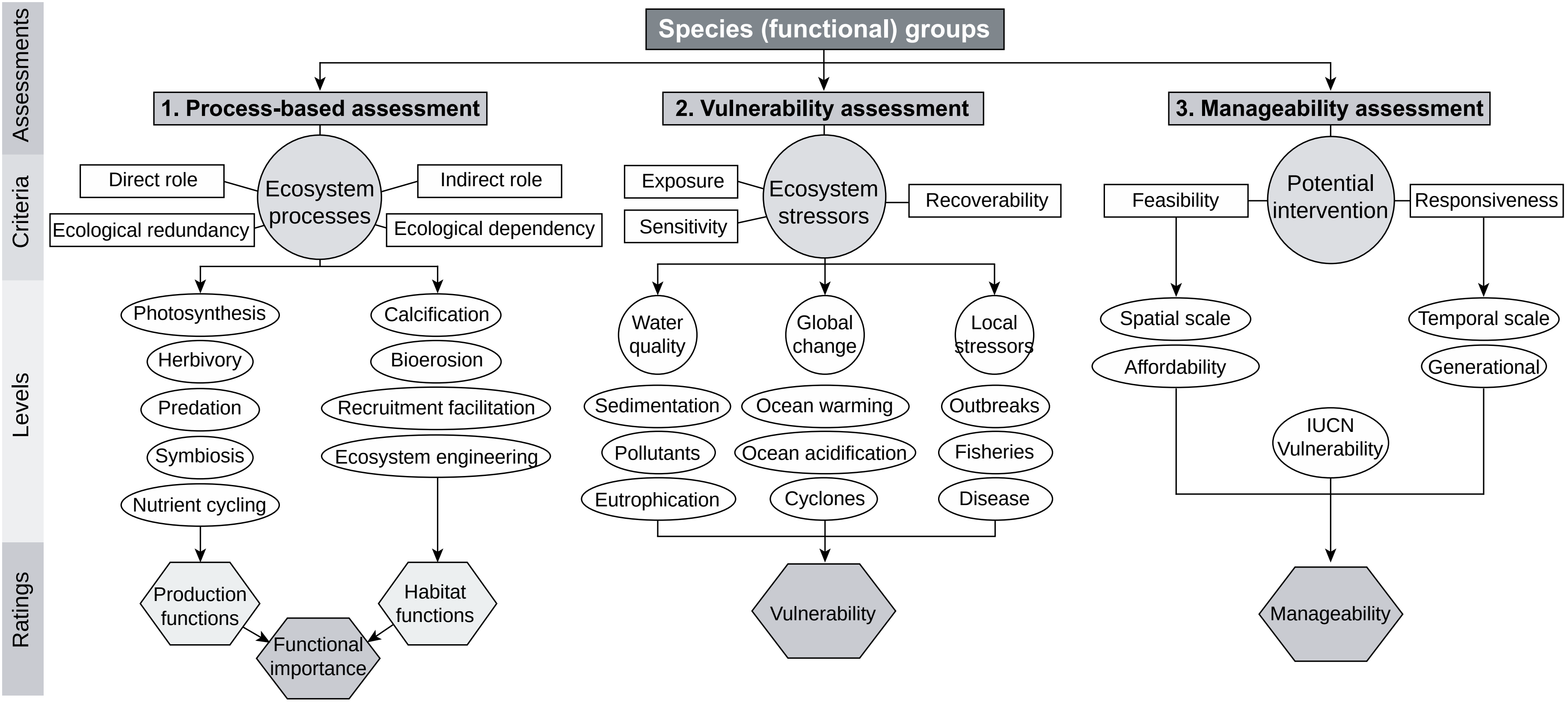

Figure 3: Framework outlining the assessment criteria employed to identify and rate priority taxa in support of ecosystem functioning based on their (1) functional importance (process-based assessment), (2) vulnerability, and (3) manageability.

2.3 Scoring criteria

2.3.1 Functional importance: a process-based assessment

Contributions of organisms to ecosystem processes (e.g. calcification, bioerosion, herbivory, predation; Figure 1) drive and support a range of ecosystem functions (e.g. reef accretion, habitat complexity, energy/trophic transfers) and services (e.g. coastal protection, fisheries, tourism). The first stage of our surveys elicited experts to score the contribution of 70 taxonomic and functional groups of coral reef species (Figure 2) to nine ecosystem processes considered critical to ecosystem functioning (Table 1; Figure 3). These processes were selected due to their broad representation in the literature and current consideration in management reports for the GBR (GBRMPA 2014b). These nine processes scale up to support habitat and production functions (Figure 1), which are fundamental to the future of coral reefs in terms of reef construction, trophic pathways and ecosystem services (de Groot et al. 2002, Harborne et al. 2017). All processes and functions were considered equally important to ensure that all were represented at their highest levels; i.e. no process was weighted as more important to a functioning ecosystem.

Table 1: Ecosystem processes that underpin habitat and production functions on coral reefs.

Production	***Habitat***
Primary production	Calcification
Herbivory	Bioerosion
Predation	Ecosystem engineering
Nutrient cycling	Recruitment facilitation
Symbiosis	

Species groups were scored based on their direct and indirect contributions to each process (Figure 3; Table 2). This was intended to capture both the immediate contribution of an individual to a process (e.g. hard corals to calcification) and, equally important, their indirect facilitation and/or mediation of the processes (e.g. algae to herbivory), as indirect effects are fundamental to the complexity of ecosystem functioning and to conservation outcomes (Wootton 1994, Wootton 2002, Dulvy et al. 2004, Jordán et al. 2008, Bergstrom et al. 2009, Ritchie and Johnson 2009). Species groups were also scored based on their ecological redundancy and dependency on a per-process basis (Figure 3; Table 2), as species interactions and functional diversity can highlight critically important species and functions (Petchey and Gaston 2002, Mouillot et al. 2013, Mouillot et al. 2014). Expert scores were compiled for these four contribution dynamics, and average scores were calculated for each functional group–ecosystem process combination. Finally, experts were elicited to rate their level of confidence (i.e. certainty; Table 2) in their scores for each functional group. These scores for certainty (or uncertainty) were used *post hoc* to weight final scores for management recommendations.

Scores for direct (D) and indirect (I) contributions were combined as a measure of the magnitude (M) of the role of each functional group to each ecosystem process, using the equation:

$$M = (D + I)^2$$

Table 2: Criteria used to score taxa based on their contributions to nine key ecosystem processes on the GBR.

Dynamic	Category	Score	Notes
Direct contribution	None	0	No direct role in this process
	Low	1	Directly contributes to this process but is not a key player
	High	2	Ecologically significant contribution to the process
Indirect facilitator/ mediator	None	0	No real indirect effect on others performing this process
	Low	1	Some level of impact on the process; competition, mutualism
	High	2	Specific impact; key predator, top-down/bottom-up control
Redundancy	None	0	Critical and specific in this space, or in mediating it
	Low	1	Some level of replaceability, similar species performing
	High	2	Replaceable in its functional role driving this process
Dependency	None	0	Self-sufficient in performing the process
	Low	1	Some level of dependence to complete this functional role
	High	2	Reliant on other organisms to complete this process
Certainty	Low	0.25	Little empirical work and expert knowledge
	Medium	0.50	Some empirical work and expert experience
	High	0.75	Extensive work and/or experience

This equation worked under the assumption that direct and indirect effects were equally as important to ecosystem processes and functions. Scores were squared to elevate organisms that scored highly for any given process, and to amplify even the slightest differences among expert responses. Scores for magnitude, redundancy and dependency were then categorised and ranked for each species–process combination (Table 3). For magnitude, the top and bottom 33-percentile of scores were classed as ‘high’ and ‘low’, respectively, with the remaining scores classed as ‘intermediate’ (Table 3). Thus, rankings were relative to the range of scores within each process. We worked under the assumption that magnitude was the most important score for determining the functional importance of species groups; i.e. how much they contribute (directly or indirectly) to the process or function outweighed their ecological redundancy and/or dependency (Table 3). Examples of ‘high’ magnitude scores existed in algal turfs to primary production, branching and tabular corals to calcification, and piscivorous fishes to predation. Examples of ‘low’ magnitude scores were worms to primary production, and piscivorous fishes to calcification.

Redundancy and dependency were used as mediators of scores for magnitude. Species with ‘low’ (or no) ecological redundancy (average scores ≤1) were considered more important for targeted management (Table 3), as this suggests specialisation and irreplaceability in their roles (Hooper et al. 2005, Jain et al. 2014, McWilliam et al. 2018). Species with ‘high’ redundancy (average scores >1) were deemed replaceable and were down-weighted (Table 3). For example, triton snails had low redundancy for the predation process, as they are essential predators of CoTS, while other predatory molluscs were considered to have higher redundancy in this process. Species groups with ‘low’ dependency (average scores ≤1) were considered more important than those with ‘high’ dependency (Table 3), under the assumption that they can effectively perform their roles exclusive of others and are thus better candidates for targeted management. Conversely, dependent species were down-weighted (Table 3), as their ecological performance requires inclusion of other species with implications for management efficacy.

Table 3: Ranking scheme for functional groups based on their magnitude, redundancy and dependency in context of nine key ecosystem processes on the GBR. H=high; M=intermediate; L=low.

Rank	Magnitude (D + I)^2	Redundancy	Dependency
1	H	L	L
2	H	L	H
3	H	H	L
4	H	H	H
5	M	L	L
6	M	L	H
7	M	H	L
8	M	H	H
9	L	L	L
10	L	L	H
11	L	H	L
12	L	H	H

Ranks were determined on a per-process basis. Within this scoring scheme, a functional group with the highest magnitude of contribution to an ecosystem process but the lowest ecological redundancy and dependency would rank the highest; an 'essential provider'. Conversely, a low-contributing group with high redundancy and dependency would rank the lowest; a 'leech'. Total functional importance *(FI)* was then calculated across the *i* = 9 process rankings using a sum of squares equation:

$$FI = \sum_{i=1}^{9} (13 - x)^2$$

where x is the rank score for each process. This ensured that highly ranked functional groups (i.e. *FI* = 1) resulted in higher final scores, and that those ranked highly for just one process were recognised. Final vales for *FI* were square root transformed to normalise data. *FI* was calculated in the same manner for habitat and production functions separately. Scores for expert scientific certainty were examined *post hoc*. Final values for *FI* with high certainty were considered top priority, while scores that were largely uncertain were up-weighted under precautionary principles.

2.3.2 Assessing the vulnerability of GBR species

Ecosystems are considered healthy if they are able to maintain (or recover) structure and functioning in the face of external pressures (Costanza and Mageau 1999). To understand potential threats to functioning on the GBR, pertinent current and near-future (2050 outlook; (DEE 2015, GBRMPA 2018b)) stressors were workshopped (Table 4). Parallel to scoring functional importance, experts were elicited to score the 70 functional groups (Figure 2) based on their vulnerability to nine critical stressors (Table 4; Figure 3), in line with previous projects, elicitation processes and reviews (Ban et al. 2014a, Ban et al. 2014b, Uthicke et al. 2016, Harborne et al. 2017). The IPCC Vulnerability Framework (IPCC 2007) formed the basis of this assessment, which uses the sensitivity and exposure of an individual, as well as its potential to recover, to calculate its total vulnerability (Figure 4).

Table 4: Nine pertinent stressors used here to assess species vulnerabilities on the GBR.

Water quality	***Climate change***	***Other***
Sedimentation	Ocean warming	Disease
Eutrophication	Ocean acidification	Fisheries
Pollutants (e.g. pesticides)	Cyclones / storm events	Population outbreaks

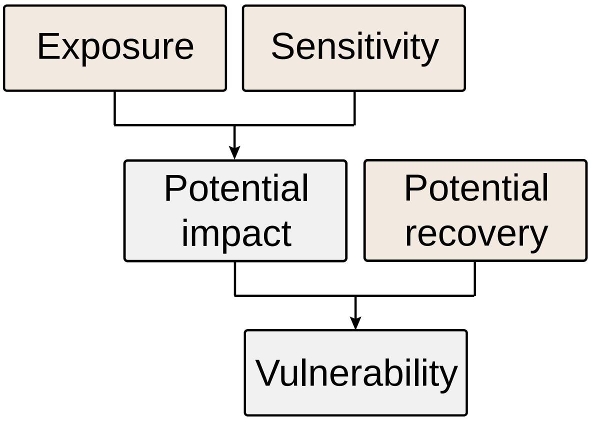

Figure 4: IPCC Vulnerability framework (IPCC 2007) used to determine the vulnerability of functional groups to potential stressors.

Experts scored species groups based on their known (and anticipated) sensitivity, exposure and recoverability to each of the nine pertinent stressors (Figure 3). Sensitivity (*S*) was scored across a range of positive to negative scores (Table 5), as some species may benefit from a particular stressor (e.g. ocean warming on algal growth, herbivore abundance due to overfishing of predators), while others may be severely impacted (e.g. calcification due to ocean change, sea cucumbers due to overfishing). However, since our focus was to identify vulnerable species for management, scores that suggested positive effects from a stressor ($S > 0$) were counted to have no effect (i.e. not sensitive; $S = 0$). Exposure (*E*) was considered generally for typical reef habitats (e.g. reef crest, reef slope), but was assessed differently for inner reefs and offshore regions on the GBR as some stressors, such as those related to water quality, are often more significant on inshore reefs proximal to terrestrial influence (Devlin and Brodie 2005, Wooldridge et al. 2006, Brodie and Waterhouse 2012, Brodie et al. 2012, Kroon et al. 2012, Waterhouse et al. 2012, Fabricius et al. 2014, Lam et al. 2018, MacNeil et al. 2019, Mellin et al. 2019).

Potential impact (*PI*) was calculated from average expert scores for each stressor–taxa combination, using the equation:

$$PI = (S \times E)^2$$

This calculation assumes that sensitive taxa that are not exposure to a stressor (*E* = 0) are not vulnerable, as for groups that are exposed but not at all sensitive (*S* = 0). *PI* was calculated for each of *i* = 9 stressors, and total vulnerability (*V*) was then calculated across all stressor values, using the equation:

$$V = \frac{\sqrt{\sum_{i=1}^{9} PI}}{PR}$$

Table 5: Criteria used to score the vulnerability of functional groups to nine pertinent stressors on the GBR.

Dynamic	Category	Rank	Notes
Sensitivity (S)	Sensitive	-2	Highly sensitive to the stressor
	Slight impact	-1	Partial negative impacts
	No impact	0	Not affected
	Slight gain	1	Partial benefit from stressor
	Beneficial	2	Stressor is highly beneficial
Exposure (E)	None	0	Not exposed to the stressor
	Low	1	Low exposure, low likelihood of exposure
	High	2	Highly exposed, highly likely to be exposed
Potential Recoverability (PR)	Low	0.25	Unlikely to recover before next event
	Medium	0.50	Some level of recoverability
	High	0.75	Highly likely to recover before next event
Certainty	Low	0.25	Little empirical work and expert knowledge
	Medium	0.50	Some empirical work and expert experience
	High	0.75	Extensive work and/or experience

This framework ensured that species with high potential recovery (*PR*) were down-weighted under the assumption that management would be less necessary for species likely to recover. Conversely, *V* would be greater for species with low *PR* under the assumption that they would require greater management attention to improve recovery chances. Experts also scored the certainty of their scores for each functional group here (Table 5), which was used *post hoc* to address the validity of vulnerability scores. Final rankings suggesting high vulnerability with high certainty were considered the most critical to address. Vulnerable species groups with a low-rated level of certainty could also be examined under precautionary principles so that data deficient groups were not overlooked.

Final scores for *V* and *FI* were combined to identify key species where both factors were high. The relative impact (*Imp*) of our nine stressors was also calculated by multiplying *V* and *FI* for each species-process-stressor combination;

$$Imp_{species} = V_{stressor} \times FI_{process}$$

From this template, we could determine the proportional impact that each stressor was considered to have on each functional group at their highest level of functioning. This was also calculated for each ecosystem process-stressor combination. The proportional impact of a given stressor would be weighted higher by taxa scored to be more functionally important. Conversely, the proportional impact of a stressor would be less driven by species with marginal importance. This information could be used to identify combinations of species, stressor and/or processes that may be most critical to address and protect.

2.3.3 Assessing manageability of GBR species

Each functional group was assessed on their relative manageability on the GBR. This assessment was in context of the biological functioning of each species group and was not an assessment of other attributes such as social, cultural and economic values. These additional attributes would be important to consider if building out from the current framework. Experts were elicited to score groups based on their likely (1) responsiveness to management intervention, (2) feasibility of implementation (affordability, geographic scale, etc.) (Figure 3), and (3) availability and attainability of information (i.e. monitorability) (Table 6). Conservation status (e.g. IUCN Red List species) was also considered *post hoc* to address 'at risk' populations (Richards and Day 2018) (Figure 3).

Table 6: Criteria used to score the manageability of functional groups on the GBR.

Dynamic	Category	Rank	Notes
Responsiveness	None	0	Species/populations unlikely to change following intervention
	Low	1	Some response predicted through action
	High	2	Action is likely to have a strong effect on populations
Feasibility	None	0	Broad scale, not affordable, inefficient, impossible
	Low	1	Plausible but likely restricted to some locations/populations
	High	2	Very possible with good scope-cost benefits
Information	None	0	Little existing work, hard to monitor
	Low	1	Some work exists, monitoring possible (but patchy)
	High	2	Extensive work exists, easy to monitor

Manageability (*Mg*) was calculated using average expert scores for responsiveness (*R*) and feasibility (*F*), using the equation:

$$Mg = (R + F)^2$$

Scores for information/monitorability were not included in this calculation under the assumption that functionally important and vulnerable species should be a priority regardless of their ability to be monitored. Thus, the predicted ability for species to respond to management (*R*) and feasibility (*F*) of implementation formed the foundations of our *Mg* calculation. Groups were categorised as a high priority for management if they were in the top 66-percentile of scores for *Mg*, while those in the bottom 33-percentile were deemed lower management priorities. Top-scoring organisms for functional importance, vulnerability and management priority were considered top candidates overall. High scoring groups that were considered lower priority for management would be highlighted as groups that may require innovative approaches.

2.3.4 Incorporating uncertainty

Experts were elicited to score the certainty of their scores for functional importance and vulnerability. Certainty was scored categorically as low (0.25), medium (0.50) or high (0.75) (Tables 2, 5). These scores were used *post hoc* to support our recommendations, particularly when scientific certainty was comparatively high or low. High certainty solidified the merit of our recommendations, particularly for highly ranking functional groups. Under precautionary principles, scores that were uncertain were highlighted so that functional groups that 'slipped through the cracks' in our ranking system due to data deficiencies were not missed. Thus, low-ranked functional groups had the potential to be elevated in their importance and/or vulnerability if certainty was low.

2.4 Identifying knowledge gaps in ecosystem functioning on the GBR

Formal expert elicitation is a structured and transparent methodology that effectively addresses uncertainties in scientific knowledge (Knol et al. 2010, Polasky et al. 2011). In addition to the scoring criteria above, critical knowledge gaps in our understanding of reef functioning were made evident by our expert panel (Appendix 1). These research gaps were developed into five subprojects, which reflect our multidisciplinary expert assemblage. Within the lifetime of this project, teams of researchers addressed these knowledge gaps, which are presented here as case studies that highlight pivotal species (and groups of species) at specific levels of ecosystem functioning to directly inform this project and future research:

Case Study 1 *(Appendix 4):* Invertivory on the GBR: a poorly understood link in the trophic chain.

Case Study 2 *(Appendix 5):* Calculating the carbonate budget for the GBR: coral cover and coralline growth.

Case Study 3 *(Appendix 6):* Microbial communities on the GBR: links to water quality parameters that indicate healthy reef systems.

Case Study 4 *(Appendix 7):* Spatial patterns and functional impacts of recreational spearfishing on the GBR.

Case Study 5 *(Appendix 8):* Juvenile CoTS ‘in waiting’: the missing link in population and connectivity models.

3.0 RESULTS & DISCUSSION

Species of particular functional importance on the GBR are outlined below using an ecosystem process-based assessment for 70 functional groups. Rankings for functional importance are provided at various levels of ecosystem functioning: for each ecosystem process (Section 3.1), for habitat and production functions, and combined overall (Section 3.2). Additional rankings are outlined for species groups based on their perceived vulnerability to nine key environmental stressors (Section 3.3), and for their relative manageability (Section 3.4). Final scores are presented across these three components and weighted to scientific certainty (Section 3.4). Note that all processes and functions were considered equally important to a functioning reef to reflect all species and processes at their highest level of functioning.

3.1 Process-specific functional importance

Top-ranked species groups within each process are outlined in Table 7. Results met expectations in many cases, but due to our assessment of both direct and indirect effects, and ecological redundancy and dependency (Figure 3), we highlight novel and sometimes unexpected players. Scores are supported with case-specific reviews of the literature available for coral reefs, primarily for the GBR, at various levels of ecosystem processes and functions.

3.1.1 Primary productivity

Algal turfs, phytoplankton, CCA and host-associated phototrophic microbes were the top ranked groups for primary productivity (Table 7). Approximately 70% of the carbon fixed by primary producers on the GBR originates from phytoplankton (Furnas and Mitchell 1987, Furnas and Mitchell 1988, McKinnon et al. 2007). Typical of tropical ecosystems, phytoplankton communities on the GBR are diverse, including a range of diatoms, dinoflagellates, cyanobacteria and picophytoplankton, which form the baseline of pelagic food webs (Revelante and Gilmartin 1982, Revelante et al. 1982, McKinnon et al. 2007, Davies et al. 2016). Microbial metabolic pathways are involved with 59–100% of the net primary production on coral reefs, including within the phytoplankton (Arias-Gonzalez et al. 1997, Silveira et al. 2017). This sweeping contribution to primary production is captured here for all microbial groups (FI ≥ 4). Host-associated phototrophic groups (e.g. Symbiodiniaceae) ranked highest, owing to their niche role facilitating productivity and organic carbon cycling in corals (and other hosts) (Silveira et al. 2017), and supporting the physiology, ecology and evolution of coral reefs (LaJeunesse et al. 2018).

Turf algae (Figure 5) are critical primary producers in oligotrophic coral reef waters, exhibiting high mass-specific rates of productivity (Adey and Goertemiller 1987), though we acknowledge the high diversity and ubiquitous nature of this group. Turf growth and productivity can be enhanced by high wave energy (Roff et al. 2019) and nutrient enrichment with links to water quality (Vermeij et al. 2010, Gordon et al. 2016a), particularly on inshore reefs of the GBR (Lam et al. 2018). Turf algae are rapid colonisers of bare substrates on coral reefs, particularly in degraded systems (Roth et al. 2018). The contribution of algal turfs to net primary production on the GBR is 100–500 g.C.m^{-2}.yr^{-1} for both inshore and offshore habitats (Klumpp and McKinnon 1992, Russ 2003), lower than estimates for fleshy macroalgae (e.g. *Sargassum*; 1000 g.C.m^{-2}.yr^{-1}) (Schaffelke and Klumpp 1997). The contradiction in ranks between turf and macroalgal groups here may reflect the relatively low biomass of fleshy macroalgae across much of the offshore area of the GBR.

Table 7: Functional importance (FI) rankings for 70 functional groups per-process on the GBR; H=herbivores, P=predators; DF=deposit feeders; SF=suspension feeders. Colours denote highest scores: 1st (red), 2nd (yellow), and 3rd (green).

Taxa	Functional group	Primary production	Herbivory	Predation	Nutrient cycling	Symbiosis	Calcification	Bioerosion	Ecosystem engineering	Recruitment
Microbes	Phototrophic	4	7	7	4	4	7	4	4	7
	Host-associated	2	7	7	4	2	2	2	2	4
	Chemoautotrophic	4	7	7	4	4	6	4	4	4
	Heterotrophic	4	7	7	4	4	8	4	4	4
Algae	Phytoplankton	2	7	7	2	7	7	5	11	5
	Algal turfs	2	3	7	2	7	7	2	8	2
	Leathery	8	3	7	8	7	5	11	4	11
	Foliose	4	3	7	8	7	5	11	4	2
	Calcareous	6	3	7	6	7	2	11	8	5
	CCA	2	5	7	6	7	2	11	4	2
Sponges	Heterotrophic	7	7	7	6	4	7	7	3	3
	Phototrophic	3	7	7	6	4	7	7	3	3
	Boring	3	7	7	10	4	4	2	6	4
	Cryptic	7	7	7	6	4	3	3	5	3
Coral	Tabular	4	7	7	2	2	2	7	2	2
	Staghorn	4	7	7	4	4	4	7	2	2
	Branching (other)	4	7	7	8	4	4	11	4	2
	Massive	4	7	7	8	2	4	11	2	4
	Encrusting	4	11	7	8	4	4	7	4	4
	Free-living	8	11	7	8	4	8	11	8	8
	Soft corals	4	7	7	4	2	7	11	4	8
	Foraminifera	8	11	11	8	4	4	7	12	12
Worms	Nematodes	11	11	7	7	8	7	3	7	11
	Nemertea	11	11	7	7	8	7	3	7	11
	Polychaetes	11	11	3	7	8	7	3	7	7
	Spirobranchus	11	11	8	11	4	7	3	7	5
Crustaceans	Decapods (H)	7	3	7	7	8	7	7	7	7
	Decapods (P)	11	11	3	7	7	7	7	7	11
	Coral-associated	7	11	4	6	2	2	3	8	7
	Barnacles	11	11	7	11	8	7	7	7	7
	Stomatopods	11	11	3	7	8	7	3	7	7
	Cleaner shrimp	7	11	8	10	6	5	11	7	5
	Infauna	7	7	3	7	8	7	7	7	7
	Zooplankton	7	3	3	2	7	7	11	11	11
	Parasitic	11	11	7	7	8	7	11	11	11
Molluscs	Gastropods (H)	7	3	7	7	7	3	7	7	7
	Gastropods (P)	11	7	3	7	7	3	7	7	11
	Triton snails	7	7	1	7	5	3	7	5	11
	Drupella	7	11	7	7	7	3	7	7	7
	Tridacnidae	7	7	7	7	8	3	7	7	3
	Bivalves (other)	7	7	7	8	7	3	7	7	3
	Chitons	7	7	7	7	7	3	3	7	7
	Cephalopods	11	7	1	7	8	7	7	7	11
Echinoderms	Seastars (H)	7	3	7	7	7	7	7	7	11
	Seastars (P)	11	11	7	7	7	7	7	7	7
	CoTS	7	3	3	7	7	3	3	7	7
	Sea cucumbers (DF)	7	7	7	5	8	5	7	7	11
	Sea cucumbers (SF)	7	11	7	11	7	11	7	11	11
	Sea urchins (regular)	7	3	7	7	7	3	3	7	7
	Sea urchins (irregular)	7	7	7	11	7	7	7	7	11
	Brittle stars	7	7	7	7	7	7	7	7	11
	Feather stars	7	11	11	11	7	7	7	7	11
Fishes	Cryptobenthic	7	7	3	2	8	11	11	7	7
	Farmers	7	2	9	8	7	5	9	3	2
	Scrapers (scarids)	7	4	9	4	11	5	3	3	1
	Browsers (nasos)	7	4	9	8	11	5	11	7	3
	Browsers (siganids)	7	4	9	8	11	5	11	7	3

Browsers (other)	7	4	9	8	11	5	11	7	3
Bolbometopon	7	2	7	6	11	5	3	1	3
Excavators (other)	7	2	5	8	11	5	3	3	3
Detritivores	7	2	9	1	11	7	11	7	5
Planktivores	11	9	7	7	11	11	11	11	5
Corallivores	11	9	7	11	11	7	11	7	9
Invertivores (labrids)	7	11	4	7	11	11	7	7	9
Invertivores (other)	7	7	7	7	11	11	5	7	11
Invertivores (lutjanids)	7	5	7	11	11	11	5	7	9
Eels	11	6	5	5	11	11	11	7	7
Piscivores (residents)	11	8	4	7	11	11	11	7	7
Piscivores (transients)	11	7	3	7	11	11	11	7	9
Cleaner wrasse	7	5	5	10	2	5	9	6	5

Figure 5: Turf algae are a predominant habitat type on coral reefs with a significant influence on ecosystem functioning in both healthy and degraded reefs.

Primary production by CCA is similar to that by turf algae (Chisholm 2003, Diaz-Pulido and McCook 2008, Lewis et al. 2017). Despite lower direct contributions to primary productivity, algal turfs and CCA ranked higher than fleshy macroalgae due to a suggested lower redundancy with expansive assemblages at scales from centimetres to kilometres (Harris et al. 2015). Turfs and CCA dominate the epilithic algal matrix (EAM) across the GBR, with direct links to total benthic and grazer (i.e. fisheries) productivity (Klumpp and McKinnon 1992, Russ 2003, Littler and Littler 2007, Arnold et al. 2010), and recruitment dynamics (Doropoulos et al. 2017a, Doropoulos et al. 2017b).

Interestingly, no group scored the top ranking (FI = 1; Table 7), attributing to the broad ecological redundancy in primary production across and within functional groups, and/or dependency of some species on others to complete this role (i.e. host-associated phototrophic microbes). Corals are active primary producers through their association with their microbial partners (Zooxanthellae; Symbiodiniacaea, and endolithic algae) but scored lower here (FI ≤ 4) as they have high levels of dependency and generally lower rates of production than most algae. Experts noted that the contribution of corals to photosynthesis was considered largely redundant as it would be readily replaced by algal productivity (Appendix 2).

3.1.2 Herbivory

Farming (e.g. damselfishes) and excavating (e.g. parrotfishes) fishes were the highest rated groups for herbivory (FI = 2; Table 7). Farming damselfishes are well recognised for their role regulating the growth and composition of algal assemblages within their territories (Ceccarelli et al. 2001, Hata and Kato 2004, Hoey and Bellwood 2010c, Ceccarelli et al. 2011), where they shape benthic coral reef communities (Ceccarelli et al. 2001, Ceccarelli 2007, Casey et al. 2015a), and reef fish behaviour and assemblages (Eurich et al. 2018). Densities of herbivorous fishes and intensity of herbivory can be influenced by proximity to reef structure. Distinct grazing halos around reef structures are a physical indication of top-down behavioural interactions between herbivores and predators (Sweatman and Robertson 1994, Madin et al. 2011, Downie et al. 2013, Ollivier et al. 2018), particularly for species that are closely associated with reef refugia, like farming damselfishes.

Nominally herbivorous parrotfishes are typically attracted to the endolithic algal growth on dead coral surfaces, and their scraping and excavating feeding behaviour promotes reef bioerosion (Clements et al. 2017). The green humphead parrotfish, *Bolbometopon muricatum*, is one of the largest roaming herbivores on coral reefs. Its high score for herbivory here is likely a reflection of its functionally explicit contribution to reef bioerosion through its feeding ecology. Despite being a nominal herbivore, each individual ingests around 5 tonnes of structural carbonate per year (around half is living coral) (Bonaldo et al. 2014). Replacement of the functional roles of *B. muricatum* by other species is unlikely (i.e. low ecological redundancy), as observed on some coral reefs where this species has experienced extreme population declines from overfishing (Myers 1999, Donaldson and Dulvy 2004).

All nominally herbivorous reef fishes scored highly for their magnitude of contribution to the herbivory process (FI ≥ 4). Certain species of scrapers (e.g. parrotfishes) and browsers (e.g. rabbitfishes, unicornfishes) are considered particularly important herbivores at various scales across the GBR, with several key species highlighted in the literature; *Naso lituratus*, *N. unicornis*, *Siganus canaliculatus*, *S. doliatus, Calotomus carolinus*, *Kyphosus vaigiensis* (Hoey and Bellwood 2009, 2010a, Hoey et al. 2013, Loffler et al. 2015a, b, Streit et al. 2015). Their slightly lower ranked importance for herbivory here (Table 7), may reflect an arguably broader level of ecological redundancy in the scrapers and browsers compared to excavators on the GBR. However, dietary groupings of nominal herbivores do not necessarily reflect taxonomy (Choat et al. 2002), and key herbivorous species appear to have specialised traits in their feeding ecology that can have specific and dynamic influences on algal communities at local and regional scales (Bellwood et al. 2006b, Hoey and Bellwood 2009, Wismer et al. 2009, Johansson et al. 2013, Loffler et al. 2015a, Streit et al. 2015, Loffler and Hoey 2018).

Interestingly, detritivorous fishes, including blennies and surgeonfishes, ranked among the highest for herbivory despite having a lower magnitude of contribution (direct and indirect) than nominally herbivorous groups (Table 7). This may be an artefact of their low functional redundancy, outlined as fundamental components of nutrient pathways and the transfer of energy from the EAM (i.e. algal turfs) to secondary consumers (Crossman et al. 2001, Wilson et al. 2003, Crossman et al. 2005, Bellwood et al. 2014). Regardless, this group represents ~40% of the biomass of EAM-grazing assemblages on the GBR (Wilson et al. 2003). The surgeonfish, *Ctenochaetus striatus*, was highlighted as particularly important due to its active role removing sediment and detritus from the EAM, facilitating herbivory by other species (Goatley and Bellwood 2010, Marshell and Mumby 2012, 2015). Detritivores can be key nuclear species that affect the behaviour and distribution of other species, and provide high contributions to the export of nutrients across reefs from sand flats to hard reef structure (Lukoschek and McCormick 2000, Crossman et al. 2001, Goatley and Bellwood 2010, Marshell and Mumby 2012). Interestingly, detritivores and other functional groups (including herbivores) can supplement their diet with a range of other food sources (e.g. invertebrates, microbes, diatoms), which have a higher protein, fatty acid and/or total energy content than their primary food source (Montgomery and Galzin 1993, Choat et al. 2002, Choat et al. 2004, Clements et al. 2009, Hernaman et al. 2009, Kramer et al. 2013, Clements et al. 2017). Notably, diet partitioning and selectivity are currently underestimated for many nominal detritovores and herbivores (Choat and Clements 1998, Clements et al. 2017).

Most benthic algal groups scored highly for herbivory (FI = 3) due to their role as food for herbivores, demonstrating the importance of assessing indirect effects in ecosystem functioning. Interestingly, this was not captured for phytoplankton, which are ubiquitously important for grazers in the plankton including early life stages of most marine invertebrates and fishes (Hamner et al. 1988, Furnas et al. 2005, McKinnon et al. 2005, McKinnon et al. 2015). Zooplankton, and a range of other invertebrates (sea urchins, decapods, gastropods, seastars), scored highly for herbivory (FI = 3). Pelagic grazers, such as copepods, larvaceans and salps, provide the fundamental links in production and energy flow to higher order consumers. Mesozooplankton (the medium-sized zooplankton) can graze ~40% of the production by phytoplankton in oligotrophic regions (Calbet 2001), including essentially all production in certain size classes, yet zooplankton may still be food-limited on the GBR (McKinnon and Thorrold 1993, McKinnon et al. 2005, Skerratt et al. 2019).

Many micro- and macro-invertebrates occupy specific functional space, but since they typically have a lower magnitude of herbivory compared to reef fishes, their roles often go unappreciated (Brawley and Adey 1981, Klumpp and Pulfrich 1989, Altman-Kurosaki et al. 2018). Sea urchins are top herbivores on some coral reefs, usually after populations of herbivorous fishes and/or urchin predators are depleted through fishing (Ogden and Lobel 1978, Carpenter 1986, McClanahan 1988). Echinoids are often considered keystone species with a range of contributions to reef ecosystem functioning (Birkeland 1989). Detrimental coral-algal phase shifts can occur in their absence, as shown in the Caribbean (Carpenter 1990, Mumby 2006, Mumby et al. 2006b). Some urchin species are also outplanted as biocontrol (e.g. *Tripneustes*) to maintain invasive algal growth on some reefs (Conklin and Smith 2005, Stimson et al. 2007, Westbrook et al. 2015, Neilson et al. 2018). Other benthic herbivores (e.g. trochus snails, diogenid hermit crabs, amphipods) can be active in areas not accessible to reef fishes, limiting algal growth and facilitating coral recruitment in refugia from higher order grazers (Brawley and Adey 1981, Coen 1988, Klumpp and Pulfrich 1989, Doropoulos et al. 2012b, Doropoulos et al. 2016). Conversely, grazing by some herbivorous invertebrates may disrupt coral recruitment and regeneration, as posited for the blue starfish, *Linckia laevigata* (Laxton 1974b), but there is surprisingly little information available on the ecology of this vibrant well-known species.

3.1.3 Predation

Somewhat unexpectedly, the top-ranked groups for the predation process were triton snails and cephalopods (FI = 1; Table 7). Triton snails, specifically the giant triton, *Charonia tritonis*, are among the largest mobile predatory invertebrates on the GBR, and are a key predator of adult CoTS (Endean 1969, Pratchett et al. 2014, Cowan et al. 2017, Hall et al. 2017). Some have attributed CoTS population outbreaks to the removal of *C. tritonis* from the GBR in the mid-1900s (the ‘predator removal hypothesis’), although controlled laboratory experiments suggest they only consume ~0.7 CoTS ind^{-1} week^{-1} and that they also target a range of other marine invertebrates (Pearson and Endean 1969). Regardless, their ranking here reflects this important predatory niche, which has been addressed for the GBR previously in the context of conservation and CoTS outbreak management (Hall et al. 2017).

Interestingly, invertivorous fishes did not score highly in the predation process (Table 7), including those that target CoTS at various life stages (e.g. emperors, pufferfishes, triggerfishes) (Cowan et al. 2017). It has been estimated that ~70% of fishes on the GBR feed predominantly on invertebrates (Kramer et al. 2015), including many with specialised feeding mechanisms and roles, such as tuskfishes (*Choerodon*) that use tools to break open mollusc shells (Jones et al. 2011), cleaner wrasses (*Labroides*) that target gnathiid isopods over other parasites (Grutter 1997), and rockmover wrasses (*Novaculichthys*) that overturn the benthos to access hidden prey (Wainwright et al. 2002). The lack of consideration of invertivores here reflected their broad ecological redundancy at this level of functioning and the data gaps regarding empirical observations of invertivory on the GBR (Case Study 1; Appendix 4).

Cephalopods also received the top score for the predation process (FI = 1), despite the literature being largely restricted to their taxonomy (Roper and Hochberg 1987, Norman 1992, Norman and Finn 2001), and surprisingly little information existing on their functional ecology on the GBR, and in general (Ponder et al. 2002). The functional importance of cephalopods is perhaps mostly presumed from their fast growth rates (Pecl and Jackson 2008), broad cross-shelf distributions occupying cryptobenthic to pelagic habitats (Moltschaniwskyj and Doherty 1995), and their contributions to fisheries productivity as both predators and prey (Connell 1998, Beukers-Stewart and Jones 2004, Taylor and Bennett 2008). The relatively high feeding rates and densities of squid and other cephalopods have the potential to control recruitment dynamics of many commercially and ecologically important fishes (Hunsicker and Essington 2008). Changes to predatory-prey dynamics of cephalopods could have ecosystem-level implications (Pecl and Jackson 2008, Spady et al. 2014, Spady et al. 2018). Benthic shallow-water octopuses are likely key predators within the reef matrix where large predatory fishes cannot access. Their behaviours are complex for an invertebrate and can involve interesting mutualistic hunting relationships with predatory fishes such as coral trout (Vail et al. 2013). Moray eels (muranids) occupy a similar niche in the reef matrix and demonstrate the same hunting mutualism (Vail et al. 2013) but were rated slightly lower for predation processes (FI = 5). Overall, trophic interactions in cryptic habitats are difficult to quantify and are poorly characterised.

Cryptobenthic fishes (Figure 6), which also occupy the reef matrix, rated highly for predation (FI = 3), despite the lack of empirical information on their functional roles (Bellwood et al. 2019, Brandl et al. 2019). This group, which includes the gobies, represent around half the total number of reef fishes on the GBR with around 8% of this population consumed daily (Depczynski and Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018), producing almost 60% of the consumed reef fish biomass (Brandl et al. 2019). Representing some of the smallest marine vertebrates, cryptobenthic fishes are fundamental to predation processes and production functioning as prey. They are also important crypto-invertebrate predators (Goatley et al. 2017), particularly of microcrustaceans (e.g. copepods) (Case Study 1; Appendix 4). Copepods are the most speciose group in the zooplankton on the GBR, and are at the base of marine food webs that directly and indirectly support fisheries production (McKinnon and Thorrold 1993, McKinnon et al. 2005). It is estimated that the flux of zooplankton to the coral reef 'wall of mouths' is ~0.5 kg m^{-1} d^{-1} (Hamner et al. 1988), with extrapolations that suggest copepod production across the entire GBR is >630,000 tonnes Carbon yr^{-1} (McKinnon and

Thorrold 1993, McKinnon et al. 2005, McKinnon et al. 2007). Given their fundamental contribution to reef trophodynamics, zooplankton scored highly for the predation process (FI = 3). Notably, the zooplankton group also includes macro- and mega-plankton, which includes cnidarian and ctenophoran jellyfishes that can be large (>200 mm) with explicit roles in ecosystem functioning through their typically carnivorous predation on smaller zooplankton groups (Hutchings et al. 2019) and as an important food source themselves (Ates 1988, 1991, Purcell and Arai 2001). Jellyfish blooms are documented around the world, including on the GBR, with impacts on ecosystem stability and functioning (Hutchings et al. 2019). This includes cubozoans (box jellyfish and *Irukandji*), which have socioeconomic impacts on inshore reefs of the GBR resulting from their sometimes fatal envenomation (Huynh et al. 2003, Kingsford et al. 2012, Gershwin et al. 2014).

Figure 6: Small and often cryptic fishes occupy a range of microhabitats where they serve as important micropredators and provide direct links from the benthos to fisheries productivity. Photo credit: P. Mumby.

In context of the ‘wall of mouths’ (Hamner et al. 1988), planktivorous fishes (e.g. damselfishes, fusiliers, anthias) scored surprisingly low (FI = 7), despite their well-appreciated roles transferring carbon (in plankton) from the water column into trophic networks, especially within close proximity of reef structure and refugia (Holzman et al. 2005, Motro et al. 2005, Yahel et al. 2005), and their contribution as prey to a multitude of species (Hamner et al. 1988, Hamner et al. 2007, Johansen and Jones 2013). The unexpectedly low score for planktivorous fishes may, in part, reflect their broad ecological redundancy, as they represent >20% of all coral reef fishes and account for >60% of the total fish biomass (Bellwood and Hughes 2001, Bellwood et al. 2004). It is also possible that experts scored the predation process from a top-down perspective, resulting in lower scores for many intermediate level predators like planktivores and invertivores.

Other invertebrates, including predatory polychaete worms, crustaceans (decapods, stomatopods, infauna) and molluscs (e.g. *Conus*, nudibranchs), ranked highly (FI = 3). Both pelagic and benthic micro- and crypto-predators provide the foundations of energy transfer to higher trophic levels (Goatley et al. 2017). This includes impressive cases for key benthic predators like mantis shrimp (e.g. *Odontodacylus*) (deVries et al. 2016, Goatley et al. 2017) and cone snails (e.g. *Conus*) (Kohn 2015), which can be highly specialised physically and/or chemically to target larger vertebrate prey. Harlequin shrimp (*Hymenocera*) and a number of other predatory invertebrates may be important cryptic predators, including of juvenile life stages of CoTS hidden in the reef and rubble framework (Glynn 1984, Cowan et al. 2017, Keesing et al. 2018). Nudibranchs can influence benthic cyanobacterial productivity through top-down effects on key herbivores (Geange and Stier 2010), and sponge-feeding nudibranchs sequester chemical defences that can alter fish feeding behaviour (Proksch 1994, Becerro et al. 1998, Ritson-Williams and Paul 2007). Nudibranchs are among the most abundant spongivores on coral reefs but their low relative densities limit their ability to shape sponge abundance and distributions (Powell et al. 2015).

CoTS also ranked among these invertebrates for the predation process (Table 7), as top corallivores with extreme predatory potential during population outbreaks (Pratchett et al. 2014). Outbreaks aside, CoTS adults can consume up to 250 cm^2 of live coral per day (Chesher 1969, Glynn 1973), around 2–5 times the rate of other similarly sized corallivorous starfish, such as *Culcita novaeguineae* (Glynn and Krupp 1986, Birkeland 1989). Non-*Acanthaster* predatory asteroids scored lower for predation (FI =7), although their selective feeding habits can influence the relative abundance of some coral species (Glynn and Krupp 1986). Even the nominally herbivorous sea star, *Linckia laevigata*, is reported to feed on live coral, but this behaviour is rare with little impact as their stomachs are relatively small (Laxton 1974b). Corals did not score highly for predation (FI ≥ 7), likely due to their broad redundancy regarding this process and propensity to switch between autotrophy and heterotrophy to meet energy requirements (Anthony and Fabricius 2000, Grottoli et al. 2006, Ferrier-Pages et al. 2011, Hoogenboom et al. 2015). This ability is highly dynamic depending on species and location, with some corals on turbid inshore reefs 10–20 times more heterotrophic than their counterparts in oligotrophic waters (Anthony 2000, 2006).

Large predatory reef fishes (transients and residents) were among the highest scoring fishes within the predation process but were rated lower than a range of other taxa (Table 7), in line with previous suggestions that top-down forces on the GBR are weak (Rizzari et al. 2015, Casey et al. 2017). While top-down effects of predatory reef fishes can alter reef fish recruitment and community structure (Webster and Almany 2002, Almany 2004b, Almany and Webster 2004, Rizzari et al. 2014, Palacios et al. 2016a, Palacios et al. 2016b), their relative rarity and limited links across trophic networks can reduce their overall functional importance (Roff et al. 2016, Casey et al. 2017). In contrast to common ecological theory, there is a degree of ecological redundancy in the mesopredator group on the GBR, which includes the sharks (Rizzari et al. 2015, Frisch et al. 2016b). Most reef-associated sharks do not act as apex predators but instead function as mesopredators along with a diverse group of reef fishes (Roff et al. 2016). Interestingly, resident fishes (e.g. coral trout) scored lower (FI = 4) than transient predatory fishes (e.g. sharks, barracudas) (FI = 3), reflecting the dependency of residents on habitat refugia (Rogers et al. 2014, Rogers et al. 2018b). Hunting regularity and success are typically greater in resident reef fishes, but transient predators can be the primary source of mortality for non-reef associated fishes (Hixon and Carr 1997, Almany 2004a).

Case Study 1: Invertivory on the GBR: a poorly understood link in the trophic chain

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It has been estimated that ~70% of fishes on the GBR feed predominantly on invertebrates (Kramer et al. 2015), but data gaps remain regarding invertivory on benthic mobile invertebrates (BMIs) including crustaceans, gastropods, worms and echinoderms. In a review of over 550 studies, only 35 reported nominally invertivorous fishes to incorporate BMIs in their diet on the GBR. This included 174 species from 20 families (Figure CS1.1, Appendix 4), ~10% of the total known number of fish species on the GBR. This diversity spans a range of life stages, sizes, morphologies and feeding modes, and exceeds that of herbivorous (178 species from 9 families; (Cvitanovic et al. 2007)), detritivorous (24 species from 5 families; (Wilson et al. 2003)) and corallivorous (128 species from 11 families; (Cole et al. 2008)) fishes on the GBR. Quantitative measures of invertivory on BMIs were only found for 18 families in 33 studies, including three families that consumed <10% invertebrates (Acanthuridae, Blennidae, Siganidae). Further, data was also only comparable for 11 of these families (Figure CS1.2) (see Appendix 4). This highlights the paucity of direct observations and quantification of fish invertivory on BMIs. It should be noted that this does not include fishes that target CoTS, as this has already received considerable attention (see Cowan et al. 2017).

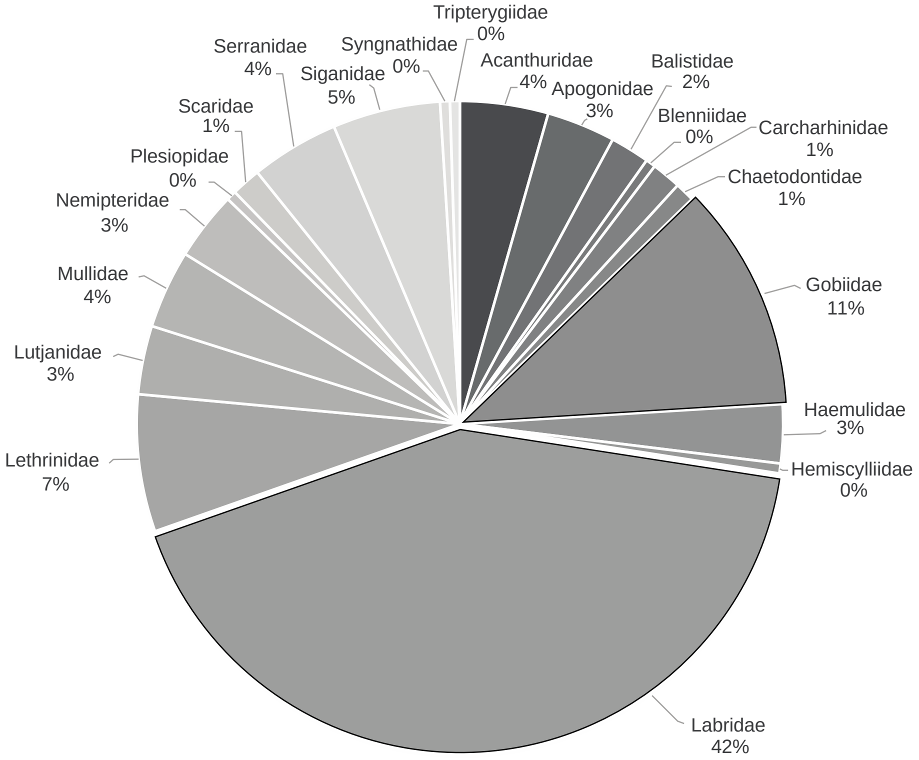

Figure CS1.1: Proportion of coral reef fishes and sharks (by Family) that are reported to consume benthic mobile invertebrates on the GBR; see Appendix 4 for full details.

The greatest diversity of BMI invertivores came from the Labridae (wrasses), followed by the Gobiidae (gobies) (Figure CS1.1). Labrids are one of the most functionally and ecologically diverse groups of fishes on coral reefs and account for the highest biomass of invertivores on the GBR (Williams and Hatcher 1983, Bellwood et al. 2006c, Kramer et al. 2015). While this may suggest high functional redundancy (Bellwood et al. 2006c), labrids exhibit the greatest range of specialised feeding mechanisms and species with key roles, e.g. tuskfishes (*Choerodon*) use tools to break open mollusc shells (Jones et al. 2011), cleaner wrasses (*Labroides*) target gnathiid isopods over other parasites (Grutter 1997), rockmover wrasse (*Novaculichthys*) overturn the benthos to access hidden prey (Wainwright et al. 2002). Cryptobenthic fishes (e.g. gobies) (Figure 6) represent around half the total number of reef fishes on the GBR, are particularly important predators of microcrustaceans (e.g. copepods), and themselves provide direct trophic pathways to higher order consumers (Depczynski and Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, Brandl et al. 2019). Apogonids (cardinalfishes) and a range of other nocturnally active species (e.g. reef sharks, epaulette sharks, sweetlips and emperors) are functionally significant invertivores at night, particularly regarding larger crustaceans (e.g. Malacostraca) (Marnane and Bellwood 2002, Boaden and Kingsford 2012).

For species where invertivory was quantified (Figure CS1.2), ~40% were obligate consumers of BMIs. Crustaceans were the predominant prey across all families of invertivorous fishes (Figure CS1.2). Annelid worms represented the greatest proportion of the diet of the Hemiscylliidae (epaulette sharks) and Mullidae (goatfishes) (Figure CS1.2), but this was only quantified for one species in each family. Many species not classified as nominal invertivores in the literature are documented to ingest significant amounts of benthic invertebrates (e.g. carnivores: *Chelodipterus quinquelineatus* and *Carcharhinus melanopterus* >35% of stomach contents; herbivores and detritivores: *Amblygobius phalaena* and *Bathygobius fuscus* >15%; carnivores/piscivores: *Lethrinus nebulosus* >50%) (Appendix 4). Detritivores and other functional groups may supplement their diet with invertebrates to avail of the higher protein and energy content (Hernaman et al. 2009, Kramer et al. 2013).

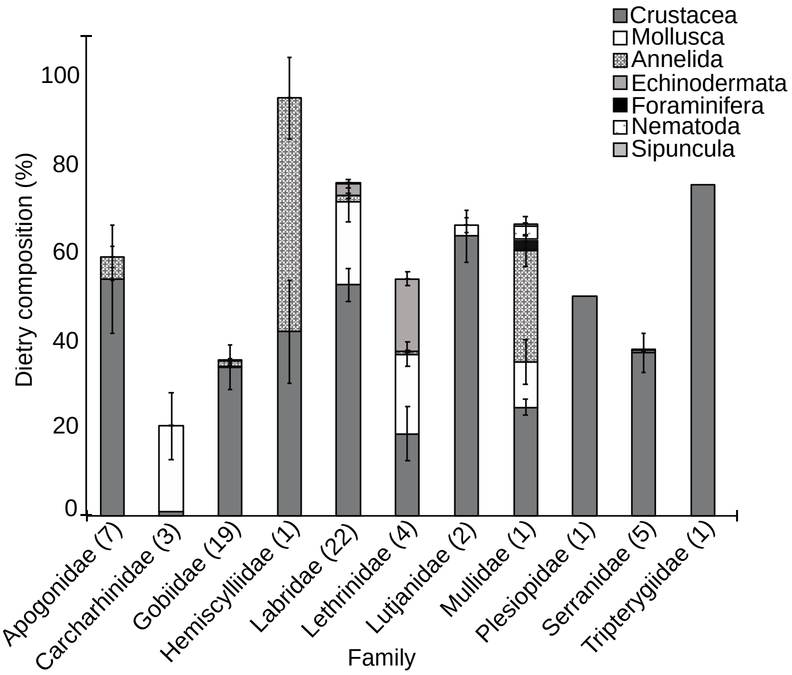

Figure CS1.2: Mean proportion (±SE) of invertebrates (by Phyla) in the diet of nominally invertivorous fishes (by Family). Number of species are indicated in parentheses after family name. Note only 11 of 18 families are presented as other data were not comparable.

From a bottom-up perspective, crustaceans comprised >40% of invertebrate prey and were consumed by all invertivorous fish taxa (Figures CS1.2, CS1.3), particularly by smaller fishes (Figure CS1.3a), and notably during early development and for those with ontogenetic shifts in diet. Echinoderms were the most abundant conspicuous macroinvertebrate group across the GBR (see Figure 1 in Appendix 4), but this was not reflected in their contribution to the invertivore diet (~4%), likely due to a lack of direct observations on key echinoderm predators, such as the Balistidae (triggerfishes; (Young and Bellwood

2012)). Echinoderms were mainly targeted by larger invertivores (Figure CS1.3a), perhaps owing to their well-defended morphologies (e.g. sea urchins; (Birkeland 1989)). Better description and quantification of invertebrate fauna, particularly for less-conspicuous groups, is essential to the characterisation of reef trophodynamics and mapping fisheries productivity beyond the herbivores and piscivores.

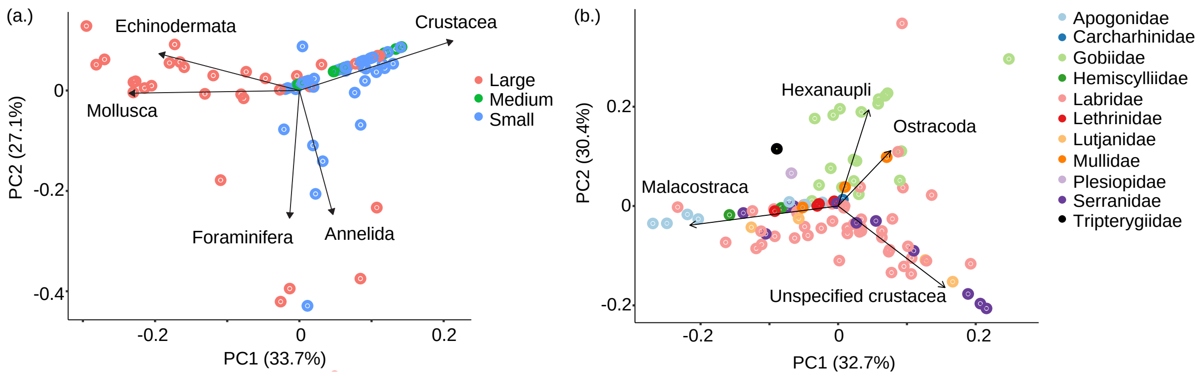

Figure CS1.3: Principal components analyses (PCA) of invertebrate prey items of invertivorous fishes on the GBR, indicating (a) prey taxa by predator size, and (b) crustacean-specific feeding grouped by fish family.

Vulnerability of invertivores to climate change and habitat degradation may be highest for those that rely on coral habitat for survival (e.g. cryptobenthic fishes) and those that rely on coral-associated invertebrates as their main prey items (e.g. juvenile coral trout). Even following recovery of the coral reef itself, fish communities can struggle to recover (Bellwood et al. 2006a, Graham et al. 2007, Bellwood et al. 2012a). Interestingly, dietary shifts in response to habitat degradation have been observed in both young (Wen et al. 2016) and adult (Hempson et al. 2017) coral trout (*Plectropomus* spp.). In response to extensive habitat loss due to a cyclone, some invertivorous fishes increased in biomass (e.g. the titan triggerfish (*Balistoides viridescens*), darkspot tuskfish (*Choerodon monostigma*), and sidespot goatfish (*Parupeneus pleurostigma*)), suggesting they may benefit from novel resources post-disturbance (Brandl et al. 2016). However, some species exhibited a decline in biomass, highlighting species-specific responses to perturbation. Dead coral and rubble habitats can host a greater density and diversity of invertebrates (Enochs et al. 2011, Enochs and Manzello 2012, Nelson et al. 2016), which could benefit those able to access these microhabitats (e.g. rockmover wrasse) as reefs degrade. However, the bioavailability of cryptic invertebrates to higher order consumers is yet to be adequately quantified. Characterising these trophic pathways would have implications for fisheries management, particularly for key fishery targets that are invertivores as recruits, such as coral trout and stripey snapper (*Lutjanus*).

This data compilation highlights disparate knowledge gaps for BMI-feeding invertivores. Targeted research is imperative to quantify predator-prey dynamics for invertivores on the GBR. This should focus on characterising direct measures of invertivory, prey availability, trophic transfers from within the reef matrix and beyond, and the potential for invertivores to mediate trophic functioning in degraded reef systems.

3.1.4 Nutrient cycling

Detritivorous fishes were the highest ranked group regarding nutrient cycling (FI = 1; Table 7). They are fundamental components of nutrient pathways transferring energy from the EAM (i.e. algal turfs) to secondary consumers (Crossman et al. 2001, Wilson et al. 2003, Crossman et al. 2005, Bellwood et al. 2014), and in the export of nutrients and detritus from sand patches across the calcified reef structure (Lukoschek and McCormick 2000, Crossman et al. 2001, Goatley and Bellwood 2010, Marshell and Mumby 2012). They are somewhat unanticipated top players, outside of the archetypal algae–herbivore–predator trophic continuum, making this an important finding. Blennies are considered key detritivores on the GBR, representing ~60% of this trophic group's density in some habitats (Wilson 2001), and exhibiting incredible population productivity with estimates that <1% survive for more than one year (Wilson 2004). This is similar for cryptobenthic fishes (e.g. gobies) (FI = 2), which are super abundant, highly productive, and provide direct links from the hidden and largely inaccessible reef matrix to higher consumers (Depczynski and Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018). The small size (<50 mm length) and rapid population turnover of cryptobenthic fishes (Figure 6) reflect their niche roles in top-down trophodynamics within the reef matrix, and bottom-up pathways that support fisheries productivity (Depczynski and Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, Brandl et al. 2019). The high scores for blennies and gobies here capture their critical roles in coral reef trophodynamics.

Phytoplankton and turf algae also scored highly for nutrient cycling (FI = 2), at the baselines of pelagic and benthic productivity, respectively (Furnas and Mitchell 1987, Furnas and Mitchell 1988, Klumpp and McKinnon 1992, Russ 2003, Littler and Littler 2007, McKinnon et al. 2007). In the context of productivity, *in situ* growth rates of dominant phytoplankton species range from one to several doublings per day, resulting in fast growth rates and substantial contributions to nutrient cycling. Phytoplankton species are important in nitrogen fixation, particularly *Trichodesmium*, which form extensive cyanobacterial rafts (Revelante and Gilmartin 1982, Revelante et al. 1982, Furnas 1992). Similarly, turf algae are particularly important in the fixation of nitrogen on coral reefs and its rapid distribution across trophic pathways (Borowitzka et al. 1977, Borowitzka 1981, Wilkinson et al. 1984, Hatcher 1988, Larkum et al. 1988). On turf and macroalgal-rich reefs, microbial community density and diversity increase with the potential to shape nutrient pathways and reef health (Haas et al. 2016, Brown et al. 2019).

All four functional groups of microbes, as partitioned here, also scored highly (FI = 4). Microbial communities are key drivers of large-scale biogeochemical processes in the oceans (Falkowski et al. 2008), with fundamental roles in mediating nutrient cycling (e.g. phosphorus, nitrogen) (Charpy et al. 2012, Tout et al. 2014, Ferrier-Pages et al. 2016) and influencing water quality (Glasl et al. 2017, Glasl et al. 2018a). Impressively, host-associated microbes (the 'coral microbiome') (FI = 2) can provide >90% of a coral's nutritional requirements (Muscatine and Porter 1977, Bourne et al. 2016). Tabular corals (FI = 2) ranked higher than other corals (FI = 4–8), likely a result of their broader functional importance regarding rapid reef growth and recovery (Connolly and Muko 2003, Ortiz et al. 2014, Ortiz et al. 2018). The relative contribution of autotrophy and heterotrophy in corals is variable, dynamic and plastic (Grottoli et al. 2006, Ferrier-Pages et al. 2011, Hoogenboom et al. 2015), with some species exhibiting higher rates of heterotrophy in turbid environments nearshore compared to the same species in oligotrophic water (Anthony 2000, Anthony and Fabricius 2000). Interestingly, sponges rated fairly low (FI ≤ 6), despite their well-documented roles in benthic-pelagic coupling and detrital pathways (de Goeij et al. 2013, Mumby and Steneck 2018). This may be a result of most information on the trophic ecology of sponges being derived from the Caribbean, with comparatively little known for sponges (particularly cryptic species) on Pacific reefs (Wilkinson 1983, 1987, Mumby and Steneck 2018).

The highest scoring mobile invertebrates were the zooplankton (FI = 2; Table 7), which includes a diversity of pelagic crustaceans (e.g. copepods and mysids), doliolids, salps, larvaceans (Appendicularia) and chaetognaths. Zooplankton are intermediate trophic levels in pelagic food webs, linking primary production by phytoplankton with higher order fishes, and thus support oceanic and coastal fisheries. Zooplankton are also key players in benthic-pelagic coupling, as they are consumed by benthic fishes and invertebrates including corals (Bishop and Greenwood 1994, Marnane and Bellwood 2002, Holzman and Genin 2003, Holzman et al. 2005), and there are demersal zooplankton that move directly between the sediment and water column daily (Jacoby and Greenwood 1988). Zooplankton can be highly abundant with distinct cross-shelf community assemblages (Sammarco and Crenshaw 1984, Williams et al. 1988, McKinnon and Thorrold 1993, McKinnon et al. 2005). Their biomass is greatest inshore and around shallow reef areas in the southern and central GBR, and is greater in summer months (Russell 1935, Skerratt et al. 2019). Appendicularia have been found to grow faster than any other multicellular organism (Hopcroft and Roff 1995), and can be nearly as abundant as copepods on coral reefs where they are important food source for planktivores and fish larvae (Noda et al. 1992, Llopiz 2013, Carrillo-Baltodano and Morales-Ramirez 2016, Dupuy et al. 2016).

Most benthic mobile invertebrate groups scored low with deposit-feeding sea cucumbers (FI = 5) and coral-associated decapods (FI = 6) among the highest ranked groups (Table 7). Sea cucumbers have been coined the ‘vacuum cleaners’ of the reef (Samyn and Tallon 2005), with functionally important roles in bioturbation, carbonate chemistry and nutrient cycling, and a strong influence on benthic productivity and infaunal community structure (Uthicke and Klumpp 1998, Uthicke 1999, 2001, Wolkenhauer et al. 2010, Schneider et al. 2011, Schneider et al. 2013, Purcell et al. 2016a, Lee et al. 2017, Wolfe and Byrne 2017a, Wolfe et al. 2018). In terms of ecosystem functioning, the relative importance of sea cucumbers would likely be greater in lagoon systems, outside of the focal coral reef habitat here. Coral-associated decapods (e.g. Tetraliidae, Trapeziidae) have direct relationships with their hosts, typically acroporid and pocilloporid corals (Stella et al. 2011b, Gonzalez-Gomez et al. 2018). They play important roles utilising large amounts of coral mucus, recycling detritus and organic matter (Glynn 1983, Hutchings 1983, Stimson 1990), and even physically defending their coral host from predators (e.g. CoTS, *Drupella*) (Pratchett 2001, Stella et al. 2011b). Their high dependency on their coral host (and thus highly localised benefits) worked to lower their overall score here.

3.1.5 Symbiosis

As organismal symbioses are defined by interactions and interdependency, it was not possible to receive the highest score for this process within our scoring scheme. Top-rated (FI = 2) taxa for symbiosis were microbes (host-associated phototrophic), corals (tabular, massive, soft), decapods (coral-associated), and fishes (cleaner wrasse) (Table 7). The coral microbiome (i.e. coral-associated microbes) can exist at densities exceeding one million cells per cm^2 of host tissue (Garren and Azam 2012a), with diversities in the thousands in some host species (Mouchka et al. 2010, Blackall et al. 2015, Bourne et al. 2016). These microbes are at the foundation of coral reefs, particularly in their relationships with benthos-dominating species such as corals, sponges and algae, where they are pivotal to host fitness through nutrient provisioning and waste removal pathways (Egan et al. 2013, Blackall et al. 2015, Bourne et al. 2016, Ferrier-Pages et al. 2016, Glasl et al. 2016, Glasl et al. 2018b, Ramsby et al. 2018b). The relative abundance of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, Howells et al. 2013, Stat et al. 2013, Bay et al. 2016). All corals scored highly (FI ≥ 4), reflecting their important symbioses, not only with microbial communities, but also their diverse and fundamental associations with a range of reef taxa spanning from worms to fishes that depend on corals as habitat. Recent observations suggest that soft corals (FI = 2) may be particularly important in providing reef structure post disturbance (i.e. bleaching), with potential to promote fish diversity and density at a critical time of recovery (Ferrari 2017).

Corals co-exist with a great diversity of symbiotic reef biota. Coral-associated decapods are strongly bound to their coral hosts, where they can increase coral growth, deter predators, and even reduce disease in their coral host (e.g. *Cymo*) (Glynn 1980, 1983, Pratchett 2001, Stella et al. 2011b, Pollock et al. 2013). Christmas tree worms (*Spirobranchus*) (Figure 7) also scored highly (FI = 4), with similar coral-host associations, enhancing water circulation across coral polyps influencing coral nutrition, growth and recovery (Strathmann et al. 1984, Dai and Yang 1995, Ben-Tzvi et al. 2006), and aiding in the protection of corals from predators (e.g. CoTS) (DeVantier et al. 1986, Rowley 2008). However, corals exist in the absence of these associates, meaning they may not be functionally imperative. Similar to corals, giant clams (Tridacnidae) host symbiotic autotrophs that can provide >50% of the individuals carbon needs for both respiration and growth, superseding their need for heterotrophy through filter-feeding as they grow (Klumpp et al. 1992). This symbiotic association was not captured for giant clams here (FI = 8).

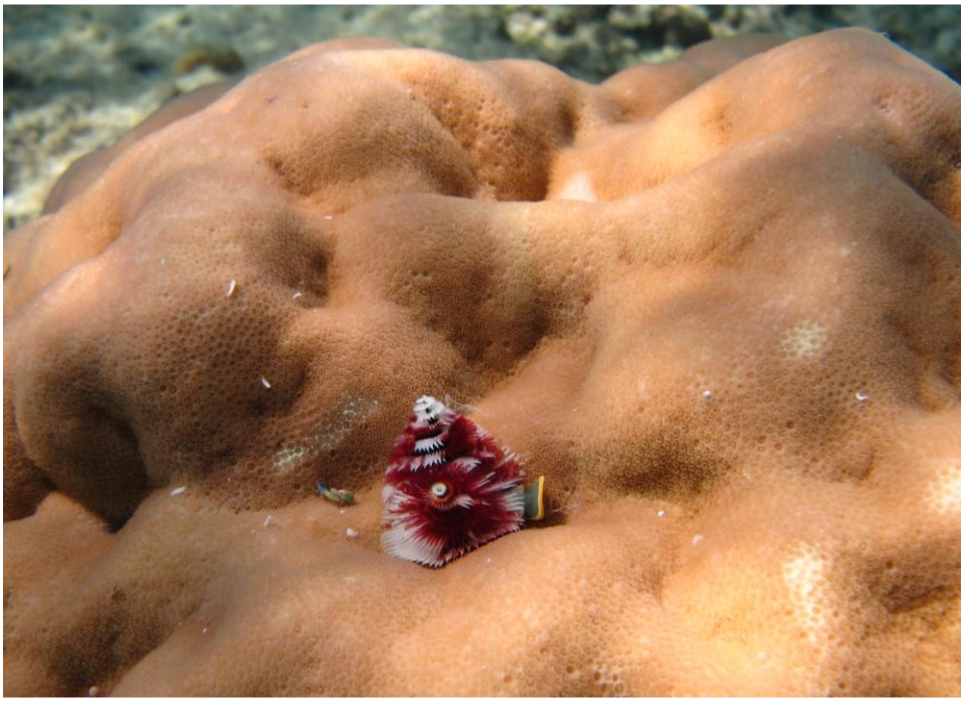

Figure 7: Christmas tree worms (*Spirobranchus*) embed into live coral where they can enhance water flow across the coral polyp interface, as well as deter predators such as CoTS and *Drupella*.

For the reef fishes, cleaner wrasses (*Labroides*) (Figure 8) scored highest (FI = 2; Table 7). Cleaners, particularly *L. dimidiatus* on the GBR, have highly developed interspecies communication and ‘cleaning’ services, removing ectoparasites, dead skin and mucus from their clients (Grutter and Poulin 1998, Bshary and Grutter 2002). Ranging from small fishes to charismatic megafauna, clients frequent cleaning stations to ensure their bodies are well-maintained and parasite free. This service has been documented to reduce stress hormones in the client (Soares et al. 2011), and increase fish density, diversity and size (Grutter et al. 2003, Clague et al. 2011, Waldie et al. 2011), recruitment (Sun et al. 2015) and cognitive performance (Binning et al. 2018). Cleaner wrasses may also be self-aware – a hallmark of cognition and intelligence (Kohda et al. 2019). Cleaner wrasses appear to fill an ecological niche with little ecological redundancy, but more information is needed on other cleaning species (e.g. *Lysmata* shrimp, other fishes) (Cote 2000, Vaughan et al. 2017) and how their symbioses scale up to support greater reef functioning.

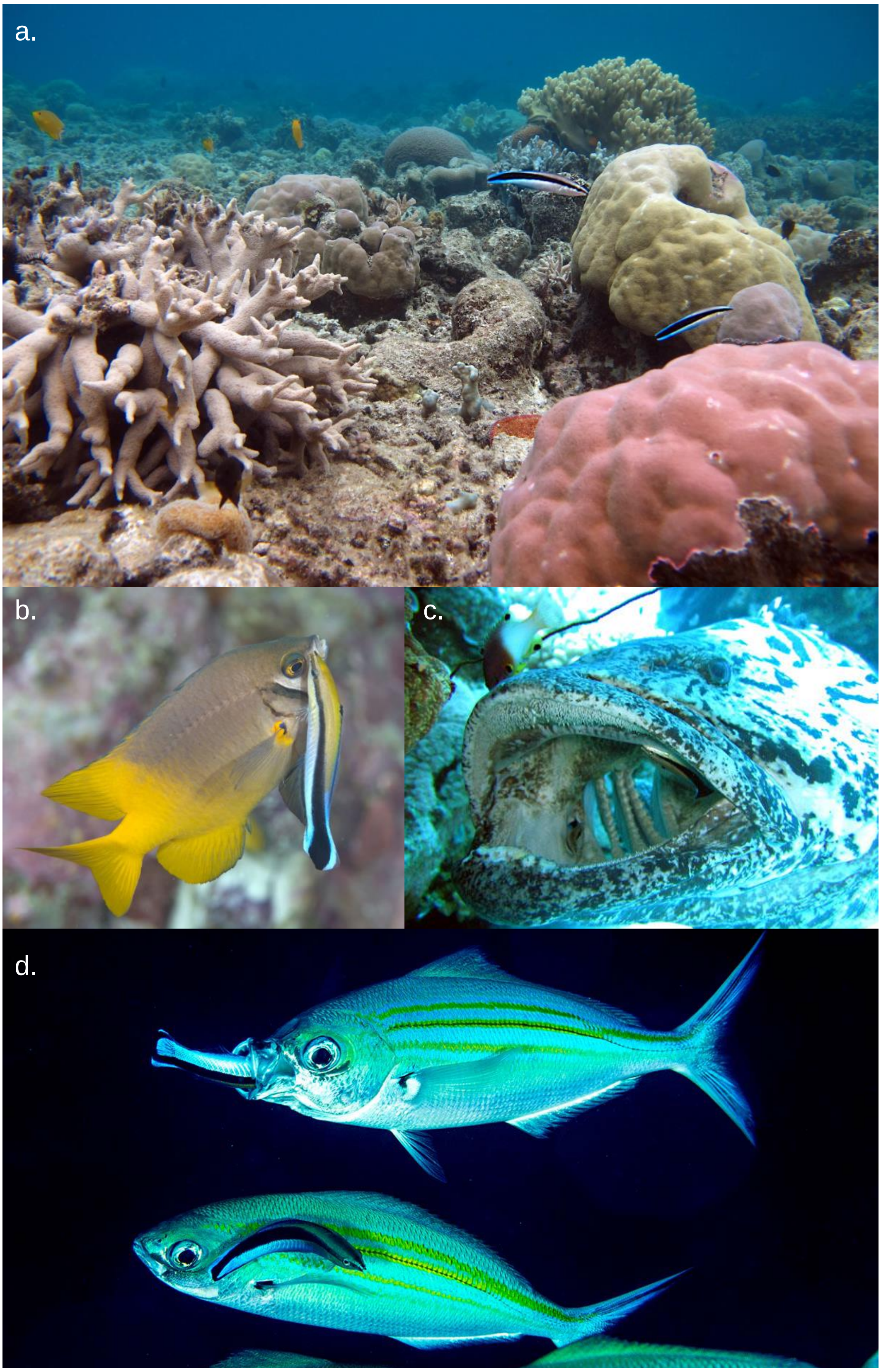

Figure 8: Cleaner wrasse (*Labroides dimidiatus*) offer their cleaning service to a range of marine species, including (b.) damselfish (Pomacentridae), and (c.) grouper (Serranidae). Photo credit: (b.) Richard Smith (Ocean Realms Images), (c.) A. Grutter, (d.) P. Mumby.

3.1.6 Calcification

Microbes (host-associated phototrophic), calcifying algae (CCA, calcareous species) and corals (tabular) scored highest for their roles in calcification (Table 7). The influence of the coral microbiome on coral health and functioning is widely appreciated (Egan et al. 2013, Blackall et al. 2015, Bourne et al. 2016, Glasl et al. 2016, Glasl et al. 2018b), so their functional ranks here even outweighed some coral species. Coral calcification provides the framework and complexity of the reef, so not surprisingly, most corals scored highly (FI ≥ 4). Tabular corals were considered the most functionally significant contributors to calcification on the GBR, owing to the rapid growth characteristic of acroporids (Pratchett et al. 2015, Anderson et al. 2017, Anderson et al. 2018), including those on turbid inshore reefs (Thompson and Dolman 2010, Browne 2012, Browne et al. 2013, Rocker et al. 2017). Acroporids (including tabular corals) generally exhibit the highest calcification rates with the greatest influence on the carbonate budget (Case Study 2; Appendix 5).

Case Study 2: Calculating the carbonate budget for the GBR: coral cover and coralline growth

Tries Razak, Guillermo Diaz-Pulido

Coral reefs exist in a dynamic state between reef construction (calcification) and destruction (erosion). The balance between these processes (i.e. the carbonate budget) can be used as a key metric to assess reef health and to forecast the ability of reefs to cope with environmental change (Perry et al. 2008, Kennedy et al. 2013, Mace et al. 2014, Perry et al. 2018). Some studies quantify the rates of carbonate production (e.g. Kinsey 1983, Browne et al. 2012, Silverman et al. 2012) and bioerosion (Kiene and Hutchings 1994, Osorno et al. 2005, Hoey and Bellwood 2008) in specific taxa and/or locations on the GBR. Variability in these rates is the result of complex interactions between these processes and terrestrial influences (e.g. water quality) (Mallela and Perry 2007), reef metabolism (e.g. calcification and dissolution, and photosynthesis and respiration) (DeCarlo et al. 2017, Woodroffe et al. 2017), reef topography and hydrodynamics (Vargas-Ángel et al. 2015), and ocean change (Kennedy et al. 2013, Shaw et al. 2016, Manzello et al. 2018, McMahon et al. 2019). For example, net ecosystem calcification dropped by 46% on a reef flat at Lizard Island, GBR, between 2009 and 2016, immediately after a mass-bleaching event (McMahon et al. 2019). Such dramatic changes in reef-scale calcification rates would impact reef functioning. Ocean change stressors are likely to retard reef carbonate systems at the global scale (Dove et al. 2013, Kennedy et al. 2013, Manzello et al. 2017, Albright et al. 2018, Cyronak et al. 2018), though examples of resilience and recovery at local scales are promising (Manzello et al. 2018). Critically, current carbonate budget estimates are largely restricted to specific regions (Yamano et al. 2000, Suzuki et al. 2001, Browne et al. 2013, Hamylton et al. 2013, Hamylton et al. 2014, Hamylton et al. 2017), making it imperative to upscale this information to establish a baseline carbonate budget at the whole-of-reef scale in the face of global change. This Case Study calculated carbonate production, bioerosion rates and the total carbonate budget for the GBR from coral cover reported for 92 reefs across the GBR between 2014 and 2018 using the long-term monitoring program (LTMP) data provided by the Australian Institute of Marine Science (AIMS) (Jonker et al. 2008) (see Appendix 5).

Hard coral assemblages contributed to approximately 94% of the total reef carbonate production (calcification) on the GBR, with the remaining 6% contributed by calcareous algae, including both CCA and the green algae *Halimeda* spp. (Table CS2.1). *Acropora* species exhibit the fastest calcification rates on the GBR compared to other carbonate producers (i.e. non-*Acropora* corals and calcareous algae), particularly in the southern GBR (Appendix 5; Table CS2.1). Total carbonate production increased from north (16.5 kg m^{-2} yr^{-1}) to south (51.5 kg m^{-2} yr^{-1}) (Table CS2.1; Figure CS2.1). Mean bioerosion rates were similar across the GBR (15.98–18.32 kg m^{-2} yr^{-1}) (Figure CS2.1), driven almost entirely by grazing parrotfishes (Table CS2.1). *Cliona* sponge bioerosion was negligible (Table CS2.1), but there is a general lack of data available for non-fish bioeroders (e.g. sponges, worms, endolithic algae) and their reef-scale densities on the GBR to accurately estimate their contributions. Overall, a negative carbonate budget was recorded for the northern GBR (-1.82 kg m^{-2} yr^{-1}), driven by low carbonate production rather than high bioerosion rates (Figure CS2.1). The total carbonate budget was positive in the central (18.31 kg m^{-2} yr^{-1}) and greatest in the southern (34.24 kg m^{-2} yr^{-1}) GBR. Lower carbonate budgets in the north may be attributable to the major bleaching events on the GBR in 2016 and 2017, which severely affected 81% of northern reefs (Hughes et al. 2017b, Hughes et al. 2018b).

Table CS2.1: Mean rates (±SD) of carbonate production, bioerosion and carbonate budget (kg m^{-2} yr^{-1}) in the North, Central and South GBR.

	North	Central	South
Carbonate production (total)	**16.51 ± 11.74**	**34.29 ± 30.02**	**51.51 ± 52.47**
Calcareous algae	1.59 ± 1.39	1.00 ± 0.72	0.83 ± 0.67
Hard corals	14.91 ± 10.88	33.29 ± 30.09	50.68 ± 52.37
Bioerosion rate (total)	**18.32 ± 16.75**	**15.98 ± 11.74**	**17.27 ± 12.47**
Parrotfish	18.32 ± 16.75	15.97 ± 11.74	17.26± 12.47
Cliona sponge	0.0004 ± 0.003	0.010 ± 0.035	0.010 ± 0.033
Carbonate budget	**–1.82 ± 18.54**	**18.31 ± 33.17**	**34.24 ± 53.13**

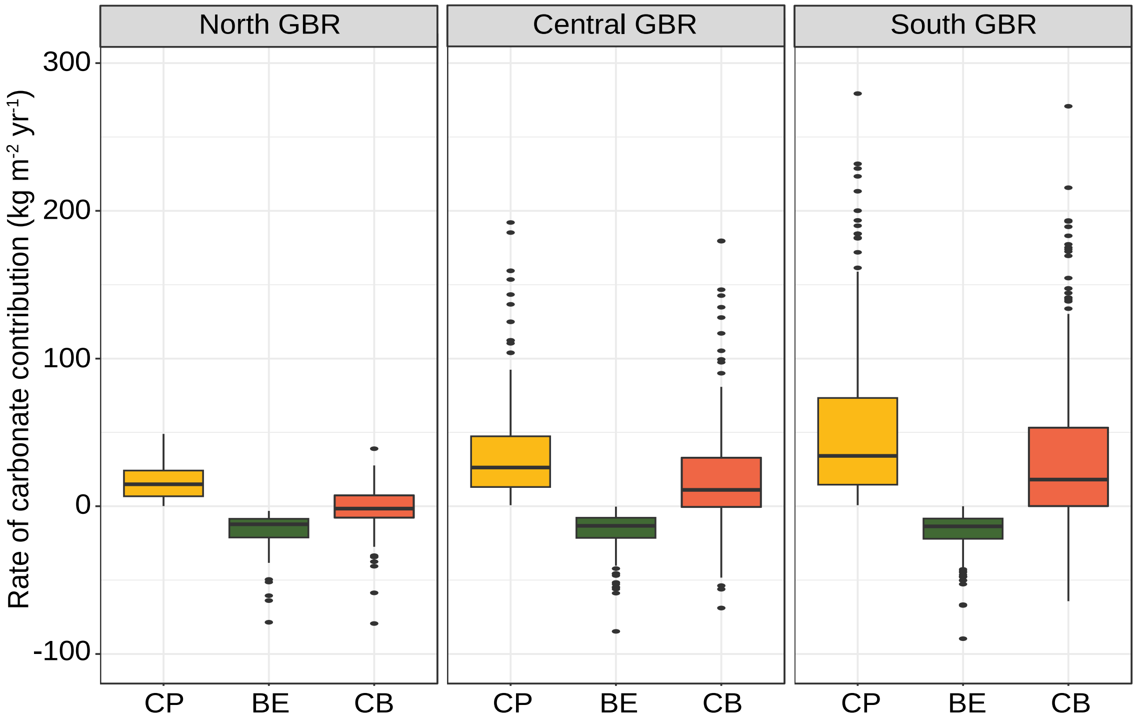

Figure CS2.1: Rates (kg m^{-2} yr^{-1}) of carbonate production (CP), bioerosion (BE) and the carbonate budget (CB) along the latitudinal gradient of the GBR.

There is marked temporal and spatial variability in rates of calcification and bioerosion on coral reefs, as found for reefs captured in the AIMS LTMP dataset (Appendix 5). There was a general increase in the carbonate budget for reefs between 2014 and 2016, but a reduced budget thereafter (Figure CS2.2). This trend was particularly evident for reefs grouped in the north and south, perhaps attributable to the major bleaching events on the GBR in 2016 and 2017 (Hughes et al. 2017b, Hughes et al. 2018b), while the carbonate budget in the central GBR plateaued from 2016 onwards (Figure CS2.2). Ocean change stressors are likely to retard reef carbonate systems at the global scale (Dove et al. 2013, Kennedy et al. 2013, Manzello et al. 2017, Albright et al. 2018, Cyronak et al. 2018), though examples of resilience and recovery at local scales are promising (Manzello et al. 2018). How the relative abundance of different coral taxa contributed to the observed variability in the carbonate budget will be important to differentiate in order to determine potential thresholds in coral cover to maintain reef resilience and recovery in a future ocean.

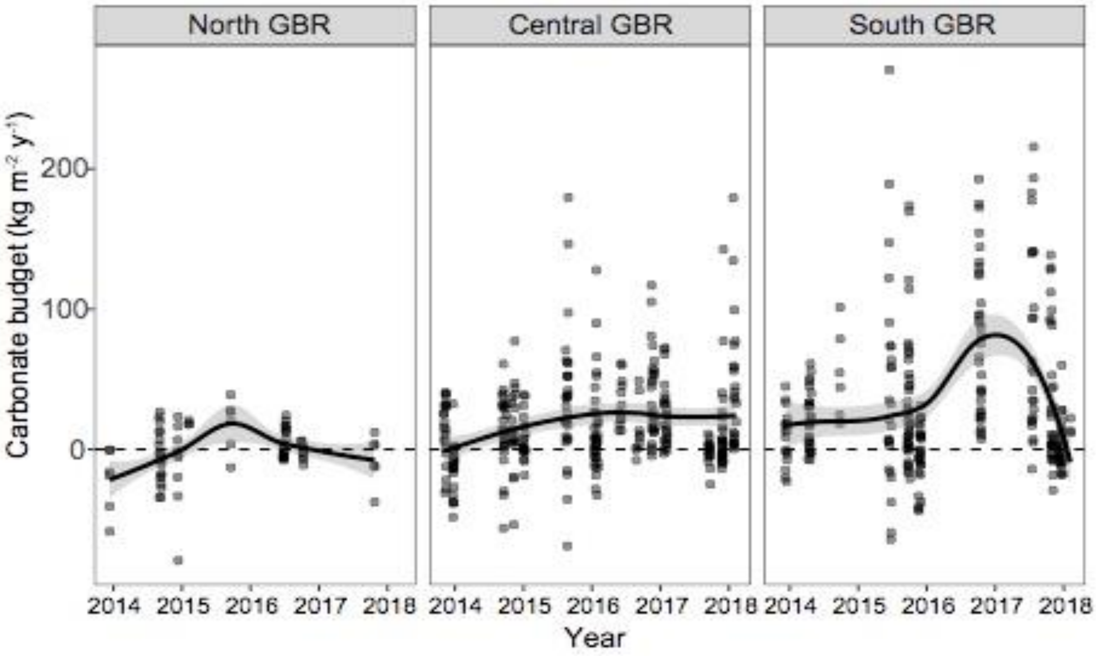

Figure CS2.2: Temporal change in the total carbonate budget on the north, central and south GBR between 2014 and 2018.

Calcification by CCA can be particularly fast in shallow-water habitats (up to 10 kg $CaCO_3$ m^{-2} yr^{-1}) (Kinsey 1983, Chisholm 2000), where they can completely dominate benthic cover (90–100%) (Atkinson and Grigg 1984, Glynn et al. 1996). CCA calcification in deeper (≥6 m) reef slope habitats (as focused on here) is likely to be slower (≤ 5 kg $CaCO_3$ m^{-2} yr^{-1}) (Chisholm 2000, Lewis et al. 2017). Calcareous algae (e.g. *Halimeda*) contribute to the production of marine sediments and can be major contributors to beach and lagoonal sediments (Marshall and Davies 1988, Delaney et al. 1996), with carbonate production around 2.2 kg $CaCO_3$ m^{-2} yr^{-1} (Drew 1983). While this is lower in comparison to calcification by scleractinian corals (Case Study 2), such as *Porites* (>10 kg $CaCO_3$ m^{-2} yr^{-1}) (Cooper et al. 2008, De'ath et al. 2009), the breakdown of calcareous alga can be much faster and can rapidly fill inter-reefal space. Overall, hard scleractinian corals are calculated to be responsible for ~94% of carbonate production on the GBR, with CCA accounting for the remaining 6% (Case Study 2).

The contribution of non-coral, non-algal species to reef carbonate production (i.e. calcification) was not captured in Case Study 2, as other calcifiers are not captured in the long-term monitoring program and/or their contributions are often comparatively marginal. However, little is known of the contribution of very small but highly abundant calcifying invertebrate groups (e.g. micro-molluscs and foraminiferans), many of which are yet to be named. For many of these taxa, their contributions to calcification are often overlooked but can be presumed from their presence in carbonate sands. For example, benthic and pelagic Foraminifera can make considerable contributions to the carbonate budget of coral reefs (Langer et al. 1997, McKinnon et al. 2007, Fujita et al. 2009, Doo et al. 2017, Hamylton et al. 2017), and are particularly important attributes in lagoon and reef sediment facies (Yamano et al. 2002, Wilson and Vecsei 2005, Yamano et al. 2015, Sarkar et al. 2016, Schmitt and Gischler 2017). Zooplankton such as pteropods and heteropods (molluscs) are relatively uncommon in GBR waters, although the pteropod, *Cavolinia longirostris*, can form aggregations in summer (Russell 1935). Large benthic foraminiferans (e.g. *Marginopora*, *Baculogypsina*) can be the single most important contributors to mass sediment production on the GBR where they can comprise >60% of biogenic sediment (Yamano et al. 2000, Dawson and Smithers 2014, Dawson et al. 2014). As such, foraminiferans received their highest score across all processes for calcification (FI = 4).

Coral-associated decapods scored highly for the calcification process (FI = 2), demonstrating the robust design of our methodology, which emphasises the importance of looking beyond direct roles when evaluating ecosystem functioning. While the direct magnitude of calcification by decapods is likely to be minimal at best, the influence of coral-associated crabs in regulating coral mucus can enhance the growth and survival of their coral hosts (Glynn 1983, Hutchings 1983, Stimson 1990). They can also have pronounced effects on corals by reducing fouling algal epibionts (Coen 1988). These symbiotic benefits that facilitate coral calcification upregulated coral-associates within this process compared to other crustaceans.

Molluscs generally scored highly (FI = 3), but as for crustaceans, have lower direct contributions to calcification compared to corals. Calcification in the Mollusca is perhaps greatest for giant clams (Tridacnidae) with some species reaching >120 cm across and weighing >200 kg (Rosewater 1965). Further, shell and 'bed' construction by giant clams and other bivalves provides structural complexity to the reef that provides substrate for colonisation by a diversity of holobionts, epibionts, commensal and ectoparasitic organisms (Neo et al. 2017). Corallivorous molluscs (e.g. *Drupella*) have indirect impacts on calcification through coral predation (Cumming 1999, Cumming 2009, Glynn and Enochs 2011), as for CoTS (FI = 3), which have been attributed to >40% of the decline in coral cover on the GBR (De'ath et al. 2012). Sea urchins (e.g. *Diadema*) scored similarly due to their indirect role in the balance between reef accretion and erosion through their herbivorous grazing (Birkeland 1989, Alvarado et al. 2016), as well as the direct calcification of their tests and spines. In addition, during winter when algal production slows down on Caribbean reefs, up to 25% of the diet of *Diadema antittarum* can be derived from living scleractinian corals (Carpenter 1981), an unsuspected coral predator.

3.1.7 Bioerosion

No group received the top ranking for bioerosion reflecting the high redundancy within this process (Table 7). Host-associated phototrophic microbes, algal turfs and boring sponges scored highest (FI = 2). A diversity of bacteria, fungi and endolithic algae ('microborers') biochemically penetrate live and dead coral and CCA substrates (Golubic et al. 1981, Golubic et al. 2005, Tribollet 2008, Hutchings 2011, Diaz-Pulido et al. 2014, Reyes-Nivia et al. 2014). These groups represent somewhat hidden bioerosion pathways operating on micro-biological scales on and within the reef matrix (Hutchings 1986, Glynn and Manzello 2015). All groups of microbes scored highly (FI ≥ 4) with significant roles in carbonate dissolution–calcification processes. Cyanobacteria are estimated to be responsible for 18–30% of sediment dissolution of coral reef and lagoon sediments on the GBR (Tudhope and Risk 1985). Epilithic (surface) microfloral (e.g. algal turfs) and microbial communities can shape bioerosion pathways and biological community structure (Chazottes et al. 2002). Microborers are often the primary agents of bioerosion in the first year following coral mortality, which promotes larger bioeroding grazers (e.g. parrotfishes) to dominate in the years to follow (Tribollet et al. 2002, Tribollet and Golubic 2005). However, the contributions of microborers to net reef erosion are difficult to quantify and large knowledge gaps remain (Case Study 2; Appendix 5) (Hutchings 1986, Glynn and Manzello 2015). Likewise, there is a need to quantify and distinguish the contribution of microbial metabolic processes from that of purely thermodynamic and chemical processes (e.g. low saturation of interstitial seawater with respect to calcium carbonates, e.g. omega under-saturation) to the rates of internal biological carbonate erosion (e.g. Reyes-Nivia et al. 2014). Both biological and chemically-driven processes are fundamental for an accurate quantification of erosion rates of reef cements.

Boring and cryptic sponges ranked as important bioeroders (FI = 3). The most important genera of siliceous sponges to bioerosion are *Cliona*, *Anthosigmella* and *Spheciospongia* (Wilkinson 1983, Schönberg 2000, Fang et al. 2017). Sponges can be the most significant invertebrate bioeroders on coral reefs, with *Cliona* species reported to contribute up to 23 kg $CaCO_3$ m^{-2} yr^{-1} (Neumann 1966, Glynn and Manzello 2015). Around 2–3% of the carbonate skeleton is dissolved in this process with the remainder passed on as sediments (Glynn and Manzello 2015). In extreme cases, sponges can also infest and kill live coral colonies (Lopez-Victoria et al. 2006, Marulanda-Gomez et al. 2017). *Cliona* and non-*Cliona* sponges are the only bioeroding invertebrates captured in the AIMS LTMP, as densities of other (often cryptic) invertebrate species are hard to quantify. This makes it difficult to upscale their contributions to bioerosion and reef carbonate budgets at the whole-reef scale (Case Study 2). This might explain why bioeroding molluscs (e.g. lithophagid bivalves, boring clams) scored low for bioerosion here (FI = 7) despite their documented contribution to bioerosive and biocorrosive processes (Hutchings 1986, Lazar and Loya 1991, Krumm 1999, Londono-Cruz et al. 2003, Chen et al. 2013, Schönberg et al. 2017).

All groups of worms (‘macroborers’) scored highly for bioerosion (FI = 3), but as an incredibly diverse assemblage they are likely to have diversity and redundancy in their roles. The first suite of macroeroders to proliferate in dead coral substrate are typically short-lived polychaetes (e.g. *Polydora*, fabriciniids), which can be extremely abundant, followed by longer-lived polychaetes (e.g. Cirratulidae, Eunicidae, Sabellidae) (Hutchings et al. 1992, Hutchings 2011). In high densities (up to 80,000 ind. m^{-2}), these worms can contribute to erosional losses around 0.7–1.8 kg $CaCO_3$ m^{-2} yr^{-1} (Davies and Hutchings 1983). *Spirobranchus* (Serpulidae) scored highly among the other worm groups, but importantly, do not bore into live coral directly. Instead, these worms stimulate corals to grow around their thinly calcified tube, where they can have significant indirect effects on calcification, bioerosion and the deterrence of some corallivores (DeVantier et al. 1986, Rowley 2008, Hutchings et al. 2019).

A range of other mobile invertebrates also scored highly (FI = 3; Table 7). Mean bioerosion rates of chitons on One Tree Island, southern GBR, were 0.16 kg $CaCO_3$ ind^{-1} yr^{-1} (Barbosa et al. 2008). At high densities, chitons may have an equivocal role in carbonate erosion budgets as other macroeroders like sea urchins and parrotfishes, but namely in the intertidal. Regular sea urchins (e.g. diadematids, echinometrids) contribute to erosion rates >10 kg $CaCO_3$ m^{-2} yr^{-1} on some reefs (Glynn and Manzello 2015, Alvarado et al. 2016), but rates on the GBR are comparatively low, perhaps due to comparatively healthy fish populations regulating urchin densities (Sammarco 1985). CoTS scored among these invertebrates, possibly as its consumption of live coral promotes colonisation by bioeroders on dead coral surfaces altering the biological character of the reef (Glynn and Manzello 2015).

Scraping and excavating parrotfishes scored highly for bioerosion (FI = 3). Most of these nominally herbivorous fishes are attracted to the endolithic algal growth on dead corals with substantial bioerosion resulting from their feeding behaviour (Clements et al. 2017). Some species also target live coral in >50% of the diet (e.g. *Bolbometopon*) (Bonaldo et al. 2014). Parrotfishes are generally the greatest contributors to bioerosion on coral reefs (Figure 9) and are key drivers in total reef carbonate budgets (Case Study 2) (Perry et al. 2012a). Calculations in Case Study 2 suggest that 25 species of parrotfishes from five genera (*Bolbometopon*, *Cetoscarus*, *Chlorurus*, *Hipposcarus* and *Scarus*) are responsible for almost all of the bioerosion on the GBR. Excavating parrotfishes (*Bolbometopon* and *Chlorurus* spp.) are typically the most significant external bioeroders on coral reefs (Figure 9), contributing to erosion rates over 32 kg $CaCO_3$ m^{-2} yr^{-1} on the GBR (Hoey and Bellwood 2008), with significant contributions to sediment production (Bellwood and Choat 1990, Bellwood et al. 2003). *Bolbometopon muricatum* (Figure 9) alone accounts for around 87.5% of the erosive processes and almost all of the live coral predation by parrotfishes on outer-shelf reefs of the GBR (Bellwood et al. 2003, Hoey and Bellwood 2008).

Figure 9: Parrotfishes can contribute to a range of habitat and production functions through their consumption of live coral and the EAM, contributing to bioerosion and leaving feeding scars (right) that influence coral-algal dynamics on coral reefs. The green humphead parrotfish (*Bolbometopon muricatum*; bottom) is a key species. Photos of parrotfishes by P. Mumby.

3.1.8 Ecosystem engineering

Bolbometopon (Figure 9) scored highest for ecosystem engineering (FI = 1; Table 7). This was influenced by the low redundancy of this species, given its functionally explicit role as a mass-excavator of live and dead coral, particularly on outer-shelf reefs (Hoey and Bellwood 2008, Bonaldo et al. 2014). Other parrotfishes also scored highly for this role (FI = 3) but were down-weighted due to a comparatively higher redundancy across the group. In healthy systems on the GBR, parrotfish bioerosion can balance net reef accretion (calcification) (Hoey and Bellwood 2008) (Case Study 2), and following disturbance can potentially drive a negative carbonate budget. Farming damselfishes scored along with the parrotfishes for their roles in shaping algal communities and coral reef growth within their territories (Ceccarelli et al. 2001, Hata and Kato 2004, Ceccarelli 2007, Ceccarelli et al. 2011, Casey et al. 2015a). This can further impact reef fish behaviour and community structure (Eurich et al. 2018). Damselfishes seem to exhibit a positive association with both coral habitat and predators (e.g. coral trout) across the GBR (Emslie et al. 2019), with impacts on coral growth, resilience and recovery (Chase et al. 2014, Chase et al. 2018).

Corals (tabular, staghorn, massive) and host-associated phototrophic microbes scored highly (FI = 2). This reflects the symbiotic relationship between the coral and its microbiome, and the fundamental importance of both to the construction of the reef (Bourne et al. 2016). The rugosity and complexity of branching and tabular corals, including acroporids and pocilloporids, provide critical refugia that support the diversity of coral reefs (Hixon and Menge 1991, Cheal et al. 2008, Harborne et al. 2012, Rogers et al. 2014, 2018a, Rogers et al. 2018b). Different coral species support different fish communities (Holbrook et al. 2008, Messmer et al. 2011, Holbrook et al. 2015), suggesting that coral and fish biodiversity are tightly linked. For example, tabular coral formations provide particularly important shelter for larger predatory fishes, which inspires competition, predation and community dynamics, and scale up to support fisheries productivity (Pratchett et al. 2008a, Kerry and Bellwood 2012, 2015b, a, 2016, 2017). However, tabular and branching corals typically have ephemeral life history traits (Tanner et al. 1996), and the loss of particular coral species will have disproportionate impacts on reef fish assemblages and biodiversity (Messmer et al. 2011, Holbrook et al. 2015). The influence and importance of specific functional and morphological coral groups is dynamic over time and space (McWilliam et al. 2018, Bellwood et al. 2019).

Exhibiting high recruitment rates, tabular corals (e.g. *Acropora hyacinthus*) are key to the growth, maintenance and recovery of coral reefs (Connolly and Muko 2003, Ortiz et al. 2014, Yadav et al. 2016, Ortiz et al. 2018). Staghorn corals (e.g. *Acropora muricata*) are commonly regarded as fast-growing ‘weedy’ species, as they have greater calcification rates but exhibit disturbance-prone ‘boom-and-bust’ characteristics (Knowlton 2001, Graham et al. 2014, Anderson et al. 2017). Massive corals (e.g. *Porites*) are slow growing but their broader resilience and longevity are important characteristics regarding long-term reef accretion, persistence and recovery (Baldock et al. 2014, Ortiz et al. 2014, Yadav et al. 2016, Ortiz et al. 2018). Some corals (e.g. *Turbinaria*) may be more resilient to turbid conditions on inshore reefs, where their functional importance is likely to be comparatively greater in the absence of other groups (Anthony 2006, Browne 2012, Browne et al. 2013). In response to mass coral bleaching and mortality on the GBR (Hughes et al. 2018b), *Pocillopora* (grouped here within ‘other branching corals’) replaced acroporids as the predominant recruitment taxon for the first time recorded (Hughes et al. 2019a), and may emerge as prime features in the current reef recovery trajectory.

Sponges also scored highly for ecosystem engineering, particularly larger conspicuous groups (heterotrophs, phototrophs) (Table 7). In addition to providing structural complexity to a reef (Maldonado et al. 2015), marine sponges host a diverse microbiome, which can occupy up to 35% of sponge volume and impact host defence, metabolism and resilience to perturbation (Simister et al. 2012, Webster and Taylor 2012, Taylor et al. 2013). It is not surprising that all microbe groups also scored highly (FI ≥ 4). While scoring lower for ecosystem engineering than other sponge groups (Table 7), the role of cryptic and boring sponges to reef and rubble consolidation is well appreciated (Wulff and Buss 1979, Wilkinson 1983, Hutchings 2011), with important inferences for settlement, recruitment and recovery on coral reefs (Biggs 2013). This is similar for CCA (Matsuda 1989, Diaz-Pulido and McCook 2008, Arnold et al. 2010, Doropoulos et al. 2012a), which scored among the highest algal groups (FI = 4). The role of a range of taxa (e.g. CCA, algae, sponges and microbes) in the biogenic cementation and consolidation of degraded reef rubble habitat is likely to be critical to reef functioning and recovery in a future ocean (Johns et al. 2018), but this remains poorly characterised.

3.1.9 Recruitment facilitation

Parrotfishes scored highest for recruitment facilitation (FI ≥ 3; Table 7). As above, the bulk-excavation of both live and dead coral by scraping and excavating parrotfishes is an important process for bioerosion and ecosystem engineering. Parrotfish feeding scars are hypothesised to facilitate settlement of corals and a range of other species through the excavation of live coral polyps and/or removal of epilithic algae from hard surfaces (Bellwood and Choat 1990, Bonaldo and Bellwood 2009, Bonaldo et al. 2014). This may also be true for grazing invertebrates like sea urchins (Dart 1972). *Bolbometopon* has been attributed to 87.5% of the erosion and 99.5% of the coral predation by parrotfishes on the outer-GBR (Hoey and Bellwood 2008). The role of this parrotfish in recruitment facilitation would likely emulate these contributions but this is yet to be explicitly quantified. Farming damselfishes also scored highly (FI = 2), due to their territorial behaviour that influences coral recruitment and juvenile survival (Gleason 1996, Gochfeld 2010, Doropoulos et al. 2013, Casey et al. 2015a), as well as community dynamics of larger reef fishes (Ceccarelli et al. 2001). Generally, herbivores play functionally diverse roles in recruitment facilitation owing to their diet, behaviour and distribution on the reef (Dart 1972, Doropoulos et al. 2013).

The roles of algae in recruitment facilitation are diverse, including indirect pathways through herbivory and feeding scars (Dart 1972), adding structural complexity free from the coral polyp ‘wall of mouths’ (Hamner et al. 1988), and/or biochemical settlement cues (e.g. CCA, macroalgae) (Heyward and Negri 1999, Harrington et al. 2004, Birrell et al. 2008b, Arnold et al. 2010, Doropoulos et al. 2012a, Doropoulos et al. 2013, Brooker et al. 2016b). While turf and macroalgal growth can impair the recruitment of coral reef species (Birrell et al. 2008a, Diaz-Pulido and McCook 2008, Arnold et al. 2010, Johns et al. 2018), it has been posited that the benefits of macroalgae in protecting juvenile corals from predation by species like parrotfishes may outweigh the negative impacts of algal growth on coral settlement and coral-algal competition (Venera-Ponton et al. 2011). Interestingly, the presence of CCA can prevent such undesirable algal growth to facilitate recruitment processes (Vermeij et al. 2011, Gomez-Lemos and Diaz-Pulido 2017).

Tabular and branching corals scored highly (FI = 2), as increased complexity provides refugia on coral reefs, facilitating the settlement, recruitment and survival of corals, fishes, and other marine species (Patton 1994, Ohman et al. 1998, Pratchett et al. 2008a, Shima et al. 2008, Wilson et al. 2008, Coker et al. 2014, Yadav et al. 2016, Gallagher and Doropoulos 2017). Shading by tabular corals can reduce the settlement success of autotrophic species (e.g. corals, algae) and alter benthic community compositions towards heterotrophs (e.g. bryozoans, invertebrates) (Baird and Hughes 2000). Sponges (FI ≥ 4) also influence settlement and recruitment, perhaps most importantly in their ability to consolidate benthic habitat (e.g. rubble). Coral rubble is an important settlement and recruitment habitat, and unconsolidated rubble can reduce coral settlement and recruit survival, hindering reef recovery (Wulff and Buss 1979, Fox et al. 2003, Fox and Caldwell 2006, Biggs 2013, Johns et al. 2018).

Interestingly, bivalves including giant clams and bed-forming species like oysters scored highly (FI = 3). The structural refugia they provide can facilitate settlement of juvenile fishes and a diversity of other organisms, increasing their protection and survival post-settlement, particularly when coral cover is low (Beukers and Jones 1998, Lecchini et al. 2007, Cabaitan et al. 2008, Neo et al. 2015). In this context, the low scores for bivalves regarding symbiosis (FI = 8) and ecosystem engineering (FI = 7) are surprising but may be considered marginal in terms of reef construction compared to corals. The functional roles of bed-forming species (e.g. oysters) are greater in intertidal and estuarine regions beyond the target habitat explored here.

3.2 Functional importance ratings

3.2.1 Production functions

Across the five production functions (i.e. primary production, herbivory, predation, nutrient cycling, symbioses), algal turfs were outlined as the most important group to productivity (Table 8). This captures their contributions to primary production and their role at the baseline of marine food webs – somewhat analogous to grasslands in terrestrial systems (Diaz-Pulido and McCook 2008). Turf communities (nominally EAMs) are critical drivers of benthic productivity on coral reefs, with a propensity to rapidly occupy available space in degraded reef systems (Roth et al. 2018), but even on healthy reefs (Klumpp and McKinnon 1992, Diaz-Pulido and McCook 2008). EAMs cover high proportions of reef flats (50–80%) and reef slopes (30–70%) across the GBR, and exhibit seasonal differentiation in productivity with a summer maxima (Klumpp and McKinnon 1992). Although they have a relatively low biomass per unit area and typically only reach heights of ~1 cm, EAMs have a rapid turnover and can shape coral reef communities from cryptic species diversity (Carpenter 1985, 1986, Klumpp et al. 1988, Klumpp and McKinnon 1989, Klumpp and Pulfrich 1989, Enochs 2012, Enochs and Manzello 2012) to herbivore assemblages on reef flats (Bellwood et al. 2018). Rates of turf algal productivity strongly predict herbivore biomass (Carpenter 1986, Russ 2003, Tootell and Steele 2016), and conversely, herbivores directly regulate turf canopy height (Carpenter and Williams 1993, Mumby et al. 2013a). Herbivorous grazers are suggested to consume around half of the total annual net production of the EAM, making it directly available to the food web and a critical component of reef trophodynamics (Hatcher and Larkum 1983, Klumpp and Polunin 1990). More specifically, much of the nitrogen in coral reefs is 'fixed' (made biologically available) by blue-green algae within the EAM, which have rapid growth rates and are intensively grazed, distributing nitrogen and other nutrients throughout the reef (Borowitzka et al. 1977, Borowitzka 1981, Wilkinson et al. 1984, Hatcher 1988, Larkum et al. 1988). Turfs often persist as constant grazing by herbivores prevents overgrowth by larger, fleshy seaweeds (e.g. *Sargassum*) (Diaz-Pulido and McCook 2008). However, once established, species such as *Sargassum* are highly resilient to physical and biological removal with implications for altered trophodynamics and production functioning on degraded reefs (Loffler and Hoey 2018).

Table 8: Functional importance (FI) rankings for taxa on the GBR, calculated for production and habitat functions, and overall. H=herbivores, P=predators; DF=deposit feeders; SF=suspension feeders. Ranks: 1st (red), 2nd (yellow), and 3rd (green).

Taxa	**Functional group**	**Production functions**	**Habitat functions**	**Total importance**
Microbes	Phototrophic	10	27	17
	Host-associated	2	1	1
	Chemoautotrophic	11	12	9
	Heterotrophic	12	25	13
Algae	Phytoplankton	6	41	22
	Algal turfs	1	10	3
	Leathery	36	43	41
	Foliose	20	24	18
	Calcareous	21	28	28
	CCA	15	9	6
Sponges	Heterotrophic	30	17	24
	Phototrophic	16	18	15
	Boring	22	8	11
	Cryptic	31	5	10
Coral	Tabular	3	4	2
	Staghorn	13	7	4
	Branching (other)	23	13	19
	Massive	17	14	12
	Encrusting	35	16	25
	Free-living	45	65	62
	Soft corals	5	44	26
	Foraminifera	59	52	59
Worms	Nematodes	64	38	54
	Nemertea	65	39	53
	Polychaetes	46	29	40
	Spirobranchus	61	26	48
Crustaceans	Decapods (H)	33	45	38
	Decapods (P)	41	53	51
	Coral-associated	19	15	16
	Barnacles	69	46	65
	Stomatopods	47	30	39
	Cleaner shrimp	60	42	52
	Infauna	34	47	37
	Zooplankton	4	68	34
	Parasitic	66	69	70
Molluscs	Gastropods (H)	27	31	30
	Gastropods (P)	38	40	36
	Triton snails	9	33	21
	Drupella	55	32	47
	Tridacnidae	48	19	33
	Bivalves (other)	49	20	32
	Chitons	42	21	31
	Cephalopods	26	54	45
Echinoderms	Seastars (H)	28	55	46
	Seastars (P)	62	48	58
	CoTS	14	22	14
	Sea cucumbers (DF)	39	49	49
	Sea cucumbers (SF)	63	70	68
	Sea urchins (regular)	29	23	23
	Sea urchins (irregular)	56	56	57
	Brittle stars	43	57	50
	Feather stars	68	58	66
Fishes	Cryptobenthic	8	62	35
	Farmers	32	11	20
	Scrapers (scarids)	37	2	7
	Browsers (nasos)	50	34	44
	Browsers (siganids)	51	35	43
	Browsers (other)	52	36	42
	Bolbometopon	25	3	5
	Excavators (other)	24	6	8
	Detritivores	7	50	29

Planktivores	67	66	67
Corallivores	70	60	69
Invertivores (labrids)	53	61	61
Invertivores (other)	57	59	60
Invertivores (lutjanids)	58	51	56
Eels	40	63	55
Piscivores (residents)	54	64	64
Piscivores (transients)	44	67	63
Cleaner wrasse	18	37	27

As for turfs in benthic habitats, phytoplankton (scoring 6th for production functions; Table 8) are critical to ecosystem functioning in open-water habitats. They play a major role in the cycling of carbon dioxide, carbon and nitrogen fixation, and are fundamental components of marine food webs, even in shallow-water systems (Furnas and Mitchell 1987, Furnas et al. 2005, McKinnon et al. 2007, Davies et al. 2016). Approximately 30% of production by nano- and micro-phytoplankton is grazed by the zooplankton (scoring 4th for production functions; Table 8) on the GBR (Roman et al. 1990). The importance of both phytoplankton and zooplankton at the baseline of ecosystem productivity and functioning is well captured here. Yet, waters of the GBR are typically oligotrophic and phytoplankton grazers are often considered food limited (McKinnon and Thorrold 1993, McKinnon et al. 2005). An estimated 25–100% of particulates in the water column fall to the benthos each day, making planktonic groups, and the faeces and marine snow they produce, important components of benthic functioning (i.e. benthic-pelagic coupling) (McKinnon et al. 2007, Alongi et al. 2015, Lonborg et al. 2017). Plankton occupy the largest coral reef habitat – the pelagic ecosystem – and are key to ecosystem functioning (McKinnon et al. 2007). It should be noted that this broad scale pelagic context stretches beyond the typical reef habitat examined here for targeted management recommendations.

Host-associated phototrophic microbes ranked second highest for production functions on the GBR (Table 8). The best-known coral symbionts are photosynthetic dinoflagellates within the Symbiodiniaceae, which can reach densities $>10^6$ cm^{-2} of host tissue (Garren and Azam 2012a, Bourne et al. 2016). Coral holobionts are at the core of a healthy coral animal – and coral reef – sometimes providing corals with almost all of their nutritional requirements (Muscatine and Porter 1977, Bourne et al. 2016), including up to 100% of their carbon requirements (Falkowski et al. 1993, Palardy et al. 2008). Symbiotic algae help to recycle waste products and convert inorganic nutrients making them bioavailable to their host (Ferrier-Pages et al. 2016). Symbiotic autotrophs also provide nutrients to a range of other marine organisms, such as giant clams (Tridacnidae), reducing their dependence on heterotrophy (Klumpp et al. 1992). While the functional contribution of the coral microbiome is poorly understood, it appears to be inextricably linked to the passage and cycling of nutrients (carbon, nitrogen, sulphur, phosphorus, vitamins), and overall reef productivity (Bourne et al. 2016). The generally high scores for the remaining microbial groups (≥12th) are important to note, particularly since the roles and sensitivities of host-associated microbes can differ greatly to those that are free-living (independent of a host organism) (Glasl et al. in press). Free-living microbes and bacteria can be important indicators of reef productivity and health, including for reef seawater and sediment environments (Case Study 3; Appendix 6) (Hansen et al. 1992, Falkowski et al. 2008, Glasl et al. 2017, Glasl et al. 2018a).

Case Study 3: Microbial communities on the GBR: links to water quality parameters that indicate healthy reef systems

Pedro Frade, Nicole Webster, David Bourne

Microorganisms are fundamental drivers of biogeochemical cycling in coral reef ecosystems (Gast et al. 1998, Bourne and Webster 2013b), and are critical to the health of keystone marine invertebrates including corals (Bourne et al. 2016). The current lack of available microbial data collected at sufficient spatial and temporal resolution hinders our capacity to identify the contributions that microbes make to a functioning reef and reef resilience (Dinsdale et al. 2008). Faced with the growing impacts of rapid climate change (Hughes et al. 2017a, Osborne et al. 2017), identification of microbial taxa that contribute to a healthy reef is critical. This Case Study synthesises currently available information on pelagic microbial communities across GBR regions (Figure CS3.1; Appendix 6). Relative microbial abundances were used to identify patterns in communities along inshore to offshore gradients in context of riverine floodwaters and water quality plumes (Angly et al. 2016).

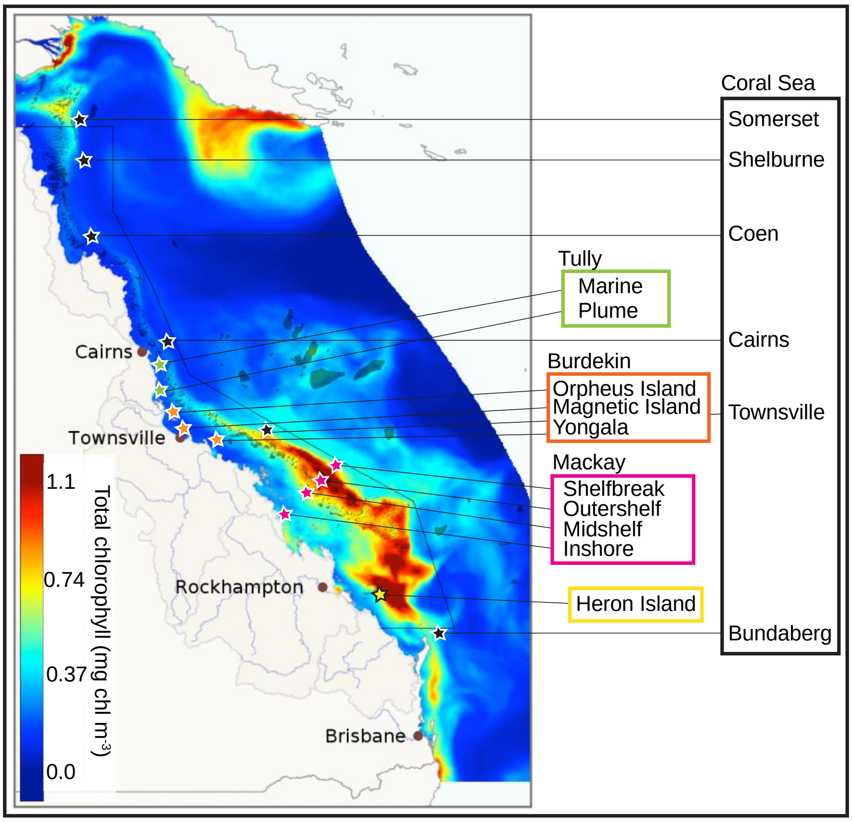

Figure CS3.1: Regions and locations on the GBR covered in the literature for pelagic microbial datasets (see Table CS3.1). Chlorophyll data (June 2016) obtained from eReefs (CSIRO GBR4 Hydrodynamic Model v2.0), with online map generation by AIMS.

Pelagic microbial communities across the GBR respond in a deterministic way to environmental fluctuations and drivers. This means that microbial community dynamics can be modeled to better understand how ecosystem functions predict changes to reef health and redress knowledge gaps that may guide future interventions aimed at mitigating environmental stressors. For example, the cyanobacterial family Prochlorococcaceae is more common under oligotrophic conditions (offshore) while Synechococcaceae becomes increasingly dominant in nutrient-rich eutrophic waters (inshore) (Figure CS3.2) (Dinsdale et al. 2008). The relative abundance of these two groups varies between wet and dry seasons as evidenced on the mid-shore Yongala reef, which switches from Prochlorococcaceae dominance to Synechococcaceae dominance in the wet season, likely owing to influence from terrestrial freshwater runoff (Figure CS3.2) (Dinsdale et al. 2008). These two photoautotrophic bacterial families have different capacities to use organic nitrogen (Scanlan and West 2002, Zubkov et al. 2003), and so the Prochlorococcaceae:Synechococcaceae relative abundance ratio can be used as an indicator for nutrient enrichment at spatial and temporal scales (Figure CS3.2).

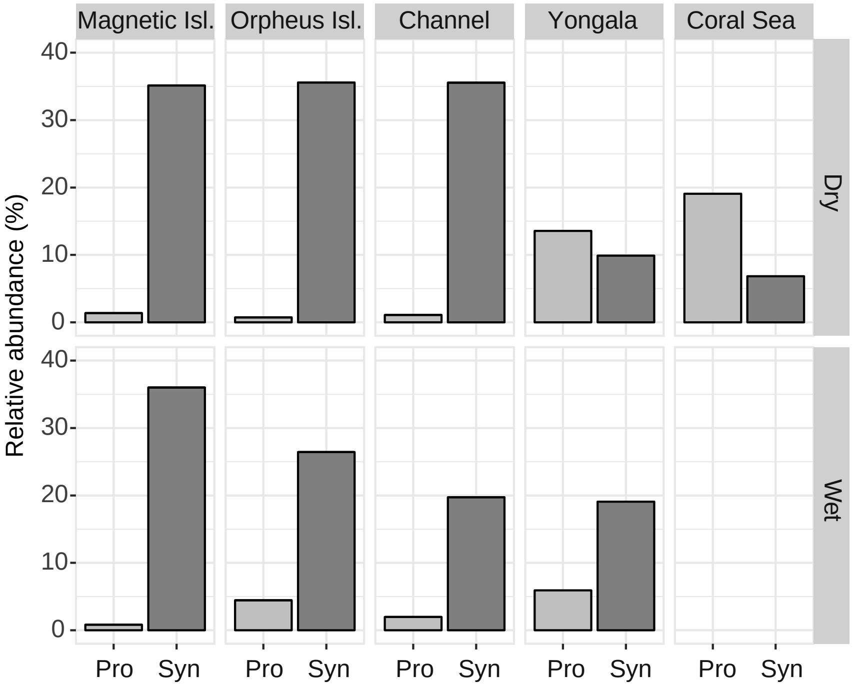

Figure CS3.2: Relative abundance of the cyanobacteria Prochlorococcaceae (Pro) and Synechococcaceae (Syn) during wet and dry seasons in the Burdekin region (see Figure CS3.1). Data provides comparison between inshore (Magnetic Island, Orpheus Island and Channel), mid-shore (Yongala) and open ocean (Coral Sea) regions. Coral Sea only sampled in dry season.

Another example of a microbial-based indicator exists in the ratio between Pelagibacteraceae and SAR86 (Appendix 6), which is negatively correlated with increasing nutrient levels. Levels of typical copiotrophs such as families OCS155, Flavobacteraceae, Cryomorphaceae and Rhodobacteraceae, could be modelled against levels of oligotrophs such as Pelagibacteraceae and SAR86 to generate new indices indicative of eutrophication (e.g. Haas et al. 2016). Typical opportunistic bacteria, including those exhibiting virulence towards benthic organisms (e.g. in the families Rhodospirillaceae, Rhodobacteraceae and Vibrionaceae), could also be used as indicators of reef health and or degradation (Appendix 6). Microbial baselines could be used to assess impacts from coastal eutrophication, anthropogenic disturbance and climate change, as microorganisms represent the first responders to environmental change and may mitigate or exacerbate the impacts of disturbance for higher trophic levels. How microbial assemblages translate to changes in benthic composition (macroalgal versus coral cover) and reef health requires attention (Glasl et al. in press). Establishment of microbial baselines through a network of microbial observatories spanning key habitats along inshore to offshore gradients in the northern, central and southern GBR would enable a robust assessment of the microbial contribution to reef function and health.

Tabular corals (Figure 10) ranked third for their role in production functions (Table 8). Despite scoring lower for primary production (FI = 4), and herbivory and predation (FI = 7), tabular corals were rated particularly high for nutrient cycling and symbiosis (FI = 2). In addition, the redundancy of key tabular corals could be considered relatively low with just three species considered common on the GBR, including *Acropora hyacinthus*, *A. cytherea* and *A. clathrata*.

Tabular corals are suggested to be key to the growth, maintenance and recovery of reefs due to their high recruitment rates and relatively large colony size, sometimes meters in diameter (Figure 10) (Connolly and Muko 2003, Ortiz et al. 2014, Ortiz et al. 2018). The morphology of tabular (and other branching) corals indirectly promotes production functions through habitat provisioning, which facilitates the recruitment and survival of post-larval corals, fishes and a range of other marine species (Patton 1994, Ohman et al. 1998, Shima et al. 2008, Wilson et al. 2008, Gallagher and Doropoulos 2017). A bulk of research indicates that increased coral complexity, largely influenced by branching and tabular corals, correlates to greater reef fish biomass and species richness (Jones and Syms 1998, Graham and Nash 2013, Graham 2014, Rogers et al. 2014, Gonzalez-Rivero et al. 2017, Richardson et al. 2017a, Richardson et al. 2017b, Rogers et al. 2018a, Rogers et al. 2018b). This is likely due to a range of factors influencing predator-prey dynamics, refuge availability and physical protection (Stewart and Jones 2001, Holbrook and Schmitt 2002, Johansen et al. 2008, Holbrook et al. 2011, Stella et al. 2011b, Verges et al. 2011, Kerry and Bellwood 2015b, a, 2017).

Figure 10: Tabular corals provide significant contributions to habitat functions, as well as supporting fisheries productivity through recruitment facilitation and structural complexity. Photo credit: P. Mumby.

Interestingly, soft corals scored fifth (Table 8), with similar scores as mentioned for tabular corals above for processes relating to production functions (Table 7). Soft corals tend to dominate the turbid waters typical of near-shore reefs on the GBR, suggesting regional specificity in functional importance between coral taxa (Fabricius 1997, Fabricius and De'ath 2001a). Some soft coral species are even herbivorous, feeding predominantly on phytoplankton – an important consideration that can shape community structure on eutrophic inshore reefs (Fabricius et al. 1995, Fabricius and De'ath 2008). Soft corals may also provide an important refugia for fishes and other marine species following mass coral bleaching events, as documented on Lizard Island (Ferrari 2017), indirectly promoting production functioning through habitat provisioning.

The highest ranked fishes for production functions were detritivores (7th) and cryptobenthic fishes (8th) (Table 8). Detritivores (e.g. blennies, surgeonfishes) are fundamental to the transfer of energy from sediments and the EAM (i.e. algal turfs) to secondary consumers (Crossman et al. 2001, Wilson et al. 2003, Crossman et al. 2005, Bellwood et al. 2014), with some surgeonfishes (e.g. *Ctenochaetus striatus*) actively facilitating herbivory processes (Goatley and Bellwood 2010, Marshell and Mumby 2012, 2015). The rapid population turnover of blennies (Wilson 2004), which can account for ~60% of detritivore biomass in some habitats (Wilson 2001), attributes to their key role in reef trophodynamics with links to fisheries productivity. Cryptobenthic fishes (e.g. gobies) have only more recently been acknowledged as a cornerstone of reef trophodynamics and ecosystem functioning (Brandl et al. 2019). With ~8% of their population consumed daily, representing almost 60% of consumed reef fish biomass, cryptobenthic fishes exhibit extremely fast population productivity for a vertebrate, and are undoubtedly a foundation in the transfer of energy from the reef matrix to higher order consumers (Depczynski and Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, Brandl et al. 2019).

Although scoring relatively low for other processes (FI ≤ 5), triton snails were considered top predators and consequently were the highest ranked invertebrate (9th) regarding total production functions on the GBR (Table 8). This was undoubtedly driven by the predation of CoTS adults by the giant triton, *Charonia tritonis* (Endean 1969, Pratchett et al. 2014, Westcott et al. 2016, Cowan et al. 2017, Hall et al. 2017), a predation pathway with very little ecological redundancy but great ecological impact. However, the direct consumption of CoTS by triton snails (Pearson and Endean 1969) is likely to be well below what would be required to restrict outbreaks as they occur today (Westcott et al. 2016), especially since they are not obligate predators of CoTS.

3.2.2 Habitat functions

Host-associated phototrophic microbes (i.e. the coral holobiont) were outlined as the most important group for habitat functioning on the GBR (Table 8). While their direct roles in processes such as calcification and ecosystem engineering may be marginal, their indirect roles facilitating these processes are pronounced and essential (Muscatine and Porter 1977, Bourne et al. 2016). Corals are largely dependent on their microbiome for their carbon requirements (Falkowski et al. 1993, Palardy et al. 2008), and restructuring of reef communities occurs when this symbiotic relationship breaks down (i.e. coral bleaching) (Fitt et al. 2001, Bourne et al. 2016, Hughes et al. 2018b, Stuart-Smith et al. 2018).

The highest ranked reef fishes for habitat functions were the parrotfishes (Figure 9) (scarids=2nd, *Bolbometopon*=3rd, other excavators=7th) (Table 8), scoring highly across all habitat-based processes (FI ≥ 5) (Table 7). Parrotfishes are generally the greatest contributors to bioerosion on reefs with a key influence on the total reef carbonate budget (Perry et al. 2012a). As addressed in Case Study 2 (Appendix 5), parrotfishes are almost entirely responsible for bioerosion processes on the GBR, though information is lacking for other contributors. The bulk-excavation of both living and dead coral by scraping and excavating parrotfishes is considered critical to reef functioning (Bellwood and Choat 1990, Bellwood et al. 2003), and feeding scars left by parrotfishes can facilitate settlement and recruitment (Bellwood and Choat 1990, Bonaldo and Bellwood 2009, Bonaldo et al. 2014). There may be limited ecological redundancy among some parrotfish species, with spatial variability documented in their contributions to bioerosion, ecosystem engineering and recruitment facilitation across GBR (Hoey and Bellwood 2008). *Bolbometopon muricatum* (Figure 9), the largest parrotfish on the Reef, is most significant offshore, while *Scarus rivulatus* (scrapers) and *Chlorurus* spp. (excavators) are more important on inner and mid-shelf reefs (Hoey and

Bellwood 2008). Interestingly, the indirect roles of parrotfishes in habitat functioning sometimes outweighed the direct importance of corals (Table 8), another example of the importance of addressing indirect roles in ecosystem functioning.

Tabular corals (Figure 10) ranked fourth, higher than other coral groups (8–65th), likely owing to their fast growth, high recruitment rates and recovery potential (Connolly and Muko 2003, Linares et al. 2011, Ortiz et al. 2014, Ortiz et al. 2018). Acroporids frequently provide the greatest contributions to coral extension rates, carbonate production (calcification) and the total carbonate budget of coral reefs (Case Study 2) (Perry et al. 2012a, Pratchett et al. 2015). The structural complexity provided by tabular (and other branching) corals provides fundamentally important refugia (Figure 10), which facilitates the recruitment and survival of a great diversity of coral reef species (Ohman et al. 1998, Pratchett et al. 2008a, Shima et al. 2008, Wilson et al. 2008, Kerry and Bellwood 2012, 2015a, Gallagher and Doropoulos 2017). In general, species diversity on coral reefs is shaped and supported by coral diversity (Messmer et al. 2011, Holbrook et al. 2015, Clements and Hay 2019).

Cryptic and boring sponges scored highly for habitat functions (6th and 9th, respectively) (Table 8). Sponges can be the most significant bioeroding invertebrates on coral reefs with notable contributions to sediment production (Neumann 1966, Glynn and Manzello 2015). Cryptic and boring sponges are also critical to reef and rubble consolidation (Wilkinson 1983, Hutchings 2011), a process that enhances settlement, recruitment and reef recovery post disturbance (Biggs 2013). They also add structural complexity that attracts a diversity of reef organisms to enhance local biodiversity, perhaps importantly as coral cover declines in a changing ocean (Maldonado et al. 2015, Bell et al. 2018). The highest ranked algae was CCA (10th), which can play a similar role in cementing unstable reef benthos (Matsuda 1989, Diaz-Pulido and McCook 2008), shaping cryptobenthic communities (Enochs and Manzello 2012), and facilitating the recruitment of habitat-forming corals (Heyward and Negri 1999, Harrington et al. 2004, Arnold et al. 2010, Doropoulos et al. 2012a, Gomez-Lemos and Diaz-Pulido 2017). CCA are responsible for ~6% of the carbonate production (calcification) on the GBR (Case Study 2).

The highest ranked benthic mobile invertebrates were host-associated crustaceans (e.g. Trapeziidae, Tetraliidae) (15th), owing to their beneficial symbioses with their coral hosts. Bivalves (Tridacnidae = 19th; other = 20th) also scored highly as an invertebrate group. As for corals, their structural formations can provide refugia for a diversity of symbiotic and commensal organisms, especially when coral cover is low (Beukers and Jones 1998, Lecchini et al. 2007, Cabaitan et al. 2008, Neo et al. 2015). Some bivalves are also important bioeroders, such as the boring clam, *Tridacna crocea* (Hutchings 1986).

3.2.3 Total functional importance

In this section, we provide a ranking across all functional groups, creating a hierarchy of species in terms of their total functional importance from our ecosystem process-based assessment. This section highlights a critical element of our analysis, in that species that performed incredibly well in context of just one ecosystem process would not necessarily be ranked highly in terms of total functional importance. The same goes for species that scored well for either production functions or habitat functions. That is, only those that scored highly across multiple processes, and those contributing to both production and habitat functions, would likely result in a high final ranking. For specific details within processes and functions with support from the literature refer to the sections above.

Host-associated phototrophic microbes ranked highest across all nine ecosystem processes (Table 7) and are outlined here to be the most broadly functionally important group on the GBR (Table 8). Microbial groups ranked highest overall, with chemoautotrophic microbes ranked 9th and the lowest scoring group (phototrophic) ranked 17th. Microorganisms play ubiquitous roles in the functioning of coral reefs from symbioses with host-associates (with corals, sponges, algae, etc.) to free-living communities in pelagic and sedimentary environments (Blackall et al. 2015, Bourne et al. 2016), as addressed in Case Study 3 (Appendix 6).

In a global assessment of over 800 zooxanthellae-hosting coral species, trait diversity was remarkably conserved across latitudinal and longitudinal gradients, suggesting functional robustness in diverse coral systems like the GBR (McWilliam et al. 2018). Yet here, tabular corals ranked second, above all other coral groups. This is in line with the literature that suggests tabular acroporids (Figure 10) – particularly *Acropora hyacinthus* on the GBR – are key to the growth, maintenance and recovery of coral reefs (Connolly and Muko 2003, Ortiz et al. 2014, Ortiz et al. 2018). Rugosity and habitat complexity are enhanced by tabular and other branching corals, providing important refugia and recruitment habitat (Ohman et al. 1998, Shima et al. 2008, Wilson et al. 2008, Kerry and Bellwood 2015b, a, Gallagher and Doropoulos 2017). It is not surprising that many corals ranked among the highest in terms of total ecosystem functioning (staghorns 4th, massives 12th, other branching 19th), as these groups form the framework of the reef. Overall, hard corals contribute to around 94% of the carbonate production on the GBR, with acroporids highlighted as the most significant group to the total carbonate budget (Case Study 2, Appendix 5).

Algal turfs scored third, as critical drivers of benthic productivity somewhat analogous to grasslands in terrestrial systems (Diaz-Pulido and McCook 2008). The second highest ranked algal group was CCA (6th; Table 8). The highest ranked fishes were the parrotfishes (scraping scarids=7th, *Bolbometopon*=5th, other excavators=8th). The low-rated contribution of cryptobenthic fishes regarding habitat functions (62nd) resulted in a low total score (35th) (Table 8). Although scoring highly for production functions (7th), detritivorous fishes also scored lower overall (29th). Sponges ranked highly overall, especially cryptic (10th) and boring (11th) species. The highest ranked mobile invertebrate group was CoTS (14th), even though others ranked higher in certain processes (Table 7), and for habitat and production functions separately (Table 8). The triton snail ranked 21st, driven by its role in predation (Table 7), while coral-associated decapods ranked 16th and sea urchins (regular) ranked 23rd. Zooplankton were among the most important to production functions (4th), but scored low overall (34th) owing to their low-ranked contributions to habitat functions (68th).

3.3 Vulnerability rankings

Vulnerability of our 70 functional groups was assessed in context of their biological functioning in the typical reef slope and reef crest habitats on the GBR, with a primary focus on offshore reef regions (Table 9). Inner-reef regions were assessed separately (see Table 10; Appendix 3), as exposure to some stressors (particularly those related to water quality) are most significant inshore (Devlin and Brodie 2005, Wooldridge et al. 2006, Brodie and Waterhouse 2012, Brodie et al. 2012, Kroon et al. 2012, Waterhouse et al. 2012, Fabricius et al. 2014, Lam et al. 2018, Mellin et al. 2019), where recovery rates are impaired (MacNeil et al. 2019). Vulnerabilities to each of our nine key stressors were considered equally, though we note that some stressors are likely to have greater and broader impacts at local and global scales, and that all stressors will occur in synergy with cumulative and multifaceted impacts (Halpern et al. 2008, Brown et al. 2014, McClanahan et al. 2015, Uthicke et al. 2016, Harborne et al. 2017, Wolff et al. 2018b).

Table 9: Potential impact (PI) of nine pertinent stressors on 70 functional groups on the GBR. Exposure was considered in context of offshore reefs. Note: maximum PI = 16 (red); high PI ≥10 (yellow); medium PI ≥ 7 (green); blank cells denote PI = 0; H=herbivores, P=predators; DF=deposit feeders; SF=suspension feeders.

Taxa	**Functional group**	**Nutrients**	**Sediments**	**Pollutants**	**Warming**	**Acidification**	**Cyclones**	**Fishing**	**Disease**	**Outbreaks**
Microbes	Phototrophic		1.0		9.0	1.0				
	Host-associated	4.0	2.3		16.0	4.0			1.0	
	Chemoautotrophic				4.0	1.0				
	Heterotrophic				9.0	1.0				
Algae	Phytoplankton		0.3							
	Algal turfs		0.3		1.0					
	Leathery		0.3		1.0		2.3			
	Foliose		2.3				0.3			
	Calcareous		2.3		4.0	4.0	2.3			
	CCA	1.0	4.0		9.0	9.0				
Sponges	Heterotrophic		1.8		1.0	7.1	16.0	1.0	1.0	
	Phototrophic		4.0		1.0	1.0	16.0	1.0	1.0	
	Boring		1.8		0.4		0.3		1.0	
	Cryptic		2.3		1.0	1.0	1.0		1.0	
Coral	Tabular	3.1	2.3		16.0	9.0	16.0	0.1	2.8	16.0
	Staghorn	3.1	2.3		16.0	9.0	16.0	0.4	2.8	16.0
	Branching (other)	3.1	1.8		16.0	9.0	16.0	0.1	1.8	16.0
	Massive	1.6	1.6		16.0	6.3	1.8	0.1	1.8	1.8
	Encrusting	1.6	2.3		16.0	6.3	1.8	0.1	1.8	2.8
	Free-living	1.0	1.6		12.3	6.3	4.0		1.8	1.8
	Soft corals	1.0	2.3		12.3	4.0	11.1	0.1	1.0	
	Foraminifera		1.6		4.0	6.3	7.1		0.4	
Worms	Nematodes									
	Nemertea						0.3			
	Polychaetes						0.3			
	Spirobranchus		1.0		9.0	4.0	1.0		1.0	
Crustaceans	Decapods (H)				9.0	16.0				
	Decapods (P)				16.0	16.0	0.3			
	Coral-associated		1.0		16.0	16.0	9.0			0.3
	Barnacles		1.0		9.0	9.0				
	Stomatopods				9.0	9.0	0.3			
	Cleaner shrimp				9.0	16.0	1.0			
	Infauna				1.0	9.0	0.3			
	Zooplankton		0.3		9.0	16.0	0.3			
	Parasitic				4.0	9.0	0.3			
Molluscs	Gastropods (H)		0.3		16.0	16.0				
	Gastropods (P)				9.0	7.1	1.0			
	Triton snails				9.0	7.1	1.0	0.3		
	Drupella				16.0	16.0	0.3			
	Tridacnidae		2.3		16.0	16.0	16.0	1.0		
	Bivalves (other)		0.3		16.0	16.0	4.0	1.0	1.0	
	Chitons				9.0	9.0	1.0			
	Cephalopods	0.3			1.0	4.0	0.3	2.3		
Echinoderms	Seastars (H)		0.3		9.0	4.0				
	Seastars (P)				9.0	1.0	1.0			
	CoTS				1.0	9.0	1.0			
	Sea cucumbers (DF)				9.0	4.0	2.3	16.0		
	Sea cucumbers (SF)		0.3		9.0	1.0	1.0	1.0		
	Sea urchins (regular)		0.3		9.0	16.0				
	Sea urchins (irregular)				9.0	16.0	0.3			
	Brittle stars				9.0	4.0	0.3			
	Feather stars				9.0	4.0	1.0			
Fishes	Cryptobenthic	0.1	1.0		11.1	4.0	11.1			1.8
	Farmers		2.8			1.8	7.1			

Scrapers (scarids)		4.0			1.8	0.1	0.1		
Browsers (nasos)		1.8			1.8	0.4	0.1		
Browsers (siganids)		1.8			1.8	0.4	0.4		
Browsers (other)		1.8			1.8	0.4	0.4		
Bolbometopon	0.1	2.8		1.8	4.0	1.8	0.4		
Excavators (other)		4.0			1.8	1.8	0.1		
Detritivores	0.4	1.8		0.4	1.8	7.1			
Planktivores	0.1	1.0		11.1	4.0	11.1			2.8
Corallivores	1.8	2.8		16.0	11.1	2.8			4.0
Invertivores (labrids)		1.8		4.0	4.0	1.8	0.1		
Invertivores (other)		1.8		4.0	4.0	1.8	1.8		
Invertivores (lutjanids)		1.0		4.0	4.0	1.0	0.4		
Eels	0.4	1.8		7.1	4.0	1.0			
Piscivores (residents)	1.0	1.8		11.1	4.0	2.8	16.0		
Piscivores (transients)	0.4	1.8		7.1	4.0	1.8	16.0		
Cleaner wrasse	0.1	0.4		7.1	1.8	11.1			

3.3.1 Stressor-specific vulnerabilities - Climate change

Changes in the global climate are occurring faster than anticipated (IPCC 2018, Xu et al. 2018). The greatest potential impacts across our 70 functional groups were suggested for ocean warming and ocean acidification, followed by cyclones (Table 9). This indicates that climate-related stressors were the primary concern of GBR experts, as demonstrated previously (Ban et al. 2014b). This is in line with the widespread coral bleaching events documented across the GBR over recent years (Hughes et al. 2017b, Hughes et al. 2018b, Hughes et al. 2018c), with alterations to reef community assemblage and structure (Stuart-Smith et al. 2018), trophodynamics (Hempson et al. 2018a, Hempson et al. 2018b), reproduction (Hughes et al. 2019a), community calcification (McMahon et al. 2019), and reduced recovery rates (Osborne et al. 2017, MacNeil et al. 2019) already observed, including for deep (or mesophotic) reefs (Frade et al. 2018). It is also calculated that rates of change in ocean chemistry are likely to be steeper on the GBR than currently projected by the IPCC (Mongin et al. 2016b), perhaps even more so for inshore reefs (Uthicke et al. 2014), and that cyclones will have significant spatial and temporal impacts across the GBR (Wolff et al. 2016, Cheal et al. 2017, Mellin et al. 2019). The only comprehensive solution to reduce the impact of global change on coral reefs, and globally, is to rapidly decrease anthropogenic emissions of CO_2, but the future of coral reefs is dependent on both local and global action on local and global stressors (Kennedy et al. 2013, Albright et al. 2016a, Hoey et al. 2016a).

3.3.1.1 Ocean warming

Marine organisms are more vulnerable to warming than terrestrial taxa, making increasing ocean temperatures one of the most broadly confronting contemporary stressor (Richardson and Schoeman 2019). The effects of warming on coral reefs are most pronounced as tropical species already exist within narrow thermal tolerance ranges at their upper limits (Hoegh-Guldberg 1999, Pörtner and Farrell 2008, Pandolfi et al. 2011, Hoey et al. 2016a). While there are high levels of variability in species responses and tolerances to climate change stressors, changing temperature regimes are likely to have significant impacts on species ranges, reproduction, physiology, taxonomy and diversity, productivity and functioning.

Host-associated phototrophic microbes and most coral groups rated among the most vulnerable to ocean warming (Table 9). Thermal sensitivity of the coral holobiont is well established, with the expulsion of microbial symbionts from the coral host following extended exposure to warm conditions (Brown 1997, Fitt et al. 2001, Bourne et al. 2008, Baird et al. 2009, Bourne et al. 2016). This results in a range of physiological and ecological impacts on corals – the coral bleaching phenomenon – with similar effects on other zooxanthellate-host organisms including tridacnid clams (Buck et al. 2002, Leggat et al. 2003), sponges (Vicente 1990), sea anemones (Lesser et al. 1990), and algal species including CCA (Anthony et al. 2008). Bleaching impairs the transfer of nutrients from the zooxanthellae to the host, impacting tissue development, skeletal growth, biomass, fecundity and autotrophy, while increasing susceptibility to disease and host mortality (Szmant and Gassman 1990, Glynn 1996, LeTissier and Brown 1996, Fitt et al. 2001). Yet, the relative abundance and local adaptation of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, Howells et al. 2013, Stat et al. 2013, Bay et al. 2016, Barfield et al. 2018).

Specific coral species and morphologies are documented to be more heavily impacted by ocean warming, with branching and tabular groups (acroporids, pocilloporids) typically most prone to bleaching (Gleason 1993, Baird and Marshall 1998, Marshall and Baird 2000, Obura 2001, Baird and Marshall 2002, McClanahan et al. 2004, Adjeroud et al. 2005, Thompson and Dolman 2010, Kennedy et al. 2018). But these faster-growing corals are critical to post bleaching recovery (Adjeroud et al. 2009, Linares et al. 2011, Ortiz et al. 2014, Ortiz et al. 2018), and there may be some resilience to the coral bleaching phenomenon in thermally tolerant zooxanthellae and microbiomes (Berkelmans and van Oppen 2006, Epstein et al. 2019), switches to heterotrophic feeding (Grottoli et al. 2006, Ferrier-Pages et al. 2011), intraspecies resilience across life stages (Putnam et al. 2010, Alvarez-Noriega et al. 2018), and adaptive responses owing to genomic history (Howells et al. 2013, Bay and Palumbi 2015, Dixon et al. 2015, Quigley et al. 2018). High levels of connectivity, most notably in the south poleward direction, along the GBR may facilitate the genetic migration and spread of warmer heat-tolerant alleles to higher latitudes as the climate warms (Matz et al. 2018).

The sensitivities and responses of free-living microbes (independent of a host organism) are often starkly different and can be important bioindicators of reef health regarding temperature, nutrients and sedimentation (Case Study 3) (Hansen et al. 1992, Falkowski et al. 2008, Glasl et al. 2017, Glasl et al. 2018a). Zooplankton were considered more vulnerable to climate change stressors than phytoplankton (Table 9), but impacts will be highly variable across the diversity of these two groups. Anthropogenic stressors and their interactions will impact phyto- and zoo-plankton growth, development, physiology, abundance and distribution, altering blooms, benthic-pelagic coupling and functioning (Huntley and Lopez 1992, Edwards and Richardson 2004, Richardson and Schoeman 2004, Kirby et al. 2007, Gao et al. 2012, Häder and Gao 2015, Carrillo-Baltodano and Morales-Ramirez 2016, Dupuy et al. 2016). Cyclone and storm events can drive homogenisation of zooplankton communities (McKinnon et al. 2003). Indirect influences of climate change on oceanographic processes (e.g. currents, upwelling, etc) are suggested to drive vulnerabilities in the plankton across the GBR region, as reviewed by McKinnon et al. (2007). Any alteration to phytoplankton or zooplankton abundance, composition, productivity and timing of occurrence is likely to have a cascading effect on higher trophic levels and functioning of the GBR (McKinnon et al. 2007).

For coral reef fishes, current evidence suggests that increased water temperature will be a major determinant of future assemblages through habitat degradation and direct effects on larval dispersal, recruitment, physiology and behaviour (Munday et al. 2009b, Hoey et al. 2016a). The positive associations between a great diversity of reef fishes and their coral habitat exemplifies the fundamental importance of coral as the foundation of healthy reef communities (Coker et al. 2014, Pratchett et al. 2018, Emslie et al. 2019). Thus, there are specific concerns for species that depend on corals as a food source and/or for shelter including coral-associated decapods (Stella et al. 2011a, Stella et al. 2011b), and corallivorous, planktivorous and cryptobenthic fishes (Munday 2004, Pratchett et al. 2004, Wilson et al. 2006, Pratchett et al. 2008b, Cole et al. 2010, Bellwood et al. 2012a, Wilson et al. 2014, Hempson et al. 2018c, Rice et al. 2019) (Table 9). Specialist and obligate corallivorous fishes (e.g. butterflyfishes and tubelip wrasses) are likely to be highly impacted by the combined impacts of global change through prey depletion, starvation, and even reduced sociality and reproductive potential (Pratchett et al. 2004, Berumen and Pratchett 2006, Cole et al. 2008, Graham et al. 2009, Cole et al. 2010, Thompson et al. 2019), while their feeding adds further pressure on coral condition (Cole et al. 2009). Chaetodont abundance and species richness seem to be primarily influenced by bottom-up drivers making physical changes to their coral habitat a significant concern (Brooker et al. 2016a, Leahy et al. 2016). Yet, trophic and foraging plasticity as documented for a range of coral reef fishes, including some considered to be specialist obligate feeders, will likely offer some resilience in a degraded reef setting (Wen et al. 2016, Hempson et al. 2017, Karkarey et al. 2017, Letourneur et al. 2017, Feary et al. 2018, Zambre and Arthur 2018). The close contact relationships between host-associated fishes (e.g. damselfishes) and coral refugia can enhance water circulation (Goldshmid et al. 2004), which can moderate bleaching susceptibility of the coral host itself (Chase et al. 2018).

In extreme cases, the abundance and richness of reef fishes may decline >60% following extensive collapse of reef habitat and structure (Pratchett et al. 2018). Resident predatory fishes that depend on reef structure, including the top fisheries targets on the GBR (coral trout), show a range of vulnerabilities to projected future conditions at both larval and adult life stages (Munday et al. 2013a, Johansen et al. 2014, Johansen et al. 2015, Clark et al. 2017, Messmer et al. 2017, Pratchett et al. 2017b). In context of direct effects, unable to meet the energetic costs of living in a warmer environment, larger-bodied coral trout may be more heavily impacted than smaller sized individuals, with significant ramifications to fisheries and functioning (Messmer et al. 2017, Scott et al. 2017b). Indirectly, the dependency of resident predatory fishes on tabular corals in particular presents a concerning case where changes in habitat functioning through the loss of coral complexity could have cascading impacts on fisheries production functions (Kerry and Bellwood 2012, 2015b, a).

Most herbivorous fish groups were considered generally resilient, with densities of some grazing species (e.g. parrotfishes) even documented to increase post disturbance, perhaps due to the increased algal production that typically follows coral mortality (Diaz-Pulido and McCook 2002, Cheal et al. 2008, Wilson et al. 2009, Cheal et al. 2010, Graham et al. 2015, Russ et al. 2015, Hempson et al. 2018c, Roth et al. 2018). However, grazing intensity can decline in line with reduced coral cover as denser algal growth outweighs and minimises the impact of grazers, and simplified habitat complexity increases predation exposure (Cheal et al. 2010, Bozec et al. 2013, Pratchett et al. 2018, Rogers et al. 2018a). The functional roles of the diversity of nominally herbivorous species will vary depending on algal density and the state of the reef (Chong-Seng et al. 2014). Coral-algal phase shifts have documented impacts on fisheries productivity (Ainsworth and Mumby 2015, Rogers et al. 2018a), and herbivores protected from fisheries activity in no-take areas may enhance reef recovery (Mumby et al. 2014, Chung et al. 2019). While changes in ecosystem states are a dynamics process (van de Leemput et al. 2016), in general, resilience and recovery of coral reefs will depend on the reversibility of seaweed blooms post disturbance, with grazing herbivores deemed particularly critical (Arthur et al. 2006, Bellwood et al. 2006b, Hughes et al. 2007b, Diaz-Pulido et al. 2009, Adam et al. 2011, Doropoulos et al. 2013, Bonaldo et al. 2014, Mumby et al. 2014, Adam et al. 2015b, Bennett et al. 2015, Graham et al. 2015). Effective herbivore management through Herbivore Management Areas (HMAs) is an emerging resilience-building tool in response to widespread and severe coral bleaching events (Chung et al. 2019).

Sponge-dominated reefs may increase in occurrence in a future ocean (Norstrom et al. 2009, Gonzalez-Rivero et al. 2011, Pawlik 2011, Bell et al. 2013, Easson et al. 2014, Farnham and Bell 2018), although for *Cliona*, the most abundant bioeroding sponges on the GBR, densities and benthic cover have not increased and trends are likely to be site-specific (Ramsby et al. 2017). Interestingly, phototrophic sponges appear to be more resilient to ocean warming and acidification than their heterotrophic counterparts, which may influence community structures towards phototrophic species (Bennett et al. 2017, Bennett et al. 2018). Stark increases in the density of the colonial ascidian, *Didemnum molle*, have also been documented following warming and widespread coral bleaching on the GBR, perhaps linked to reduced competition for space and nutrients and/or reduced predation pressure (Tebbett et al. 2019). It will be increasingly important to determine the competitive relationships between non-coral phase shift drivers (e.g. algae, sponges, ascidians) and how they alter trophic pathways and energy flows on future coral reefs (Norstrom et al. 2009, Maldonado et al. 2015, Bell et al. 2018, Tebbett et al. 2019).

For other marine invertebrates, additive stress from corallivorous gastropods (e.g. *Drupella*) and sea stars (e.g. CoTS) through coral predation may reduce the resilience and recovery of corals to thermal stress and bleaching (Bruckner et al. 2017, Shaver et al. 2018, Keesing et al. 2019). Marine worms were not considered vulnerable to any stressor, except for *Spirobranchus* to ocean warming, owing to its dependence on live coral substrate and a range of coral-host associations (Strathmann et al. 1984, DeVantier et al. 1986, Dai and Yang 1995, Ben-Tzvi et al. 2006, Rowley 2008). Though, increased water circulation close to the coral surface as caused by *Spirobranchus* (Figure 7) may decrease host susceptibility to bleaching (Strathmann et al. 1984), as posited for other coral-associated groups (Chase et al. 2018).

3.3.1.2 Ocean acidification

Changes in ocean chemistry (e.g. pH and carbonate ions) are attributable to increased anthropogenic CO_2 in the atmosphere and corresponding CO_2 dissolved by the world's oceans (Kleypas et al. 1999, Caldeira and Wickett 2005, Orr et al. 2005). Resultant decreases in seawater pH and the reduced availability of carbonate ions will directly impair the ability for calcifying organisms to develop their skeletons and shells, including for corals (Hoegh-Guldberg 2005, Przeslawski et al. 2008, De'ath et al. 2009, Anthony et al. 2011b, Fabricius et al. 2011, Wild et al. 2011, Connell et al. 2013, Dove et al. 2013). Coral reefs are among the most sensitive ecosystems to changes in ocean chemistry as they are fundamentally dependent on calcification to support both habitat and production functioning (Hoegh-Guldberg 2005, Anthony et al. 2011b, Albright et al. 2016a).

CCA ranked as the most vulnerable algal group to climate change stressors (Table 9), while other algae may benefit from waters higher in temperature (warming) and CO_2 (acidification) with a competitive advantage over corals (Diaz-Pulido and McCook 2002, Diaz-Pulido et al. 2007, Diaz-Pulido et al. 2009, Diaz-Pulido et al. 2011b); though this is not the case for all macroalgae (Bender et al. 2012, 2014a). CCA may even be more sensitive than some corals, exhibiting greater skeletal dissolution due to its high magnesium-calcite carbonate form, and reduced productivity, diversity, growth and survival when exposed to ocean acidification and/or warming (Anthony et al. 2008, Nelson 2009, Diaz-Pulido et al. 2012, Ordonez et al. 2014, McCoy and Kamenos 2015, Cornwall et al. 2019). Variability in natural conditions as driven by diel cycles (particularly in the intertidal) may heighten the sensitivity of CCA to decreases in ocean pH, converse to that suggested for organisms exposed and adapted to naturally extreme conditions (Camp et al. 2018a, Johnson et al. 2019). For example, it is suggested that large benthic Foraminifera show varied responses to ocean change stressors due to their exposure to extreme conditions in shallow-water intertidal environments (Fujita et al. 2011, Doo et al. 2014, Schmidt et al. 2014, Prazeres et al. 2015, Schmidt et al. 2016). However, any impact on the ability for foraminiferans to calcify will have long-term impacts on reef carbonate dynamics and sediment processes (Dawson et al. 2014).

Records of skeletal growth of massive *Porites* corals indicate a measurable decrease in coral calcification on the GBR over the past few decades (De'ath et al. 2009, De'ath et al. 2013), but with high spatial and temporal variability in trends (D'Olivo et al. 2013) and potentially just reflecting short-term responses to thermal stress events (Cantin and Lough 2014). Reduced calcification rates have also been reported for a range of branching corals on the GBR and elsewhere, including for acroporids and pocilloporids (Manzello 2010, Pratchett et al. 2015, Anderson et al. 2017, Anderson et al. 2018), and in total carbonate budgets (Case Study 2). Structural branching coral forms are possibly more vulnerable to ocean acidification than robust massive forms (Fabricius et al. 2011, Madin et al. 2012). There are also notable changes in the diversity of the coral microbiome under acidified conditions, which may have concomitant implications for reef structure, recruitment and total functioning (Mouchka et al. 2010, Krause et al. 2012, Doropoulos and Diaz-Pulido 2013, Webster et al. 2013a, Webster et al. 2013b, Webster et al. 2016, Grottoli et al. 2018, Wee et al. 2019). However, the coral microbiome can enhance the transgenerational adaptive plasticity of corals in support of reef adaptation and resilience (Torda et al. 2017, Webster and Reusch 2017).

Coral reefs may switch to a state of net dissolution in the coming decades due to changes in ocean temperature and chemistry, with significant impacts on net ecosystem calcification (Silverman et al. 2012, Albright et al. 2013, Kennedy et al. 2013, Silverman et al. 2014, Albright et al. 2018, Cyronak et al. 2018, Eyre et al. 2018, McMahon et al. 2019), sediment dynamics (Eyre et al. 2014, Cyronak and Eyre 2016), and reef recovery (Osborne et al. 2017). On Lizard Island, GBR, net ecosystem calcification decreased by ~46% between 2009 and 2016, measured immediately after extensive coral bleaching (McMahon et al. 2019). Parallel to decreases in calcification, bioerosion rates are accelerating in line with ocean change, which is itself emerging as a significant stressor in terms of reef health and future reef resilience (Reyes-Nivia et al. 2013, DeCarlo et al. 2015, Manzello et al. 2017, Schönberg et al. 2017). The total carbonate budget across the GBR may soon be in a state of net dissolution and erosion, as may already be the case for some reefs (Case Study 2). This trajectory indicates that the GBR may enter a critical negative state in which erosive processes surpass carbonate accretion in a changing ocean with critical impacts on habitat and production functions, as suggested for other reefs (Kennedy et al. 2013, Manzello et al. 2017). However, the ability for some bioeroding organisms, like clionid sponges, to persist in a future ocean may too be impacted (Achlatis et al. 2017, Fang et al. 2018, Ramsby et al. 2018a).

Most marine invertebrate groups rated as highly vulnerable to the impacts of ocean warming and acidification (Table 9), with an abundance of research and reviews documenting survival bottlenecks across life-history stages, particularly for calcifying marine larvae and adults (Przeslawski et al. 2008, Byrne 2011, Bhadury 2015, Przeslawski et al. 2015, Espinel-Velasco et al. 2018). Tropical sea urchin larvae are considered among the most vulnerable (Byrne et al. 2013). It is not surprising that calcifiers were considered the most vulnerable to ocean acidification here (Table 9). Yet, the effects of ocean acidification and the energetic stress of hypercapnia extend well beyond the calcification process, being observed to cause a range of sensory, cognitive and behavioural abnormalities across reef invertebrate and fish life histories (Munday et al. 2009a, Briffa et al. 2012, Devine et al. 2012, Domenici et al. 2012, Munday et al. 2012, Allan et al. 2013, Munday et al. 2014, Watson et al. 2014, Ferrari et al. 2017, Jarrold et al. 2017, Watson et al. 2017, Espinel-Velasco et al. 2018), as well as altered predatory-prey dynamics (Munday et al. 2010, Allan et al. 2013, Heinrich et al. 2016, Watson et al. 2017, Spady et al. 2018). Ocean acidification will also impact settlement success on coral reefs through changes in the nature and distribution of suitable settlement cues and substrates, including CCA and biofilm (Doropoulos et al. 2012a, Doropoulos and Diaz-Pulido 2013, Espinel-Velasco et al. 2018). Habitat degradation reduces post-settlement success of corals and shifts towards algal-dominated systems may limit reef recovery (Roth et al. 2018).

There will be spatial variability in the responses of reef organisms to climate change stressors, owing to thermal histories, local adaptation and regional disparities in exposure (Uthicke et al. 2014, Siboni et al. 2015, Hughes et al. 2018b, Stuart-Smith et al. 2018). Intertidal and coastal organisms may be less susceptible to future conditions owing to their current exposure to diel fluctuations (e.g. pH, temperature, oxygen), while offshore and open-ocean organisms may be most vulnerable as they typically experience the most constant conditions (Byrne 2011, Jarrold et al. 2017, Jarrold and Munday 2018). Biota permanently in the plankton (e.g. copepods, pteropods), which typically have short generation times, may have resilience in their ability to respond to changes in ocean conditions compared to species with longer generational turnover (McKinnon et al. 2007). Ocean acidification may even enhance certain processes including bioerosion rates (Reyes-Nivia et al. 2013, Enochs et al. 2015, Schönberg et al. 2017) with potential impacts on reef carbonate budgets (Wisshak et al. 2014, Manzello et al. 2017). Light intensity may work to ameliorate the negative effects of acidification on photosynthesising species like corals (Dufault et al. 2013, Wall et al. 2017) and giant clams (Watson 2015). Tropical deposit-feeding sea cucumbers may partially buffer the impacts of ocean acidification through their bioturbation activity and contributions to reef biogeochemistry (Schneider et al. 2011, Schneider et al. 2013, Wolfe et al. 2018). This has been posited for the mega-consumer and excreter of coral carbonates, *Bolbometopon muricatum* (Goldberg et al. 2019), but this remains poorly addressed for parrotfishes in general. Seagrasses, macroalgae and a range of other species may also contribute to the biogenic buffering of reef carbonate chemistry owing to their relative roles in the balance between photosynthesis (i.e. O_2 production) and respiration (i.e. CO_2 production) (Anthony et al. 2011a, McCulloch et al. 2012, Smith et al. 2013, Cornwall et al. 2014, Mongin et al. 2016a, Page et al. 2016, DeCarlo et al. 2017). This presents a potential management strategy through *in situ* cultivation of macroalgae (Mongin et al. 2016a).

3.3.1.3 Cyclones

While tropical cyclones are not expected to increase in occurrence in a changing climate, they are predicted to increase in severity. The likelihood of more intense cyclones within timeframes of coral recovery by the mid-century presents significant global threat to coral reefs and those that depend on them (Cheal et al. 2017). Cyclones were suggested to have the strongest impact on sessile marine invertebrates; branching corals (tabular, staghorn, other species), sponges (heterotrophic, phototrophic), and giant clams (Tridacnidae) (Table 9). At the whole-reef scale, mean rates of coral loss on the GBR are projected to be -0.67% y^{-1}, largely attributed to cyclone damage (Mellin et al. 2019). At the colony level, morphology plays an important role in the biophysical impacts of cyclones, which are often most severe for fragile branching corals compared to robust massive forms (Woodley et al. 1981, Connell et al. 1997, Hughes and Connell 1999, Adjeroud et al. 2005, Madin 2005, Madin and Connolly 2006, Madin et al. 2014).

The long-term effects of cyclones (i.e. habitat degradation) may have the greatest impact on coral reef fishes and fisheries production (Cheal et al. 2002), but impacts will vary across communities depending on species, depth ranges and exposure gradients (windward, protected) (Ceccarelli et al. 2016). Site-attached reef fishes (e.g. cryptobenthics, damsels, planktivores, cleaner wrasse) scored as the most vulnerable fish groups to cyclones (Table 9). Small fish species that rely on corals for survival may be particularly vulnerable to the habitat loss and increased predation pressure attributed to cyclone damage (Lassig 1983, Harmelin-Vivien 1994, Coker et al. 2009, Ceccarelli et al. 2016). Conversely, resident predatory fishes, which also depend on coral habitat, may be largely resilient to a range of environmental disturbances on the GBR (Emslie et al. 2017). Damselfish assemblages have generally been well retained within their relative regional settings on the GBR with assemblage degradation only associated with major coral losses (Emslie et al. 2019). Operating on site-specific cleaning stations, cleaner wrasse populations were documented to decline by 80% following a sequential cyclone and El Niño (warming) event on Lizard Island, GBR (Triki et al. 2018). Following extensive habitat loss due to tropical Cyclone Ita, some invertivorous fishes increased in biomass (the titan triggerfish (*Balistoides viridescens*), darkspot tuskfish (*Choerodon monostigma*) and sidespot goatfish (*Parupeneus pleurostigma*), suggesting they may benefit from novel resources made available for exploitation post-disturbance (Brandl et al. 2016). Grazing fishes (e.g. detritivores, parrotfishes) may help to maintain fish diversity post-disturbance on some reefs (Wilson et al. 2009, Ceccarelli et al. 2016).

3.3.2 Stressor-specific vulnerabilities - Fisheries

Ultimately, management of climate change stressors depends on fast action towards a low-carbon economy, but this must be augmented with local action to prevent degradation of reef structures and associated losses of ecosystem functions and services (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Overfishing is considered one of the greatest local threats to coral reefs (Jackson et al. 2001, Garcia and Moreno 2003, Bellwood et al. 2004, Newton et al. 2007, Cinner et al. 2016, Cinner et al. 2018). Our partitioning of species here to broader taxonomic and functional levels does not fully encapsulate species-specific vulnerabilities to overfishing, but rather the groups most broadly at risk. Impacts from fishing were greatest for predatory reef fishes (resident and transient), and for deposit-feeding sea cucumbers (Table 9). While fishing intensity is relatively low at regional scales, commercial fisheries have increased in effort (~40%) and catch (~50%) since the 1990s (Mapstone et al. 2004). Regardless, fin-fish fisheries are generally well-managed on the GBR (Williamson et al. 2004, DEE 2017), with reef resilience enhanced through marine park zoning (Mellin et al. 2016). Unlike on other reefs globally, the fishing of herbivores is marginal on the GBR (Case Study 4; Appendix 7).

The primary fin-fish species targeted on the GBR is the coral trout (*Plectropomus* spp.), considered here as a resident piscivore. An estimated 749 tonnes of coral trout are commercially harvested from the GBR each year, with >100,000 additional individuals harvested by recreational spear and line fishers, annually (DEE 2017). Globally, many *Plectropomus* populations are in decline due to the combined effects of overfishing and habitat degradation (Frisch et al. 2016a). On the GBR, coral trout, and a range of other predatory fishes, benefit from no-take zones through increases in biomass, density and size compared to sites open to fishing (Williamson et al. 2004, Heupel et al. 2009, Miller et al. 2012, Emslie et al. 2015, Casey et al. 2017, Castro-Sanguino et al. 2017, Frisch and Rizzari 2019), including in context of recreational spearfishing (Case Study 4; Appendix 7). No-take reserves also preserve the natural behaviour of coral trout with potential influences on genetic and social structures (Bergseth et al. 2016). In a global context, the status of *P. leopardus* was recently re-evaluated from a Near Threatened to a Least Concern species (Choat and Samoilys 2018), and its fishery on the GBR is well monitored and managed (DEE 2017). For some larger target species, such as sharks, illegal harvest in no-take zones may continue to have significant impacts on population structures (Stevens et al. 2000, Davis et al. 2004, Robbins et al. 2006, McCook et al. 2010, Bergseth et al. 2017, Weekers and Zahnow 2018, Frisch and Rizzari 2019). The Queensland shark control program also contributes to the extraction of these predators, with around 500–700 sharks removed from Queensland waters each year (QGSO 2019). There has been a regional depletion of shark populations over the past half-century since the onset of this control program with concurrent declines in body size and probability of encountering mature individuals, suggesting sharks on the Queensland coastline are more vulnerable to exploitation than previously thought (Roff et al. 2018).

Case Study 4: Spatial patterns and functional impacts of recreational spearfishing on the GBR

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Of the recreational fishing methods, spearfishing is a small but contentious component (Godoy et al. 2010, Young et al. 2015). Given the well-documented impacts of line fishing from discarded pollution, lost gear, the requirement of bait and frequent levels of bycatch, spearfishing may be considered the more sustainable practice (Frisch et al. 2008). Yet, in a comparison between line and spearfishers on the GBR, despite a similar catch composition and landing fewer fish overall, the mean size of fish caught by spearfishers was significantly greater (Frisch et al. 2008). Spearfishing is a highly selective method where participants can target specific individuals based on species and size, with limited impacts on non-target species (Dalzell et al. 1996, Bejarano Chavarro et al. 2014). So, while spearfishing may have a seemingly smaller impact on the marine environment, selectivity towards large individuals (that are likely fecund) and particular trophy species, may result in negative impacts to viable breeding stocks (Hughes et al. 2007a, Meyer 2007, Frisch et al. 2008, Godoy et al. 2010, Frisch et al. 2012). For example, just three years after the introduction of spearfishing on an inshore reef near Townsville, vast decreases in the number (54%) and size (27%) of coral trout (*Plectropomus* spp.) – the primary fisheries target on the GBR – were recorded (Frisch et al. 2012). There is potential for recreational line and spearfishing to have broadly equivalent impacts on the marine environment (Frisch et al. 2008), but the lack of information on spearfishing often causes it to be overlooked in fisheries management (Johansson et al. 2013, Pavlowich and Kapuscinski 2017), as for recreational fishing in general.

In a survey of over 140 spearfishers that operate on the GBR, the proportion of time spent spearfishing in coastal, inshore and offshore regions varied from Bundaberg (south) to Cooktown (north) (Figure CS4.1). Spearfishers from the North GBR (Cooktown, Cairns, Townsville) spent the greatest proportion time on offshore reefs. Those from Mackay represented the greatest proportion operating directly from the coastline, while spearfishers from Bowen preferred inshore regions. The incremental level of spearfishing pressure from coastal (14%) to inshore (32%) to offshore (54%) regions from Townsville may reflect historical patterns of overfishing on near-shore reefs around this location (Frisch et al. 2012), and an increased necessity to travel offshore in search of a successful catch (Young et al. 2016a).

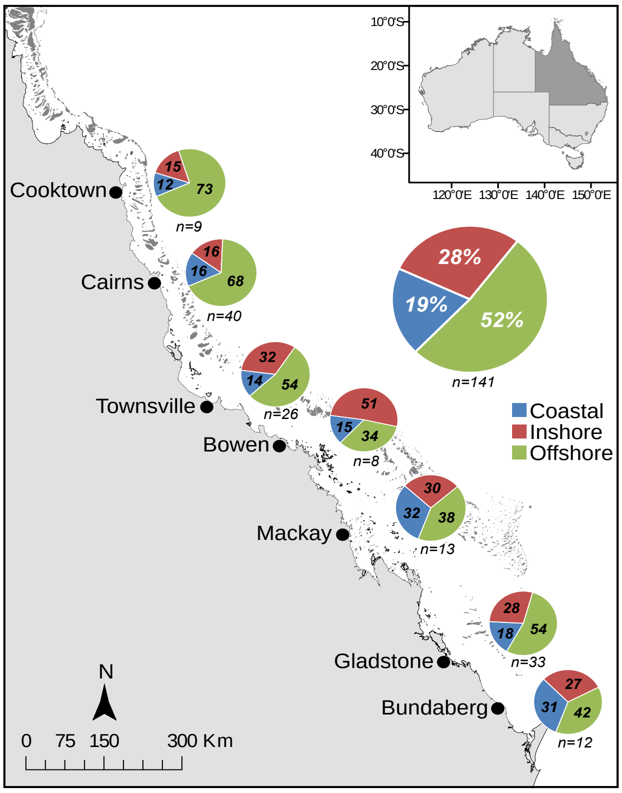

Figure CS4.1: Proportion of time spent on the GBR by spearfishers from major cities along the Queensland coast. Colours reflect the percentage of time spent on coastal, inshore and offshore reefs.

Twenty-two common coral reef fishes were used to examine spearfishing catches on the GBR (for a full list see Table 1, Appendix 7). Species included herbivorous, invertivorous and piscivorous representatives. Nominally piscivorous species including Lutjanidae, Lethrinidae and *Plectropomus*, represented ~75% of the recalled catch of spearfishers, while herbivorous fishes were lesser preferred (Figure CS4.2). Coral trout (*Plectropomus* spp.) dominated catches (34% total catch) (Figure CS4.2), which is also the primary target of recreational line-based and commercial fisheries on the GBR (Leigh et al. 2014, DEE 2017). In a global context, the status of *P. leopardus* was recently re-evaluated from a Near Threatened to a Least Concern species (Choat and Samoilys 2018), and its fishery on the GBR is considered to be well monitored and managed (DEE 2017). Invertivorous tuskfishes (*Choerodon* spp.) were often the primary drivers of catch differences among locations, most favoured by spearfishers operating from Bowen and Cairns (Figure CS4.2). The drivers of these spatial differences in tuskfish preferences remain unknown, especially given their broad distribution across the GBR (Platten et al. 2002, Fairclough et al. 2008). As a Near Threatened and monandric protogynous hermaphrotidic species where males only occur in the largest size bracket (Fairclough and Nakazono 2004), the black-spot tuskfish (*C. schoenleinii*) may be particularly vulnerable to the selectivity of spearfishing. Interestingly, the venus tuskfish (*C. venustus*) can alter its sex-ratio in response to overfishing (Platten et al. 2002). Regardless, the reproductive biology of tuskfishes has resulted in rapid population declines on other coral reefs owing to overfishing (Ebisawa et al. 1995, Cornish 2003, Fairclough and Nakazono 2004), highlighting the importance of (1) educating groups on fishing-selectivity for species with vulnerable reproduction, and (2) monitoring catch trends for key species within the spearfishing community.

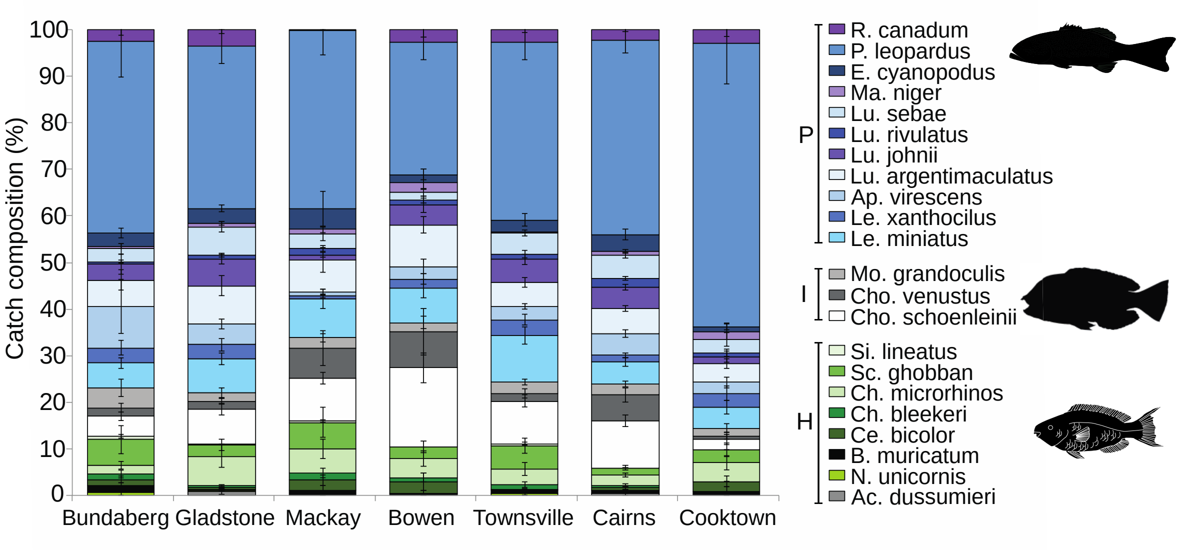

Figure CS4.2: Mean proportion of study species in spearfishing catches across seven major cities along the GBR coastline. Species grouped by functional guild (H: herbivores=greens; I: invertivores=greys; P: piscivores=blues).

Herbivorous coral reef fishes were rarely included in the catches of spearfishers (Figure CS4.2), but the steephead parrotfish (*Chlorurus microrhinos*) and the blue-barred parrotfish (*Scarus ghobban*) were among the greatest contributors to variations in predicted catches among locations. Both species represented ~3% of the total catch composition of spearfishers, are broadly distributed on the GBR (Cheal et al. 2012), but vary in their ecological and functional significance. The steephead parrotfish is particularly important on midshelf reefs, while *Scarus* spp. are more functionally important inshore (Bellwood and Choat 1990, Bellwood et al. 2003, Hoey and Bellwood 2008). Generally, parrotfishes were more heavily targeted in coastal and inshore regions, where their functional importance might be comparatively high (Bellwood et al. 2003, Hoey and Bellwood 2008). Despite their relatively low contribution to the total catch of spearfishers across the GBR, the selectivity of spearfishing towards some herbivores could drive significant alterations to the ecological functioning of inshore reefs, particularly given the propensity for algal growth inshore (Diaz-Pulido et al. 2009, Wolff et al. 2018a). Interestingly, the region with the greatest reported catch composition of herbivores (Mackay) (Figure CS4.2), also most frequently fished from the coastline (Figure CS4.1). A demographic analysis of fishery impacts on parrotfishes would be desirable for the GBR, as has been done elsewhere (e.g. (Bozec et al. 2016).

Deposit-feeding sea cucumbers are particularly prone to overfishing due to their ease of collection and our general lack of scientific information on their biology and ecology to empower management (Uthicke et al. 2004, Purcell et al. 2013). The sea cucumber (bêche-de-mer) fishery currently operating on the GBR has a history of exploitation, with trends of sequential population declines across species with high market value (Eriksson and Byrne 2015), and continued occurrence of illegal harvest inside the Marine Park bounds (Conand 2018). In 2004, a rotational harvest scheme was implemented as a management tool, but concerns have been raised regarding its effectiveness as recovery of depleted populations may still be marginal, and caches of high-valued species continue to decline (GBRMPA 2014b, Purcell et al. 2016b). At least ten sea cucumber species found on the GBR are listed as Vulnerable to extinction on the IUCN Red List for Threatened Species (Conand et al. 2014, Purcell et al. 2014, Richards and Day 2018). There is particular concern for the black teatfish (*Holothuria whitmaei*), as its fishery, which was closed in 1999 due to widespread overharvest (Uthicke et al. 2004, Eriksson and Byrne 2015), may be reopening (DAF 2018) without fisheries-independent data to indicate whether populations have recovered. Quantitative information on bêche-de-mer populations along and across the GBR is imperative to inform management independent of fisheries.

Interestingly, no other group scored as vulnerable to fisheries (Table 9; Appendix 3). We acknowledge that an assessment beyond the broad taxonomic and functional groups here is necessary to determine specific impacts from fisheries on the GBR. Such future work should include additional consideration of social, cultural and economic values on the reef. A range of fishing-related impacts are documented on the GBR, resulting from derelict fishing gear that can entangle corals and increase disease susceptibility (Williamson et al. 2014a), anchor and vessel damage (Beeden et al. 2014a, Kininmonth et al. 2014), frequent by-catch from commercial fisheries (Hill and Wassenberg 2000), and illegal practices in no-take zones (Davis et al. 2004, Arias and Sutton 2013, Williamson et al. 2014a, Bergseth et al. 2015, Weekers and Zahnow 2018). The impact of recreational spearfishing is assessed in detail in Case Study 4. While this fishing method has the potential to impact viable fish stocks (Hughes et al. 2007a, Meyer 2007, Frisch et al. 2008, Godoy et al. 2010, Frisch et al. 2012), the Queensland (and Australian) spearfishing community has been highly responsive to previous management campaigns, and exhibit self-regulatory and monitoring approaches that are vital to fisheries conservation and advocacy (Young et al. 2014, GBRMPA 2016, Young et al. 2016b).

3.3.3 Stressor-specific vulnerabilities – Population outbreaks

There are a range of species, particularly non-coral marine invertebrates, that exhibit marked population fluxes on coral reefs (Norstrom et al. 2009). The boom-and-bust phenomenon of echnioderms is well documented (Uthicke et al. 2009). On the GBR, outbreaks of *Acanthaster* cf. *solaris* (CoTS; Figure 11) are the most extensive, destructive and researched outbreak candidate, gaining considerable traction in reef management (Westcott et al. 2016, Sweatman and Cappo 2018). As scored here, population outbreaks (namely regarding CoTS) were outlined to have the greatest potential impact on tabular, staghorn and other branching corals (Table 9). *Acropora* and *Montipora* are the preferred coral genera of CoTS across the Pacific (Laxton 1974a, Pratchett et al. 2014, Westcott et al. 2016), though even the lesser-preferred coral species are consumed during extreme outbreaks or when food is scarce (Chesher 1969, Pearson and Endean 1969). At the whole-reef scale, corallivory by CoTS in outbreak densities has been attributed to ~42% of the declines in live coral cover on the GBR (De'ath et al. 2012). However, this statistic is likely to be much lower at present in light of extensive coral bleaching in 2016 and 2017 (Hughes et al. 2017b, Hughes et al. 2018b, Hughes et al. 2018c).

Figure 11: Population outbreaks of CoTS (Acanthaster spp.) (left) and Drupella (right) can exacerbate reefs, leaving a bleached-white feeding scar on their coral prey.

Outbreaks of other marine invertebrates have received considerably less attention on the GBR, and in general. High densities of *Drupella* (Mollusca) (Figure 11) can have significant impacts on reef condition, documented to reduce live coral cover by >75% on some reefs (Turner 1994, Scott et al. 2017a). Their effects can be even more significant following bleaching-induced coral mortality, which can impact coral resilience and recovery (Bruckner et al. 2017, Keesing et al. 2019), as for other corallivorous gastropods (Shaver et al. 2018). But while *Drupella* spp. are present on the GBR, such extensive impacts have not been documented (Cumming 2009). Stark increases in the density of the colonial ascidian, *Didemnum molle*, were recently documented on Lizard Island following pervasive coral bleaching (Tebbett et al. 2019). While corallivorous species like CoTS and *Drupella* (Figure 11) have direct impacts on corals through predation, rapid expansions of opportunistic sessile organisms, like these ascidians, can impact reef recovery and resilience through competition for food and space, and potential toxicity (Bak et al. 1996, Tebbett et al. 2019). Even at highly localised scales, population outbreaks of alternative opportunistic and ephemeral invertebrates can have repercussions on coral recruitment, recovery and functioning (Zhang et al. 2018). Ecosystem states are dynamic in terms of time and space (van de Leemput et al. 2016), and phase shifts beyond the typical coral-algal model are increasingly common as reefs degrade (Norstrom et al. 2009).

In general, there has been little documentation of extensive impacts from invasive or introduced species in the marine environment of the GBR, with a greater representation and impacts documented for mainland and island habitats (GBRMPA 2014b).

3.3.4 Stressor-specific vulnerabilities – Water quality and disease

Diseases are poorly understood for corals and other marine species on the GBR, despite documentation of widespread proliferation in some cases (Richardson 1998, Willis et al. 2004, Roff et al. 2011, Shore and Caldwell 2019). While scores were considerably lower for disease than for a number of other stressors, acroporids (tabular and staghorn) rated as the most vulnerable to disease (Table 9). White Syndrome primarily impacts tabular acroporids compared to other coral species and functional forms (Hobbs and Frisch 2010, Hobbs et al. 2015). Coral disease can reduce net growth rates of corals, particularly tabular acroporids, by ~20% (Roff et al. 2008, Maynard et al. 2011). Disease proliferation is largely induced by temperature anomalies (Bruno et al. 2007, Harvell et al. 2007, Sato et al. 2009, Maynard et al. 2011, Sato et al. 2011, Ruiz-Morenol et al. 2012, Sato et al. 2016, van de Water et al. 2016, Chen et al. 2017), but can also be expedited by plastic pollution (Lamb et al. 2018), runoff and sedimentation (Haapkyla et al. 2011, Pollock et al. 2016), cyclone damage (Sato et al. 2018), tourism (Lamb and Willis 2011, Lamb et al. 2014, van de Water et al. 2015), and fisheries activity (Diaz-Pulido et al. 2009, Page et al. 2009, Graham et al. 2011a, Williamson et al. 2014a, Lamb et al. 2015, Lamb et al. 2016). While the transmission of coral disease between individuals and among populations remains understudied (Shore and Caldwell 2019), it seems that any considerable stressor can enhance disease susceptibility on coral reefs, particularly inshore on the GBR (MacNeil et al. 2019). Disease management on the GBR focuses on continued research and monitoring of disease outbreaks to facilitate local response plans (Maynard et al. 2011, Beeden et al. 2012).

Water quality stressors (nutrients, sediments, pollutants) were not considered huge threats in the context of offshore reefs (Table 9), assumedly driven by low exposure at distance from the coastline. When assessed in context of near-shore reefs, nutrients, sediments and pollutants were considered to have greater impacts across our functional groups (Appendix 3). Declining water quality is considered one of the greatest threats to the long-term health of the GBR, but most critically for inshore reefs (Brodie and Waterhouse 2012, Lam et al. 2018, MacNeil et al. 2019). While consistent exposure to poor water quality may render inshore reefs more resilient (Browne 2012, Perry et al. 2012b), they may exhibit slower rates of growth and recovery (MacNeil et al. 2019, Mellin et al. 2019). Spatially, nutrient (e.g. chlorophyll *a*) levels on the GBR typically increase from north to south, and from outer to inner coastal regions, supporting bottom-up processes from the plankton along these gradients (Skerratt et al. 2019). It appears that dissolved inorganic nitrogen, primary production, phytoplankton biomass and zooplankton grazing are elevated in La Niña years, driven by greater average winds, rainfall and river discharge (Skerratt et al. 2019). A range of species in the plankton (e.g. copepods, Appendicularia) are reported to increase in abundance on anthropogenically-disturbed reefs possibly due to increases in terrestrial runoff and nutrients (Carrillo-Baltodano and Morales-Ramirez 2016, Dupuy et al. 2016).

Sediment loads on inshore reefs were considered a significant stressor for many of the species examined here (Table 9; Appendix 3), in line with the literature (Bainbridge et al. 2009, Brodie et al. 2013, Tsatsaros et al. 2013, Waterhouse et al. 2013, Bainbridge et al. 2014). Only a small proportion of land-derived sediment reaches mid- to outer-reefs on the GBR (Bartley et al. 2014). Sediments can have a range of impacts on coral reef communities through elevated turbidity gradients, reduced light availability and the physical smothering of sessile organisms, and fine sediments typically have greater impacts on coral reefs than course sediments (Erftemeijer et al. 2012). On the GBR, macroalgal and bioeroding communities show a positive relationship with suspended sediment concentrations, contrasting the negative relationship observed for coral and CCA cover (Fabricius and De'ath 2001b, 2004, Fabricius et al. 2005, Hutchings et al. 2005, Bessell-Browne et al. 2017b). Sediments and high turbidity alter reef structure, reproduction, larval success, recruitment, bioerosion and species interactions on inshore reefs (Babcock and Davies 1991, Fabricius 2005, Fabricius et al. 2005, Hutchings et al. 2005), with extensive dredging activity posing considerable risk (Erftemeijer et al. 2012, Jones et al. 2016, Bessell-Browne et al. 2017a, Pineda et al. 2017b, Tebbett et al. 2017d).

Sessile and filter-feeding invertebrates are possibly most susceptible to sediment loads, including corals, sponges and giant clams (Elfwing et al. 2003, Przeslawski et al. 2008). However, some nearshore reefs appear resilient to turbidity, maintaining relatively rapid accretion rates and high coral cover (Browne et al. 2010, Browne 2012, Perry et al. 2012b, Browne et al. 2013), but with trade-offs in feeding regimes (Anthony 2000, Anthony and Fabricius 2000, Anthony and Connolly 2004), morphology (Browne et al. 2010, Padilla-Gamino et al. 2012, Duckworth et al. 2017) and skeletal density (Rocker et al. 2017). Sponges rated among the most vulnerable to sediments and pollutants (Table 9; Appendix 3), yet both sponges and their microbiomes seem resilient to high sediment loads on the GBR (Pineda et al. 2017b, Pineda et al. 2017c, Strehlow et al. 2017), and some species may even thrive (Bell et al. 2015). While responses are variable (Pineda et al. 2017a), the diversity of sponges, even at small cryptic scales, may offer some resilience to sediment and pollutant loads (Schönberg 2001, 2016). Increases in the benthic cover of *Cliona*, the most abundant bioeroding sponge on the GBR, are greatest when algal cover and nutrient levels are low (Ramsby et al. 2017).

For reef fish communities, increased suspended sediments can impact foraging, growth, larval development, behaviour and predator-prey interactions (Wenger et al. 2011, 2012, Wenger et al. 2013, Wenger et al. 2014). Foraging success of visual predators like planktivorous damselfishes can be significantly impaired in turbid environments (Wenger et al. 2012, Johansen and Jones 2013). Herbivorous fishes rated among the most vulnerable to sediments (Table 9; Appendix 3), with some species shown to decrease grazing activity when sediments loads are too high in the EAM (Bellwood and Fulton 2008, Goatley and Bellwood 2012, Goatley et al. 2016, Gordon et al. 2016b). This can be expedited by turf canopy height, whereby taller canopies trap sediments with negative impacts on herbivory and coral recruitment (Carpenter and Williams 1993, Birrell et al. 2005, Bellwood and Fulton 2008, Arnold et al. 2010, Goatley and Bellwood 2012, Clausing et al. 2014, Lam et al. 2018). Interestingly, some detritivores may be particularly important in removing sediment and detritus from the EAM, facilitating herbivory by other species (Goatley and Bellwood 2010, Marshell and Mumby 2012, 2015).

Habitat degradation associated with coral bleaching and freshwater flood plumes (Williamson et al. 2014b), has been shown to drive dietary shifts in both juvenile (Wen et al. 2016) and adult (Hempson et al. 2017) coral trout. This trophic plasticity involved consumption of non-preferred fishes in line with changes in foraging behaviour (Wen et al. 2016) and prey biomass (Hempson et al. 2017). Although dietary adaptive capacity may mitigate short-term impacts of sedimentation and habitat degradation, it may result in a shortened and simplified trophic structure with a longer-term toll on ecosystem functioning (Graham et al. 2007, Estes et al. 2011, Hempson et al. 2017, Feary et al. 2018). How these stressors impact predator-prey dynamics are particularly important to characterise, particularly for key fisheries targets with ontogenetic shifts in diet, like coral trout (Case Study 1; Appendix 4).

Pesticides, herbicides, trace metals and agricultural nutrients (e.g. nitrogen, phosphorus) that influence eutrophication are commonly measured on near-shore reefs of the GBR at concentrations above Australian water quality guidelines (Lewis et al. 2009, Brodie and Waterhouse 2012, Lewis et al. 2012, Waterhouse et al. 2012, Brodie et al. 2013). However, few toxic pollutants on the GBR approach harmful concentrations, and if so, are typically only recorded during short-term runoff pulses (van Dam et al. 2011). Further, there is limited empirical evidence on how pesticides scale up to impact inshore ecosystem processes, functions and services (Fichez et al. 2005, van Dam et al. 2011, De Valck and Rolfe 2018). In context of nearshore systems, there is a lack of evidence that mangrove and seagrass biomes are negatively impacted by water quality stressors, but elevated nutrient levels, substrate availability and low grazing pressure suggest that nearshore benthic communities are shifting towards macroalgal dominance with impacts on reef functioning (Schaffelke et al. 2005).

On the GBR, the herbicide Diuron has received considerable attention, which can impact photosynthesis, fecundity, larval development and survival in a range of groups including corals, CCA, foraminiferans and sea urchins (Negri et al. 2005, Cantin et al. 2007, Magnusson et al. 2008, Shaw et al. 2009, Magnusson et al. 2012). Regarding bottom-up effects, biofilms (EAMs) may be resilient to herbicides but their community structure can be altered depending on exposure thresholds (Magnusson et al. 2012). *In situ* nutrient dosages of nitrogen and phosphorus impacted coral growth, recruitment and skeletal density, but only when loading was high and generally with sublethal effects (Koop et al. 2001, Bell et al. 2007). Elevated nutrient levels can also enhance microbioerosion, making it imperative to manage water quality as coral reefs degrade (Chazottes et al. 2017). Most significantly, elevated nutrients have been attributed to CoTS outbreaks on the GBR through the enhancement of success in pelagic larval life stages, which has received considerable attention in the literature (Brodie et al. 2005, Fabricius et al. 2010, Wooldridge and Brodie 2015, Babcock et al. 2016a, Wolfe et al. 2017, Uthicke et al. 2018, Wolff et al. 2018b), although the links are tenuous and unresolved (Pratchett et al. 2014, Pratchett et al. 2017a, Wolfe et al. 2017).

Overall, water quality stressors are likely to combine with other environmental factors with significant additive impacts, particularly in context of thermal stress (Wooldridge and Done 2009, Negri et al. 2011, van Dam et al. 2011, Lewis et al. 2012, van Dam et al. 2012, van Dam et al. 2015, Banc-Prandi and Fine 2019). Early monitoring of runoff loads, particularly following heavy rainfall and flood events, has resulted in tighter regulations and catchment management in the GBR region (Brodie and Waterhouse 2012, Brodie et al. 2012). Even though water quality issues have been a strong management focus on the GBR, current initiatives to improve or reverse pollutant loads are not being met (De Valck and Rolfe 2018). Better understanding of the direct impacts of pollutants on coral reef organisms, and the functions and services they provide, is essential to ensure management goals are biologically relevant and post-disturbance recovery is supported (Fichez et al. 2005, van Dam et al. 2011).

3.3.5 Total vulnerability and recoverability

Using the IPCC Vulnerability Framework (IPCC 2007), corals were outlined as the most vulnerable across the nine stressors for both inner reef and offshore regions (Table 10). Vulnerability scores were generally higher for inner reefs compared to reefs offshore, owing to the additional impacts from water quality in close proximity to the coastline. Branching and tabular corals were rated the most vulnerable of our 70 groups, but with tabular corals rated to have a higher level of recoverability (Table 10). Host-associated phototrophic microbes were the most vulnerable microbial group, considered especially vulnerable inshore, as for CCA (Table 10). The most vulnerable invertebrates were coral-associated decapods, several mollusc groups (particularly giant clams; Tridacnidae), and deposit-feeding sea cucumbers (Table 10). Piscivores (resident, transient) were considered the most vulnerable of the reef fishes with the lowest recovery potential, strongly influenced by their potential to be impacted by fisheries (Table 9; Appendix 3). Staghorn and massive corals were predicted to have the lowest recovery potential for corals, and the triton snail was rated lowest for recovery overall (Table 10). Once considered abundant, densities of triton snails on the GBR have remained extremely low since their extensive overharvest in the 1930s (Endean 1969, Endean and Stablum 1973, Hall et al. 2017). Deposit-feeding sea cucumbers were also suggested to have particularly low recovery potential (Table 10), as bêche-de-mer fisheries operating on the GBR follow global trends of overharvest with no fisheries-independent data available to suggest overfished populations have recovered (Eriksson and Byrne 2015, Purcell et al. 2016b).

Table 10: Total potential impact (PI) and vulnerability (V) of 70 functional groups on the GBR, including their predicted recoverability and certainty of scores. Values are shown for inshore and offshore reefs. H=herbivores, P=predators; DF=deposit feeders; SF=suspension feeders. Red cells = top 10th percentile of scores (bottom 10th for recoverability); yellow cells = top 75th percentile.

Taxa	Functional group	PI (Inner GBR)	V (Inner GBR)	PI (Outer GBR)	V (Outer GBR)	Recoverability	Certainty
Microbes	Phototrophic	30.00	40.00	11.00	14.67	0.75	0.75
	Host-associated	62.00	99.20	27.25	43.60	0.63	0.50
	Chemoautotrophic	14.00	18.67	5.00	6.67	0.75	0.63
	Heterotrophic	19.00	25.33	10.00	13.33	0.75	0.63
Algae	Phytoplankton	10.00	13.33	0.25	0.33	0.75	0.75
	Algal turfs	11.00	14.67	1.25	1.67	0.75	0.75
	Leathery	8.25	16.50	3.50	7.00	0.50	0.50
	Foliose	13.25	17.67	2.50	3.33	0.75	0.63
	Calcareous	23.25	46.50	12.50	25.00	0.50	0.50
	CCA	47.00	62.67	23.00	30.67	0.75	0.50
Sponges	Heterotrophic	44.33	76.00	27.89	47.81	0.58	0.50
	Phototrophic	47.11	80.76	24.00	41.14	0.58	0.50
	Boring	17.81	26.71	3.47	5.21	0.67	0.58
	Cryptic	29.00	49.71	6.25	10.71	0.58	0.50
Coral	Tabular	82.70	110.27	65.20	86.94	0.75	0.75
	Staghorn	83.03	147.62	65.53	116.51	0.56	0.69
	Branching (other)	79.81	116.09	63.73	92.70	0.69	0.69
	Massive	41.76	83.51	30.82	61.64	0.50	0.75
	Encrusting	45.51	66.19	32.51	47.28	0.69	0.69
	Free-living	37.87	55.08	28.62	41.63	0.69	0.56
	Soft corals	43.03	68.86	31.72	50.76	0.63	0.63
	Foraminifera	26.31	38.26	19.37	28.17	0.69	0.44
Worms	Nematodes	0.00	0.00	0.00	0.00	0.75	0.63
	Nemertea	0.25	0.33	0.25	0.33	0.75	0.38
	Polychaetes	0.25	0.33	0.25	0.33	0.75	0.38
	Spirobranchus	28.00	37.33	16.00	21.33	0.75	0.38
Crustaceans	Decapods (H)	29.00	38.67	25.00	33.33	0.75	0.38
	Decapods (P)	36.25	58.00	32.25	51.60	0.63	0.38
	Coral-associated	54.25	108.50	42.25	84.50	0.50	0.50
	Barnacles	26.00	34.67	19.00	25.33	0.75	0.38
	Stomatopods	22.25	29.67	18.25	24.33	0.75	0.38
	Cleaner shrimp	30.00	48.00	26.00	41.60	0.63	0.50
	Infauna	11.25	18.00	10.25	16.40	0.63	0.50
	Zooplankton	30.25	40.33	25.50	34.00	0.75	0.50
	Parasitic	14.25	19.00	13.25	17.67	0.75	0.50
Molluscs	Gastropods (H)	37.00	59.20	32.25	51.60	0.63	0.50
	Gastropods (P)	21.11	33.78	17.11	27.38	0.63	0.50
	Triton snails	21.36	56.96	17.36	46.30	0.38	0.50
	Drupella	36.25	48.33	32.25	43.00	0.75	0.63

	Tridacnidae	62.00	106.29	51.25	87.86	0.58	0.67
	Bivalves (other)	46.00	73.60	38.25	61.20	0.63	0.63
	Chitons	19.00	25.33	19.00	25.33	0.75	0.50
	Cephalopods	19.61	26.15	7.75	10.33	0.75	0.50
Echinoderms	Seastars (H)	18.00	24.00	13.25	17.67	0.75	0.50
	Seastars (P)	15.00	20.00	11.00	14.67	0.75	0.50
	CoTS	12.00	16.00	11.00	14.67	0.75	0.75
	Sea cucumbers (DF)	35.25	70.50	31.25	62.50	0.50	0.50
	Sea cucumbers (SF)	17.00	22.67	12.25	16.33	0.75	0.50
	Sea urchins (regular)	30.00	40.00	25.25	33.67	0.75	0.50
	Sea urchins (irregular)	26.25	42.00	25.25	40.40	0.63	0.50
	Brittle stars	14.25	19.00	13.25	17.67	0.75	0.50
	Feather stars	18.00	24.00	14.00	18.67	0.75	0.50
Fishes	Cryptobenthic	39.56	52.74	29.11	38.81	0.75	0.67
	Farmers	27.11	36.15	11.67	15.56	0.75	0.67
	Scrapers (scarids)	22.00	29.33	6.00	8.00	0.75	0.67
	Browsers (nasos)	13.44	20.17	4.11	6.17	0.67	0.67
	Browsers (siganids)	13.78	20.67	4.44	6.67	0.67	0.75
	Browsers (other)	13.78	23.62	4.44	7.62	0.58	0.50
	Bolbometopon	23.56	40.38	10.89	18.67	0.58	0.75
	Excavators (other)	23.67	35.50	7.67	11.50	0.67	0.67
	Detritivores	22.22	29.63	11.56	15.41	0.75	0.58
	Planktivores	40.56	60.83	30.11	45.17	0.67	0.75
	Corallivores	56.11	96.19	38.44	65.90	0.58	0.58
	Invertivores (labrids)	24.11	32.15	11.67	15.56	0.75	0.67
	Invertivores (other)	25.78	44.19	13.33	22.86	0.58	0.67
	Invertivores (lutjanids)	17.44	34.89	10.44	20.89	0.50	0.58
	Eels	25.00	50.00	14.33	28.67	0.50	0.50
	Piscivores (residents)	52.11	104.22	36.67	73.33	0.50	0.58
	Piscivores (transients)	44.89	89.78	31.11	62.22	0.50	0.75
	Cleaner wrasse	26.22	34.96	20.56	27.41	0.75	0.63

3.4 Combined assessment of functionally important and vulnerable taxa

In order to identify key species for targeted management on the GBR, we compared scores for functional importance against scores for vulnerability (Figure 12). Using the median values for both axes, four quadrats were established to represent priority targets (Figure 12);

1. **Intervention (high priority):** Functionally important and vulnerable groups that should be considered top priorities for management.
2. **Intervention (low priority):** Important groups that are not as vulnerable but may still be considered for management to conserve a functioning reef.
3. **Protection:** Vulnerable groups that were not considered as critical to reef functioning but may require protection to ensure they are not lost.
4. **Monitor:** Low rated importance and vulnerability suggests little action may be needed, but populations should still be monitored, especially when certainty is low.

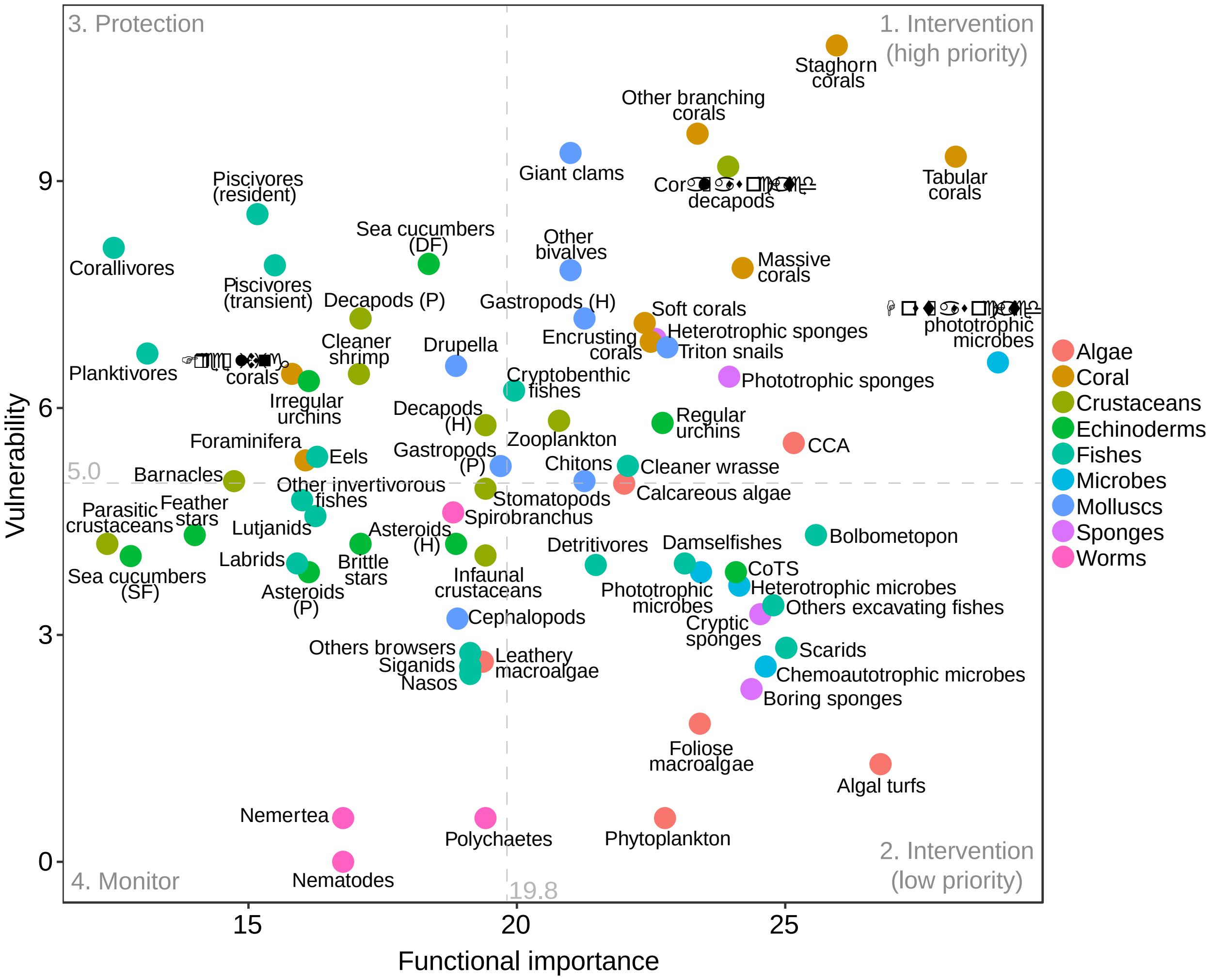

Figure 12: Assessment of the functional importance of 70 species groups relative to their rated vulnerabilities on the GBR. Dotted grey lines represent the median values for each axis creating four management quadrats; 1. Intervention (top priority), 2. Intervention (low priority), 3. Protection, and 4. Monitor. Colours reflect taxonomy. H=herbivores, P=predators, DF=deposit feeders, SF=suspension feeders.

Not surprisingly, most coral groups scored highly for both measures and are considered top priority (Figure 12). Specifically, tabular and branching groups (staghorn, other) ranked highest. Host-associated phototrophic microbes also ranked as a top priority, although they were scored to be less vulnerable than these coral groups (Figure 12). The remaining microbial groups were considered lower priority owing to their low scores for vulnerability (Figure 12), despite free-living microbes (i.e. those in seawater or sediment) and bacteria emerging as important bioindicator tools for monitoring reef health (Case Study 3; Appendix 6) (Glasl et al. 2017, Glasl et al. 2018a), as for phytoplankton (Revelante and Gilmartin 1982, Revelante et al. 1982, Furnas 1992). Coral-associated decapods ranked highly, along with a range of other invertebrates including zooplankton, bivalves and giant clams, triton snails and other gastropods (herbivores, predators). Regular sea urchins (e.g. *Diadema*) also fell within this top priority space, perhaps due to lessons learned from the Caribbean (Hughes 1994, Mumby et al. 2006a, Mumby et al. 2006b). Top priority algal groups were the calcifiers (CCA, calcareous) owing to their higher rated vulnerabilities compared to the remaining algal groups. Despite their great contributions to a functioning reef, algal turfs and macroalgae were categorically considered low priority for management owing to lower rated vulnerabilities (Figure 12). However, the opportunistic nature of these algal groups can drive phase shifts away from coral dominance, and for this very reason they should not be ignored in management, particularly on inshore reefs where nutrient enrichment from water quality can enhance algal growth (Vermeij et al. 2010, Gordon et al. 2016a), including on the GBR (Schaffelke et al. 2005, Lam et al. 2018). Phototrophic and heterotrophic sponges were top priority sponge groups, while the more functionally important cryptic and boring sponges were considered more resilient (Figure 12).

For the reef fishes, although scoring lower for their total functional importance compared to other fish groups, cleaner wrasse and cryptobenthic fishes were the only two fish groups to fall within the top priority space (Figure 12). For cleaner wrasse, which may not be the most directly important or vulnerable of the reef fishes, this score was largely attributed to their low ecological redundancy. Interestingly, those that were considered among the most functionally important groups (e.g. *Bolbometopon*, scarids, damselfishes, detritivores) were not considered highly vulnerable (low priority), while those that were the most vulnerable (e.g. piscivores, corallivores, planktivores) were not ranked among the key groups for maintaining a functioning reef (Figure 12). This highlights the importance of using a multi-level approach in assessing species' functionality.

3.4.1 Proportional impacts of stressors on taxa

For each group of species, we combined their functional importance per-process and vulnerability per-stressor in every combination to calculate the relative impact of each stressor at various levels of taxonomy and ecosystem processes (see methods). This analysis presents weighted impacts of stressors for species at their highest levels of functioning and vulnerability. This data may be particularly useful in guiding where attention could be focused to maintain highly weighted species-stressor-process combinations.

The proportional impact of each stressor varied across our taxonomic groups, and between inner reef and offshore regions (Figure 13A, B). As above, global change stressors (ocean warming, ocean acidification, cyclones) were considered to have the greatest potential impact overall, especially offshore (Figure 13B). On inshore reefs, the proportional impact of global change stressors on biological functioning was dampened by a greater influence from water quality stressors (nutrients, sediments, pollutants) (Figure 13B), as would be expected (Brodie and Waterhouse 2012, Lam et al. 2018, MacNeil et al. 2019). Interestingly, the proportional impact of water quality stressors superseded ocean change stressors on inshore reefs for some taxa (e.g. microbes, algae, sponges, fishes) (Figure 13A), attributing to the importance of addressing local management in conjunction with global stressors and a low-carbon economy (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Corals were the primary taxonomic group considered to be impacted by outbreaks, likely almost entirely in context of CoTS on the GBR. Echinoderms and fishes were the major groups impacted by fisheries (Figure 13A, B). The functional contributions of sponges seemed disproportionately impacted by cyclones compared to other taxonomic groups, particularly offshore where there was less exposure to impacts from sediments and pollutants (Figure 13B).

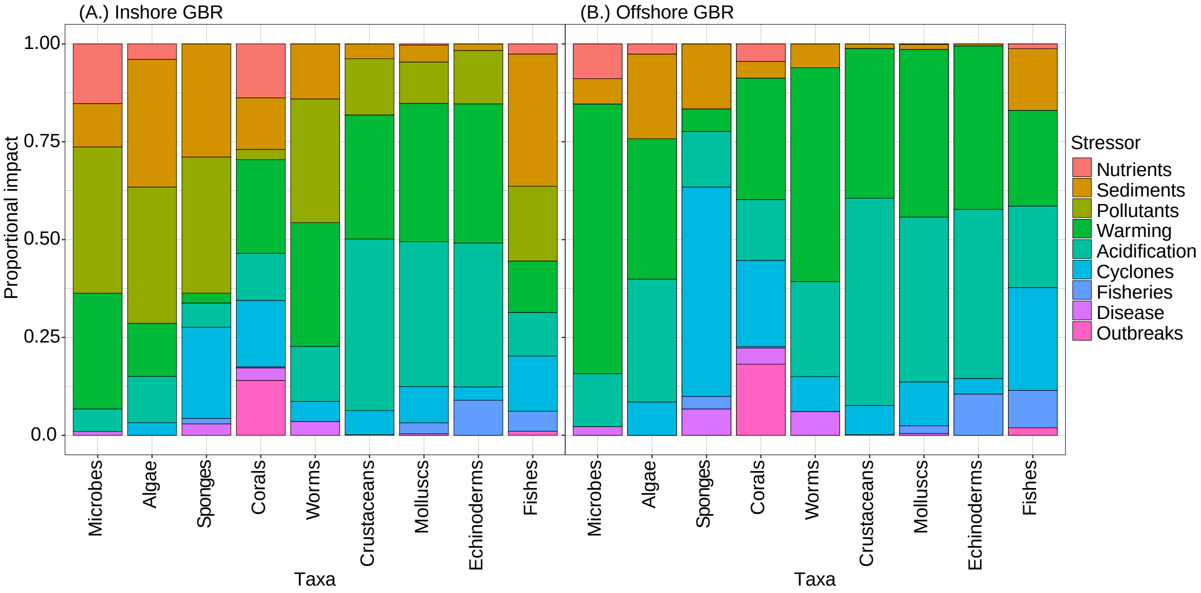

Figure 13: The proportional impact of each stressor on taxonomic groupings (A.) inshore and (B.) offshore. Each column is a relative proportion of the functional importance and vulnerability of all species groups within the taxa-stressor combination (see methods).

This analysis was deconstructed at the level of our 70 functional groups, providing important information on the most critical stressors to consider when looking to maintain each species group at their highest level of functioning. For many of the mobile invertebrate groups (i.e. crustaceans, molluscs and echinoderms) the impact of ocean change stressors was greatest, even in context of inshore reefs (Figure 14), as reviewed for adult and larval life stages across this great diversity of species (Przeslawski et al. 2008, Byrne 2011, Przeslawski et al. 2015). For most herbivorous fish groups (e.g. browsers, excavators and scrapers), water quality stressors, particularly sediments, were considered to have the greatest proportional impact on their functioning (Figure 14), including offshore (Figure 15). This is in line with the literature that suggests grazing activity can be significantly impaired when sediments loads are too high in their algal food source (Bellwood and Fulton 2008, Goatley and Bellwood 2012, Goatley et al. 2016, Gordon et al. 2016b). As such, functioning of several algal groups, including turfs, was considered to be greatly impacted by sediment loads (Figures 14, 15). Of the marine worms, only *Spirobranchus* was considered vulnerable to a number of stressors. Nemerteans and polychaetes were suggested to be almost entirely impacted by cyclones (Figures 14, 15) – an artefact of their low rated vulnerabilities as a whole. Scores for nematodes, nemerteans and polychaetes reflect the data gaps and uncertainty in the biology and ecology of these groups in broader context of reef functioning and threat sensitivity. Fisheries was suggested to have a disproportionate impact on deposit-feeding sea cucumbers, and was the major stressor impacting functioning of piscivorous fishes (resident and transient) (Figures 14, 15). It would be important to partition these broad functional categories for piscivores at greater resolution in future work. Tabular, staghorn and other branching corals were the groups most impacted by outbreaks, with the functioning of some fish groups that depend on corals for shelter (i.e. corallivores, cryptobenthic, planktivores) also partially impacted. This reflects the ability for our scoring system to capture indirect impacts of stressors on reef functioning. Interestingly, water quality stressors seemed to have a broader and proportionately greater impact on functioning for many species than outbreaks, including offshore (Figure 15).

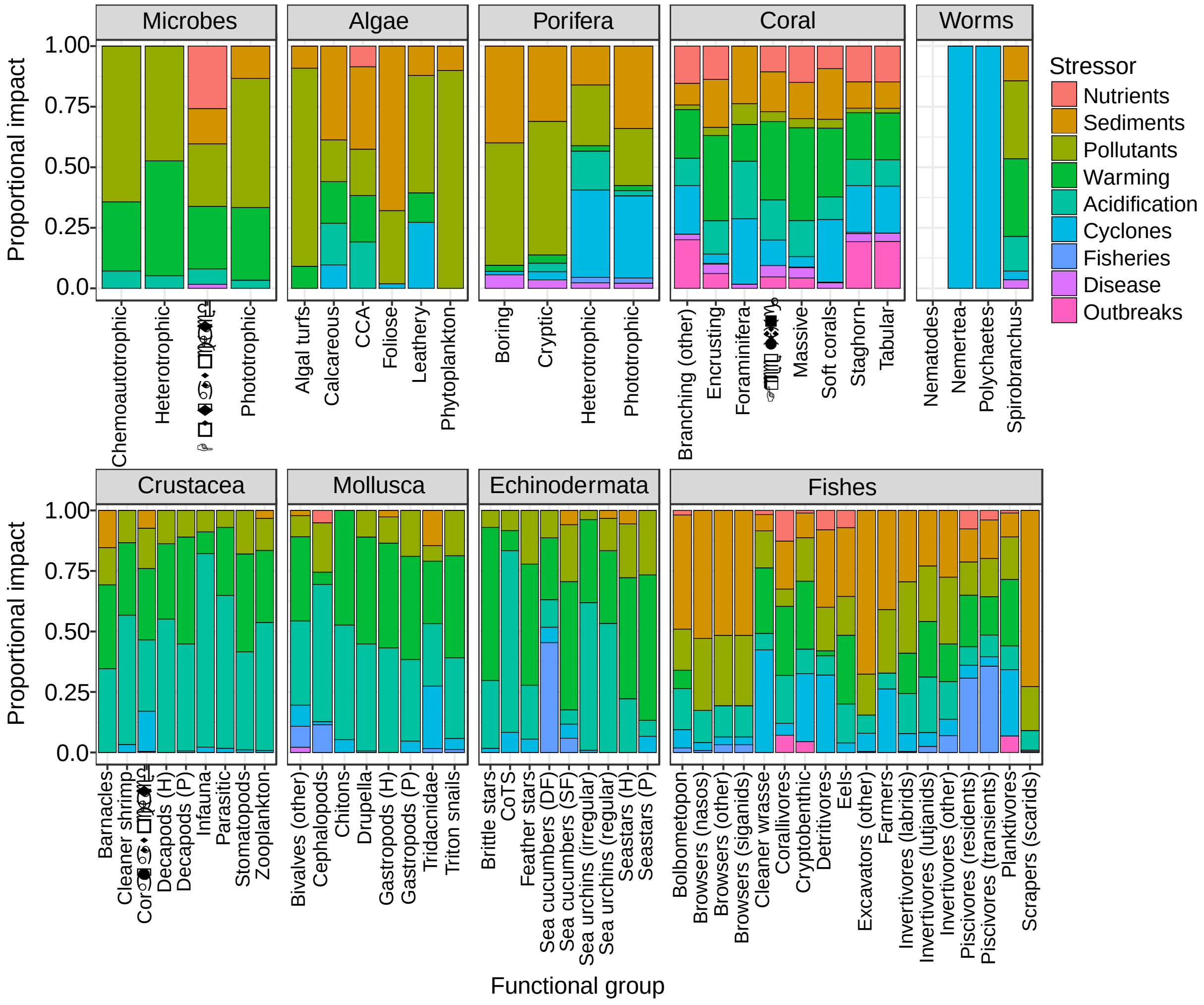

Figure 14: The proportional impact of each stressor on our 70 groups of species as a factor of their functional importance inshore.

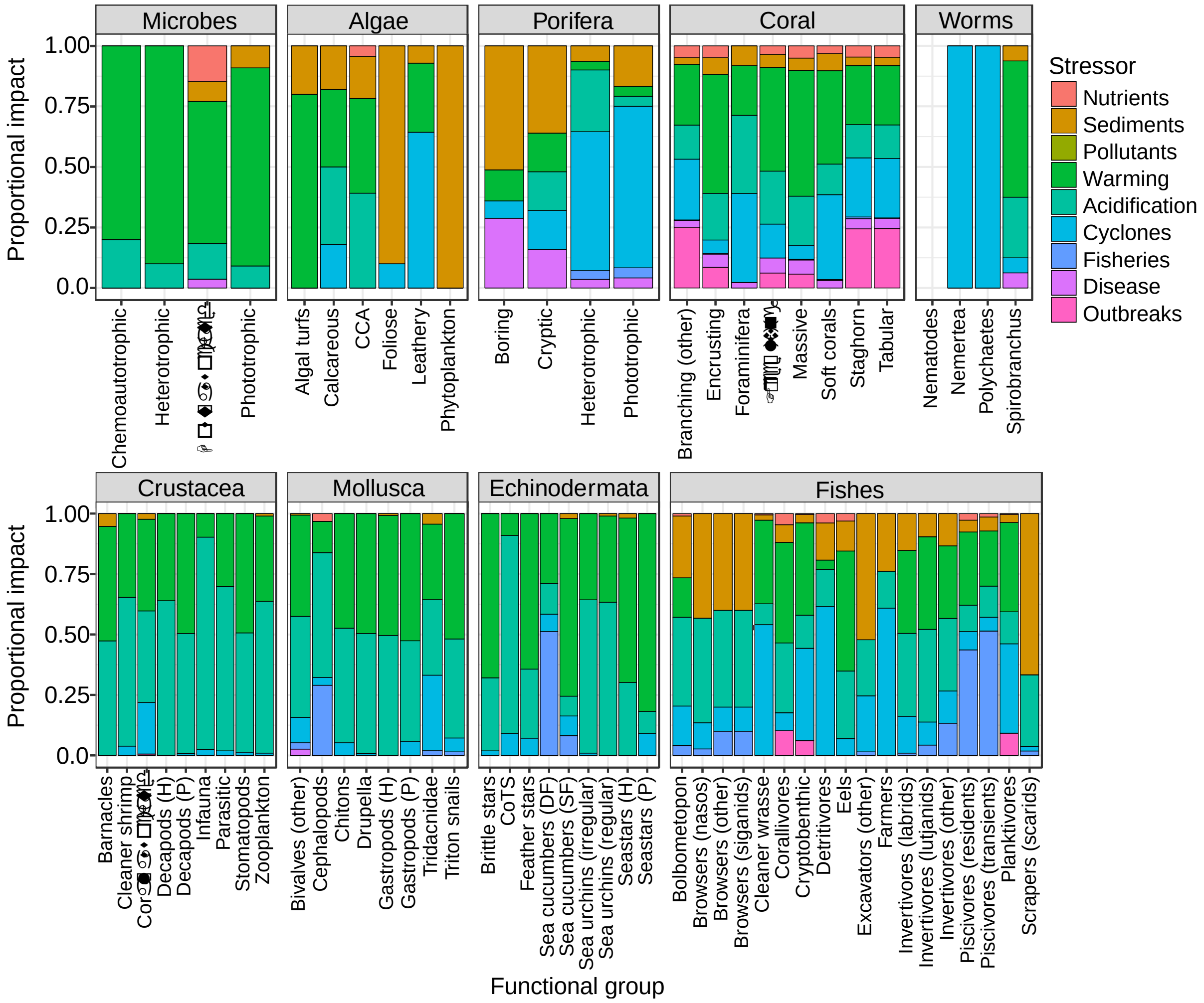

Figure 15: The proportional impact of each stressor on our 70 groups of species as a factor of their functional importance offshore.

3.4.2 Proportional impacts of stressors on ecosystem processes

To examine the impact of our nine stressors on ecosystem processes, the additive functional importance and vulnerability of each taxa was calculated across each process-stressor combination. This allowed the determination of the relative impact of each stressor at the level of our nine ecosystem processes, which was weighted by species at their highest level of functioning. Despite the observed differences in the proportional impact of stressors on taxa separately (as above), analyses at the level of ecosystem processes showed little variation in potential impact (Figure 16A, B). Global change stressors were calculated to have the greatest proportional impact on ecosystem processes, especially offshore (Figure 16B). As above, impact from water quality stressors on ecosystem processes were proportionately greater inshore (Figure 16A). Though generally, there was little difference in the proportional impact of stressors between inshore and offshore habitats other than the added stress from pollutants (Figures 16-18). Few toxic pollutants on the GBR approach harmful concentrations, and if so, are typically only recorded during short-term runoff pulses near shore (van Dam et al. 2011).

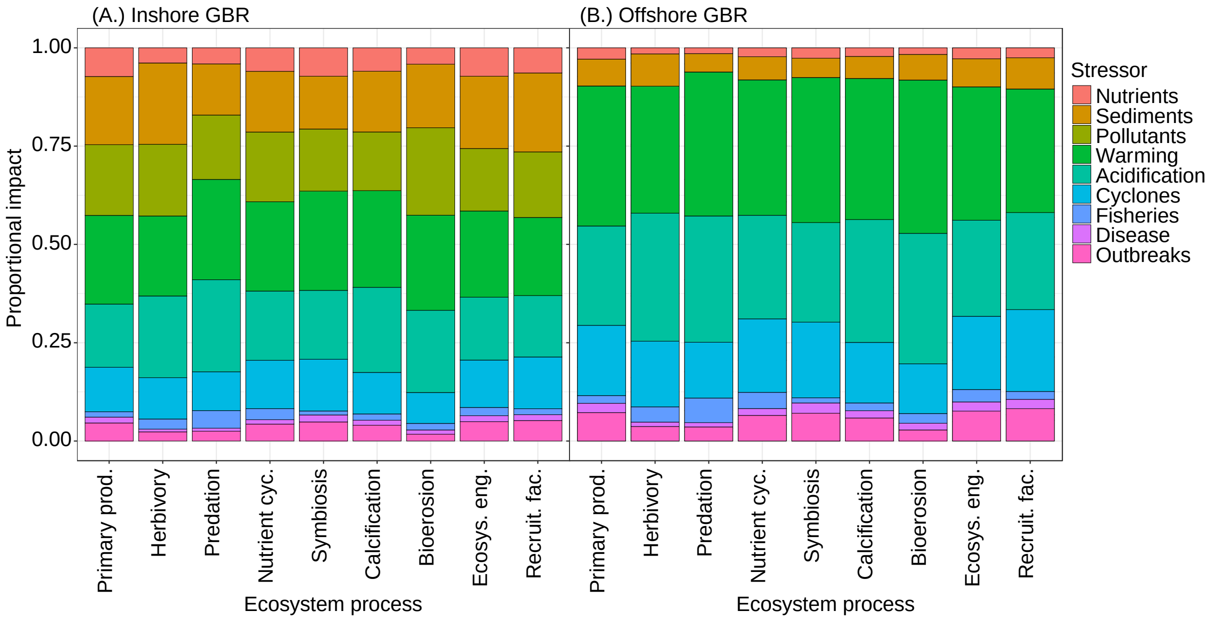

Figure 16: The proportional impact of each stressor on ecosystem processes (A.) inshore and (B.) offshore. Each column is a relative proportion of the functional importance and vulnerability of all species groups within each process-stressor combination.

This analysis became particularly informative when examined as a proportion of each stressor separately. The impact of fisheries was evidently greatest for the predation process (Figures 17, 18), likely driven by combined importance and vulnerability of the two large predatory fish groups (residents and transients) at this level of functioning. This could be assumed to be driven by triton snails, which rated highest for predation in context of CoTS, but these gastropods were not considered vulnerable to fisheries here as historical records of exploitation are namely anecdotal (Endean 1969) and collection of *Charonia tritonis* on the GBR has been prohibited for several decades (Hall et al. 2017). Generally, stressors had the lowest proportional impact on the bioerosion process (Figures 17, 18), in line with the literature suggesting bioerosion is likely to increase in a future ocean and is itself an emergent stressor on coral reefs (DeCarlo et al. 2015, Manzello et al. 2017, Schönberg et al. 2017). Ocean acidification had the greatest proportional impact of species considered important for the calcification process (Figures 17, 18), as would be expected. For a number of stressors (nutrients, warming, cyclones, outbreaks and disease), potential impacts were tightly coupled for symbiosis, calcification, ecosystem engineering and recruitment facilitation processes (Figures 17, 18). This likely reflects the fundamental role of corals and their symbionts in the ecosystem process that support habitat functioning. Yet overall, the proportional impacts on many ecosystem processes within each stressor were relatively homogenous (Figures 17, 18) attributed to the broad sweeping effects stressors can have in complex systems like coral reefs.

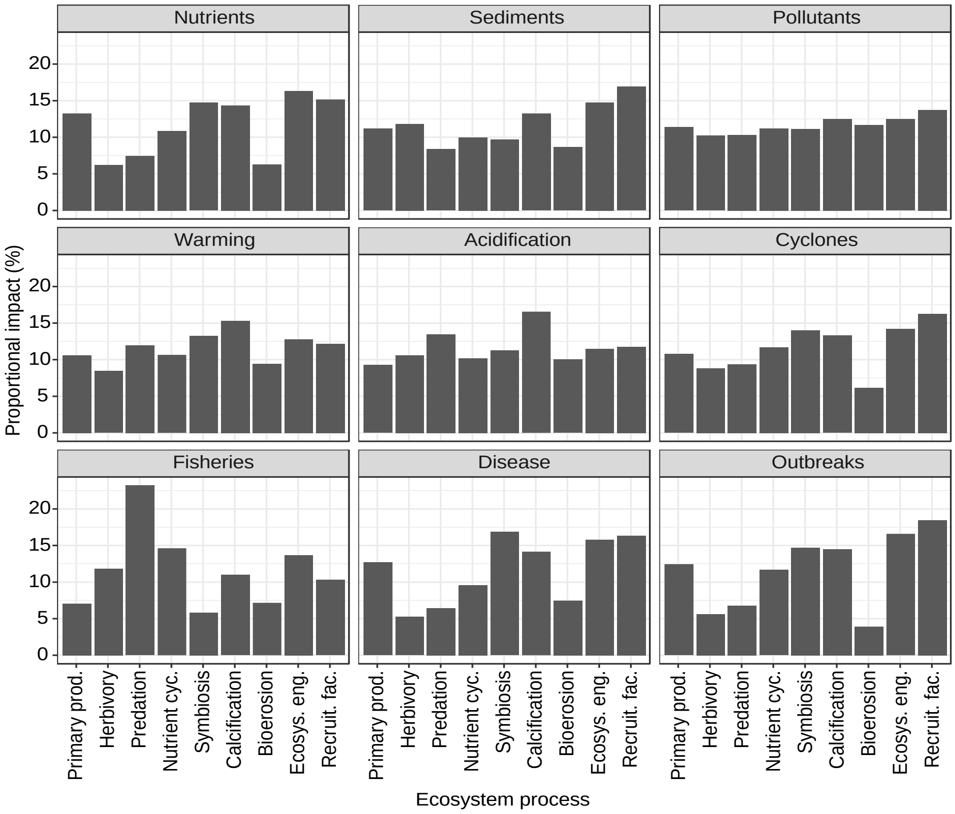

Figure 17: The proportional impact of each stressor on ecosystem processes in context of inshore regions of the GBR. Each column is a relative proportion of the functional importance and vulnerability within each stressor.

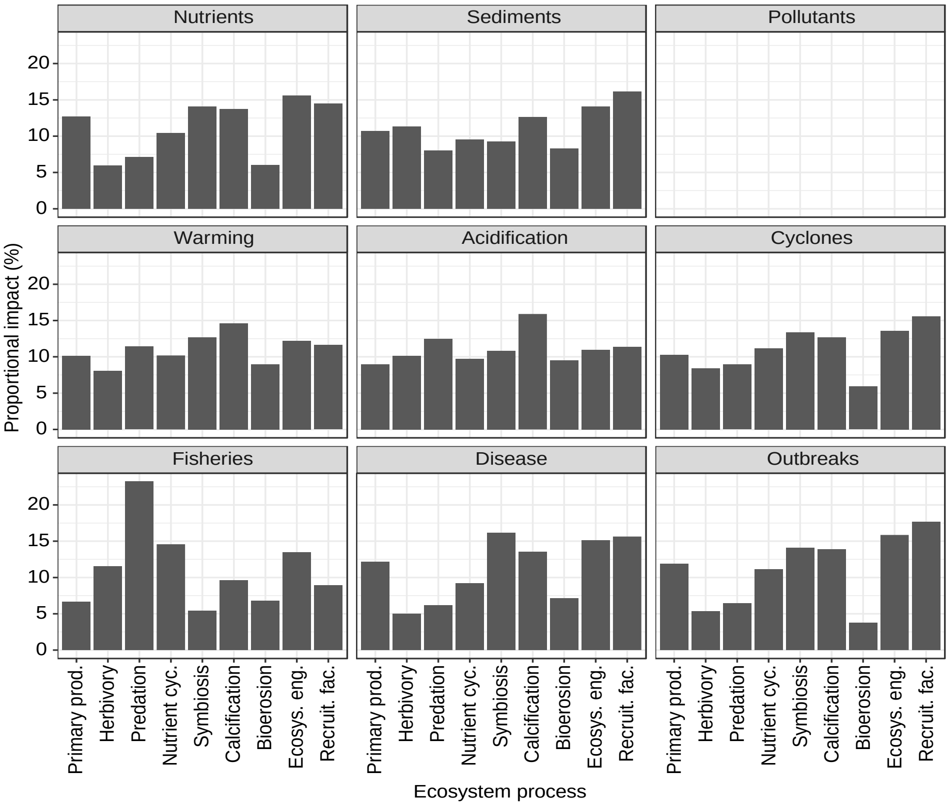

Figure 18: The proportional impact of each stressor on ecosystem processes in context of offshore regions of the GBR. Each column is a relative proportion of the functional importance and vulnerability within each stressor. Data absent for pollutants offshore due to null score for exposure.

3.4.3 Addressing manageability

Experts were elicited to rate species based on their potential responsiveness to management action, and the feasibility of implementing management strategies (i.e. spatial scale, time, energy, cost) (Table 11). Groups that scored in the top 66-percentile were categorised as a higher priority for management (Figure 19) that would likely benefit from direct measures of protection or even represent cases where management has already proved effective. Those in the bottom 33-percentile were deemed lower management priorities (Figure 19) that may indirectly benefit from broader scale management schemes (e.g. marine zoning) and/or require innovative approaches. In any case, maintaining current systems of zoning and compliance provides a baseline to management to preserve species, functioning and biodiversity on coral reefs (GBRMPA 2014c, 2018b). Note that this assessment was in context of the biological functioning of each taxa and was not an assessment of other important elements in strategic assessments including social, cultural and economic reef values (GBRMPA 2014c).

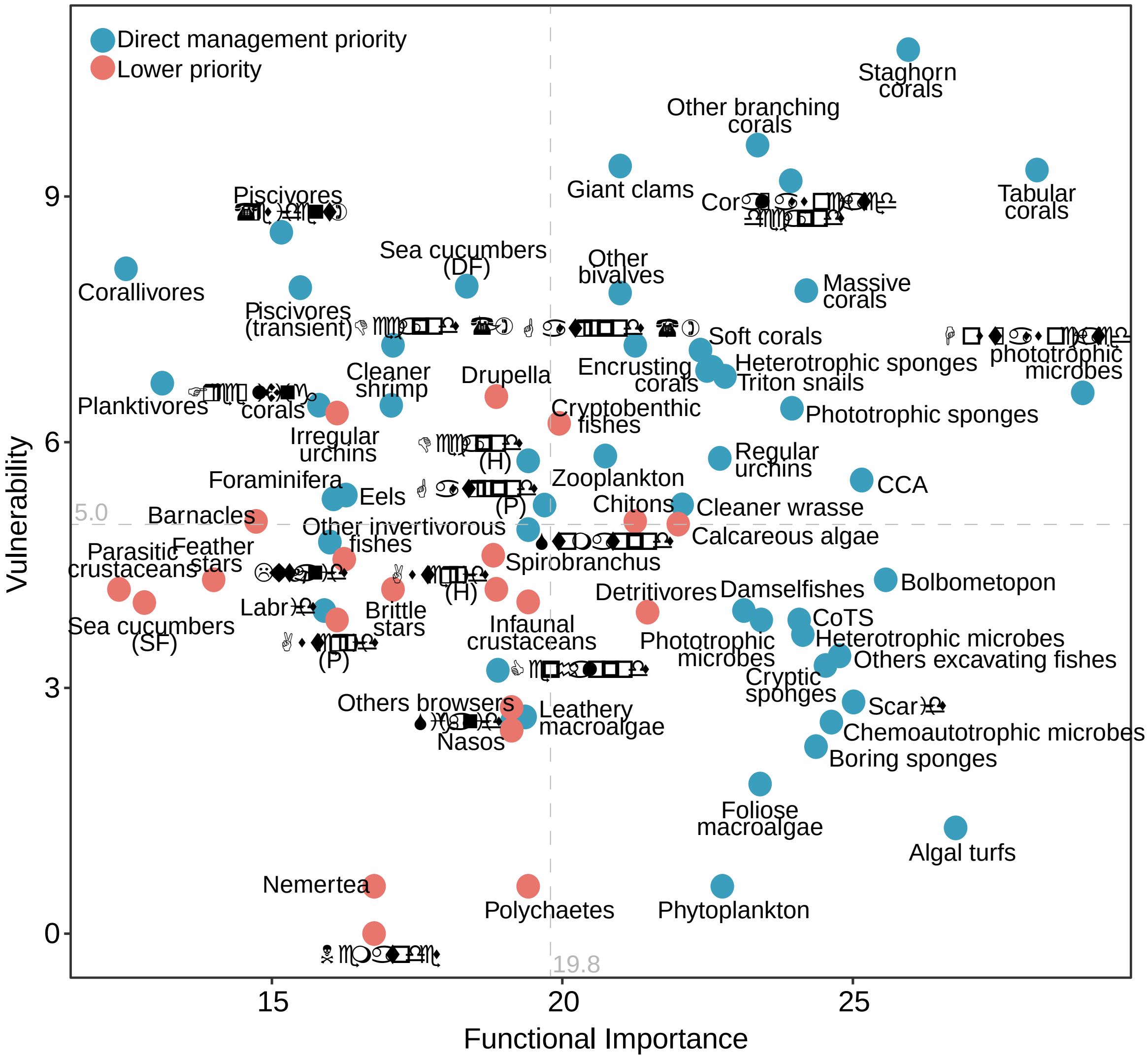

Figure 19: Perceived manageability of each taxa relative to their rated functional importance and vulnerabilities on the GBR. Dotted grey lines represent the median values for each axis. H=herbivores, P=predators, DF=deposit feeders, SF=suspension feeders.

Table 11: Manageability of functional groups on the GBR based on their responsiveness to and feasibility of intervention. Direct management priority (M) = top 66-percentile of scores; lower management priority (L) = lowest 33-percentile. H=herbivores, P=predators; DF=deposit feeders; SF=suspension feeders.

Taxa	Functional group	Responsiveness	Feasibility	Manageability
Microbes	Phototrophic	1.5	1.0	M
	Host-associated	1.5	1.0	M
	Chemoautotrophic	1.5	1.0	M
	Heterotrophic	1.5	1.0	M
Algae	Phytoplankton	1.5	1.5	M
	Algal turfs	1.0	0.5	M
	Leathery	1.5	1.5	M
	Foliose	1.0	1.0	M
	Calcareous	0.5	0.0	L
	CCA	1.5	1.0	M
Sponges	Heterotrophic	1.7	1.3	M
	Phototrophic	1.7	1.3	M
	Boring	1.0	1.0	M
	Cryptic	0.7	1.0	M
Coral	Tabular	1.5	1.0	M
	Staghorn	1.5	1.3	M
	Branching (other)	1.3	1.0	M
	Massive	1.0	1.0	M

	Encrusting	1.3	1.0	M
	Free-living	0.8	0.8	M
	Soft corals	1.0	1.0	M
	Foraminifera	1.0	1.0	M
Worms	Nematodes	0.0	0.0	L
	Nemertea	0.5	0.0	L
	Polychaetes	0.5	0.0	L
	Spirobranchus	0.5	0.5	L
Crustaceans	Decapods (H)	0.5	1.0	M
	Decapods (P)	1.0	1.0	M
	Coral-associated	1.5	2.0	M
	Barnacles	0.0	0.0	L
	Stomatopods	0.5	1.0	M
	Cleaner shrimp	0.5	1.0	M
	Infauna	0.0	0.0	L
	Zooplankton	0.5	1.0	M
	Parasitic	0.0	0.0	L
Molluscs	Gastropods (H)	1.0	1.0	M
	Gastropods (P)	0.5	1.0	M
	Triton snails	1.0	1.5	M
	Drupella	0.5	0.5	L
	Tridacnidae	1.3	2.0	M
	Bivalves (other)	1.0	1.3	M
	Chitons	0.5	0.0	L
	Cephalopods	1.0	1.5	M
Echinoderms	Seastars (H)	0.5	0.0	L
	Seastars (P)	0.5	0.5	L
	CoTS	1.5	1.5	M
	Sea cucumbers (DF)	2.0	1.5	M
	Sea cucumbers (SF)	0.0	0.0	L
	Sea urchins (regular)	1.0	0.5	M
	Sea urchins (irregular)	0.5	0.0	L
	Brittle stars	0.0	0.0	L
	Feather stars	0.0	0.0	L
Fishes	Cryptobenthic	0.7	0.3	L
	Farmers	1.0	1.0	M
	Scrapers (scarids)	0.7	0.7	M
	Browsers (nasos)	0.3	0.7	L
	Browsers (siganids)	0.7	0.7	M
	Browsers (other)	0.3	0.3	L
	Bolbometopon	0.7	0.7	M
	Excavators (other)	0.7	0.7	M
	Detritivores	0.7	0.3	L
	Planktivores	1.3	0.7	M
	Corallivores	1.0	1.3	M
	Invertivores (labrids)	0.7	0.7	M
	Invertivores (other)	1.3	1.0	M
	Invertivores (lutjanids)	0.3	0.3	L
	Eels	0.7	0.7	M
	Piscivores (residents)	2.0	2.0	M
	Piscivores (transients)	1.3	1.7	M
	Cleaner wrasse	0.7	1.7	M

Interestingly, species that scored lowest for their functional importance and vulnerability on the GBR were also regarded as the least manageable (Figure 19; Table 11). This may reflect expert bias and the assumption that important and vulnerable groups should be managed, but also demonstrates strong support for the protection of highly rated groups. Invertebrates were most frequently considered unmanageable (Figure 19), reflecting the difficulties inherent in monitoring and managing small, often cryptic species. This was reflected in the Crustacea, where barnacles, infaunal species and parasites scored low, along with all four groups marine worms (Figure 19). Five groups of reef fishes (cryptobenthics, *Naso* sp., other browsers, detritivores, lutjanids) rated as low priority (Figure 19), most likely stemming from the direct comparison of these groups to other reef fishes rather than their actual inability to be managed.

In context of the biology of these groups, cryptobenthic fishes are incredibly diverse and abundant, with rapid population turnovers that ensure persistence against extreme predation pressure (Depczynski and Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, Brandl et al. 2019), suggesting an inherent resilience. This is also true for the broad distributions and/or high densities of many detritivorous fishes including blennies (Wilson 2000, Wilson 2001, Wilson 2004), and surgeonfishes, particularly *Ctenochaetus striatus* (Tebbett et al. 2018). Interestingly, microbes, which are ubiquitous and relatively poorly understood, were considered manageable candidates. This may reflect recent research suggesting that some groups (e.g. bacteria and free-living microbes in seawater or sediment) can be used as bioindicators to monitoring reef health, particularly regarding water quality (Case Study 3) (Glasl et al. 2017, Glasl et al. 2018a), and potential Symbiodiniaceae community regulation in support of reef restoration (Quigley et al. 2018). All corals were considered manageable, including the non-coral group Foraminifera, as were phytoplankton and zooplankton (Figure 19; Table 11).

3.4.4 Accounting for scientific certainty

Scientific certainty, as expressed by our expert panel, varied among the 70 functional groups (Figure 20). Uncertainty was most evident for mobile marine invertebrate groups, reflecting the comparatively poor knowledgebase we have regarding non-coral invertebrates on the GBR, and generally (Ponder et al. 2002, Przeslawski et al. 2008). While certainty was high for some key species, such as CoTS and bivalves, for most non-coral marine invertebrates including marine worms, crustaceans and echinoderms, certainty was poor (Figure 20). Along with CoTS, scientific certainty was greatest for *Bolbometopon*, tabular corals and algal turfs, which have received great attention both in the literature and in this review. The lowest certainty for a reef fish group was for eels (muraenids) (Figure 20). Interestingly, certainty was relatively high for cephalopods despite surprising data deficiencies regarding the biology and ecology of this group on the GBR and elsewhere. Conversely, certainty was low for triton snails despite the body of literature devoted to this gastropod owing to its role in CoTS predation (Endean 1969, Pratchett et al. 2014, Westcott et al. 2016, Cowan et al. 2017, Hall et al. 2017). The perceived depletion of *Charonia tritonis* on the GBR, and elsewhere, was the basis for the ‘predator removal hypothesis’ regarding CoTS outbreaks (Endean 1969). However, records of their exploitation are mainly anecdotal, and the lack of scientific data and official harvest records suggest these gastropods may have always been rare on many coral reefs (Hall et al. 2017). Regardless, triton snails were scored to have low potential recoverability (Table 10), as while limited data exists, exploitation has occurred for *Charonia* species on many coral reefs globally where their numbers remain low (Salm 1978, Nijman et al. 2016, Hall et al. 2017).

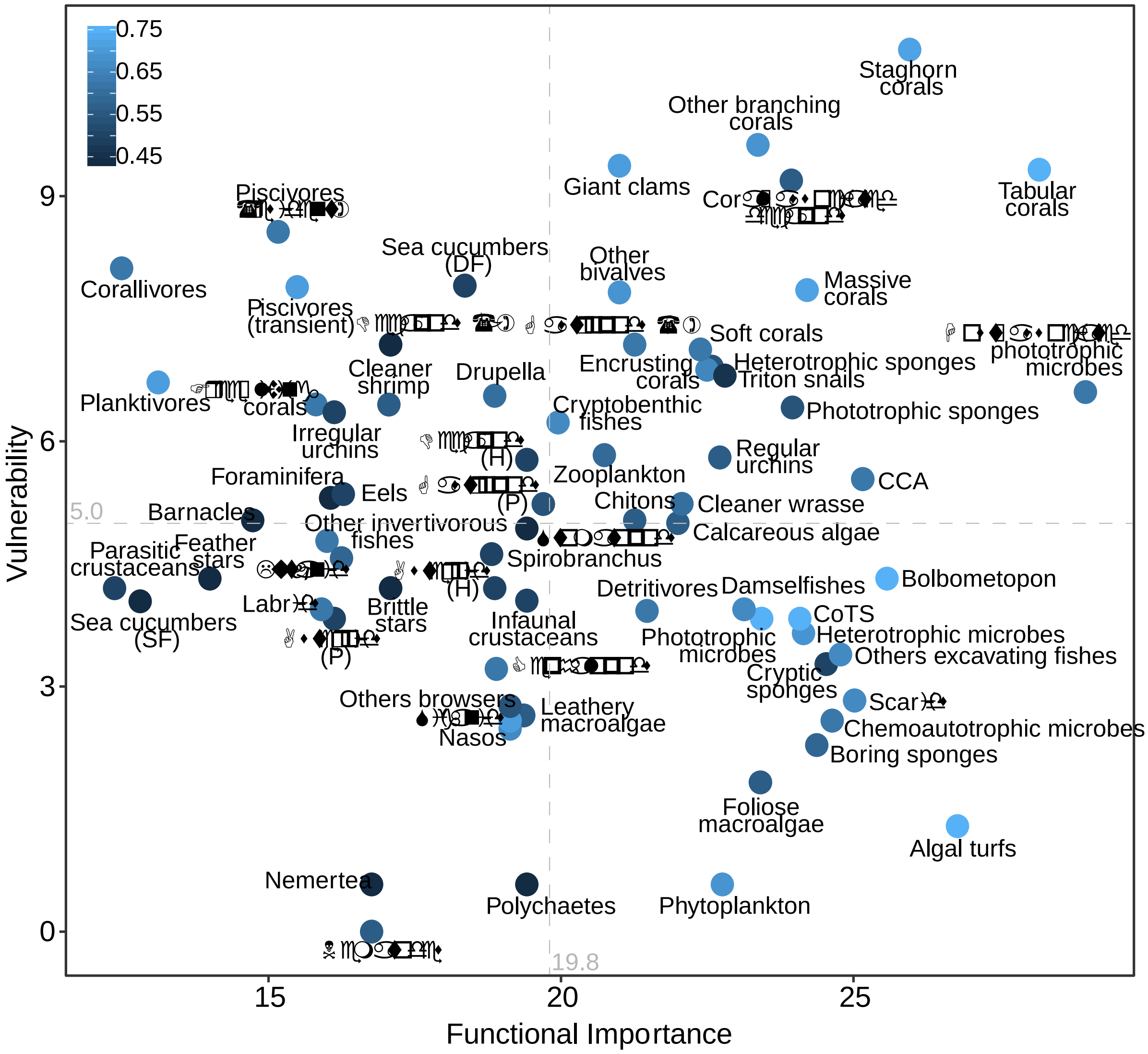

Figure 20: Scientific (expert) certainty in scores for functional importance and vulnerability of the 70 functional groups. Shading reflects scores of high (light) to low (dark) certainty. Dotted grey lines represent the median values for each axis. H=herbivores, P=predators, DF=deposit feeders, SF=suspension feeders.

These high or low relative values for certainty are highlighted here to inform and support our findings and recommendations – an important elicitation process (Knol et al. 2010, Polasky et al. 2011). For groups that scored highly overall with a high level of certainty, management seems most appropriate; i.e. we are sure that they are functionally important, vulnerable and manageable on the GBR. Groups with comparatively low levels of certainty are briefly reviewed below under precautionary principles so that no groups were overlooked due to data deficiencies, particularly for those where uncertainty was disproportionate to their relative importance and/or vulnerability. In most cases of uncertainty, we conclude that more empirical data are required to explicitly characterise their functional significance and vulnerabilities, and to predict ecological consequences in their absence. The desired outcome for these data deficient groups is to reduce uncertainty through increased research and monitoring.

3.4.4.1 Cryptic predators: eels and octopuses

Due to the difficulties surveying the cryptic habitats they typically occupy, very little data exist for muraenids (eels; Figure 21a, b) on the GBR, and reefs in general. They likely span many trophic levels with adults ranging from just a few centimetres to >3 m, and from sandy-bottom to complex reef rubble and intertidal habitats (Böhlke and Randall 2000). Many muraenids actively hunt within the intricacies of the reef framework often inaccessible to other large predators, sometimes occupying nocturnal niches with diets that include fishes, crustaceans, worms and cephalopods (Hiatt and Strasburg 1960, Hixon and Beets 1993, Fishelson 1997, Young and Winn 2003, Gilbert et al. 2005). Unlike a diversity of other reef fishes, including large resident piscivores, muraenids optimise habitat use within the reef and rubble matrix (i.e. dead coral) rather than exhibiting dependence on live coral, suggesting they may fare better as coral reefs degrade. Yet, how trophic pathways within the reef matrix scale up to fisheries productivity are poorly understood. As for muraenids, a broad knowledge gap is evident for cephalopods, particularly octopuses (Figure 21c) that exist in a similar 'hidden' trophic space. Benthic predators like octopuses and muraenids (Figure 21) are likely key predators within the reef matrix where large predatory fishes cannot access, but this remains to be quantified. Data gaps for cephalopods are surprising given their broad cross-shelf distributions occupying cryptobenthic to pelagic habitats (Moltschaniwskyj and Doherty 1995), and their contributions to fisheries productivity as both predators and prey (Connell 1998, Beukers-Stewart and Jones 2004, Taylor and Bennett 2008). Surprisingly little information exists regarding their functional ecology on the GBR, and in general (Ponder et al. 2002).

Figure 21: Muraenids (eels) (a,b) and cephalopods (e.g. octopuses; c) may be functionally significant predators within the reef matrix, but this is a poorly defined habitat and trophic group. Photo credit: T. Kenyon (b).

3.4.4.2 Deposit-feeding sea cucumbers

Although they have important roles in bioturbation, carbonate chemistry, nutrient cycling, benthic productivity and infaunal community structure (Uthicke and Klumpp 1998, Uthicke 1999, 2001, Wolkenhauer et al. 2010, Schneider et al. 2011, Schneider et al. 2013, Lee et al. 2017, Wolfe and Byrne 2017a, Wolfe et al. 2018), sea cucumbers (Figure 22) may be more influential in lagoon systems – outside of the focal habitat here. However, large deposit-feeding holothuroids are likely to have a greater influence on ecosystem-scale carbonate chemistry in closer association to reef structures (Schneider et al. 2013, Wolfe et al. 2018). As recognised by our expert panel, they are among the most vulnerable species to overfishing on the GBR (Uthicke et al. 2004, Purcell et al. 2013, Eriksson and Byrne 2015, Purcell et al. 2016b), as globally recognised (IUCN Red List for Threatened Species) (Conand et al. 2014, Purcell et al. 2014, Richards and Day 2018). Empirical data on their recruitment and reproduction (e.g. Wolfe and Byrne 2017b, Balogh et al. 2019), and natural population densities are essential to characterise before fisheries impacts on wild populations can no longer be differentiated. This is particularly true for the black teatfish, *Holothuria whitmaei* (Figure 22b), which is frequently addressed in management reports for the GBR (GBRMPA 2014b, c), yet there have been recent discussions to reopen its fishery (DAF 2018) without any fisheries-independent data since its closure (owing to overfishing) in 1999.

Figure 22: Deposit-feeding sea cucumbers use (a.) specialised feeding tentacles to feed. (b.) The black teatfish is one of the highest yielding sea cucumbers on the GBR but is also historically overfished. Overall, sea cucumbers may have greater roles in (c.) sediment-based habitats compared to on structured reefs.

3.4.4.3 Marine worms

This broad group boasts an incredible diversity across a range of functions and taxa, from microscopic infaunal nematodes, to parasitic platyhelminths, to large predatory polychaetes, to sessile filter-feeders (Hutchings et al. 2019). For polychaetes alone, there are currently over 130,000 species recognised worldwide, but there has not yet been a comprehensive survey of the polychaetes, or marine worms, of the GBR. Marine worms are often highly cryptic and new species are frequently identified when taking the time to look, as demonstrated from a two-week polychaete workshop on Lizard Island that described 91 new species (Aguado et al. 2015, Capa et al. 2015, Hutchings and Kupriyanova 2015). Bioerosion is perhaps the most well documented functional role of marine worms on the GBR (Hutchings and Kiene 1986, Hutchings 2008), but the lack of information on their population densities across the GBR hinders the ability to upscale their contributions into carbonate budget calculations (Case Study 2; Appendix 5). The Christmas tree worm (*Spirobranchus*) has received specific attention in the literature, owing to the benefits it provides for its coral host (Strathmann et al. 1984, DeVantier et al. 1986, Dai and Yang 1995, Ben-Tzvi et al. 2006, Rowley 2008). Marine worms are an important food source for many reef organisms including invertivorous reef fishes (Case

Study 1; Appendix 4), but explicit trophic contributions are notoriously difficult to quantify for soft-bodied cryptic fauna, and attention to these gaps in knowledge require urgent attention.

3.4.4.4 Cryptic sponges

The functional ecology of sponges is better documented on Caribbean reefs than for the Pacific and GBR (Wilkinson 1983, 1987, Maldonado et al. 2015, Mumby and Steneck 2018). Although conspicuous sponges ranked in the top-priority space owing to their greater vulnerability, cryptic (and boring) sponges (Figure 23) scored higher in their functional importance and are highlighted here under precautionary principles owing to the relative uncertainty in their scores (Figure 20). Cryptic sponges can be the most significant invertebrate bioeroders on coral reefs (Neumann 1966, Glynn and Manzello 2015), a process likely to be accelerated in a future ocean (Wisshak et al. 2014). The contribution of cryptic sponges to reef and rubble consolidation (Figure 23) is well appreciated (Wulff and Buss 1979, Wilkinson 1983, Hutchings 2011), facilitating recruitment processes and reef recovery (Fox et al. 2003, Fox and Caldwell 2006, Biggs 2013). Sponge aggregations can enhance local biodiversity through habitat provisioning, making it important to determine the competitive relationships between sponges and other phase-shift drivers (e.g. algae), and how the changing dominance of these organisms may alter trophic pathways and energy flows on coral reefs (Maldonado et al. 2015, Bell et al. 2018). There may be interesting outcomes in a future ocean as sponge-dominated reefs become increasingly common (Norstrom et al. 2009, Gonzalez-Rivero et al. 2011, Pawlik 2011, Bell et al. 2013, Easson et al. 2014, Farnham and Bell 2018), but possibly shifting towards phototrophic communities (Bennett et al. 2017, Bell et al. 2018, Bennett et al. 2018). For *Cliona*, the most abundant bioeroding sponge on the GBR, tolerance to ocean warming may be low (Ramsby et al. 2018a), and while clionid benthic cover does not appear to be increasing at the regional scale, it seems greatest when algal cover and nutrient levels are low (Ramsby et al. 2017).

Figure 23: Cryptic sponges consolidate unstable reef/rubble environments with benefits to recruitment, often in association with turf algae and CCA. Photo credit: T. Kenyon (left).

3.4.4.5 Crustaceans

As for the marine worms, the functional and taxonomic diversity of crustaceans (Figure 24) on the GBR is poorly characterised. Crustaceans are the most diverse marine arthropods and are often termed ‘insects of the sea’ spanning from microscopic copepods, to parasitic isopods, to predatory decapods, to filter-feeding barnacles (Hutchings et al. 2019). Crustaceans are abundant in all habitats of the GBR, with ~1300 recorded species, but the cryptic nature of many of these groups makes them inherently difficult to examine and quantify (Ponder et al. 2002). This includes those that exist in the plankton, such as copepods (Figure 24e, f), which are the most well-studied and important group numerically in the zooplankton in waters of the GBR, constituting ~80% of the mesozooplankton abundance (McKinnon and Thorrold 1993, McKinnon et al. 2005, McKinnon et al. 2007). Among the most well-known crustaceans are the decapods (crabs, shrimps and lobsters), owing to their larger size and commercial value. The dendrobranchiates (prawns) are not generally common on coral reef structures but are common in coastal and inter-reefal sediment habitats where they support an important trawl fishery on the GBR (Gribble 2003, GBRMPA 2014b). Stomatopods (e.g. mantis shrimp) are possibly the most flamboyant crustaceans on coral reefs, with vivid colouration, remarkable vision (Marshall et al. 1994, Porter et al. 2010), and active and aggressive 'spearing' and 'smashing' hunting techniques, sometimes targeting larger fish prey (deVries et al. 2016, Goatley et al. 2017, Hutchings et al. 2019). Owing to their association with corals, coral-associated decapods (e.g. *Trapezia*, *Tetralia*) (Figure 24a) have received considerable attention in the literature (see: Stella et al. 2011b), as reflected by a higher relative certainty in expert scores here (Figure 20). The contribution of crustaceans to marine food webs is fundamental and has gained slightly more traction than for the worms, as the hard exoskeletons of crustaceans are more easily identified in gut content analyses (Case Study 1; Appendix 4). However, explicit quantification of population productivity, bioavailability and trophic transfers of crustaceans to higher order predators is essential to our understanding of reef trophodynamics and production functioning.

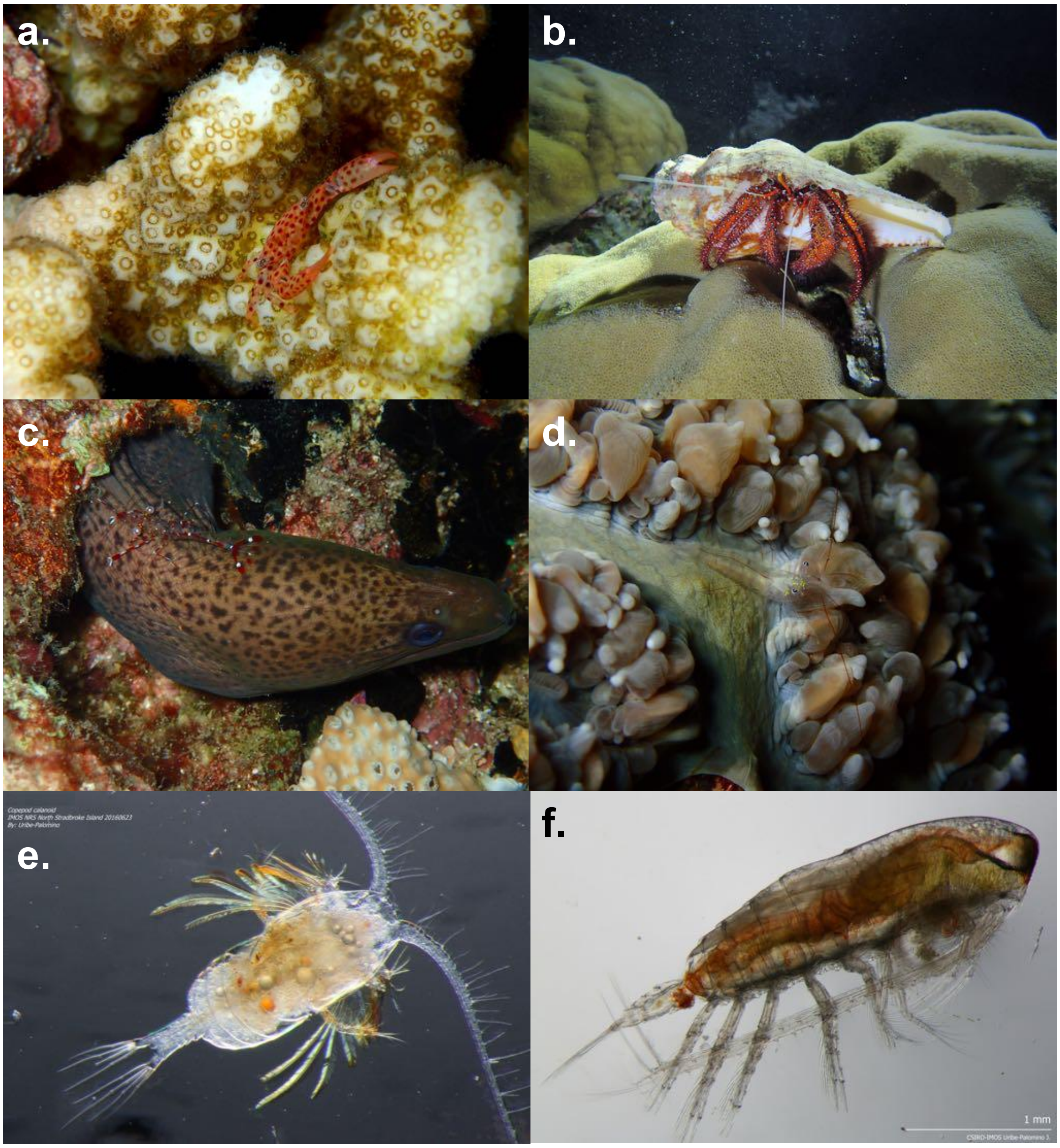

Figure 24: Crustaceans (Arthropoda) are a functionally and taxonomically diverse group, including (a.) symbiotic coral crabs, (b.) herbivorous hermit crabs, (c.) cleaner and (d.) commensal shrimp, and (e,f) microscopic copepods in the zooplankton. Photo credit: T. Kenyon (a-d), J. Uribe (CSIRO; e-f).

4.0 RECOMMENDATIONS AND CONCLUSION

In this comprehensive review guided by expert elicitation, we document a diversity of species that are critical to ecosystem functioning on the GBR. This presents the first attempt to rate and compare the functional importance, vulnerability and manageability of the incredible diversity of organisms on a coral reef spanning from microbes to predatory fishes. As a result, functional groups remained relatively broad, but greater detail can be found in the following sections where priority groups and species are highlighted. It is noted that this assessment was through the lens of classical reef crest and reef slope habitats on the GBR, and that whole-ecosystem management is necessary to maintain the integrity of the reef. Regardless, many of the attributes examined here, at the level of species, ecological processes and ecosystem functions, are of OUV and contribute greatly to the integrity and cultural values of the GBR and its World Heritage property (GBRMPA 2014c), and for coral reefs in general. So here we provide a first step to inform holistic management approaches aiming to preserve important reef species, values and processes.

Ultimately, global protection of coral reefs depends on fast action towards a low-carbon economy, but this must be augmented with local action to prevent degradation of reef structures and associated losses of ecosystem functions and services (Kennedy et al. 2013, Albright et al. 2016a, Cinner et al. 2016). Explicit identification and protection of key species that support positive ecological interactions is imperative to conservation success, and in providing targeted information to safeguard species, biodiversity and functioning into the future (Halpern et al. 2007, Mumby and Steneck 2008, McClanahan et al. 2014, Rogers et al. 2015, Shaver and Silliman 2017, Richards and Day 2018).

In the following sections, we reiterate findings in case-specific compilations of the literature for priority groups that met expectations (*Who were the winners?*) and provided novel cases (*Who were the surprises?*). Future work aiming to protect the biodiversity values of coral reefs may use the information compiled here to inform dynamic research and management to safeguard ecosystem functioning at its highest degree (Richards and Day 2018). We highlight suggested areas where management and/or science could increase monitoring and integrate novel approaches, while commending current management success in spatial planning (Day 2002) and conservation initiatives (e.g. GBRMPA 2017, 2018a) on the GBR, which seem to effectively capture priority groups and functional entities. In any case, a default management strategy should exist in education, which can enhance pro-environmentalism, stewardship, compliance and the transfer of information regarding reef conservation (Zeppel 2008, Myers et al. 2012, Beeden et al. 2014b, Elmer et al. 2017, Vercelloni et al. 2018).

4.1 Who were the winners?

4.1.1 Branching and tabular corals

Of the coral groups addressed here, tabular, staghorn and other branching corals scored highest in combination for their functional importance and vulnerability on the GBR. The roles of branching and tabular corals in reef ecosystem functioning are fundamental and have been extensively documented. Throughout the Indo-Pacific, fast-growing branching species like *Acropora* and *Pocillopora* contribute most to rapid increases in coral cover (Connell et al. 1997, Pratchett et al. 2015), most notably during years without major disturbance events (Thompson and Dolman 2010). As addressed in Case Study 2 (Appendix 5), the relative contribution of corals of the *Acropora* genus to net ecosystem calcification outweighs that of other coral groups and calcareous algae, with the greatest contribution to the carbonate budget of the GBR. Reproduction, recruitment and growth rates of structural branching and tabular species are highly variable across time and space (Browne 2012, Browne et al. 2013, Pratchett et al. 2015, Anderson et al. 2017, Anderson et al. 2018), as they can be the most susceptible groups to a range of stressors including coral bleaching (Baird and Marshall 1998, Marshall and Baird 2000, Loya et al. 2001) and ocean acidification (Fabricius et al. 2011, Madin et al. 2012). Yet, they appear to be persistently key to rapid reef growth and post-disturbance recovery (Pearson 1981, Connolly and Muko 2003, Ortiz et al. 2014, Ortiz et al. 2018). Ensuring that species key to carbonate production, a positive carbonate budget and reef recovery are protected is a key focus of resilience-based management on the GBR (GBRMPA 2017, 2018a) (Table 12).

Rates of recovery for coral assemblages are dependent on the relative contributions of new recruits and adult persistence (Connell et al. 1997, Linares et al. 2011, Gilmour et al. 2013, Pratchett et al. 2015). Following localised bleaching in the central GBR in 2001–2002, increases in coral cover up to 10% y^{-1} were primarily driven by tabular *Acropora hyacinthus*, almost entirely attributed to growth of existing corals (Linares et al. 2011). Recent mass-bleaching on the GBR resulted in significant declines in coral recruitment by ~89% with brooding *Pocillopora* species replacing spawning *Acropora* in the recruitment panel for the first time documented (Hughes et al. 2019a). This supports the suggestion that *Pocillopora* species may be more thermally resilient (Epstein et al. 2019) owing to the local adaptation required in brooding reproductive modes where gene flow is retained (Ayre and Miller 2004, Miller and Ayre 2004, Baums 2008). It is increasingly important to determine how coral larval density and supply may scale up to support reef recovery (Doropoulos et al. 2017a, Doropoulos et al. 2018). If the recovery trajectory of *Acropora* and other branching corals are increasingly compromised then shifts in dominance towards more robust and resilient taxa (e.g. *Porites*) can be expected (Fabricius et al. 2011, Pratchett et al. 2015).

Branching and tabular corals are the preferred target of CoTS (Colgan 1987, Pratchett 2007), and so current CoTS control initiatives should be maintained in support of reef resilience (Westcott et al. 2016). Tabular corals are also more susceptible to coral diseases, including the epizootic White Syndrome (Roff et al. 2006, Roff et al. 2008, Hobbs and Frisch 2010, Maynard et al. 2011, Roff et al. 2011, Hobbs et al. 2015). The five diseases found to affect *A. hyacinthus* also increase in prevalence as water temperature warms (Willis et al. 2004). Due to their morphology, physical impacts from storms, cyclones, vessel groundings and anchor damage are often more significant for branching and tabular corals compared to other morphologies (Riegl and Velimirov 1991, Riegl and Riegl 1996, Connell et al. 1997, Hughes and Connell 1999, Dinsdale and Harriott 2004, Madin 2005). While frequent, anchor damage is considered to have a relatively low impact across the GBR (GBRMPA 2014b, Kininmonth et al. 2014), and current management efforts are proving effective in reducing coral damage in high-use areas through increased awareness and stewardship (Beeden et al. 2014a).

As recognised here and previously (Ortiz et al. 2014, GBRMPA 2017, Ortiz et al. 2018), tabular corals are paramount to the resilience of the GBR. However, there may be low ecological redundancy of key tabular corals on the GBR with just three species considered common; *A. hyacinthus*, *A. cytherea* and *A. clathrata*. There should be continued momentum in the protection of tabular corals on the GBR (GBRMPA 2017, 2018a), in conjunction with research, long-term monitoring programs and plans to operationalise resilience-based management (GBRMPA 2018b) (Table 12). Tabular corals are easily recognised and render themselves important features for monitoring by citizen science groups and in education in support of reef awareness, compliance and protection at the greatest levels of functioning (Table 12).

Acropora hyacinthus often dominates the reef crest and shallow reef slope on the GBR and coral reefs throughout the Indo-Pacific (Veron 1986), where it exhibits both asexual and sexual reproduction (Wallace 1985, Smith and Hughes 1999). This species is listed as Near Threatened on the IUCN Red List of Threatened Species (Aeby et al. 2008), along with a range of other scleractinian corals on the GBR (Richards and Day 2018). Internationally, all corals are listed on CITES Appendix II, which restricts and controls trade of ‘at risk’ species, and are important attributes of OUV that contribute to the World Heritage status of the GBR (GBRMPA 2014c). Acroporids have historically been the main targets of coral fisheries on the GBR, but with minimal impact on their populations (McCormack et al. 2005).

In situ enhancement of coral larval supply and recruitment is an emerging tool to replenish degraded reefs (Heyward et al. 2002, Cooper et al. 2014, dela Cruz and Harrison 2017, Doropoulos et al. 2019). Similarly, the culture of ‘super corals’ is an emerging management strategy aiming to enhance reef resilience and recovery via transplanting and outplanting of adapted corals (Auberson 1982, van Oppen et al. 2015, Barton et al. 2017, Van Oppen et al. 2017, Beyer et al. 2018, Camp et al. 2018b, Forsman et al. 2018). There has been success transplanting fragments of *A. hyacinthus* and a range of other coral species onto reefs including in Japan (Okubo et al. 2005), the Maldives (Clark and Edwards 1995), and the Caribbean (Bruckner and Bruckner 2001, Bruckner and Borneman 2010, Ladd et al. 2018, Ladd et al. 2019). However, there are potential limitations in larval seeding and transplant methods through altered coral-microbe communities and increased disease proliferation (Casey et al. 2015b), reduced species diversity and ecological functioning (Ladd et al. 2018, Ladd et al. 2019), as well as spatial limitations at whole-reef scales. Regarding larval seeding techniques, enhancement of a diverse assemblage of coral species is imperative to reef recovery and functioning, and seeding from natural spawning slicks may offer promising opportunities for large-scale coral reef restoration (Heyward et al. 2002, Doropoulos et al. 2019). If targeted research on transplanting and outplanting corals for restoration was to develop further, then functionally important species like *A. hyacinthus* are suggested (Table 12).

Table 12: Recommendations and desired outcomes for tabular and branching corals; management (green), science (orange).

Knowledge and recommendations	Desired Outcomes	Relevant groups and end-users
Current GBRMPA initiatives capture tabular corals as a key group on the GBR (GBRMPA 2017, 2018a).	Maintain momentum in the protection of tabular *Acropora* spp. in line with current management programs.	GBRMPA Blueprint for Resilience RIMReP IUCN Red List
Coral resilience and recovery are dynamic. Branching coral taxa are important to consider regarding trajectories of recovery.	Consider branching coral taxa (e.g. *Pocillopora*) for enhanced protection and educational awareness.	RIMReP GBRMPA Blueprint for Resilience IUCN Red List Education
Current long-term monitoring programs provide invaluable information to both management and research. Consider key tabular and branching taxa in demographic-level monitoring (e.g. growth and mortality rates).	Maintain (or enhance) long-term monitoring datasets that track reef performance and recovery.	AIMS LTMP and MMP Citizen science
If GBRMPA were to engage in targeted research on transplanting corals for restoration, then functionally important species like *A. hyacinthus* are suggested.	Targeted restoration for key coral taxa.	Transplanting / aquaculture RRAP Citizen science
Tabular corals are easily recognised and render themselves important features for monitoring by citizen science groups in support of monitoring corals and their recovery.	Integrate tabular corals in citizen science and education programs to enhance protection, awareness and stewardship.	Eye on the Reef Citizens of the GBR Great Reef Census Education Anchor management
Refine carbonate budgets to resolve the contribution of individual coral taxa, including thresholds in coral cover necessary to maintain a positive carbonate budget.	Ensure that taxa key to a positive carbonate budget are protected to support reef performance and recovery.	RIMReP Research
Experiments aiming to characterise coral resilience and recovery should consider realistic thermal and chemical (e.g. pH, alkalinity) cycles to capture local habitat-specific tolerances and genomics.	Research should move away from snapshots of projected end-of-Century conditions to understand local adaptation to diel cycles.	Research

4.1.2 Microorganisms

Microbial communities, spanning both host-associated (e.g. corals, sponges, algae) and free-living (e.g. seawater, sediments) taxa, drive biogeochemical cycles in the ocean and undertake numerous functions that underpin the health of coral reef ecosystems (Falkowski et al. 2008, Krediet et al. 2013). They are key to the remineralisation of organic matter and efficient recycling of nutrients, especially in oligotrophic tropical waters (Capone et al. 1992, Tribble et al. 1994, Rasheed et al. 2002, Wild et al. 2005, Ferrier-Pages et al. 2016). The role of microbes in marine invertebrate recruitment and settlement dynamics are also well-recognised (Webster et al. 2004, Webster et al. 2011, Siboni et al. 2012a). Their sweeping ratings to ecosystem functioning here are not surprising, though most groups had lower rated vulnerabilities on the GBR compared to other functional groups.

We outline host-associated phototrophic microbes (e.g. Symbiodiniaceae) as the most critical microbe group to consider in management to maintain a healthy reef, as they are inextricably linked to the survival of their coral hosts (Bourne et al. 2016). Importantly, the relative abundance of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, Howells et al. 2013, Stat et al. 2013, Bay et al. 2016), an important feature in a warming climate. As we become more aware of the functional roles of microbial communities on coral reefs it is increasingly apparent that broad-scale community sequencing of the coral holobiont (coral host and microbial symbionts) is required in order to characterise metabolic pathways, coevolution and the acclimation/adaptation of coral reefs to environmental change (Bourne et al. 2016) (Table 13).

Microbes can be the first biological responders to environmental perturbation (Bourne et al. 2016, Glasl et al. 2017, Glasl et al. 2018a), with populations that vary in response to external conditions (e.g. season, water quality) and habitat type (Kelly et al. 2014, Tout et al. 2014, Angly et al. 2016, Frade et al. 2016, Agusti et al. 2019). Such environmental parameters can drive the spatial distribution and temporal dynamics of pelagic microorganisms across different habitats of the GBR (Case Study 3). Free-living microbes and bacteria in reef seawater and sediments may be more sensitive indicators of environmental change than coral-microbes (Glasl et al. in press). Specifically, the Prochlorococcaceae:Synechococcaceae relative abundance ratio provides an indicator of the contribution of nutrient enrichment in GBR waters (Table 13), which seems to be sensitive both at spatial and temporal scales (Case Study 3; Appendix 6). Yet, despite this potential, we have a poor understanding of how microbes to provide resilience and buffering across the greater reef system or how they could be used as early warning signals for tipping points as habitats degrade (Table 13).

Given that microbes have great potential to be used as early warning signals, it would be highly beneficial to establish baseline conditions of the coral reef microbiome, from host-associates to free-living assemblages, as the current lack of data hinders our potential to use microbes in reef-monitoring programs (Table 13). Incorporating the coral reef microbiome into long-term monitoring schemes could provide useful information to assess and predict broader reef impacts from coastal eutrophication and climate change. Establishment of microbial baselines through a network of microbial observatories spanning key habitats along inshore to offshore gradients of the GBR would enable a robust assessment of the microbial contribution to reef functioning (Table 13). This would require a combination of analytical techniques (omic approaches: genomic and transcriptomic sequencing, metabolomics, epigenetics) to characterise assemblages, including *in situ* visualisation to link localisation with broader reef functioning.

Table 13: Recommendations and desired outcomes for microorganisms; management (green), science (orange).

Knowledge and recommendations	Desired Outcomes	Relevant groups and end-users
The current lack of data on the coral reef microbiome, from host-associates to free-living assemblages, hinders our potential to use microbes in reef-monitoring programs.	Support establishment of a network of microbial observatories spanning key habitats along inshore to offshore gradients in the northern, central and southern GBR. This network would help develop a potential science-case to implement microbial assemblages in monitoring.	RIMReP AIMS LTMP and MMP Research
Incorporating microorganisms into long-term monitoring programs and resilience-based management could provide useful information on early warning signals through the relative abundances of key taxa over time. E.g. the Prochlorococcaceae: Synechococcaceae relative abundance ratio provides an indicator of nutrient enrichment in GBR waters, which is sensitive both at spatial and temporal scales (Case Study 3).	Use microbial baselines as early warning signals to assess impacts from coastal eutrophication and climate change. Continue support for data development through the eReefs platform regarding environmental conditions (e.g. water quality, temperature and chemistry).	RIMReP AIMS LTMP and MMP Water quality management Research eReefs
Broad-scale sequencing of the coral holobiont (coral host and microbial symbionts) is required to characterise metabolic pathways, coevolution and the acclimation/adaptation of coral reefs to environmental change.	Determine the relative abundance of key groups in the coral microbiome to predict coral resilience and performance.	Research
Combine analytical techniques (omic approaches: genomic and transcriptomic sequencing, metabolomics, epigenetics) to characterise microbial assemblages, including *in situ* visualisation.	Establish baseline information to upscale microorganism localisation to broader reef functioning.	Research

4.1.3 Crustose coralline algae (CCA)

CCA (Figure 25) was outlined as the most important and vulnerable of the algal groups, in light of the low rated vulnerability of algal turfs and other macroalgal groups to ecosystem stressors. It is broadly understood that some CCA are important components of the EAM, aiding in reef consolidation (e.g. *Porolithon*) (Figure 25) (Matsuda 1989, Diaz-Pulido and McCook 2008), shaping cryptobenthic communities within the reef matrix (e.g. *Mesophyllum*, *Lithothamnion*) (Enochs and Manzello 2012), and in coral recruitment facilitation (e.g. *Titanoderma*) (Heyward and Negri 1999, Harrington et al. 2004, Arnold et al. 2010, Diaz-Pulido et al. 2010, Doropoulos et al. 2012a, Doropoulos et al. 2018). CCA are calculated to be the primary non-coral contributors to net carbonate production on the GBR (Case Study 2; Appendix 5), and elsewhere (Bak 1976, Perry et al. 2012a). The functional roles of CCA may be particularly important on reef crests, where they can dominate benthic cover >90% (Atkinson and Grigg 1984, Glynn et al. 1996), including for vertical surfaces with lower rates of sediment accumulation (Kennedy et al. 2017, Duran et al. 2018). Surveys of CCA on the GBR indicate that assemblages vary considerably in abundance, diversity and composition across the continental shelf, and suggest that shelf positioning, habitat, grazing and water quality (e.g. sediment deposition and nutrient loads) are key factors affecting their distribution (Fabricius and De'ath 2001b, Dean et al. 2015). To ensure CCA is preserved at its highest level of functioning, it seems important to maintain the key processes necessary for CCA growth, which primarily involves facilitating high rates of herbivory and reducing sediment loads (Table 14).

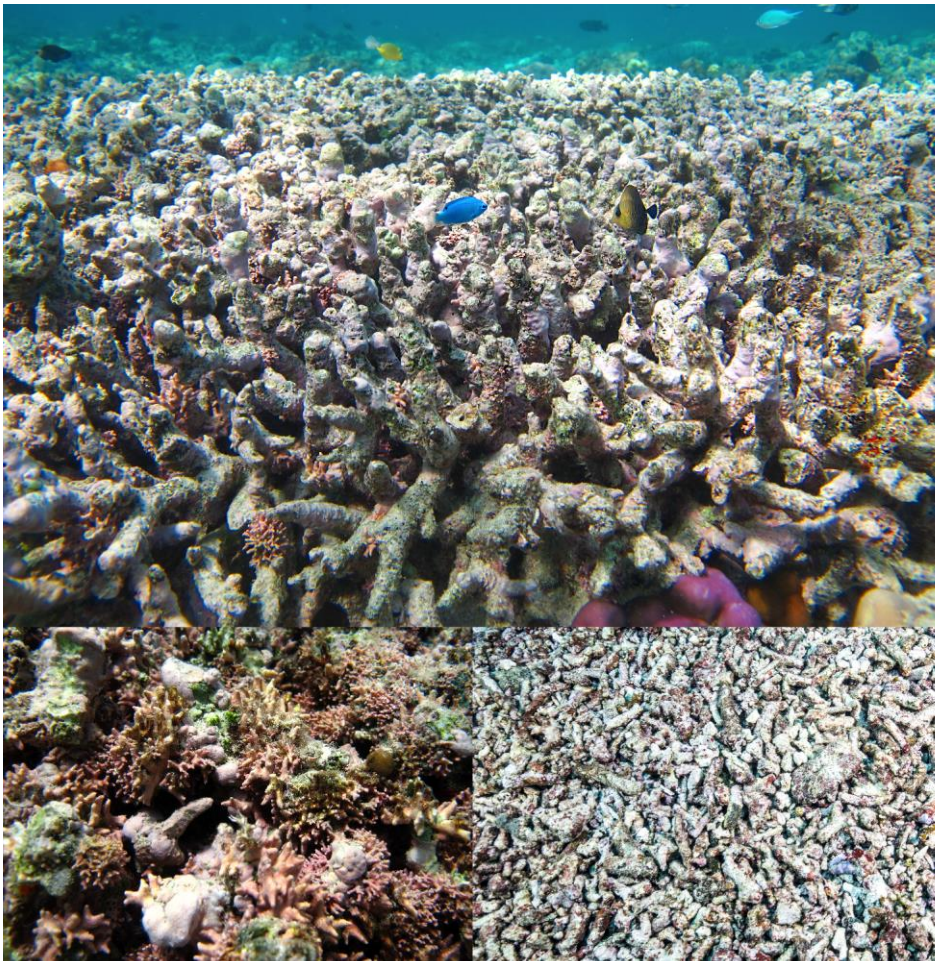

Figure 25: CCA can encrust over dead coral and rubble habitats, contributing to processes such as primary productivity, calcification, reef consolidation and recruitment facilitation. Photo credit: T. Kenyon (bottom right).

Currently, species-specific information on the distribution and relative abundance of key CCA taxa (e.g. *Titanoderma*, *Porolithon*) is limited, and these groups would benefit from consideration in long-term monitoring programs (Table 14). On the GBR, CCA taxa abundant on offshore reefs include *Neogoniolithon*, *Lithophyllum* and *Porolithon* species (Diaz-Pulido and McCook 2008), but generally, they are data deficient and information is restricted to a few locations on the GBR (Dean et al. 2015). Taxonomic information is very scarce and the cryptic diversity evident in even the most well-known genera (e.g. *Porolithon*) is quite high (Gabrielson et al. 2018), and attention to these gaps requires urgent action. Species-specific information is essential for consideration by global protection agencies (e.g. IUCN Red List), especially for priority species with key roles, like *Titanoderma* and *Porolithon*, that work to uphold the OUV of the GBR (Table 14).

Some common GBR species (*T. pustulatum*, *P. onkodes*, *Neogoniolithon* sp.) have the remarkable capacity to deter settlement of seaweed spores, which may be an increasingly important feature on future coral reefs to minimise coral-algal phase shifts (Arnold et al. 2010, Vermeij et al. 2011, Gomez-Lemos and Diaz-Pulido 2017), especially considering the active removal of macroalgae is an emergent management strategy (Ceccarelli et al. 2018). *Titanoderma* spp. is one of the preferred substrates for coral settlement, with one experiment showing settlement rates to be 15 time higher on this species compared to other CCA

(Harrington et al. 2004). How this translates at the ecosystem level *in situ* remains unclear (Table 14). Ocean acidification may have direct impacts on coral reef settlement success through impacts on CCA (Doropoulos et al. 2012a, Doropoulos and Diaz-Pulido 2013, Espinel-Velasco et al. 2018), and so it seems critical to assess the potential ecosystem-level consequences that a loss of key coral settlement inducers could have on the recruitment success on coral reef species (Table 14). Interestingly, coral larvae seem to show settlement preference towards red coloured objects (e.g. plastic cable ties, buttons), compared to blue, green and white substrates, which reflects their propensity to settle to pink CCA and – at least in part – decouples the paradigm that settlement cues are solely biochemically driven (Mason et al. 2011, Gómez-Lemos et al. 2018). This may become an important consideration for reef restoration (Mason et al. 2011), particularly since CCA appear to be highly vulnerable to changes in ocean condition (i.e. warming and acidification), even more so than some coral species (Diaz-Pulido et al. 2007, Anthony et al. 2008, Diaz-Pulido et al. 2012).

Table 14: Recommendations and desired outcomes for CCA; management (green), science (orange).

Knowledge and recommendations	**Desired Outcomes**	**Relevant groups and end-users**
CCA assemblages vary considerably in abundance, diversity and composition due to herbivory and water quality (e.g. sediment deposition and nutrient loads).	Maintain the key processes necessary for CCA growth, which primarily involves facilitating high rates of herbivory and reducing sediment loads.	Improved water quality Land use management Dredge management Fisheries management
CCA can be more vulnerable to ocean warming and acidification than some corals.	Produce exposure maps for CCA with eReefs along major disturbance gradients.	eReefs
Species-specific information on the distribution and relative abundance of key CCA taxa (e.g. *Titanoderma*, *Porolithon*) is limited. These groups would benefit from consideration in long-term monitoring programs.	Undertake periodic assessments (3–5 years) of the distribution and abundance of key CCA taxa at a subset of sites, particularly along major disturbance gradients.	RIMReP Research
Policies would be well-served by having species- or genus-level data for CCA.	Fill gaps in knowledge to inform protection agencies. Focus should be on species with key roles and/or vulnerability (*Titanoderma*, *Porolithon*).	IUCN Red List
Some CCA facilitate coral recruitment (e.g. *Titanoderm* spp.), but how this process scales up at the ecosystem level *in situ* remains unclear.	Critically assess the ecosystem-level consequences of a loss of key coral settlement inducers on recruitment processes.	Research

CCA are important non-coral calcifiers with a significant influence on reef-scale carbonate budget estimates.	Calculate how the relative abundance of explicit CCA taxa contribute to variability in the carbonate budget and determine thresholds and tipping points in benthic cover to maintain a positive carbonate budget.	Resilience-based management RIMReP Research

4.1.4 Algal turfs and the EAM

Algal turfs were rated the most functionally important group regarding production functions, and third for total functioning, but were considered largely resilient to the range of stressors examined here. For this very reason, this group is highlighted here under precautionary principles in context of algal phase shifts in a changing ocean (Roth et al. 2018). Algal turfs are an assemblage of minute often filamentous algae that exhibit fast growth, high productivity and rapid colonisation rates. Within the epilithic algal matrix (EAM), turfing species dominate surprisingly large proportions of coral reefs (Diaz-Pulido et al. 2016), where they are critical to primary production in oligotrophic waters (Adey and Goertemiller 1987, Klumpp and McKinnon 1989), harbour detritus, microorganisms (Wilson et al. 2003), and host a diversity of cryptic invertebrates (Kramer et al. 2012). While the taxonomy of turfs and EAMs is complex, offshore reefs are often dominated by the red alga *Ceramium punctatum* and the blue-green algal family, *Nostococaceae* (Scott and Russ 1987), while inshore reefs are typically dominated by the green algae *Acetabularia calyclus* and *Cladophora fascicularis*, the filamentous brown algae *Sphacelaria* spp. and the *Falkenbergia* stage of the red alga *Asparagopsis taxiformis* (Diaz-Pulido and McCook 2008).

EAMs cover high proportions of reef flats (50–80%) and reef slopes (30–70%) on the GBR, with particularly high productivity in summer (Klumpp and McKinnon 1992). They lay the foundations for benthic production functions, with particularly important roles in the fixation of nitrogen and its rapid distribution across trophic pathways (Borowitzka et al. 1977, Borowitzka 1981, Wilkinson et al. 1984, Hatcher 1988, Larkum et al. 1988). Rates of turf algal productivity strongly predict herbivore biomass (Carpenter 1986, Russ 2003, Tootell and Steele 2016), and conversely, herbivores directly regulate turf canopy height (Carpenter and Williams 1993, Mumby et al. 2013a). Herbivorous grazers are suggested to consume around half of the total annual net production of the EAM, making it directly available to the food web (Hatcher and Larkum 1983, Klumpp and Polunin 1990), particularly on reef flats (Bellwood et al. 2018).

There can be interesting top-down and bottom-up drivers of turfing seascapes on coral reefs, including from wave exposure, nutrification, sedimentation and herbivory (Carpenter and Williams 1993, Vermeij et al. 2010, Clausing et al. 2014, Tebbett et al. 2017a, Roff et al. 2019). Variability in turf assemblages occurs at small spatial scales (Harris et al. 2015), with thresholds in canopy heights and sediment depths (>3 mm) found to reduce herbivory, alter turf metabolism and impair coral recruitment (Carpenter and Williams 1993, Birrell et al. 2005, Bellwood and Fulton 2008, Arnold et al. 2010, Goatley and Bellwood 2012, Clausing et al. 2014, Doropoulos et al. 2017a, Doropoulos et al. 2017b, Lam et al. 2018). There is compelling evidence that the canopy height of turf algae can predict productivity, sedimentation, herbivory, wave exposure and recruitment success, which could be an important attribute to monitor so as to establish spatial data for this priority group on the GBR (Table 15). Further, turfs are a more pertinent stress when combined with sedimentation and/or nitrification. How dynamic states in turf algal productivity (e.g. turf height), nutrification, sedimentation and wave exposure (hydrodynamics) interact to impact ecological functioning needs to be explicitly characterised (Table 15). Precautionary measures should continue focus on water quality (e.g. eutrophication, sedimentation) in catchment and riparian management to facilitate natural moderation of turf growth through herbivory. Keeping turf canopy height low (<3 mm) is important for the successful recruitment of corals and other reef species (Roth et al. 2018). Maintaining herbivore assemblages, particularly those that regulate the EAM, would help facilitate the competitive dominance of reef-building corals (Table 15).

Despite the lack of information on long-term trends in algal condition, major changes are expected to occur regarding their distribution, abundance and composition in a changing ocean, driving significant alterations to ecological functioning (Diaz-Pulido et al. 2007, Diaz-Pulido et al. 2011a). On turf- and macroalgal-rich reefs, the relative abundance and diversity of microbial assemblages also increase with the potential to influence nutrient pathways and reef health (Haas et al. 2016, Brown et al. 2019). Ocean acidification is likely to enhance algal turf productivity and biomass (Ober et al. 2016), cause shifts in epilithic communities to turfing and cyanobacteria assemblages (Diaz-Pulido and McCook 2002, Bender et al. 2014b), and increase rates of bioerosion and reef carbonate dissolution (Carreiro-Silva et al. 2005, Tribollet et al. 2006, Schönberg et al. 2017). Even marginal differences in turf canopy height impacts micro-scale circulation can alter turf metabolism and chemistry across diffusive boundary layers (Carpenter and Williams 1993). This will directly influence the balance between reef growth (calcification) and destruction (dissolution) in a future ocean, with predictions that coral reefs will switch to a state of net dissolution by the end of this century (Albright et al. 2018, Eyre et al. 2018). However, the raw contribution of microfloral borers to net reef erosion are difficult to quantify and knowledge gaps remain (Case Study 2; Appendix 5) (Hutchings 1986, Glynn and Manzello 2015). Concerns over shifting carbonate budgets should address all forms of bioerosion, including rates within the EAM and endolithic algae (Table 15), especially given the propensity for turf algae to rapidly colonise dead coral substrate following perturbation (Diaz-Pulido and McCook 2002), and that bioerosion rates are likely to increase due to environmental change with significant impacts on reef health and resilience. Rates of carbonate dissolution within the reef matrix also need to be quantified, as these cements may be more responsive to changes in the saturation state of calcium carbonate under ocean acidification scenarios (Reyes-Nivia et al. 2013). More positively, *in situ* cultivation of some algal species has been suggested as a potential management strategy to, at least in part, mitigate or buffer ocean acidification and its effects on coral reefs through biogeochemical functioning (Mongin et al. 2016a).

Table 15: Recommendations and desired outcomes for algal turfs; management (green), science (orange).

Knowledge and recommendations	**Desired Outcomes**	**Relevant groups and end-users**
Keeping turf canopy height low (<3 mm) is important for the successful recruitment of corals and other reef species.	Maintain herbivore assemblages, particularly those that regulate the EAM, to facilitate the competitive dominance of reef-building corals.	Fisheries management GBRMPA Blueprint for Resilience
Turfs are a more pertinent stress when combined with sedimentation and/or nitrification.	Precautionary measures should continue focus on water quality (e.g. eutrophication, sedimentation) in catchment and riparian management.	Land use management Improved water quality Dredge management
There is compelling evidence that the canopy height of turf algae can predict productivity, sedimentation, herbivory, wave exposure and recruitment success.	Monitor canopy heights of turf algae (and macroalgae) to establish spatial data for algae on the GBR.	RIMReP Citizen science Research
Turf canopy height could be used to highlight areas susceptible to impacts from sediment and nutrient loads, wave exposure and herbivory.	Produce maps of potential turf productivity to compare with eReefs water quality and suspended sediment layers.	eReefs
How dynamic states in turf algal productivity interact with nutrification, sedimentation and wave exposure to impact ecological functioning needs to be explicitly characterised.	*In situ* and experimental quantification of the key drivers influencing turf productivity.	Research
Current tools (e.g. eReefs) could be employed to upscale knowledge on turf productivity at the whole-reef scale through proxies of wave, nutrient and sediment load data.	Use turfs as bioindicators of reef performance and condition.	Research eReefs
The raw contribution of turfs (and the EAM) to net reef bioerosion are difficult to quantify and knowledge gaps remain (Case Study 2).	Quantify the contribution of turfs (including epilithic and endolithic algae) to net bioerosion to inform carbonate budget calculations and future reef states.	Research

4.1.5 CoTS outbreaks (and triton snails)

The pervasive impacts of coral predation by CoTS have been extensively documented (e.g. Pratchett et al. 2014, Babcock et al. 2016a, Cowan et al. 2017, Pratchett et al. 2017a, Wilmes et al. 2018). While high-density populations of CoTS can adversely affect whole reefs, their impacts at low densities are minor (Branham et al. 1971), as observed on the GBR for decades at One Tree Island (Maria Byrne, pers. comm.) and other largely unaffected reefs of the Capricorn Bunker Group (Sweatman et al. 2015). The driving forces behind CoTS population outbreaks are widely debated, but their extreme fecundity and reproductive potential (Uthicke et al. 2009, Babcock et al. 2016b, Rogers et al. 2017) and high levels of connectivity across the GBR (Matz et al. 2018) are likely strong determinants (Hock et al. 2014, Hock et al. 2017). Historically, research on the CoTS outbreak phenomenon has been significantly weighted towards the larvae (e.g. the nutrient runoff hypothesis; Lucas 1982) and adults (e.g. the predator removal hypothesis; Endean 1969), and management strategies and their implementation have developed in line with this research focus (Westcott et al. 2016).

For larvae, management has been centred on improving water quality in catchment areas to limit the potential success of early developmental stages in the plankton (Fabricius et al. 2010, Wolfe et al. 2015b, Wooldridge and Brodie 2015). Although, CoTS larvae appear to have high resilience to oligotrophy (Olson 1987, Wolfe et al. 2015a, 2017, Carrier et al. 2018), and the remarkable ability to clone in the plankton (Allen et al. 2019). Outbreaks are also documented on reefs not influenced by anthropogenically-driven eutrophication, including on the GBR and elsewhere (Lane 2012, Miller et al. 2015, Roche et al. 2015). Yet, in the absence of strong evidence for the contrary, precautionary measures should continue focus on improving water quality across catchment areas to mitigate the potential for runoff-induced eutrophy to enhance larval success (Table 16).

For CoTS adults, management on the GBR has included the protection of the once overfished triton snail (*Charonia tritonis*) (Endean 1969, Cowan et al. 2017), and the active and labour-intensive removal or culling of adults (Pratchett et al. 2014), including innovative injection and detection methods (Dayoub et al. 2015, Moutardier et al. 2015, Bostrom-Einarsson and Rivera-Posada 2016, Bostrom-Einarsson et al. 2018). Current measures of control (e.g. the NESP Integrated Pest Management project; Westcott et al. 2016) are commended, and continued development of this and other such program is encouraged, including involvement with citizen science groups and in education (Table 16). The high rankings for triton snails within this report, particularly for the predation process, reflect their perceived niche role as key predators of CoTS, and their historical vulnerability to overharvest, as reviewed previously (see Hall et al. 2017). Biocontrol of CoTS populations through triton snail predation would be most effective when aiming to keep non-outbreak populations at low densities, so as to lessen the potential for outbreaks to initiate (Hall et al. 2017). There is evidence that CoTS are less abundant in no-take fishing zones on the GBR and elsewhere (Dulvy et al. 2004, Sweatman 2008, McCook et al. 2010), suggesting that heavy fishing may encourage outbreaks through suppression of a multi-level trophic cascade (i.e. reduced predation pressure across various life stages) (Cowan et al. 2017). Yet, the lack of information on the basic biology of CoTS of any age-class *in situ* means that the relationship between fishing and outbreaks remains elusive (Sweatman and Cappo 2018). Information is particularly limited for CoTS juveniles (Case Study 5; Appendix 8), although recent work demonstrates high densities of juvenile CoTS can be detected *in situ* (Wilmes et al. 2016, Wilmes et al. 2018). Characterising this life stage may provide an important opportunity to improve the early detection of outbreaks and their management (Sweatman and Cappo 2018) (Table 16).

Case Study 5: Juvenile CoTS ‘in waiting’: the missing link in population and connectivity models

Dione Deaker, Maria Byrne

Settlement of CoTS larvae is typically triggered by CCA or biofilm (Johnson et al. 1991, Wolfe et al. 2015b), where they begin their benthic life stage as small herbivorous juveniles (Figure CS5.1) with an ontogenetic shift in diet to become coral predators as they grow (Yamaguchi 1974, Johansson et al. 2016, Kamya et al. 2018). As for the great diversity of marine invertebrates, the early life history stages of CoTS experience high mortality rates (Keesing et al. 2018, Wilmes et al. 2018). In order to seed a population outbreak of deleterious corallivorous adults, high survival rates of the herbivorous juvenile are required. However, the biology and ecology of juvenile CoTS are poorly characterised due to their highly cryptic nature.

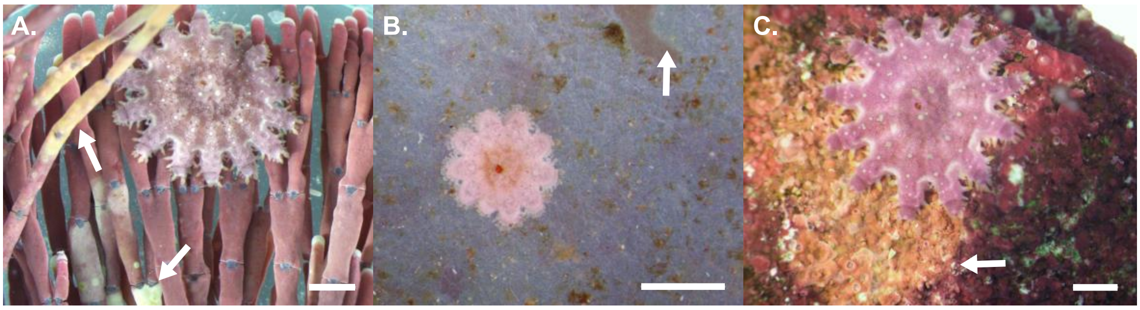

Figure CS5.1: Juvenile CoTS leave feeding scars (white arrows) on a range of algal food sources, including (A) *Amphiroa*, (B) biofilm, and (C) CCA (scale bars = 1 mm).

In an experiment over 4.5 months (139 days), juvenile CoTS were raised on one of three diets: crustose coralline algae (CCA), *Amphiroa* sp. (calcifying algae) or biofilm (Figure CS5.1), and their growth rates quantified. As for adult CoTS, juveniles leave feeding scars on their algal food source (Figure CS5.1). Juveniles fed CCA and *Amphiroa* grew the same number of arms (Figure CS5.2a) and at the same rate until day-43, when those fed CCA began to grow faster (Figure CS5.2b). Juveniles were able to consume and survive on biofilm, although growth was marginal (Figure CS5.2a, b). When offered a choice between the three diets, they selected either CCA or *Amphiroa* over biofilm, indicating that they can identify preferred food at this early life stage.

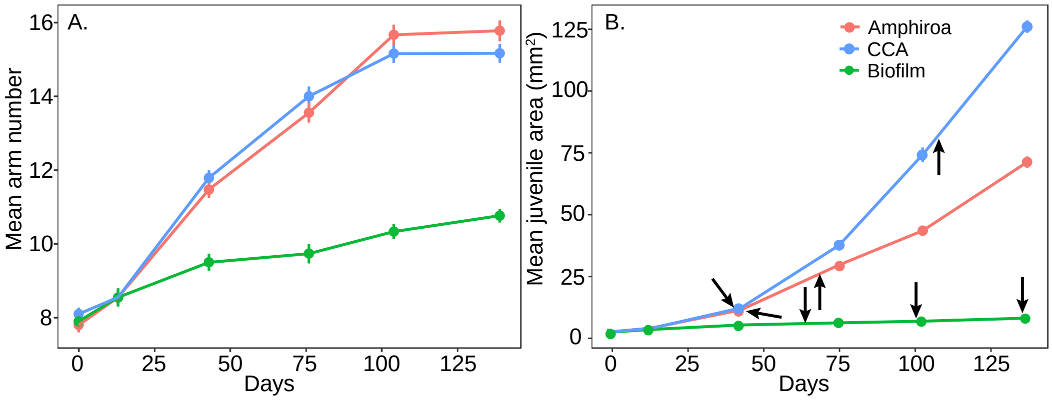

Figure CS5.2: Mean number of arms (A) and area (B) of CoTS juveniles raised on three separate diets (arrows indicate single mortality events, which occurred in all treatments).

In general, CoTS have a broader diet range than previously recognised. Their ability to subsist on biofilm alone suggests that juvenile CoTS may be able to survive for extended periods of time in the coral rubble matrix (or other EAM habitat) following settlement and prior to their ontogenetic switch to corallivory. This may create a time lag across the larval–settlement–juvenile–outbreak continuum of the CoTS life history, which is currently uncaptured in population models. As juvenile growth rates are strongly linked to resource availability, current growth estimates that are largely based on laboratory cultures (e.g. Wilmes et al. 2016) may not reflect size-age relationships in nature. These juveniles 'in waiting' complicate our ability to understand the processes that drive CoTS outbreaks and require extra attention. Early warning signals for outbreaks may exist in the benthos through juvenile reserves, but where these exist remains largely unknown (Johnson et al. 1991, Wilmes et al. 2016, Wilmes et al. 2018). The characterisation of habitat preferences of CoTS juveniles has the potential to reshape how we survey, detect and manage CoTS on the GBR and on coral reefs in general.

Table 16: Recommendations and desired outcomes for CoTS; management (green), science (orange).

Knowledge and recommendations	**Desired Outcomes**	**Relevant groups and end-users**
Current CoTS culling and removal efforts through continued development of the NESP Integrated Pest Management project (Westcott et al. 2016) are commended.	Maintain focus on reducing CoTS numbers to reduce direct impacts of outbreaks on coral cover.	NESP Integrated Pest Management project Citizen science
Precautionary measures should continue focus on improving water quality across catchment areas to mitigate the potential for runoff-induced eutrophy to enhance larval success.	Reduce impacts of water quality and nutrient loads through land use management in catchment and riparian areas.	Land use management Improved water quality
Ensure that CoTS outbreak populations are identified early for effective management.	Continue momentum of citizen science groups documenting CoTS populations on the GBR.	Eye on the Reef Education Great Reef Census
Early warning signals for outbreaks may exist in the benthos through juvenile populations, but where these exist remains largely unknown.	Consider juvenile CoTS densities as a potential early-warning indicator for outbreaks.	NESP Integrated Pest Management project
Information is particularly limited for CoTS juveniles (Case Study 5).	Focus on characterising juvenile (a) densities in situ, (b) settlement and habitat preferences, (c) nursery sites, (d) growth rates, and (e) ontogenetic shifts in diet (herbivory to corallivory).	Research
Population models (e.g. *Hock et al. 2014*, *Morello et al. 2014*, *Hock et al. 2017*) provide important information on CoTS connectivity and outbreak potential through larval dispersal.	Continued development of CoTS population models that integrate newly available information to inform predictions and management.	NESP Integrated Pest Management project Research

4.1.6 Herbivorous parrotfishes

There is a diverse but critical range of roles in the regulation and removal of algae by nominally herbivorous fishes in coral reef ecosystems (Bellwood et al. 2006b, Burkepile and Hay 2008, 2011, Steneck et al. 2017). In our process-based assessment, scraping and excavating parrotfishes were among the most ecologically significant, driven by their roles shaping habitat functions (bioerosion, ecosystem engineering, recruitment facilitation). Parrotfishes are the primary contributors to bioerosion on the GBR, as on other reefs (Perry et al. 2012a), with the capacity to exacerbate the total carbonate budget through their bioerosive processes (Case Study 2; Appendix 5). The potential for this activity to influence or buffer reef biogeochemistry would be interesting to quantify in context of ocean acidification, particularly for mass excavators such as *Bolbometopon* (Goldberg et al. 2019), as posited for deposit-feeding sea cucumbers (Schneider et al. 2011, Purcell et al. 2016a, Vidal-Ramirez and Dove 2016, Wolfe et al. 2018).

There may be limited functional redundancy among parrotfishes, which demonstrate spatial variability in their contributions to herbivory, bioerosion, ecosystem engineering and recruitment facilitation across GBR (Hoey and Bellwood 2008). *Bolbometopon muricatum*, one of the largest parrotfishes on coral reefs, appears to be most significant on outer-shelf reefs, while *Scarus rivulatus* (scraper) and *Chlorurus* spp. (excavators) are more important on inner- and mid-shelf reefs (Hoey and Bellwood 2008). *Bolbometopon muricatum* is listed as Vulnerable on the IUCN Red List owing to its susceptibility to overfishing, globally (Dalzell et al. 1996, Aswani and Hamilton 2004, Donaldson and Dulvy 2004, Chan et al. 2012, Bejarano et al. 2013, Bejarano Chavarro et al. 2014); though it is generally not fished on the GBR (Case Study 4; Appendix 7). Recruitment of this species may also be vulnerable to habitat loss attributed to water quality issues (Hamilton et al. 2017). Other parrotfishes common on the GBR are listed as Data Deficient or Least Concern by the IUCN and are currently seldom targeted by commercial and recreational fishers on the GBR. While the impact from fisheries seems low for herbivores at present, there has not yet been an assessment on the total extractive use of herbivores for the GBR (Table 17).

Changes in herbivory can result in undesirable shifts in coral reef ecosystems (Carpenter 1990, Newman et al. 2006, Bozec et al. 2013, Mumby et al. 2013b, Ainsworth and Mumby 2015, Graham et al. 2015, Roff et al. 2015, Mumby et al. 2016), with natural reversals from algal dominance back to coral dominated states rarely observed (Diaz-Pulido et al. 2009, Rasher et al. 2013). It appears that high-diversity reefs across the Indo-Pacific have a better capacity to recover from disturbance without entering an algal-dominated phase, as observed on Caribbean reefs (Roff and Mumby 2012), though alternate ecosystem states are dynamic in terms of time and space on coral reefs (van de Leemput et al. 2016). Most herbivorous fish groups were considered resilient to environmental stressors here, with densities of some grazers (e.g. parrotfishes) even documented to increase post-disturbance, perhaps due to the increased algal production that typically follows coral mortality (Cheal et al. 2008, Wilson et al. 2009, Cheal et al. 2010, Graham et al. 2015, Russ et al. 2015, Hempson et al. 2018c). Removal of particular larger herbivores can even reduce coral recovery at least three-fold by allowing modest increases in some macroalgal genera that deter coral settlement (Doropoulos et al. 2016, Mumby et al. 2016). Long-term maintenance of reef habitat and production functions requires sufficient parrotfish stocks (Mumby 2016). Protection through Herbivore Management

Areas (HMAs) is an emerging resilience-building tool in response to severe coral bleaching on reefs where herbivores are key targets (Chung et al. 2019).

While herbivorous fishes were generally considered less vulnerable on the GBR than other functional groups, lessons learned from other coral reefs where they have been intensively overfished suggest that early protection should be considered to avoid shifting baselines (Bozec et al. 2016). In support of this, GBRMPA released a conservation initiative in 2016 aimed to deter fishers from targeting herbivorous groups that act as “natural lawnmowers and keep seaweed levels under control by grazing” (GBRMPA 2016, 2017), which seems to be effective (Case Study 4; Appendix 7) (Table 17). Maintaining herbivore assemblages, particularly those that regulate the EAM, would facilitate the competitive dominance of reef-building corals (Table 17). In extreme cases of algal growth where intervention is necessary, protection of herbivores may be best coupled with active removal of macroalgae (Ceccarelli et al. 2018), though likely labour-intensive. Outplanting of the native herbivorous grazing sea urchin, *Tripneustes gratilla*, to reduce the overgrowth of invasive algal species has been a successful management focus on Hawaiian reefs for over a decade (Conklin and Smith 2005, Stimson et al. 2007, Westbrook et al. 2015, Neilson et al. 2018).

Wave exposure, nutrification and sedimentation can determine relationships between turf algal productivity and herbivory (Carpenter and Williams 1993, Vermeij et al. 2010, Clausing et al. 2014, Tebbett et al. 2017a, Roff et al. 2019), but tipping points need to be explicitly quantified to inform holistic management aiming to enhance the recruitment and the competitive dominance of reef-building corals (Table 17). It is critical to note that the functional importance of key herbivores is dynamic with changing ecosystem states (Hempson et al. 2018c). For example, the removal of carbonates by mass-excavators (*Bolbometopon*) may be critical in systems where some corals dominate, but as fast-growing corals are lost and states shift to turf-dominance, species that regulate turfs would emerge as the key functional groups (Bellwood et al. 2019). Both research and management must be flexible to the dynamics of changing ecosystems to remain ecologically relevant.

Table 17: Recommendations and desired outcomes for herbivorous parrotfishes; management (green), science (orange).

Knowledge and recommendations	Desired Outcomes	Relevant groups and end-users
Herbivores are likely to increase in importance as coral cover declines. Current education schemes (e.g. GBRMPA Blueprint) on the importance of herbivores seem to be sufficient at raising awareness at this stage.	Maintain momentum raising awareness on key herbivorous parrotfishes (*Bolbometopon*, *Scarus*, *Chlorurus*). Integrate key taxa into citizen science monitoring and education programs.	GBRMPA Blueprint for Resilience Fisheries management Education Eye on the Reef Great Reef Census
There has not been an assessment of the catch of herbivores for the GBR. While the risk seems low at present, commissioning such an assessment would be useful.	Undertake periodic assessments (3–5 years) of commercial and recreational catches of herbivorous fishes at a subset of sites, particularly along potential exploitation gradients.	RIMReP
Lessons learned from other coral reefs where herbivores have been intensively overfished suggest that early protection should be considered to avoid shifting baselines.	If monitoring indicates that herbivore catches increase, there needs to be action into determining catch limits, etc., to quantify what level of harvest might be feasible without impacting reef resilience.	Research DAF
There is compelling evidence that herbivory can indicate turf canopy height, sedimentation and wave exposure, and influence recruitment success.	Quantify tipping points between rates of herbivory, algal productivity, nutrification, sediment loads and wave exposure to enhance processes that facilitate recruitment and the competitive dominance of reef-building corals.	Research

4.2 Who were the surprises?

4.2.1 Chemoautotrophic microbes

There is a growing awareness of the importance of chemoautotrophic microbes (e.g. Archaea) in many marine habitats, including coral reefs (Figure 26). More information is known for this group in the water column, where they are highly prevalent and may have significant roles in carbon and energy cycling, particularly for the Thaumarchaeota of the Marine Group II Archaea (Jiao et al. 2010, Zhang et al. 2015, Angly et al. 2016, Liu et al. 2017). In benthic systems, they were probably first recognised as important components of the sponge microbiome, with specific roles in nitrogen and ammonia cycling (e.g. Thaumarchaeota, *Nitrospira*) (Taylor et al.

2007, Bayer et al. 2008, Webster and Taylor 2012, Bourne and Webster 2013a), and altered community dynamics following bleaching stress (e.g. *Crenarchaeota*) (Lopez-Legentil et al. 2008, Lopez-Legentil et al. 2010). In corals, a diverse endolithic community has also been identified, which is likely to be important for sustaining coral health through the exchange of nutrients, especially during periods of bleaching-related stress (Fine and Loya 2002). Motile archaeal assemblages are prevalent within the coral mucus, and are likely involved in complex nutrient cycling (Kellogg 2004, Frade et al. 2016), while anaerobic methanotrophic Archaea can be tightly coupled with nitrogen cycling and sulphate reduction in complex assemblages within coral polyps (Figure 26) (Wegley et al. 2007, Kimes et al. 2010, Bourne and Webster 2013a). There has also been an increased interest in microaerophilic and anaerobic processes within benthic substrates. Microbial assemblages vary between oxic (e.g. *Planctomycetaceae*, *Proteobacteria*) and anoxic (e.g. anaerobic methanotrophic Archaea; ANME) sediments, where they play functionally important roles in organic matter degradation and nutrient cycling (Figure 26) (Rusch et al. 2009, Rusch and Gaidos 2013).

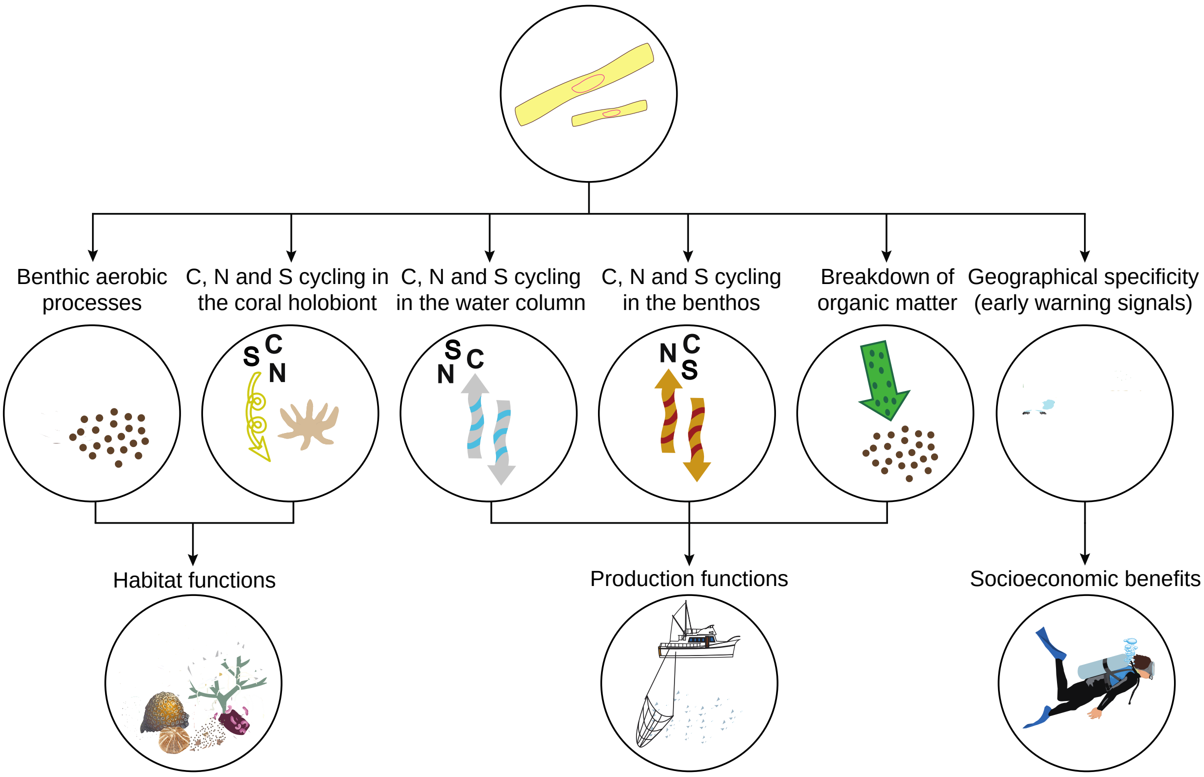

Figure 26: Schematic of the influences of chemoautotrophic microbes (e.g. Archaea) on ecosystem processes, functions and services on the GBR. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

To date, chemoautotrophic microbes have been poorly represented in the literature owing to difficulties in culturing and detecting these groups. As such, their final ranking above phototrophic and heterotrophic microbes here is somewhat surprising. It appears that archaeal assemblages are more strongly shaped by geography rather than host-specificity as displayed by other microbes and bacteria (Siboni et al. 2012b, Frade et al. 2016), although this may simply be an artefact of insufficient investigations that include archaeal-specific primers. On the GBR, prevalence of some chemoautotrophic microorganisms in the inshore lagoon system suggests seasonal variation in assemblages driven by floodwaters and consequent differences in water quality and suspended sediments (Case Study 3; Appendix 6) (Angly et al. 2016), but improved detection and monitoring of microbial groups is required, including for spatially explicit Archaea (Table 18). It is likely that microbial assemblages can be used to provide early warning signals for ecosystem change (Bourne et al. 2016, Glasl et al. 2017, Glasl et al. 2018a), but this emerging bioindicator tool requires further development (Table 18). Precautionary measures should maintain focus on water quality while links between runoff (eutrophy, sediments, etc.) and microbial assemblages are characterised (Table 18).

Table 18: Recommendations and desired outcomes for chemoautotrophic microbes; management (green), science (orange).

Knowledge and recommendations	**Desired Outcomes**	**Relevant groups and end-users**
Archaeal assemblages seem to be influenced by geography, but improved detection and monitoring of this microbial group is required.	Improved detection of microbial groups in long-term monitoring schemes, including for spatially explicit Archaea.	RIMReP AIMS LTMP and MMP Research
Free-living microorganisms are often more sensitive bioindicators than the host-specific coral microbiome.	Consider free-living chemoautotrophic microorganisms as early warning signals to assess impacts from coastal eutrophication and climate change.	RIMReP Research
Prevalence of some chemoautotrophic microorganisms demonstrate seasonal variation in assemblages driven by floodwaters and consequent differences in water quality and suspended sediments.	Precautionary measures should maintain focus on water quality while links between runoff (eutrophy, sediments, etc.) and microbial assemblages are characterised. Continue support for data development through the eReefs platform regarding environmental conditions (e.g. water quality, temperature and chemistry).	Land use management Improved water quality eReefs
Characterise spatial population dynamics of microbial groups using omic analytical approaches, including *in situ* visualisation, particularly for spatially explicit microbes (e.g. Archaea).	Establish baseline information to upscale microorganism localisation to broader reef functioning.	Research

4.2.2 Cleaner wrasse

Cleaner wrasses were the only fish group that scored in the top priority quadrant for important and vulnerable species (Figure 12) that were also considered a higher priority candidate for management (Figure 19). This ranking was likely upweighted by their low functional redundancy, as cleaner wrasse scored lower for most processes compared to other fish groups. Cryptobenthic fishes scored alongside cleaner wrasse in their combination of functional importance and potential vulnerability (Figure 12) but were deemed a lower priority for management compared to the other fishes examined (Table 19), likely owing to their incredible display of population productivity for a vertebrate (Depczynski and Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, Brandl et al. 2019).

The ecological importance of cleaning organisms and their cleaning stations in marine community dynamics (Figure 27) has long been recognised but is largely overlooked (Cote 2000, Vaughan et al. 2017). There are over 200 species of cleaner fishes from 106 genera, and over 50 species of cleaner shrimp from 11 genera, recorded to exhibit cleaning behaviour (Cote 2000, Vaughan et al. 2017). In context of the GBR, here we draw focus on the bluestreak cleaner wrasse (*Labroides dimidiatus*), as it has received considerable attention in the literature as a dedicated specialist cleaner. Though typically existing at low densities, cleaner wrasse can shape reef fish assemblages through the active removal of deleterious ectoparasites, dead skin and mucus from client fishes (Figure 27). Parasitic gnathiid isopods rapidly reoccupy their fish hosts within 24 hrs on the GBR – where they are in high abundance – a process that requires clients to frequently return to cleaning stations (Grutter 1996, 2003). The effects of gnathiids on hosts vary, ranging from partial blemishes and lesions to death, with early life history stages of fishes most susceptible to parasitic micropredation (Grutter et al. 2008, Penfold et al. 2008, Grutter et al. 2011, Sun et al. 2012, Jenkins et al. 2018, Duong et al. 2019).

Through the cleaning process, *L. dimidiatus* have been documented to reduce stress hormones in the client (Soares et al. 2011), increase fish size, density, diversity and survival (Grutter et al. 2003, Clague et al. 2011, Waldie et al. 2011), encourage juvenile recruitment (Sun et al. 2015), and enhance fish cognitive performance (Binning et al. 2018) (Figure 27). In a series of long-term (>8 year) removal experiments on the GBR, some reefs were up to 66% lower in fish abundance and 33% less species rich in the absence of *L. dimidiatus* (Waldie et al. 2011), with a 27% increase in the size of a model damselfish (Clague et al. 2011). In context of ecosystem functioning, the symbiotic relationship established between cleaners and a diversity of marine fauna is likely to improve production functions on coral reefs (Figure 27) – although direct links to fisheries productivity are yet to be quantified. Cleaners also have the potential to influence habitat functions indirectly, by attracting excavating (e.g. parrotfishes) and corallivorous (e.g. butterflyfishes) species to cleaning stations, increasing the exposure of coral communities to bioerosion and predation processes (Adam 2012). How cleaners influence reef resilience and health beyond fish-fish interactions (i.e. coral growth, reef recovery) requires attention (Table 19). Owing to their site fidelity, local-scale assessments in support of reef resilience might assign some high priority to cleaners and cleaning stations as key features (Table 19), as outlined in the GBRMPA Blueprint for Resilience regarding herbivores and tabular corals (GBRMPA 2017, 2018a).

In the context of ecosystem services, cleaners attract a diversity of marine megafauna, including manta rays, turtles, mola mola, sharks and predatory fishes, to specific reef locations (Oliver et al. 2011, Jaine et al. 2012, Couturier et al. 2014, Murie and Marshall 2016, Couturier et al. 2018). Established ‘mega stations’ (cleaning stations that attract megafauna) are primary targets for recreational divers and tourist operators on reefs from Mozambique, through the Indo-Pacific and Caribbean, with direct socioeconomic benefits (Figure 27). Manta rays can spend ~8 hr per day engaging in cleaning activity, which inspire tourist hotspots (Marshall and Bennett 2010a, b, Rohner et al. 2013, Germanov et al. 2019). Additionally, their presence on cleaning stations can be used as indicators of environmental conditions of water quality, hydrodynamics and food availability (Armstrong et al. 2016, Barr and Abelson 2019). On the GBR, ecotourism in the southern-most coral cay, Lady Elliot Island, largely benefits from manta ray associations with cleaning stations (Couturier et al. 2014). Mega cleaning stations are also found on Osprey Reef in the Coral Sea (O'Shea et al. 2010), supporting high revenue tourist operations (Stoeckl et al. 2010a, Stoeckl et al. 2010b). The influence of cleaners to regional and global scale socioeconomics seems so poorly appreciated and their broader integration into ecosystem monitoring, citizen science and tourism initiatives seems important (Table 19).

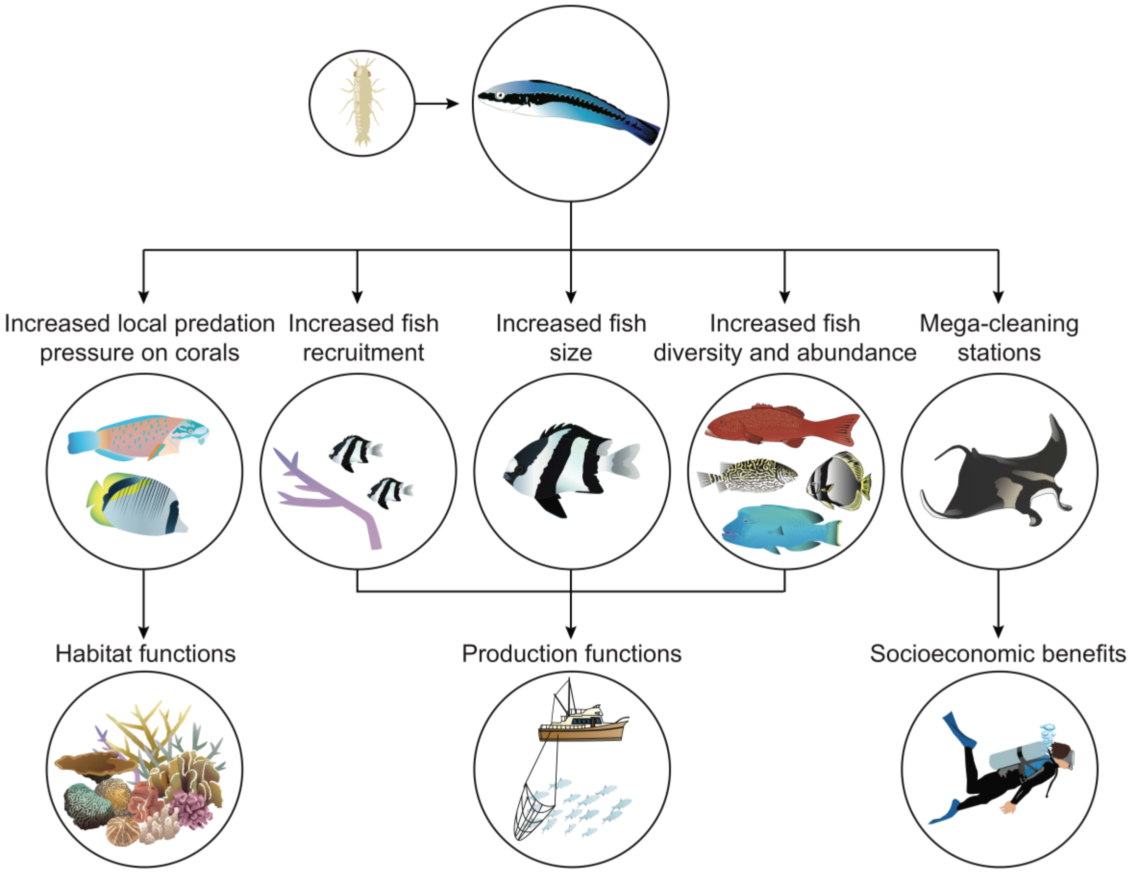

Figure 27: Schematic of the influences of cleaner wrasse (*Labroides dimidiatus*) on ecosystem processes, functions and services on the GBR. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/) and (Hutson et al. 2018).

The biological, functional and socioeconomic benefits of cleaning stations provide a strong case for the need to protect these localised habitats to maintain the ecosystem functions and services they support (Figure 27; Table 19). However, little information exists regarding their vulnerabilities. Globally, cleaner wrasses are primary targets for the aquarium industry but they are among the lowest survivors in amateur tank setups owing to their highly specialised diets and symbioses (Rhyne et al. 2017); though they are rarely harvested from the GBR (Roelofs 2008). *Labroides dimidiatus* is considered Least Concern by the IUCN (Shea and Liu 2010), but naturally existing at low densities with strong site fidelity, cleaner wrasse (and other cleaning organisms) may be particularly vulnerable to environmental perturbation (Rosa et al. 2014, Vaughan et al. 2017, Triki et al. 2018, Vaughan et al. 2018). Following the extreme weather events that affected the GBR during 2016, *L. dimidiatus* densities decreased by ~80% from long-term monitoring sites on Lizard Island (Triki et al. 2018). However, surveys beyond these long-term sites suggest *L. dimidiatus* may have increased in abundance around Lizard Island between 2011–15 (Ceccarelli et al. 2016). Though poorly characterised, it is probable that fast recovery of cleaner populations post-disturbance would help re-establish cleaning interactions and the benefits they provide (Triki et al. 2018). It is important to understand how environmental stressors (e.g. bleaching) impact cleaners and their interactions on cleaning stations, and to what extent a loss of cleaners would affect reef functioning (Table 19).

Table 19: Recommendations and desired outcomes for cleaner wrasse; management (green), science (orange).

Knowledge and recommendations	**Desired Outcomes**	**Relevant groups and end-users**
The biological, functional and socioeconomic benefits of cleaning organisms and their cleaning stations provide a strong case for the need to protect these localised habitats to maintain the ecosystem functions and services they provide.	Local-scale assessments in support of resilient reefs might assign some high priority to cleaners and cleaning stations as key features, as outlined in the regarding herbivores and plating corals (GBRMPA 2017, 2018a).	GBRMPA Blueprint for Resilience Education
Current practice and future efforts to support coral resilience should benefit site-specific cleaners and their cleaning symbioses.	Explore the potential for restoration methods to have a significant role in repairing damaged cleaning stations (i.e. coral cover).	RIMReP RRAP
‘Mega stations’ are present on the GBR (e.g. Lady Elliott Island), which support high revenue tourist operations, but spatial data on key cleaning stations is not explicitly characterised.	Optimise interest and involvement of tourist operators and citizen science groups in reporting cleaning stations and their communities.	Eye on the Reef Education Great Reef Census
Most information on the importance of cleaners is angled at fish-fish interactions, but how these scale up to support production and habitat functions requires attention.	Characterise how cleaners influence reef functioning beyond fish-fish interactions (i.e. coral cover, reef recovery).	Research
There is little information on the impacts of environmental stressors (e.g. bleaching) on cleaners and their interactions on cleaning stations.	Quantify to what extent a loss of cleaners would affect reef functioning.	Research Eye on the Reef AIMS LTMP RIMReP

Cleaners exhibit site fidelity, and their interactions with species on cleaning stations can indicate water quality, hydrodynamics and food availability.	Characterise the potential for cleaning stations and interactions to be informative bioindicators on the GBR.	Research RIMReP

4.2.3 Bivalves

Giant clams (Tridacnidae) and other bivalves (e.g. oysters) scored surprisingly high for habitat functions, driven by processes of calcification and recruitment facilitation. Shell and 'bed' construction by bivalves can contribute structural complexity to the reef (Figure 28), with both alive and dead structures encouraging recruitment and providing refugia for a diversity of symbiotic and commensal organisms, a particularly important feature when coral cover is low (Beukers and Jones 1998, Lecchini et al. 2007, Cabaitan et al. 2008, Neo et al. 2015). This may be an increasingly important attribute to document and protect in a changing ocean (Table 20). Shallow-water benthic bivalves are natural controllers of eutrophication and water quality through their filter-feeding processes (Figure 29), perhaps most importantly on near-shore reefs (Klumpp et al. 1992, Klumpp and Lucas 1994, Neo et al. 2015), enhancing an important aesthetic reef value (GBRMPA 2014c, Marshall et al. 2018, Vercelloni et al. 2018). Some bivalves are also important bioeroders such as the boring clam, *Tridacna crocea* (Figure 28), which can dominate reef and intertidal areas on near-shore (e.g. Orpheus Island) and offshore (e.g. One Tree Island) reefs (Hutchings 1986). As bioerosive processes become more pervasive on coral reefs, knowledge gaps for non-parrotfish bioeroders on the GBR (including bivalves, sponges, microborers) should be filled to empower calculations on the total carbonate budget for the reef and predictions on future reef accretion and recovery processes (Table 20).

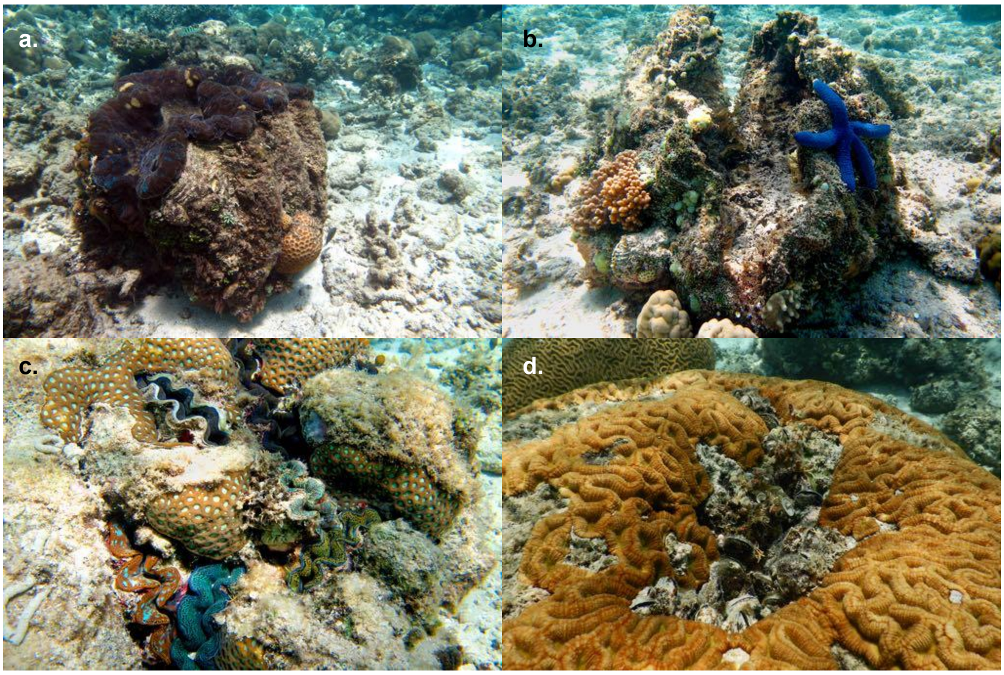

Figure 28: Giant clams (top) and boring bivalves (bottom) are important ecosystem engineers contributing to calcification, bioerosion and recruitment facilitation. They provide important structural complexity to the reef, while improving water quality through filter feeding processes.

As for corals, giant clams host zooxanthellae that aid in respiration and growth (Klumpp et al. 1992), but this makes them prone to bleaching under warm-water exposure (Buck et al. 2002, Leggat et al. 2003). As calcifying organisms, molluscs and their thinly-calcified veliger larvae are among the most vulnerable to changing ocean temperature (warming) and chemistry (acidification) (Przeslawski et al. 2008, Byrne 2011, Przeslawski et al. 2015), including impacts on juvenile survival of some tridacnids (Watson et al. 2012). Ocean acidification may also accelerate bioerosion processes within bivalve bed formations (Wisshak et al. 2014), but suitably high levels of light may work to ameliorate the negative effects of ocean acidification on some tridacnids (Watson 2015). Improving water quality would enhance the potential for light levels to ameliorate the negative impacts of ocean change on photosynthetic tridacnids, particularly for near-shore populations (Table 20).

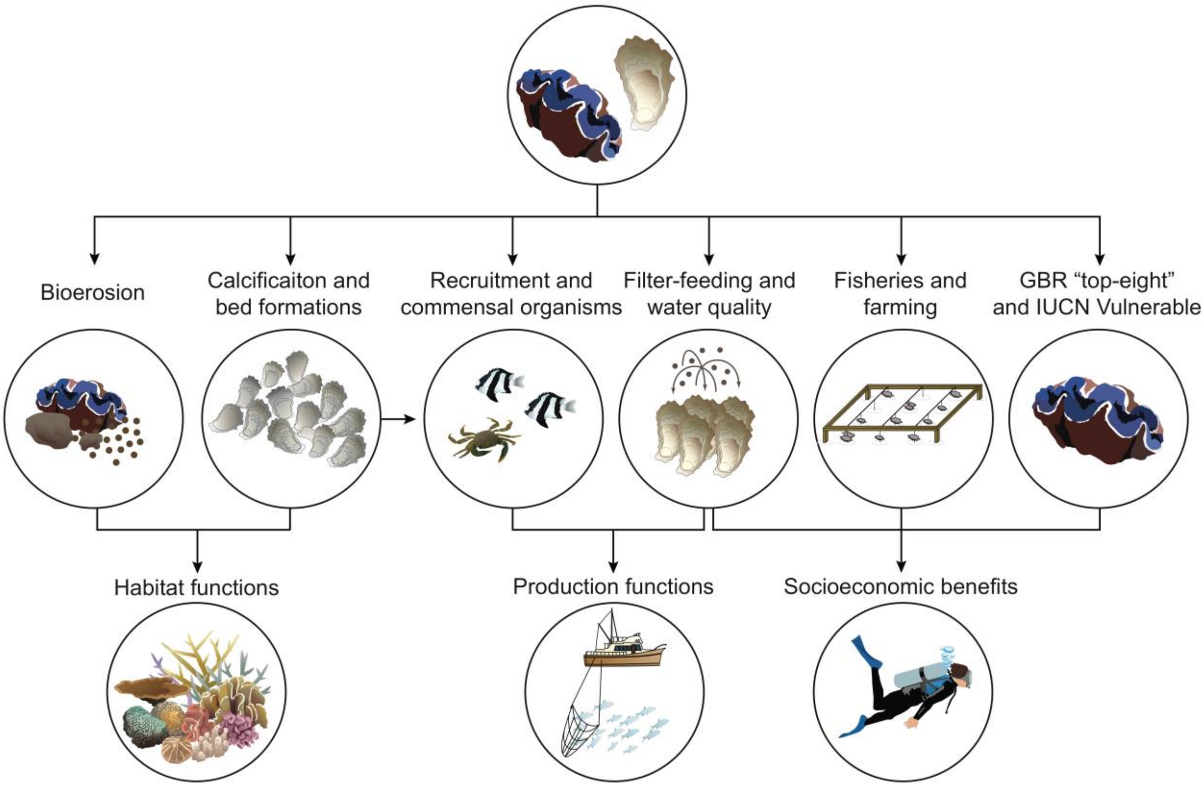

Figure 29: Schematic of the influences of bivalves (e.g. Tridacnidae, oysters) on ecosystem processes, functions and services on the GBR. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

Globally, many commercially important bivalves have been decimated by local stressors such as fisheries, and habitat and water quality degradation (Kirby 2004, Bersoza Hernández et al. 2018), including on the GBR (Gillies et al. 2015). The most important bivalve to fisheries on the GBR may be the saucer scallop, *Amusium japonicum ballotti*, which operates as a trawl-fishery with a range of management implications (Courtney et al. 2008, Courtney et al. 2015), but this occurs beyond the focal reef habitat investigated here. Oysters (*Saccostrea cucullate*, *Saccostrea echinate*, *Isognomon ephippium*, *Pinctada* spp.) and mussels (*Trichomya hirsuta*) may have once been significant reef formers on the GBR, particularly in the sheltered and intertidal habitats of estuaries, near-shore reefs and mangroves, but were also primary shellfish fisheries targets (Gillies et al. 2015, Lewis et al. 2015). Subtidal oyster reefs appear to be functionally extinct over their former range along the east coast of Australia (Beck et al. 2011), but the extent of this on the GBR is historically poorly characterised.

Giant clams, namely the larger species *T. gigas* and *T. derasa*, experienced heavy exploitation through poaching on the GBR (Pearson 1977, Dawson 1985), with all tridacnids consequently listed on Appendix II of CITES by 1985. Both *T. gigas* and *T. derasa* are also listed as Vulnerable on the IUCN Red List of Threatened Species (Wells 1996b, a, Richards and Day 2018). Giant clams are the only invertebrates listed in the 'top-eight' species to see on the GBR (https://www.barrierreefaustralia.com/info/great8/), a significant tourism drawcard (Figure 29; Table 20). Experimental aquaculture and cultivation of *T. gigas* has occurred on the GBR previously (Orpheus Island) (Crawford et al. 1988, Lucas et al. 1989), with bed formations that still exist integrated in the reef framework today. Population transplants and aquaculture of functionally important bivalves deserves consideration (Table 20) to optimise benefits from the natural infrastructures of reef-forming molluscs, including fisheries production, shoreline protection, water filtration and tourism (Figure 29).

Table 20: Recommendations and desired outcomes for bivalves; management (green), science (orange).

Knowledge and recommendations	Desired Outcomes	Relevant groups and end-users
Current practice and future efforts to support coral resilience should benefit associated bivalve taxa directly.	Maintain protection of key coral taxa to benefit bivalve assemblages and biodiversity.	GBRMPA Blueprint for Resilience
Shallow-water benthic bivalves are natural controllers of eutrophication and water quality through their filter-feeding processes, perhaps most importantly on near-shore reefs.	Maintain and protect bivalve populations as natural mediators of water quality, particularly inshore.	GBRMPA IUCN Red List
Suitably high levels of light may work to ameliorate the negative effects of ocean acidification on photosynthetic tridacnids.	Precautionary measures should maintain momentum regarding water quality guidelines to improve recovery and resilience of near-shore bivalve populations.	Land use management Improved water quality Dredge management
Population transplants and aquaculture of functionally important bivalves deserves consideration to optimise benefits from the natural infrastructures of reef-forming molluscs, including fisheries production, shoreline protection, water filtration and tourism.	Consider population transplants/aquaculture of bivalves (e.g. clam gardens, Orpheus Island) where appropriate.	Transplant/ aquaculture RRAP Citizen science
Giant clams are the only invertebrates listed in the "top-eight" species to see on the GBR.	Work closely with tourist operators and citizen science groups to map key giant clam habitats as a tourist attraction,	Eye on the Reef Citizen science Education

	and to increase educational awareness and interest in important non-coral taxa.	Great Reef Census
Shell and 'bed' construction by bivalves can contribute significant structural complexity, encouraging recruitment, biodiversity and refugia, a particularly important feature when coral cover is low.	Characterise communities occupying giant clam and bivalve bed formations in reef ecosystems.	Research Eye on the Reef RIMReP
Some bivalves are important bioeroders such as the boring clam, *Tridacna crocea.*	Fill knowledge gaps for non-parrotfish bioeroders on the GBR (including bivalves, sponges, microborers) to ensure carbonate budget estimates are representative.	Research

4.2.4 Coral-associated crustaceans

Coral-associated decapods are strongly bound to their coral host (Figure 30), where they take refuge from a range of reef and cryptic predators including squirrel fishes, wrasses and eels (Hiatt and Strasburg 1960). From a bottom-up perspective, coral-associated crabs can form up to 70% of a reef fishes diet, particularly for species with specialised morphologies that can access prey items from the intricacies of the coral framework (Hobson 1974, Rinkevich et al. 1991). The most common and well-recognised coral-associated crabs on the GBR include the *Trapezia*, *Tetralia* and *Cymo*, which primarily occupy acroporids and pocilloporids (Stella et al. 2011b). Interestingly, *Trapezia* typically occupy pocilloporid corals, while *Tetralia* are found in acroporids (Patton 1983, 1994), where they are both often observed grazing on their host's live tissue, mucus or fat bodies (Stimson 1990, Rinkevich et al. 1991, Castro 2000, Castro et al. 2004). This grazing activity is not considered to have negative effects on their host, given these coral crabs generally exist at low densities (~2 individuals per colony) (Rotjan and Lewis 2008, Stella et al. 2010, Stella et al. 2011b). Obligate-dwellers are considered highly beneficial to their coral hosts as they actively defend the host from predation from species like CoTS and *Drupella*, and contribute to the removal of excess sediment that would otherwise smother the corals (Figure 30) (Glynn 1980, 1983, Pratchett 2001, Stewart et al. 2006, Stella et al. 2011b). Further, some obligates (e.g. *Cymo*) have been shown to slow the progression of disease in their coral host (Figure 30) (Pollock et al. 2013).

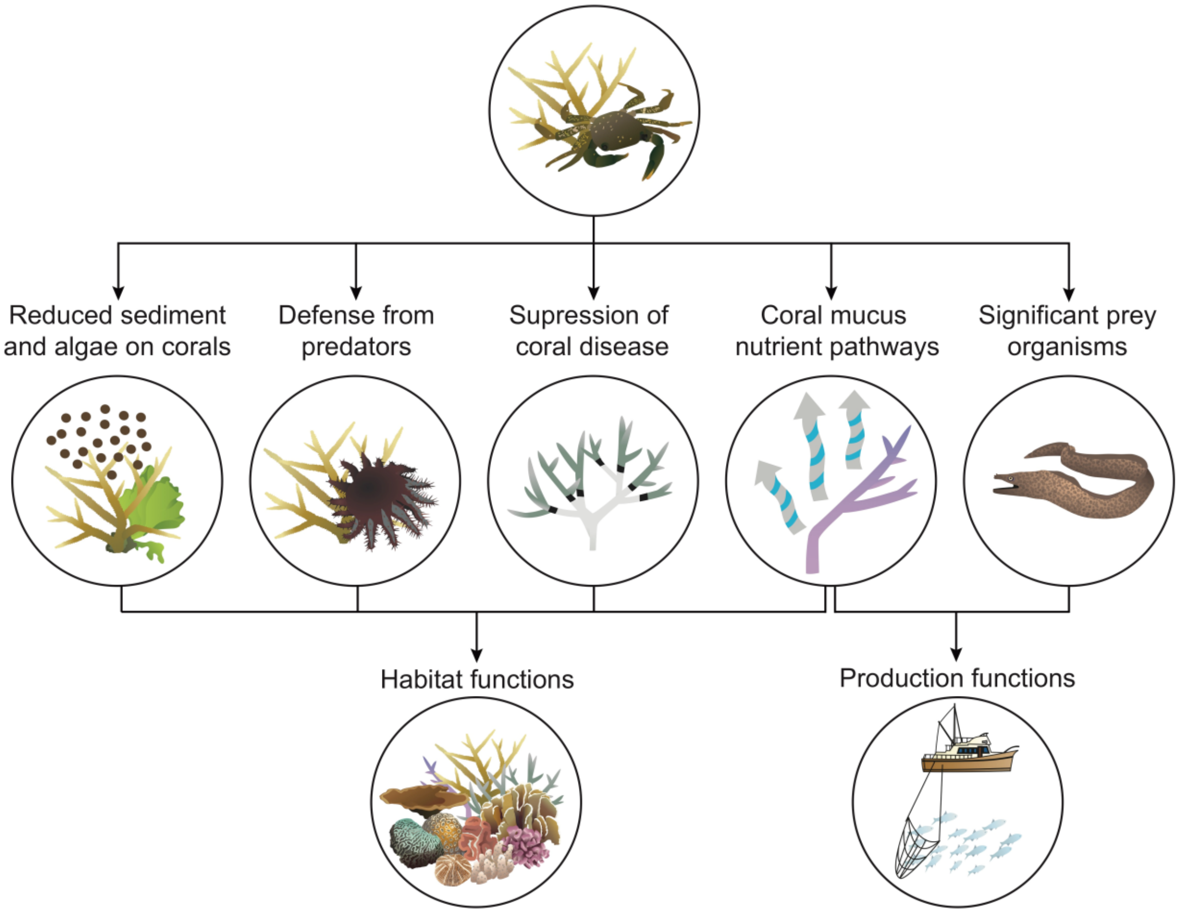

Figure 30: Schematic of the influences of coral-associated decapods on ecosystem processes and functions on the GBR. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

Coral-associated crabs can have pronounced effects on their hosts by reducing fouling algal epibionts by >65% (Coen 1988). In an experiment that removed trapezid crabs from their coral host, whole-colony mortality occurred in up to 80% of crab-less hosts within a month (Stewart et al. 2006), but how the localised benefits of coral-crabs scale up to ecosystem and socioeconomic levels is ambiguous (Table 21). The benefits and feedbacks between coral-associates and their hosts through removal experiments requires greater attention, including how shifts in baseline habitat quality (i.e. coral health) may impact invertebrate communities and trophic links to fisheries productivity (Figure 30). In light of intensifying degradation of coral reefs, any direct benefits to corals through management would surely support broader resilience of coral-associated organisms to environmental change (Table 21).

The survival of coral-associates is inextricably linked to that of their host, and so obligate associates are considered particularly vulnerable to changes in live coral cover (Caley et al. 2001, Stella et al. 2011a, Stella et al. 2011b). Among the most sensitive corals to thermal stress are *Acropora* and *Pocillopora* (Loya et al. 2001, McClanahan et al. 2004, van Woesik et al. 2011), the typical host genera of coral crabs. For trapeziids, coral bleaching has been shown to impact their densities and reproduction, which intensifies inter- and intra-species competition (Glynn et al. 1985, Stella et al. 2011a, Stella et al. 2014). There are records of some trapeziids occupying dead coral habitat, which could suggest unanticipated resilience in the ability for these coral-obligates to occupy degraded and dead coral habitats (Head et al. 2015). However, this is usually a result of saturated population densities and increased territoriality, which forces losing individuals to traverse dead coral and rubble habitats in search of suitable (and available) live coral habitat, a behavioural trait that renders them vulnerable to predation and hinders their ability to fulfil their novel roles in coral reef functioning (Stella et al. 2011b). The ability for coral-associated decapods to sustain their populations in alternative habitats during periods of coral recovery requires attention, including their potential to enhance reef resilience as corals recover (Table 21), particularly when coral mortality occurs at large spatial scales.

Table 21: Recommendations and desired outcomes for coral-associated crabs; management (green), science (orange).

Knowledge and recommendations	Desired Outcomes	Relevant groups and end-users
Current practice and future efforts to support coral resilience should benefit coral-associated taxa directly.	Maintain protection of key coral taxa to benefit reef-associated communities and biodiversity.	GBRMPA Blueprint for Resilience
There is high outreach potential and significant education value (e.g. school programs) in conveying the importance of coral-associated groups to reef functioning.	Increased stewardship regarding coral health and the diversity of associated taxa.	Education Citizen science Great Reef Census
Current understanding of the benefits and feedbacks between coral-associates and their hosts is encouraging but limited.	Quantify the localised benefits of coral-crabs on their hosts through removal experiments.	Research
Coral-associated decapods benefit their coral host, but it is ambiguous how these localised benefits scale up to ecosystem and socioeconomic levels.	Quantify to what extent a loss of coral-crabs may impact broader reef resilience, including through recovery phases.	Research
Characterise how shifts in baseline habitat quality (i.e. coral health) impacts invertebrate communities and trophic links to fisheries productivity.	Broader inclusion of non-coral reef invertebrates in monitoring and research.	Research Eye on the Reef RIMReP

4.2.5 Detritivorous fishes

Although being rated as a critical functional group, especially regarding particular ecosystem processes (e.g. nutrient cycling), detritivorous fishes were not considered vulnerable nor a high priority candidate for management (Figure 19). This is likely due to the broad distributions and/or high densities of predominant groups, including blennies (Wilson 2000, Wilson 2001, Wilson 2004), and surgeonfishes, particularly *Ctenochaetus striatus* (Tebbett et al. 2018). Regardless, detritivores are considered a key trophic group, representing ~40% of the biomass of EAM-grazing assemblages on the GBR (Wilson et al. 2003). They are fundamental components of nutrient pathways through the transfer of energy from the EAM to secondary consumers (Figure 31) (Crossman et al. 2001, Wilson et al. 2003, Crossman et al. 2005, Bellwood et al. 2014). Yet, diet partitioning and selectivity are poorly understood and currently underestimated for many nominal detritovores and herbivores (Choat and Clements 1998, Clements et al. 2017). The rapid population turnover of blennies in particular (Wilson 2004), which can account for ~60% of detritivore biomass in some habitats (Wilson 2001), attributes to their key role in reef trophodynamics with links to fisheries productivity (Figure 31). Further, post-disturbance and associated losses in coral cover, fish diversity may be maintained by detrital- and EAM-grazers (Wilson et al. 2009, Ceccarelli et al. 2016). Given the importance of detritivores to particular ecosystem processes (Figure 31), it could be important to characterise additional key contributors to detritivory and sediment processing, including for other fishes and invertebrates like deposit-feeding sea cucumbers (Table 22).

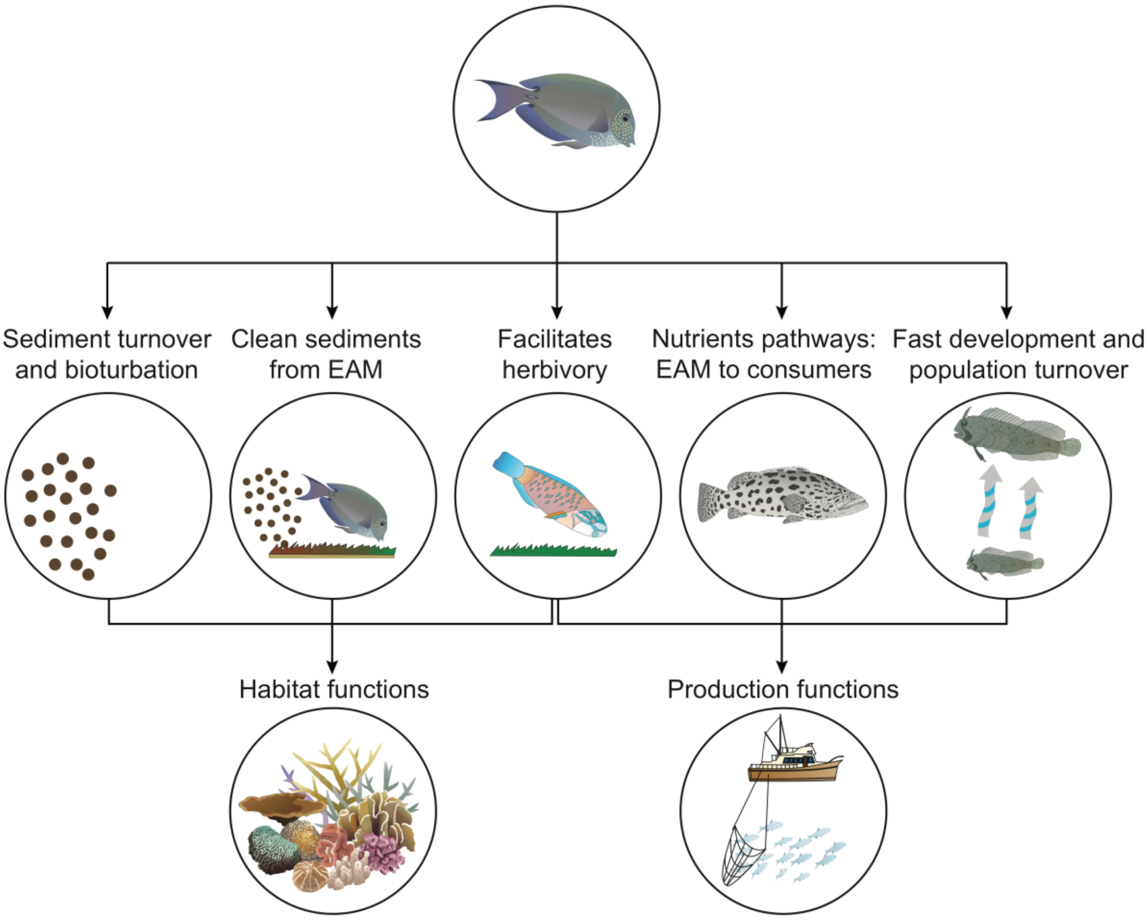

Figure 31: Schematic of the influences of detritivorous fishes (e.g. blennies, *Ctenochaetus striatus*) on ecosystem processes and functions on the GBR. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

One expert noted that their scores for detritivores were primarily in context of *C. striatus*. This species is one of the most abundant and important surgeonfishes on Indo-Pacific reefs, including on the GBR (Trip et al. 2008), through its contributions to detritivory and sediment dynamics (Purcell and Bellwood 1993, Goatley and Bellwood 2010, Krone et al. 2011, Cheal et al. 2013, Tebbett et al. 2017d, b, Tebbett et al. 2018). While feeding on components of the EAM (e.g. detritus, bacteria), *C. striatus* selectively brushes associated particles from algal turfs. They may have low functional redundancy in this role removing sediments (Tebbett et al. 2017b, Tebbett et al. 2018), which has been shown to facilitate herbivory by other species

(Goatley and Bellwood 2010, Marshell and Mumby 2012, 2015), with potential roles regulating coral-algal phase shifts (Cheal et al. 2010). *Ctenochaetus striatus* are selective feeders with a preference for coarser sediments. Fine sediments appear to impact their feeding behaviour and associations with the EAM, with implications regarding their vulnerability to sedimentation, as produced by dredging activities or heavy storm events (Tebbett et al. 2017d, c, Bellwood et al. 2018); other EAM-feeders may not be as fussy (Tebbett et al. 2017c). As some detritivores can be highly sensitive to sediment loads, improving water quality across catchment areas, including reducing impacts from dredging activity, would likely benefit this group (Table 22).

Although considered Least Concern by the IUCN, *C. striatus* has been extensively fished from some reefs like American Samoa (Trip et al. 2008, Choat et al. 2012). The aggregative spawning behaviour exhibited by this species, including on the GBR (Robertson 1983), could have specific implications for their management regarding seasonal spawning closures. There is a recreational catch limit of 5 individuals and a minimum size limit of 25 cm on the GBR, but they do not seem to be heavily targeted and exhibit particularly fast growth rates to a distinct size (Trip et al. 2008, Choat et al. 2012). As it stands, the biology of *C. striatus* may render them particularly resilient across their expansive range, given fishing intensity remains low (Trip et al. 2008).

Table 22: Recommendations and desired outcomes for detritivorous fishes; management (green), science (orange).

Knowledge and recommendations	**Desired Outcomes**	**Relevant groups and end-users**
Detritivores can be highly sensitive to sediment loads.	Maintain focus on improving water quality and sediment loads across catchment areas.	Land use management Improved water quality Dredge management
We would expect that as water quality improves (i.e. low suspended sediments), detritivorous fishes would increase. This would provide a novel opportunity to document management success.	Consider key detritivores (e.g. *Ctenochaetus*) as indicator species.	Eye on the Reef RIMReP Education GBRMPA Blueprint for Resilience Great Reef Census
High-sediment environments are challenging to monitor, so innovation may be required to census fishes in near-shore turbid waters (e.g. videography, eReefs).	Extend monitoring of detritivorous fishes (e.g. density, biomass) to inshore reefs where water quality impacts are elevated.	AIMS LTMP and MMP eReefs
There are knowledge gaps in the diet of many nominally herbivorous and detritivorous reef fishes.	Explicitly describe diet partitioning and selectivity for	Research

	nominal detritivores and herbivores.	
Characterise additional contributors to detritivory and sediment processing on the GBR, including for other reef fishes and invertebrates like deposit-feeding sea cucumbers.	Broader inclusion of novel functional groups in monitoring and research.	Research RIMReP AIMS LTMP

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APPENDIX 1: WORKSHOP DISCUSSION NOTES

Workshop #1: 7 and 8th March 2018, James Cook University, Townsville

Workshop #2: 10th April 2019, GBRMPA, Townsville

Contents

Workshop #1:

Workshop #2:

A1.1 Foreword – Workshop #1

This report summarises the outcomes of a workshop held in Townsville, Australia, on 7 and 8th March 2018. The Tropical Water Quality Hub of the National Environmental Science Programme (NESP) funded the workshop. The primary goal of this initial workshop was to bring together a diverse team of Australian coral reef scientists to harness Queensland's breadth of expertise to assess ecosystem functioning on the Great Barrier Reef (GBR). Collectively in this workshop, GBR experts worked to establish a blueprint for Project 4.6 in terms of methodology and future steps. Efforts across the two days facilitated the construction of research criteria that were employed in this Project. Workshop participants were also outlined critical knowledge gaps on ecosystem functioning on the GBR. As contracted within Project 4.6, these gaps were developed into short-term research projects funded by NESP. These subprojects are presented as case studies in the primary project report.

Participants of this workshop included representatives from the University of Queensland (UQ), the Great Barrier Reef Marine Park Authority (GBRMPA), the Commonwealth Scientific and Industrial Research Organisation (CSIRO), the Australian Institute of Marine Science (AIMS), NESP, James Cook University (JCU) and Griffith University. For a full list of participants see A1.6.

The following notes were summarised from the discussions and dialogue throughout the two-day workshop. This highlights the key concepts explored and initial criteria developed, which lay the foundations of the overarching research, data collection and conclusions of Project 4.6.

A1.2 Project 4.6: Reef functioning objectives (Peter Mumby & Kennedy Wolfe)

1. The primary objective of this Project is to make recommendations to maintain ecosystem functioning of the GBR.
2. While a healthy reef typically requires high biodiversity and species interactions, it is becoming more evident that some species play critically important roles.
3. The GBR is the world's largest coral reef ecosystem, which is an amalgamation of varying bioregions with their own (often unique) functional dynamics.
4. It must be immediately established that Project 4.6 will consider the functioning of the forereef and reef slope, as these are typically the most diverse, coral-rich reef habitats that support the greatest range of ecosystem services.
5. Other bioregions (i.e. seagrass meadows, mangroves, lagoon plains) are beyond the scope of Project 4.6.
6. Inner and outer reefs may be assessed separately (where necessary) due to the distinct species, stressors and, thus, management schemes in both regions.
7. In terms of ecosystem functioning and functionally important species, we may consider species alone or functional groups depending on the scenario.
8. Primary purposes of the workshop:
    a. What is a functional reef – how do we measure it?
    b. Construct criteria to score/rank species based on their functional roles on the GBR;
        i. Key functions
        ii. Key processes
        iii. Supporting ecosystem services
    c. Identify organisms that play critical roles on the GBR to expedite management that facilitates functioning of the GBRs degrading reef system.
    d. List the threats that GBR species are exposed to, and develop a system that works to rank their severity/vulnerabilities.
    e. Assess how to manage species based on their functional importance; develop manageability (plausibility) criteria.
    f. Identify key knowledge gaps and propose short-term research projects that work to fill these gaps. This information will be developed to directly inform this project, future NESP funded work, and otherwise.

A1.3 Group discussion to establish criteria to assess/rank reef functioning

Initial discussions on assessing the functional importance of species on the GBR were broad in scope, attributing to the complexity of the Reef and the Project. It was acknowledged that the identification of functionally important species for management needed to consider:

1. Identifying species *importance* based on their contributions to ecosystem processes, functions and services;
    a. What is a functioning reef?

    b. Who best drives/supports functioning?
    c. How can importance be measured in functional space?
2. Identifying the *vulnerability* of species to current and near-future (2050 outlook) stressors/threats;
    a. Who is actually threatened on the Reef?
    b. Is a vulnerable species important to consider if it has a low level of functional importance?
    c. Can we identify both important and vulnerable species?
3. Assessing the *manageability* of these species to enhance the effectiveness of management recommendations;
    a. How can management be incorporated into analyses?
    b. If a species is both important and vulnerable, is management even viable?
    c. What do we do if a species is critically important but notoriously difficult to manage (e.g. microbes)?

These three stages (*importance*, *vulnerability*, *manageability*) became the focal points of conversation and retrospectively formed the foundations of Project 4.6. We can predict that a species identified as functionally important that is also highly threatened (i.e. vulnerable) would require the greatest level of priority in terms of management (Figure A1.1). This Project aims to establish these functional and management hierarchies.

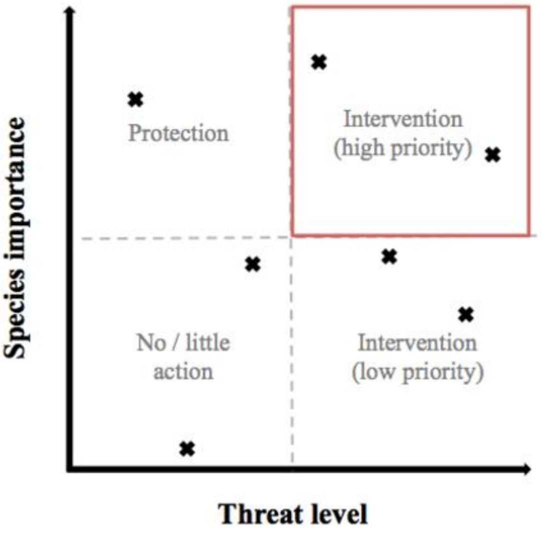

Figure A1.1: Visual representation of discussions outlining management potential based on species *importance* and *threat* level; red box indicates a high priority species for management (i.e. those that are both important and threatened on the GBR).

A1.3.1 Stage 1 – Criteria to assess species of functional *importance* on the GBR

What is a functioning reef?

There is a great diversity of interpretations of ecosystem functioning in the literature. We worked under the definition;

the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil [human] life.

Two primary ecosystem functions on coral reefs were identified; (1) habitat functions (stocks of energy and material) and (2) production functions (energy fluxes and transfers). These are essential to coral reef functioning and the ecosystem services that are attributed (e.g. coastal protection, biodiversity, fisheries production, tourism, socio-cultural importance). Thus, both biological and social elements are to be considered.

Biological, chemical and physical processes work together to maintain a functioning ecosystem. To identify species of particular functional importance, it was decided that biological processes be the focus; i.e. what does any given species bring to the table? The ecosystem processes that underpin habitat and production functions were key points to identify. Key processes were developed throughout the workshop reflecting the range of expertise within Project 4.6. The initial ecosystem processes considered were:

- Primary production
- Herbivory (farmers, browsers, grazers, excavators)
- Predation (detritivory, planktivory, corallivory, invertivory, piscivory)
- Nutrient cycling (dissolved and particulate)
- Symbiosis
- Microbial pathways
- Benthic-pelagic coupling
- Bioturbation
- Calcification
- Bioerosion
- Ecosystem engineers
- Connectivity
- Recruitment
- Competition
- Disease
- Weather/hydrology (physical parameters)
- Wave attenuation

How do we rate a species contribution to these processes?

Species would be evaluated using criteria that rate their overarching contributions to the ecosystem processes as listed above. A species could be important due to its critical importance regarding one process, while others could be important due to their partial contributions across many processes. Whether or not a species directly performs each process would be a critical value to establish. Other interacting factors (e.g. indirect effects, competition, redundancy) may enhance or reduce the capacity for organisms to perform their roles, and must therefore also be considered in the criteria. A species may become less important in their roles if they have high ecological redundancy (i.e. others would likely fill their ecological roles if they were absent, replaceable), or if there is dependency on other species (e.g. commensalism, facilitation).

Based on discussions, criteria were established to rate the contribution of any given species (or group of species) to any given ecosystem process. The criteria consider the direct role of the species to the process, as well as a range of environmental considerations that would likely influence its performance/contribution;

1. **Magnitude** of contribution: a measure of the direct contribution of the species in question to the process in question.
2. **Regulatory processes**: a measure of the indirect contribution of the species in question that may influence the ability of others to perform the process in question (e.g. predation, facilitation, competition, regulation).

3. **Resilience**: a measure to assess population dynamics (e.g. level of variability) of the species in question that provide resilience in its ability to perform the process in question.
4. **Redundancy**: a measure of ecological redundancy (replaceability) of the species in question in performing the process in question.
5. **Dependency**: a measure of the dependency of the species in question on others to perform the process in question.
6. **Distribution**: a consideration of the distribution of the species in question (GBR context; inner/outer, broad/local).
7. **Certainty**: a judgment of the level of scientific certainty behind the scores based on literature, research and/or expert opinion.

How do we score/weight these criteria? Several scoring systems were suggested:

1. Percentages or integers – a scale from 0 to 100.
2. Binary scoring: Yes/No, High/Low, Positive/Negative
3. Numerical ranges: 0-5, 0-10, 0-20, etc.

It was recognised that a broad range of values in a scoring system would likely result in a high amount of 'grey area' in responses. As such, a low-range scoring system was selected for this section, including 0 = none, 1 = low, 2 = high for each stage of the criteria. A 'mid' level was considered, but this was predicted to encourage ambivalence in scores and was discouraged. The categorisation and ranking of scores are outlined in Table A1.1.

Table A1.1: Outline of the scoring system developed to rank species [groups] based on their contribution to ecosystem processes and, thus, their functional importance.

Criteria	Category	Rank	Notes
Magnitude	None	0	No role in the process
	Low	1	Some contribution to the process
	High	2	Direct and significant role in the process
Regulatory processes	None	0	No impact on other species performing this process
	Low	1	Some level of impact on other species performing this process
	High	2	Direct impact on others (e.g. high predation pressure, competition)
Resilience*	None	0	Highly unstable populations, poor recovery
	Low	1	Some variation in populations, seasonality
	High	2	Stable population, high reproductive turnover
Redundancy*	High	0	Replaceable in its functional roles
	Low	1	Some level of replaceability, similar species
	None	2	Specific in its functional role, critical
Dependency*	None	0	Self sufficient
	Low	1	Some level of reliance to complete roles
	High	2	Reliant on other organisms
Distribution*	Broad	0	Common across the GBR
	Medium	1	Cross- or along-shelf variation
	Poor	2	Site-specific, restricted, local, endemic
Certainty	None	0	Little empirical work and expert judgment
	Low	1	Some empirical work and expert experience
	High	2	Extensive work and/or experience

*Some criteria may need reverse scoring to emphasise important species that have vulnerability in their roles; i.e. does a species with a high magnitude of contribution to a process (i.e. “important”) but low resilience and restricted distribution get a higher score, as it will require greater management attention? Conversely, do “important” species with high resilience and broad distributions get higher scores, as they will likely have a broader functional impact across the GBR?

A1.3.2 Stage 2 – Criteria to assess species *vulnerability* on the GBR

Once the scoring system was established for species functional *importance* discussion moved to address rating *vulnerability*. Addressing threat and vulnerability is essential to understanding whether the species in question requires management in the first place (Figure A1.1). The IPCC ‘Vulnerability Framework’ (Figure A1.2) was presented as an effective way to measure threats to species. This framework considers species’ *exposure* and *sensitivity* to any given stressor, and the ability for an organism to demonstrate *recoverability* (adaptive capacity) following impact. Important current and near-future (2050 outlook) threats facing species on the GBR were discussed and identified (Table A1.2).

Notes:

- Species that are known to be particularly vulnerable to a listed stressor may be necessary to assess regardless of their functional role; i.e. a species of low functional importance may still be highly threatened (see Figure A1.1).
- [Un]certainty may need to be included in the assessment of *vulnerability*, as for species *importance*.
- ‘Threat’ considered on a per-stressor and per-species basis for *sensitivity* and *exposure*

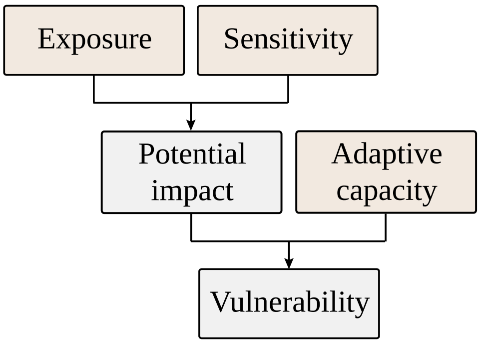

Figure A1.2: IPCC Vulnerability framework to assess species vulnerabilities to potential stressors (e.g. climate change). Measured values (exposure, sensitivity, adaptive capacity) are used to calculate vulnerability.

Table A1.2: Present and near-future (outlook 2050) stressors facing coral reef organisms and challenging functioning on the GBR.

Stressor	Sub-category
Water quality	Nutrients Sediments Salinity Pesticides
Climate change	Ocean warming Ocean acidification Hypercapnia / anoxia Cyclones
Fishing	
Disease	
Antagonistic outbreaks	

How do we score/weight these criteria? Following a similar scoring system as for species *importance* (as above), a low-range scoring system was discussed and developed (Table A1.3). Species are to be scored following the IPCC Vulnerability Framework using the criteria developed.

Note: Sensitivity can be positive or negative depending on the species' response to the stressor; e.g. positive impact of warming for algae, positive impact of fishing on prey species.

Table A1.3: Outline of the scoring system developed to rank the effects of each threat on each functional group/species (IPCC Vulnerability Framework).

Dynamic	Category	Rank	Notes
Sensitivity	Sensitive	-2	Highly sensitive to the stressor
	Slight impact	-1	Partial negative impacts
	No impact	0	Not affected
	Slight gain	1	Partially benefited
	Beneficial	2	Stressor is highly beneficial
Exposure	None	0	Not exposed to the stressor
	Low	1	Low exposure, low likelihood of exposure
	High	2	Highly exposed, highly likely to be exposed
Recoverability	None	0.3	Unlikely to recover before next event
	Low	0.7	Some level of recoverability
	High	0.9	Highly likely to recover before next event
Certainty	None	0.3	Little empirical work and expert predictions
	Low	0.7	Some empirical work and expert experience
	High	0.9	Extensive work and/or experience

A1.3.3 Stage 3 – Criteria to assess species *manageability* on the GBR

Following assessment of species *importance* and *vulnerability*, a weighted level of importance vs. threat could be produced. Species that are considered as both highly *important* and *vulnerable* will be considered as 'high priority' for management intervention (Figure A1.1). Species that are either highly important for reef function *or* highly vulnerable may still be considered for management, but approaches may vary in nature and priority. Discussions moved to address how species may then be considered for management; the end goal for Project 4.6.

Criteria were established to provide a framework to assess the manageability of any given species based on several key parameters. Scoring of these criteria followed those discussed previously, resulting in a low-range scoring system (0-2; None/Low/High) (Table A1.4).

- **Responsiveness:** how likely is the species in question to respond/recover following management intervention?
- **Feasibility**: how feasible is the potential management of this species (i.e. affordability, geographical scale, temporal scale)?
- **Conservation status:** is the species already at risk – globally or locally for the GBR?
- **Attractiveness**: does the species in question have some level of social, cultural or commercial value?
- **Information**: is there data available for this species, and is continued data collection and monitoring easy/possible?

Table A1.4: Outline of the scoring system developed to rank species [groups] based on their *manageability*.

Dynamic	Category	Rank	Notes
Responsiveness	None	0	Species/populations unlikely to change
	Low	1	Some response through action
	High	2	Action has strong effect on population
Feasibility	None	0	Broad scale, not affordable
	Low	1	Possible for some locations, patchy
	High	2	Very possible in scope-cost benefits
Conservation status	None	0	Not threatened; data deficient
	Low	1	Vulnerable; locally listed (EPBC)
	High	2	Endangered/critical; globally (IUCN)
Attractiveness	None	0	Not commercially or publicly viable
	Low	1	Some level of public or commercial benefits
	High	2	Highly attractive to public or industry
Information	None	0	Little existing work, hard to monitor
	Low	1	Some work exists, monitoring possible
	High	2	Extensive work, easy to monitor

A1.3.4 Ways forward with scoring species *importance*, *vulnerability* and *manageability* on the GBR

The primary goals of this workshop were to establish a blueprint for Project 4.6. The development of the Project criteria–established to score/rate species *importance*, *vulnerability* and *manageability*–provided the foundations to the Project's methodology. Several "practice" attempts of scoring based on the criteria occurred during the workshop, but these were not considered final scores and were namely used to refine the methodology. Following synthesis and further project development, the criteria would be constructed into workable spreadsheets and/or surveys, which would be presented back to the working group of experts to collect their scores. It was discussed that the Project team members would respond to questions relating to their expertise.

A1.4 What species should we consider for Project 4.6?

In an attempt to identify the most functionally important species on the Reef for management, this Project aims to consider all contributors. The objective is to assess species and/or functional groups of species from microbes through to apex predators. The diverse assembly of coral reef researchers harnesses a wealth of knowledge across disciplines and taxa. As initially stated, this Project does not attempt to assess species from bioregions outside the typical coral reef framework (e.g. seagrass meadows, mangroves, etc). This was an active choice of the research group as many species play functionally different roles and vary in their importance across habitat types.

During the workshop, the group was divided into several smaller teams to concentrate knowledge based on expertise. Three main groups were established; (1) corals, (2) fishes, and (3) microbes and other invertebrates. In parallel with trialing the scoring criteria for *importance*, *vulnerability* and *manageability* (as outlined above), each group developed lists of functionally important species and/or groups of species based on knowledge of the literature and expert judgment. These initial species lists formulated the basis of those considered in the scoring system/data collection. Table A1.5 outlines the original groups and species listed.

Table A1.5: Species and functional groups outlined across the workshop by teams focusing on corals, fishes, and microbes and other invertebrates. This list was to be expanded (or refined) where necessary, in constant development.

Taxa	**Group**	*E.g.s*
Algae	Algal turfs	*Cladophora*, *Lyngbya*, *Oscillatoria*, *Polysiphonia*
	Macroalgae	*Sargassum*, *Anadyomene*, *Dictyota*, *Lobophora*, *Ulva*
	CCA	*Hydrolithon*, *Porolithon*
	Calcareous	*Amphiroa*, *Halimeda*
	Phytoplankton	Cocolithophores, *Trichodesmium*
Coral	Massives	*Porites* spp.
	Tabular	*A. hyacinthus*
	Encrusting	*Montipora* spp.
	Staghorns	*Acropora* spp.
	Branching (other)	*Pocillopora* spp., *Acropora* spp.
	Free-living	Fungids
	Soft corals	*Dendronephthya*, *Sinularia*, *Xenia*
	Foraminifera	(not coral but calcifiers)
Fishes	Cryptobenthics	Gobidae, blennies
	Farmers	Damselfishes, *Pomacentrus*
	Scrapers/Grazers	Parrotfish
	Browsers	*Naso* spp., Siganids, Platax, Kyphosids
	Excavators	*Bolbometapon*, *Microrhinus*
	Detritivores	*Triostegus*, *Ctenochaetus striatus*
	Planktivores	Pomacentrids, fusiliers, chromis
	Corallivores	*Cetoscarus*, monocathids, butterflyfishes
	Invertivores	Labridae, haemulids, lutjanids, lethrinids
	Piscivores	Residents: Plectros, emperors, lutjanids
		Transients: Tunas, barracudas, sharks
	Symbiotic	*Labroides* – cleaners
Microbes	*Planktonic:*	
	Phototrophic	Synechoccoccus (inner), Prochlorococcus
	Chemoautotrophic	Archaea
	Heterotrophic	Bacteroidetes, Proteobacteria
	Benthic:	
	Phototrophic	Oscillatoria
	Chemoautotrophic	Archaea
	Heterotrophic	Proteobacteria, Planctomycetes, Acidobacteria, Verrucomicrobia
	Host-associated:	

	Phototrophic	Symbiodinium, Synechococcus
	Chemoautotrophic	Archaea
	Heterotrophic	Endozoicomonas
Porifera	*Heterotrophic:*	*Neopetrosia exigua* (*Xetospongia*), *Phopaloeidea odorabile*, *Coscinoderma matthewsi*, *Coelocarteria singaporensis*, *Stylissa flabelliformis*
	Massive	
	Encrusting	
	Erect	
	Cups	
	Phototrophic:	*Carteriospongia foliascens*, *Cymbastella coralliophilla*, *Ircinina ramose*
	Massive	
	Encrusting	
	Erect	
	Cups	
	Cliona	*Cliona* spp. (*Cliona orientalis*)
	Cryptic	
	Other bioeroding	*Aka* spp.
Echinoderms	*Asteroidea:*	
	Herbivores	*Cryptasterina* spp.
	Predators	*Culcita* spp. (excluding CoTS)
	CoTS	
	Holothuroidea:	
	Aspidochirotids	*Stichopus* spp., *Holothuria* spp.
	Dendrochirotids	Cryptic species
	Echinoidea:	
	Regular urchins	Diademids, *Echinometra* spp.
	Irregular urchins	Sand dollars, heart urchins
	Brittle stars *Ophiuroidea*	
	Crinoidea	Feather stars
Worms	Nematodes	Span across all feeding guilds
	Nemertea	Ribbon worms
	Polychaetes	Predatory species
	Filter-feeders	Spirobranchus
Crustacea	*Decapoda:*	
	Herbivores	Hermits, Xanthids, *Eripihia*
	Predators	Larger species; lobsters, crabs
	Coral-associated	*Trapezidae*, *Tetrallidae*, *Alpheus lottini*, *Hymenoceridae* (CoTS), *Cymo melanodactylus*
	Stomatopods	*Alpheidiae*
	Cleaners	*Lysmata*
	Other:	
	Barnacles	
	Infauna	Harpacticoid copepods
	Parasitic	Gnathiid isopods
Mollusca	*Gastropoda:*	
	Herbivores	Turbos, limpets, *Aplysia* spp.
	Predators	Triton snail, *Conus* spp.
	Corallivores	*Drupella*
	Bivalvia:	
	Clams	*Tridacna* spp.
	Other bivalves	Oysters, mussels
	Other:	
	Chitons	*Polyplacophora*
	Nudibranchs	
	Cephalopoda	Octopus, cuttlefish

A1.5 Identifying critical gaps in research

As contracted within Project 4.6, additional funding was available through NESP to support short-term projects aiming to fill critical knowledge gaps on coral reef ecosystem function to expedite recommendations for management on the GBR. Working group members were encouraged to develop ideas on critical knowledge gaps and propose research ideas to fill these gaps towards the end of the workshop. The main ideas for intensive research projects included:

- Threats to herbivores from fishing, specifically focusing on the poorly understood recreational spearfishing industry (Peter Mumby; Kenny Wolfe)
- Coral disease: review of information and impacts on the GBR – potential to use Betty Willis' dataset and more (Mia Hoogenboom; David Bourne)
- Threshold levels of coral cover and coralline contributions to the carbonate budget of the GBR (Guillermo Diaz-Pulido; coral team)
- Microbial switches: reviewing microbial pathways and their contribution to a functioning GBR (David Bourne; Nicole Webster)
- COTS juvenile development – the delayed life stage and missing link in our understanding of CoTS outbreaks (Kenny Wolfe; Jessica Stella)
- Invertivory on the GBR: a meta-analysis/review of a poorly understood link in the trophic chain (Kenny Wolfe; Jessica Stella)
- Primary productivity of sponges on the GBR (Manuel Gonzalez-Rivero)

A1.6 Workshop #1 participants (7-8th March 2018)

1. Dr. Russ Babcock (CSIRO)
2. Dr. Line Bay (AIMS)
3. Dr. David Bourne (JCU)
4. Damien Burrows (TWQ Hub)
5. Dr. Guillermo Diaz-Pulido (Griffith)
6. Dr. Manuel Gonzalez-Rivero (AIMS)
7. Mrs. Kate Osborne (AIMS)
8. Dr. Mia Hoogenboom (JCU)
9. Prof. Mark McCormick (JCU)
10. Prof. Peter Mumby (UQ)
11. Dr. Juan-Carlos Oritz (UQ)
12. Dr. Jessica Stella (GBRMPA)
13. Dr. Angus Thompson (AIMS)
14. Dr. Nicole Webster (AIMS)
15. Dr. Kennedy Wolfe (UQ)

A1.7 Foreword – Workshop #2

A general meeting/workshop was held at GBRMPA, Townsville, 10th April 2019, to discuss management recommendations and outputs of NESP 4.6. This was a critical meeting to align research and management priorities on the GBR. The input from workshop #2 members expanded the collaboration and they were subsequently listed as co-authors for this work (see list of participants below (A1.9).

A1.8 Notes and feedback from group discussions regarding functional species as management priorities on the GBR (Workshop #2)

General feedback on Recommendations sections

1. Suggest re-categorising the recommendation section to the following to allow more flexibility for MP Managers with determining management actions at various scales.
2. Include a diagram that shows the degree of vulnerability/ function and also the uncertain species.
3. Include science recommendations where uncertainty is high as these may be knowledge gaps that require further research.
4. Recommendations that are specific actions are best started with verbs for clarity.

Science Recommendation	**Desired Outcome for Functional Species**	**Example management actions.**
As is	Stronger language can be used. What is the real gold star desired outcome? See examples below.	Possibilities for management that shows a line of site to outcomes and monitoring and evaluation to be considered by MP Managers.
Detritivorous fishes	E.g. sediment loads are reduced by lowering sediment inputs and avoiding or mitigating resuspension in localised areas.	E.g. dredge management, anchoring management, improved runoff water quality.
Coral associated decapods		Increased stewardship for coral health and dependencies of other organisms
Bivalves	Benefits from natural infrastructures of reef forming mollusc are considered and adopted where appropriate.	E.g. transplanting/aquaculture
Cleaner wrasse	Protect ‘mega stations’ to improve ….	

Specific suggestions relating to species recommendations:

Species	**Suggestion**
Branching and tabular corals	Identify the ‘keystone’ branching and tabular Acropora sp. for additional protection.
Cleaner wrasse	Management recommendation 3 is a Science Recommendation
Detritivorous fishes	Recommendation 2 reads more like a statement. Would this be more of a science recommendation for research of these fishes as an indicator species for responses improved water quality?

A1.9 Workshop #2 participants (10th April 2019)

- Damien Burrows (NESP)
- Jesseca Carver (GBRMPA)
- Nadine Marshal (CSIRO)
- David Wachenfeld (GBRMPA)
- Roger Beeden (GBRMPA)
- Donna Audas (GBRMPA)
- Juan-Carlos Ortiz (GBRMPA)
- Chris Roelfsema (UQ)
- Peter Mumby (UQ)
- George Roff (UQ)
- Robert Mason (UQ)
- Kennedy Wolfe (UQ)
- Dylan Horne (GBRMPA)
- Neil Mattocks (GBRMPA)
- Damien Weekers (GBRMPA)
- Genevieve Williams (GBRMPA)
- Jen Dryden (GBRMPA)
- Michelle Dyer (GBRMPA)
- Vicky Bonanno (GBRMPA)
- Karen Chong-Seng (GBRMPA)
- Paul Groves (GBRMPA)
- Mel Cowlishaw (GBRMPA)
- Lauric Thiault (CRIOBE)

APPENDIX 2: EXPERT ELICITATION SUREVY RESPONSES

A2.1 Notes from survey responses on ALGAE

Score the level of contribution of each species group to primary production.

R1. Algal turfs, fleshy macroalgae and CCA contribute significantly to primary production. I have some numbers of their contribution in the following online paper: http://www.gbrmpa.gov.au/__data/assets/pdf_file/0019/3970/SORR_Macroalgae.pdf Other refs:

For turfs: Klumpp DW, McKinnon AD (1992) Community structure, biomass and productivity of epilithic algal communities on the Great Barrier Reef: dynamics at different spatial scales. Marine Ecology Progress Series 86:77-89

For CCA: Chisholm JRM (2003) Primary productivity of reef-building crustose coralline algae. Limnology and Oceanography 48:1376-1387

Fleshy macroaglae: Schaffelke B, Klumpp DW (1997) Biomass and productivity of tropical macroalgae on three near-shore fringing reefs in the central Great Barrier Reef, Australia. Botanica Marina 40:373-383

R2. (a.) Very broad functional (all encompassing) groups such as phytoplankton and turf mean that by definition there is no redundancy (unless you mean within group); (b.) Some evaluations such as sargassum are more or less context dependent e.g. Sargassum more important inshore, where contributions, redundancy and dependency might be higher.

Score the level of contribution of each species group to nutrient cycling (e.g. N & P cycles, benthic-pelagic coupling, microbial processes).

R1. Role of phytoplankton in nutrient cycling depends on zooplankton herbivory. Turfs harbour N-fixing cyanobacteria.

R2. Similar to above.

Score the level of contribution of each species group to calcification.

R1. Phytoplankton contribution to calcification would be through coccolithophores, but nothing is known about tropical forms. In temperate and cold seas, coccolithophores' contribution to production of CaCO3 is huge. Fleshy macroalgae modify carbonate chemistry, which may facilitate calcification via pH elevation during the day.

R2. Indirect positive role of fleshy and calcareous algae through shading and promotion of CCA. CCA indirect positive role through promoting coral settlement. Calcareous algae positive role higher off reef.

Score the level of contribution of each species group to bioerosion.

R1. Turfs are grazed by fish thus promoting erosion of coral and CCA skeletons.

R2. Algal turf promote parrotfish etc. grazing therefore contribute to bioerosion indirectly and are dependent on grazers e.g. fish, urchins and phytoplankton are essential for role of boring sponges (exciting!).

Score the level of contribution of each species group to ecosystem engineering.

R1. "Sargassum" here refers to other Fucales algae as well, such as Cystoseira and Hormophysa, which are also canopy forming fucalean algae, and can be locally abundant in the GBR.

R2. Algal turfs, CCA through calcification and bioerosion link. CCA redundancy =one rather than nil due to fact not all corals need it to settle.

Score the level of contribution of each species group to recruitment facilitation (e.g. habitat provisioning, biochemical cues).

R1. Some Halimeda can induce coral settlement.

R2. The direct column is a bit redundant given the question so scored all as zero. I am reading calcareous algae as halimeda rather than reds in the turf.

Score the sensitivity of each species group to the listed stressors/threats. (Note: a stressor can be 2 (positive effect) or -2 (negative effect).

R1. Nutrient effects are complicated by inducing shifts in species composition benefiting some groups over others.

R2. Surveymonkey landscape pages suck.

Score the likely recoverability of each species group to perturbation (consider: population resilience, growth rates, reproduction, susceptibility, etc), and the certainty of these scores based on literature and/or expert judgement.

R2. A lot of this depends totally on the type of perturbation.

Score the manageability of each species group to the listed stressors/threats.

R1. This is a hard one to complete as different roles are performed by different seaweeds, e.g. Sargassum may reduce coral settlement BUT provides habitat for invertebrates and fish. So intervening sargassum forests may have positive and negative effects on reef functioning.

A2.2 Notes from survey responses on MICROBES & SPONGES

Score the level of contribution of each species group to calcification.

R3. Here I am including cryptic and some heterotrophic sponges as facilitators of calcification, mainly thinking on cementation by stabilising rubble. Wulff, J. L. 1984. Sponge-mediated coral reef growth and rejuvenation. Coral Reefs 3:157-163. Wulff, J. L., and L. W. Buss. 1979. Do sponges help hold coral reefs together? Nature 281:474-475.

Score the level of contribution of each species group to bioerosion.

R3. Most of sponges depend on carbonate substrate, in particular bioeroding sponges. However, I am not including this in the dependency section because it is assumed that most benthic organisms in coral reefs depend on the reef substrate. However, it can be changed if you think otherwise.

Score the level of contribution of each species group to ecosystem engineering.

R3. Some sponges, heterotrophic and phototrophic, create complex habitats in coral reefs, hosting large diversity of invertebrate and fish species. Cryptic sponges mediate reef building by cementation. Hence my answers. Bell, J. J. 2008. The functional roles of marine sponges. Estuarine, Coastal and Shelf Science 79:341-353.

Score the level of contribution of each species group to recruitment facilitation (e.g. habitat provisioning, biochemical cues).

R3. Cryptic sponges facilitate reef cementation of rubble. Arguably this indirectly promotes recruitment. However, much of this research comes from the Caribbean and their contribution in the GBR is poorly understood.

Score the sensitivity of each species group to the listed stressors/threats. (Note: a stressor can be beneficial (positive effect) or detrimental (negative effect).

R3. Bell, James J., Alberto Rovellini, Simon K. Davy, Michael W. Taylor, Elizabeth A. Fulton, Matthew R. Dunn, Holly M. Bennett, Nora M. Kandler, Heidi M. Luter, and Nicole S. Webster. "Climate change alterations to ecosystem dominance: how might sponge-dominated reefs function?." Ecology (2018). Sponge biomass and bioerosion rates increase under ocean warming and acidification JKH Fang, MA Mello-Athayde, CHL Schönberg, DI Kline, ... Global change biology 19 (12), 3581-3591 Effects of ocean warming and acidification on the energy budget of an excavating sponge JKH Fang, CHL Schönberg, MA Mello-Athayde, O Hoegh-Guldberg, ... Global change biology 20 (4), 1043-1054 Bleaching and mortality of a photosymbiotic bioeroding sponge under future carbon dioxide emission scenarios JKH Fang, CHL Schönberg, MA Mello-Athayde, M Achlatis, ... Oecologia, 1-11 Sponge bioerosion on changing reefs: ocean warming poses physiological constraints to the success of a photosymbiotic excavating sponge M Achlatis, RM van der Zande, CHL Schönberg, JKH Fang, ... Scientific reports 7 (1), 10705

Score the manageability of each species group to the listed stressors/threats.

R3. There is very little information on how sponges are being affected in the GBR. Work from other parts of the world suggest that they can be quite susceptible to nutrients and sedimentation, hence local management actions are likely to have an impact on the status on sponges and the role they perform. However, a major recommendation from this work would be to include sponges as part of routine monitoring in order to assess their functional contribution, status and threats. This will then inform on the relevance of management actions.

A2.3 Notes from survey responses on CORAL

Score the level of contribution of each species group to primary productivity (e.g. photosynthesis).

R4. No dependency if corals etc. considered as holobiont

R5. I have scored these based on the coral host portion of the holobiont. This has implications for Dependency and Indirect contribution as the coral side of the symbiosis is clearly Dependent on the zoox and microbial partners. If the groups listed were considered at the level of the holobiont scores would be reversed. All corals are considered redundant as they would likely be replaced by algae and so photosynthesis continued.

Score the level of contribution of each species group to nutrient cycling (e.g. N & P cycles, benthic-pelagic coupling, microbial processes).

R5. Again the listed groups considered as animal portion of the holobiont. Direct contribution, although scored as 2 would be increased at the expense of Dependency and Indirect contributions at the holobiont level.

Score the level of contribution of each species group to symbiosis (e.g. commensalism, parasitism).

R4. Am excluding symbiodinium here as all are symbiotic with microalgae so direct contributions would otherwise scale to biomass

R5. Redundancy considered on the basis of biomass and the likely replacement of the group by another symbiotic group.

Score the level of contribution of each species group to calcification.

R4. No dependency if corals etc. considered as holobiont

R5. Difficulty considering redundancy as unsure of the balance between say Tabular corals and their likely replacement with CCA, I'm simply unsure as to which produces CACo3 at a great rate per unit area. On the whole I've scored redundancy as 1 for most coral groups as expect a moderate to 2 proportion of their replacement would be by non-calcifying groups.

Score the level of contribution of each species group to bioerosion.

R5. There are issues relating to redundancy. Corals don't directly contribute to bioerosion; they do however reduce bioerosion by shielding the substrate from bioeroding organisms. So, they are entirely redundant in terms of directly performing bioerosion but are not redundant in mediating bioerosion... I've scored assuming only the act of bioerosion performed by the group.

Score the level of contribution of each species group to ecosystem engineering (i.e. habitat production).

R5. Noting that Indirect contributions scoring can be 2 (or 1) in opposite directions among groups. Tabular corals may promote settlement of more habitat builders, in contrast to Soft corals that may limit settlement of habitat builders.

Score the level of contribution of each species group to recruitment facilitation (e.g. habitat provisioning, biochemical cues).

R4. Facilitation column redundant. Dependency of all on surface biota e.g. CCA, microbes etc.

R5. Again issues relating to scoring reflecting variably positive and negative contributions. Also very poor knowledge relating to settlement cues for almost all taxa other than some fish and corals. at the microbial and invert scale suspect there are may ne limited redundancy for most of these groups.

Score the manageability of each species group to the listed stressors/threats.

R5. Feasibility of management for most corals relies on management of pressures and in particular runoff, but also COTS - assuming climate is out side the feasible expectations. For stags, anchoring is an issue and there are proven successes at local scales.

A2.4 Notes from survey responses on OTHER INVERTEBRATES

Score the level of contribution of each species group to herbivory.

R1. I've considered the areas in the GBR between reefs in these responses particularly with respect to 'other bivalves'. I've also considered biomass of species group in relation to other groups on the GBR in the responses.

R2. Scale of herbivory would be important in assessing the contribution of functional roles of some invert groups to this process

Score the level of contribution of each species group to predation.

R2. Again, scale would be important. Many cephalopods hunt prey not always accessible to fishes (such as octopus hunting crustaceans in tidal pools and within the reef matrix)

Score the level of contribution of each species group to calcification.

R1. I've considered the areas in the GBR between reefs in these responses particularly with respect to 'other bivalves'. I've also considered biomass of species group in relation to other groups on the GBR in the responses.

Score the level of contribution of each species group to recruitment facilitation (e.g. habitat provisioning, biochemical cues).

R2. I found this one a bit tricky, as often species do play a role in recruitment of conspecifics. I focused more on the micro-herbivores that fulfil the role of keeping algae in check to facilitate coral recruitment.

A2.5 Notes from survey responses on FISHES

Score the level of contribution of each species group to herbivory.

R2. Recent isotopic and behavioural research in PNG by Jacob Eurich (PhD, just being published) shows that what we thought were farmers are often omnivores and that they play an important role in facilitating grazing by surgeonfish. One published article is Eurich et al. 2018.

Parrotfishes appear to also be partitioning resources in a 2ly selective way, suggesting that they may be little 'functional redundancy', though the extent to which their selection is influenced by other species (or their removal) is presently unknown. This is a quote from some recent correspondence I had with Howard Choat "We are analyzing the results of parrotfish grazing at the near micro-level by fol1owing different species, locating the feeding substratum at a very fine scale, recording the benthic substratum with macrophotography and then taking micro-cores of the epi- and endo-lithic environment in order to identify if there is any consistency in the type of substratum selected at this scale and the autotrophic elements (including microbes) associated with it. There is a far greater capacity for parrotfish species to make selections of substratum and autotrophs at this scale than we would have imagined at the complexes of co-occurring parrotfish species that appear to overlap in their grazing regimes and substratum selected are consistently partitioning resources in a very clear-cut way. "

Detritivores can be crucial for the export of nutrients/energy among reef habitats (e.g., feed in one spot, defaecate in another), for instance some goatfish feed on sand flats at the edge of the hard reef and then defaecate over the hard reef. They are also important nuclear species, which affect the behaviour and spatial impact of other species (e.g. Lukoshek & McCormick 2002).

For many of these groups, such as the balistids, it is largely unknown what their overall contribution may be, but it appears that it is likely to differ greatly between geographic locations (e.g., from Kenya and PNG). The more we study various groups, the more we are beginning to realise that generalisations are very difficult and that there is a 2 degree of selectivity which is species specific. For instance, piscivores forage on different size prey, using different foraging strategies and their feeding rates can be dependent the community around them (e.g. Maria Palacios's recent PhD, some refs below).

Lukoschek V, McCormick MI (2002) A review of multi-species foraging associations in fishes and their ecological significance. Proceedings of the Ninth International Coral Reef Symposium 1:467-474

Eurich JG, Shomaker S, McCormick MI, Jones GP (2018) Experimental evaluation of the effect of a territorial damselfish on foraging behaviour of roving herbivores on coral reefs. Journal of Experimental Marine Biology and Ecology 506:155–162

Palacios M (2017) Controlling mesopredators: importance of behavioural interactions in trophic cascades. PhD dissertation, James Cook University

Palacios MM, Warren DT, McCormick MI (2016) Sensory cues of a top-predator indirectly control a reef fish mesopredator. Oikos 125:201–209

Palacios MM, Malerba ME, McCormick MI (2018) Multiple predator effects on juvenile prey survival. Oecologia

Palacios MM, Killen SS, Nadler LE, White JR, McCormick MI (2016) Top-predators negate the effect of mesopredators on prey physiology Journal of Animal Ecology

R3. Note that I've given a 2 to detritivores only if you include *Ctenochaetus striatus* and other similar surgeonfish. Wasn't too clear how to separate two of the invertivore groups. I think balistids more important than lutjanids

Score the level of contribution of each species group to predation.

R1. Many of these species could facilitate predation by being prey, but I didn't think that was what you meant.

R2. Non-predatory groups can affect predation indirectly through their influence on the distribution and abundance patterns of habitat and other aspects of the community. Many of the taxa we would class as invertivores are probably actually omnivores (e.g., sand perches, labrids) and are likely to be opportunistically predatory on recruits, so can have a major impact on the resulting community. The truly invertivorous lutjanids are probably having less direct influence on communities. Predators tend to aggregate around where prey is located. Most piscivores target planktivores, hence their indirect effect. Most of a predator's impact has been shown to be through the fear effect and resident predators will have a greater direct effect than transient (larger) predators because of their numerical impact. The strike success of resident piscivores is very much dependent on the behaviour of the prey, which depends on the individual's interactions with other elements of the community. Predator strike rate and success will also depend on other predators in the area.

Score the level of contribution of each species group to symbiosis (e.g. commensalism, parasitism).

R1. This was kind of tough since all animals have parasites, and actually aren't we all microbial holobionts. But lets not go down that wormhole. And in a way, all organisms in an ecosystem are dependent on each other. I did not include facilitation of organisms that were a symbiosis as part of this either (e.g. herbivores make room for coral holobiont).

R2. Little is known about how important most of these species interactions are to parasitism in its many forms. Certainly external and internal parasites are certainly commonplace among fishes, though the loads differ between fish species and with habitat. Work on the microbiome symbioses suggests that that is also an important component to individual, population and community wellbeing. I can't really fill this out as I would just be guessing.

R3. Only entering data for fish engaged in symbiosis

Score the level of contribution of each species group to bioerosion.

R3. Only entered where needed.

Score the level of contribution of each species group to recruitment facilitation (e.g. habitat provisioning, biochemical cues).

R2. Detritivores (such as goatfish, some surgeonfish) could have an impact on algal and seagrass beds on sand just off the hard reef. This could be important as many species recruit into these areas (e.g. lethrinids, goatfish, some cardinalfish into seagrass; wrasses and parrotfishes into Dischistoidus algal mats). It is likely that the general activity of the fish community over the reef makes a major influence on levels of recruitment at a wide variety of spatial scales through the soundscapes they produce. *see* Gordon TAC, Harding HR, Wong KE, Merchant ND, Meekan MG, McCormick MI, Radford AN, Simpson SD (2018). Habitat degradation negatively affects auditory settlement behavior of coral reef fishes. PNAS doi: 10.1073/pnas.1719291115

Piscivores are likely to be having a large effect through their direct and indirect contributions to community dynamics. We've found that have a direct impact on recruitment through both predation and just their smell. *see* Vail A, McCormick MI (2011) Metamorphosing reef fishes avoid predator scent when choosing a home. Biology Letters 7:921-924

R3. Only entering where appropriate (zero elsewhere). Note that this is an indirect process so I didn't score 'indirect'. Assume that detritivores includes *Ctenochaetus.*

Score the sensitivity of each species group to the listed stressors/threats. (Note: a stressor can be beneficial (positive effect) or detrimental (negative effect).

R2. Antagonistic outbreaks may be detrimental to fish communities by reducing habitat 'complexity', species diversity and hence may influence communities through cues used for recruitment (sound and smell). Planktivores may be affected if anything affects 2ndary production, or the habitat complexity of the reef (= number of shelter sites). These will also be affected directly by fisheries on pelagics, groupers and snappers through mesopredator release. Regards the fisheries effects on piscivores - it depends on which group the target species are grouped into (i.e. coral trout) - obviously it will be detrimental for the target species and could be beneficial for the mesopredators that are released from top-down control. Piscivores are going to be impacted by anything that alters the lower trophic levels, so they will be detrimentally impacted by any major community shift.

R3. Same for siganids as browsers. Excavators other parrotfish same as scrapers. Corallivores same as *Bolbos* but detrimental effects of warming, cyclones and COTS. Inverts all the same.

APPENDIX 3: ASSESSMENT OF STRESSORS ON FUNCTIONAL GROUPS INSHORE

Table A3.1: Potential impact (PI) of nine pertinent stressors on 70 functional groups on the GBR. Exposure was considered in context of inshore reefs. Note: maximum PI = 16 (red); high PI ≥10 (yellow); medium PI ≥ 7 (green); blank cells denote PI = 0; H=herbivores, P=predators; DF=deposit feeders; SF=suspension feeders.

Taxa	Functional group	Nutrients	Sediments	Pollutants	Warming	Acidification	Cyclones	Fishing	Disease	Outbreaks
Microbes	Phototrophic		4.0	16.0	9.0	1.0				
	Host-associated	16.0	9.0	16.0	16.0	4.0			1.0	
	Chemoautotrophic			9.0	4.0	1.0				
	Heterotrophic			9.0	9.0	1.0				
Algae	Phytoplankton		1.0	9.0						
	Algal turfs		1.0	9.0	1.0					
	Leathery		1.0	4.0	1.0		2.3			
	Foliose		9.0	4.0			0.3			
	Calcareous		9.0	4.0	4.0	4.0	2.3			
	CCA	4.0	16.0	9.0	9.0	9.0				
Sponges	Heterotrophic		7.1	11.1	1.0	7.1	16.0	1.0	1.0	
	Phototrophic		16.0	11.1	1.0	1.0	16.0	1.0	1.0	
	Boring		7.1	9.0	0.4		0.3		1.0	
	Cryptic		9.0	16.0	1.0	1.0	1.0		1.0	
Coral	Tabular	12.3	9.0	1.6	16.0	9.0	16.0	0.1	2.8	16.0
	Staghorn	12.3	9.0	1.6	16.0	9.0	16.0	0.4	2.8	16.0
	Branching (other)	12.3	7.1	1.6	16.0	9.0	16.0	0.1	1.8	16.0
	Massive	6.3	6.3	1.6	16.0	6.3	1.8	0.1	1.8	1.8
	Encrusting	6.3	9.0	1.6	16.0	6.3	1.8	0.1	1.8	2.8
	Free-living	4.0	6.3	1.6	12.3	6.3	4.0		1.8	1.8
	Soft corals	4.0	9.0	1.6	12.3	4.0	11.1	0.1	1.0	
	Foraminifera		6.3	2.3	4.0	6.3	7.1		0.4	
Worms	Nematodes									
	Nemertea						0.3			
	Polychaetes						0.3			
	Spirobranchus		4.0	9.0	9.0	4.0	1.0		1.0	
Crustaceans	Decapods (H)			4.0	9.0	16.0				
	Decapods (P)			4.0	16.0	16.0	0.3			
	Coral-associated		4.0	9.0	16.0	16.0	9.0			0.3
	Barnacles		4.0	4.0	9.0	9.0				
	Stomatopods			4.0	9.0	9.0	0.3			
	Cleaner shrimp			4.0	9.0	16.0	1.0			
	Infauna			1.0	1.0	9.0	0.3			
	Zooplankton		1.0	4.0	9.0	16.0	0.3			
	Parasitic			1.0	4.0	9.0	0.3			
Molluscs	Gastropods (H)		1.0	4.0	16.0	16.0				
	Gastropods (P)			4.0	9.0	7.1	1.0			
	Triton snails			4.0	9.0	7.1	1.0	0.3		
	Drupella			4.0	16.0	16.0	0.3			
	Tridacna		9.0	4.0	16.0	16.0	16.0	1.0		
	Bivalves (other)		1.0	4.0	16.0	16.0	4.0	4.0	1.0	
	Chitons				9.0	9.0	1.0			
	Cephalopods	1.0		4.0	1.0	11.1	0.3	2.3		
Echinoderms	Seastars (H)		1.0	4.0	9.0	4.0				
	Seastars (P)			4.0	9.0	1.0	1.0			
	CoTS			1.0	1.0	9.0	1.0			
	Sea cucumbers (DF)			4.0	9.0	4.0	2.3	16.0		

	Sea cucumbers (SF)		1.0	4.0	9.0	1.0	1.0	1.0	
	Sea urchins (regular)		1.0	4.0	9.0	16.0			
	Sea urchins (irregular)			1.0	9.0	16.0	0.3		
	Brittle stars			1.0	9.0	4.0	0.3		
	Feather stars			4.0	9.0	4.0	1.0		
Fishes	Cryptobenthic	0.4	4.0	7.1	11.1	4.0	11.1		1.8
	Farmers		11.1	7.1		1.8	7.1		
	Grazers (scarids)		16.0	4.0		1.8	0.1	0.1	
	Browsers (nasos)		7.1	4.0		1.8	0.4	0.1	
	Browsers (siganids)		7.1	4.0		1.8	0.4	0.4	
	Browsers (other)		7.1	4.0		1.8	0.4	0.4	
	Bolbometopon	0.4	11.1	4.0	1.8	4.0	1.8	0.4	
	Excavators (other)		16.0	4.0		1.8	1.8	0.1	
	Detritivores	1.8	7.1	4.0	0.4	1.8	7.1		
	Planktivores	0.4	4.0	7.1	11.1	4.0	11.1		2.8
	Corallivores	7.1	11.1	4.0	16.0	11.1	2.8		4.0
	Invertivores (labrids)		7.1	7.1	4.0	4.0	1.8	0.1	
	Invertivores (other)		7.1	7.1	4.0	4.0	1.8	1.8	
	Invertivores (lutjanids)		4.0	4.0	4.0	4.0	1.0	0.4	
	Eels	1.8	7.1	4.0	7.1	4.0	1.0		
	Piscivores (residents)	4.0	7.1	7.1	11.1	4.0	2.8	16.0	
	Piscivores (transients)	1.8	7.1	7.1	7.1	4.0	1.8	16.0	
	Cleaner wrasse	0.4	1.8	4.0	7.1	1.8	11.1		

APPENDIX 4: INVERTIVORY

[Report submitted for Case Study 1]

Invertivory on the GBR: a poorly understood link in the trophic chain

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Abstract

One of the most specious groups of fishes on the Great Barrier Reef (GBR) are those that feed on mobile benthic invertebrates. Invertivorous fishes play important roles in ecological processes in coral reefs, shaping biodiversity by moving energy from inside the reef matrix to pelagic trophic systems. Despite their widely accepted importance, little is known about the diversity of invertivorous fishes on the GBR, the prey they target, their influence on reef function, and how they respond to stressors such as climate change and habitat degradation. As part of the reef functions project (NESP Project 4.6) we conducted a literature review to address this knowledge gap for invertivores on the GBR. In our search of over 550 studies, 35 studies identified 174 species of invertivorous fishes from 20 families, spanning diverse life stages, sizes, morphologies and feeding modes. Of these studies, 33 provided some quantitative measure of invertivory, 26 presented a measure of stomach and gut contents analyses for 14 families, and seven provided different but incomparable measures of invertivory (e.g. occurrence, handling time, partial counts) for four families. All papers are discussed in this review but only dietary composition data are presented for the 14 families, excluding three nominally herbivorous and detritivorous families that consumed <10% invertebrates (Acanthuridae, Blennidae, Siganidae). The greatest diversity of species feeding on invertebrates (~35%) and number of direct measures of invertivory (~30%) came from the Labridae (wrasses). Cryptobenthic fishes (e.g. gobies) were particularly important predators of microcrustaceans, providing direct trophic pathways to higher order consumers. From a bottom-up perspective, crustaceans comprised >40% of invertebrate prey and were consumed by all invertivorous fish species, particularly during early development and for those with ontogenetic shifts in diet (i.e. to herbivory or piscivory). Vulnerability of invertivores to climate change and habitat degradation may be highest for those that rely on coral habitat for survival (e.g. cryptobenthic fishes) and those that rely on coral-associated invertebrates as their main prey items (e.g. juvenile coral trout). This data compilation highlights disparate knowledge gaps for invertivores compared to their herbivorous and piscivorous counterparts. Targeted research is imperative to quantify predator-prey dynamics for invertivores on the GBR, including prey availability, trophic transfers from within the reef matrix and beyond, and their potential to mediate trophic cascades in degrading reef systems.

Introduction

Fishes on coral reefs play key roles in numerous important trophic pathways, moving energy from within the reef framework to higher trophic levels (Marnane and Bellwood 2002, Depczynski et al. 2007). In particular, fishes that target benthic invertebrates provide a direct link between the benthos and fisheries productivity (Klumpp et al. 1988, Depzynski and Bellwood 2003). Coral reefs such as the Great Barrier Reef (GBR), Australia, are among the most species-rich ecosystems in the world, and invertivorous fishes are among the most abundant and specious groups that inhabit them (Hiatt and Strasburg 1960, Williams and Hatcher 1983, Stella et al. 2011). Despite this, the functional roles of invertivorous reef fishes remain poorly characterised and quantified.

Invertebrates are the dominant contributors to animal diversity in the GBR ecosystem, represented by 32 phyla with an extraordinary range of morphologies. These animals exploit nearly every habitat, and are an essential source of protein to a plethora of reef organisms (Hutchings et al. 2007, Stella et al. 2011, Kramer et al. 2012). Crustaceans are thought to be a particularly important group, targeted by the majority of invertivorous reef fishes (Kramer et al. 2015). Invertebrate communities are highly variable across small and large spatial scales with the density of crypto-crustaceans reported to be highest in dead coral while mollusc densities are greatest in soft sediments (Klumpp et al. 1988, Jones et al. 1990, Enochs 2012, Enochs and Manzello 2012, Kramer et al. 2014). Therefore, it is not surprising that invertivores have evolved specialised morphologies to avail of this diversity, often occupying important trophic and ecological niches. Feeding modes of coral reef fishes can be dependent on morphology, foraging behaviour and life-stage (Bellwood et al. 2006, Holmes and McCormick 2010, Konow et al. 2017). While a range of specialised and obligate consumers exists in the invertivores, invertebrates also contribute to the diet of other functional fish groups including nominal herbivores, piscivores, planktivores and detritivores (Jones et al. 1990).

The current deficiencies in data regarding invertivory on coral reefs limits our capacity to predict functioning and productivity in a future ocean. Increasing levels of habitat degradation associated with climate change are of primary concern on coral reefs (Przeslawski et al. 2008, Stella et al. 2011). Major reductions in live coral cover are already measurable on the GBR (GBRMPA 2017, Hughes et al. 2018, De'ath et al. 2012), with consequent impacts on mobile invertebrate and reef fish assemblages (Stuart-Smith et al. 2018). Mobile invertebrates that are specialised coral-associates may be particularly vulnerable to decreasing habitat availability (Stella et al. 2011). Invertebrates are also directly susceptible to the multiple stressors associated with a changing ocean, particularly calcifying organisms with pelagic larval stage (Byrne and Przeslawski 2013). The vulnerability of invertebrates has serious implications for the invertivorous fishes that rely on them. However, our understanding of the trophic pathways between invertivorous fishes and their invertebrate prey in response to global change is limited.

To address the deficit in our current understanding of the process of invertivory on the GBR, we synthesised all relevant literature, specifically aiming to:

(a) identify the reef fish species that function as invertivores,
(b) identify the predominant invertebrate prey species and groups,
(c) identify the feeding behaviours, habitat associations and feeding methods of invertivorous fishes,

(d) outline the trophic and functional roles of invertivores, and
(e) outline known and/or predicted threats to invertivores.

We conclude with recommendations for species of particular functional importance on the GBR, namely those with highly specialised roles (i.e. low ecological redundancy) and/or predominance in reef trophodynamics.

Methods

A systematic literature review was conducted to identify the fish predators of mobile benthic invertebrates on the Great Barrier Reef (GBR). The literature was searched using the ISI Web of Science database. Searches used combinations of the terms “invertivore”, “Great Barrier Reef”, “invertebrate”, “predator”, “predation”, “diet”, “crustacea”, “molluscs”, “cephalopods”, “echinoderms”, “polychaetes”, “annelids”, “worms”, “fishes” and “fish”. The search was further supplemented by examining the reference lists of papers that were found, and subsequent searches on Google Scholar. Where possible, quantitative measures of invertivory were extracted. The predominant measure reported in the literature was dietary contribution (based on gut or stomach contents analysis), but a number of studies also measured occurrence of prey across predator diet, selection indices, measures of relative importance of prey, and direct measures of predation (e.g. handling time). Dietary contributions were most often presented as percentages, so data presented as counts were converted to percentages to facilitate comparisons between studies. Data were provided by the authors or extracted from digital publications using the measuring tool in Adobe Acrobat XI. We included hyperbenthic invertebrates as prey species as they are in the benthos during the day when many fish species are feeding. Studies of predation on the crown-of-thorns starfish (CoTS; *Acanthaster sp*.) were excluded due to recent detailed reviews of the subject (e.g. Cowan et al. 2017).

From each study, information regarding invertivorous fish species and their prey were recorded. For invertivores this included taxonomy, size, size class (small<150 mm, medium=150-300 mm, large=300-600 mm, very large>600 mm, as in Brandl et al. 2016a), preferred foraging habitat, feeding behaviour (diurnal vs. nocturnal), feeding type (facultative vs. obligate at the time of the study), feeding method (e.g. crushing vs. picking), and life-stage (recruit, juvenile, adult). Fishes were defined as obligate when invertebrates contributed >65% of their diet. If life-stage was not discussed directly then data were assumed to be for adults. Herbivores (rabbitfishes) and detritivores (surgeonfishes) that consumed small numbers of benthic invertebrates were recorded but were not included in the analysis, as this predation was considered incidental (Kramer et al. 2013). A study on the predation of crustaceans by labrids (wrasses) on the GBR (Kramer et al. 2015) was included in our analyses, but due to taxonomic resolution (genera only) species-specific information could not be determined or extrapolated (see Table 1).

For prey species and groups, information recorded included taxonomy and size, if available. Information on the abundance of invertebrate fauna, and densities of macroinvertebrates and fishes on the GBR, were obtained from papers that measured this directly, and from the Reef Life Survey database (Edgar and Stuart-Smith 2014, 2018a, 2018b). Due to time constraints data on invertebrate fauna were not extensively collected but are presented here to illustrate the potential variation in composition with habitat and location. We further collected information on the location, habitat, depth, state of the environment (ambient versus disturbed), method used to measure invertivory, season and level of replication for each study.

Current taxonomy was recorded as presented in the World Registry of Marine Species (WoRMS 2018). It should be noted that Scaridae is used here to refer to parrotfishes according to present use in WoRMS, although taxonomic revision indicates they are a subfamily (Scarinae) in the Labridae (Westneat and Alfaro 2005). If the feeding type, feeding method and life-stage of the fish were not detailed, then these data were added based on information from other studies included in the review and reference material (Randall et al. 1990, Carpenter 1996, Allen 1997, Ferry-Graham et al. 2002, Lo Galbo et al. 2002, Wainright and Bellwood 2002, Depczynski and Bellwood 2004, Wen et al. 2013a, 2013b, Rizzari et al. 2014, Brandl 2016b, Ceccarelli et al. 2018, Froese and Pauly 2018, Kingsford pers comms).

Quantitative measures of dietary composition were mostly presented as percentages of stomach and gut contents. While percentage data facilitates comparison between different species and studies that use different methods, percentage data are difficult to analyse. For each fish species the percentage contribution of prey phyla was recorded and gross averages were calculated for species found across multiple studies. Principal components analysis (PCA) was used to identify variables that explained patterns in invertivore diets. To account for non-independence, the data were rescaled as z-scores for inclusion in the analysis (as in Pineda-Munoz and Alroy 2014). Fish species were only included when invertebrates contributed >10% to their diet, and a study on invertivores feeding on crustaceans was only included in the analysis of patterns between fishes feeding on this prey group (Kramer et al. 2015). All analyses were conducted in R 3.4.3 and visualised using the ggfortify and ggplot2 packages (Wickham 2016, Horikoshi and Tang 2016, Tang et al. 2016, R core team 2017). Figures were created in R, Microsoft Excel and Adobe Illustrator.

Caveats

Most of the measures of dietary composition come from gut and stomach content analyses. These data provide us with a valuable indication of predator diet, but prey composition may be under- or over-estimated in predator diets due to variable digestion rates and post-consumption identification (e.g. crustacean exoskeletons, mollusc shells, soft-bodied worms) (Hyslop 1980). As hard exoskeletons of crabs take longer to digest, gut content analysis may overestimate their relative contribution to overall diet (Beukers-Stewart and Jones 2004). The data reviewed here spans across multiple studies and methodologies (e.g. counts of prey items vs. volume of prey items), which may have resulted in biases towards particular prey groups. Nonetheless, these data allow us to broadly compare between fishes and the invertebrates that make up their diet. We also note that there are likely to be differences in prey availability among seasons and habitats on the GBR (St John et al. 1989, Lukoschek and McCormick 2001, Beukers-Stewart and Jones 2004, Wen et al. 2016), but prey availability is not always linked to selection and consumption. Overall, the data presented here provides a snapshot of invertivory across the entire GBR, highlighting the need for increased attention in this functional space and better quantification of trophic energy transfer.

Results and Discussion

Of ~578 papers considered in this review, 35 reported on invertivorous species directly on the GBR; 33 provided a measure of invertebrates being consumed, two surveyed fish species in response to environmental stressors with trophic level reported from the literature (Appendix 1). These studies included data collected across the length of the GBR, mostly clustered around research stations (Fig. 1a). Invertivores were reported on reef habitats from waters around Lizard Island, the Keppel Islands, One Tree Island, Orpheus Island, Heron Island, Magnetic Island, Cairns, and Townsville.

Invertivorous fishes on the GBR

It is clear that invertivorous fishes are a diverse group, consisting of 174 species from 20 families of which dietary proportions are presented for eleven families (Table 1, Fig. 2). This diversity far exceeds that of herbivorous fishes (178 species from 9 families; Cvitanovic et al. 2007), detritivores (24 species from 5 families; Wilson et al. 2003) and corallivores (128 species from eleven families; Cole et al. 2008). Direct measures of invertivory on benthic mobile invertebrates were reported for 18 families, of which dietary information from stomach and gut content analysis are presented for 66 species from eleven families (Table 1, Fig. 2; data not presented for three families that consumed <10% invertebrates). Other studies that measured invertivory on the GBR presented data for six species from four families (Balistidae, Haemulidae, Nemipteridae, Scaridae) but were not directly comparable (e.g. occurrence, handling time). Densities of the eleven invertivorous families are displayed by latitude (Fig. 1d), along with macroinvertebrate prey density (Fig. 1c), and composition of small and infaunal invertebrates in different habitats along the GBR (Fig. 1b). For four of eleven families presented, data were found for just one species from one study.

Crustaceans were present in the gross diets of all eleven families, including the Carcharhinidae (consumption of crabs by the blacktip reef shark, *Carcharhinus melanopterus*) (Fig. 2). Annelids and molluscs were the next most frequently consumed taxa but were not found in all diets (Fig. 2). The highest diversity of invertivores was represented by the Labridae (wrasses), followed by the Gobiidae (Table 1). Labrids are one of the most functionally and ecologically diverse groups of fishes on coral reefs and account for the highest biomass of invertivores on the GBR (Williams and Hatcher 1983, Jones et al. 1990, Bellwood et al. 2006, Kramer et al. 2015). In general, benthic mobile invertebrate consumers are believed to be more abundant in coral reef ecosystems than other fishes (see Table 1; Jones et al. 1990).

Of the 174 fish species that are documented here as invertivorous, 89 were classified as invertivores from the literature, 17 as carnivores and/or piscivores, 12 as detritivores, six as herbivores, four as omnivores, and 46 as a combination of these or something else (Table 1). For species where invertivory was quantified, ~40% were obligate consumers of invertebrates at the time of the respective study. Interestingly, many species not classified as nominal invertivores in the literature still consumed large amounts of benthic invertebrates (e.g. carnivores: *Chelodipterus quinquelineatus* and *Carcharhinus melanopterus* >35% of stomach contents; herbivores and detritivores: *Amblygobius phalaena* and *Bathygobius fuscus* >15%; carnivores/piscivores: *Lethrinus nebulosus* >50%). Detritivores and other groups may supplement their diet with invertebrates to avail of the higher protein and energy content relative to detritus (Hernaman et al. 2009, Kramer et al. 2013).

A broad range of morphological and functional traits were found among invertivorous fishes. Body size ranged from less than 50 mm (juvenile Scaridae, Serranidae, Gobiidae) to >1 m (Carcharhinidae, Labridae) in length, reflecting the broad trophic spectra of this group. Invertivores employed a variety of feeding methods, such as striking (ramming or lunging at prey), suction, winnowing, picking, crushing and biting and varying combinations of these. The use of these terms for feeding methods varied among studies. Due to the diversity of prey consumed by labrids, broad differences in feeding method are illustrated for this family (Fig. 3). However, it should be noted that species often use multiple feeding methods (Wainright and Bellwood 2002). Some intuitive patterns were present; for example, fish with crushing mouthparts (e.g. tuskfishes, *Choerodon schoenleinii*, Bellwood et al. 2006, Young and Bellwood 2012) were recorded to more readily consume macroinvertebrates and hard-shelled molluscs (Fig. 3). Labrids of the genera *Bodianus*, *Cheilinus*, *Coris*, *Halichoeres* and *Thalassoma* also incorporated high proportions of molluscs in their diets across a range of feeding strategies (Fig. 3). In contrast, winnowing and picking species (thicklip wrasse, *Hemigymnus* spp. and Hoeven's wrasse, *H. melanurus*, Green 1994, Bellwood et al. 2006. Kramer et al. 2013, 2015) consumed more crustacea and soft-bodied worms (Fig. 3).

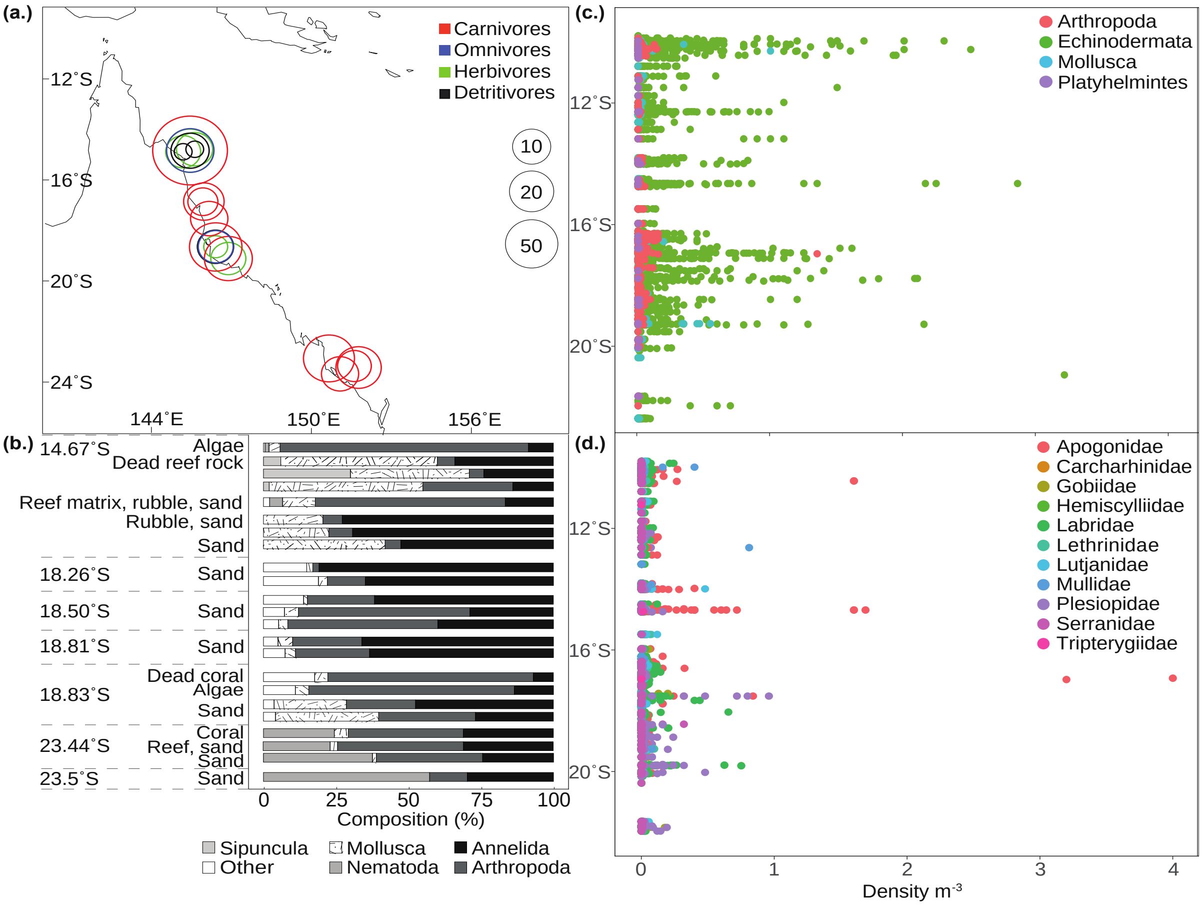

Figure A4.1: (a) Locations of studies of fishes feeding on mobile benthic invertebrates on the Great Barrier Reef. Circles indicate the number of measures taken at each site. Broad feeding guilds are indicated by colour. (b) Composition of invertebrates in different reef habitats, (c) macroinvertebrate density/m^3, and (d) fish density/m^3 on the Great Barrier Reef. Absolute latitudes and habitats for invertebrate composition are indicated on the y-axes. One data point in (c) where sea urchin density was 8.89/m^3 was removed for ease of visualisation. Data are from: (b) Hutchings and Weate 1977, Klumpp et al. 1988, Riddle 1988, St John et al. 1989, Riddle et al. 1990, Green 1994, Lukoschek and McCormick 2001, Ollivier et al. 2018; and (c) and (d) Edgar and Stuart-Smith 2014, 2018a, 2018b.

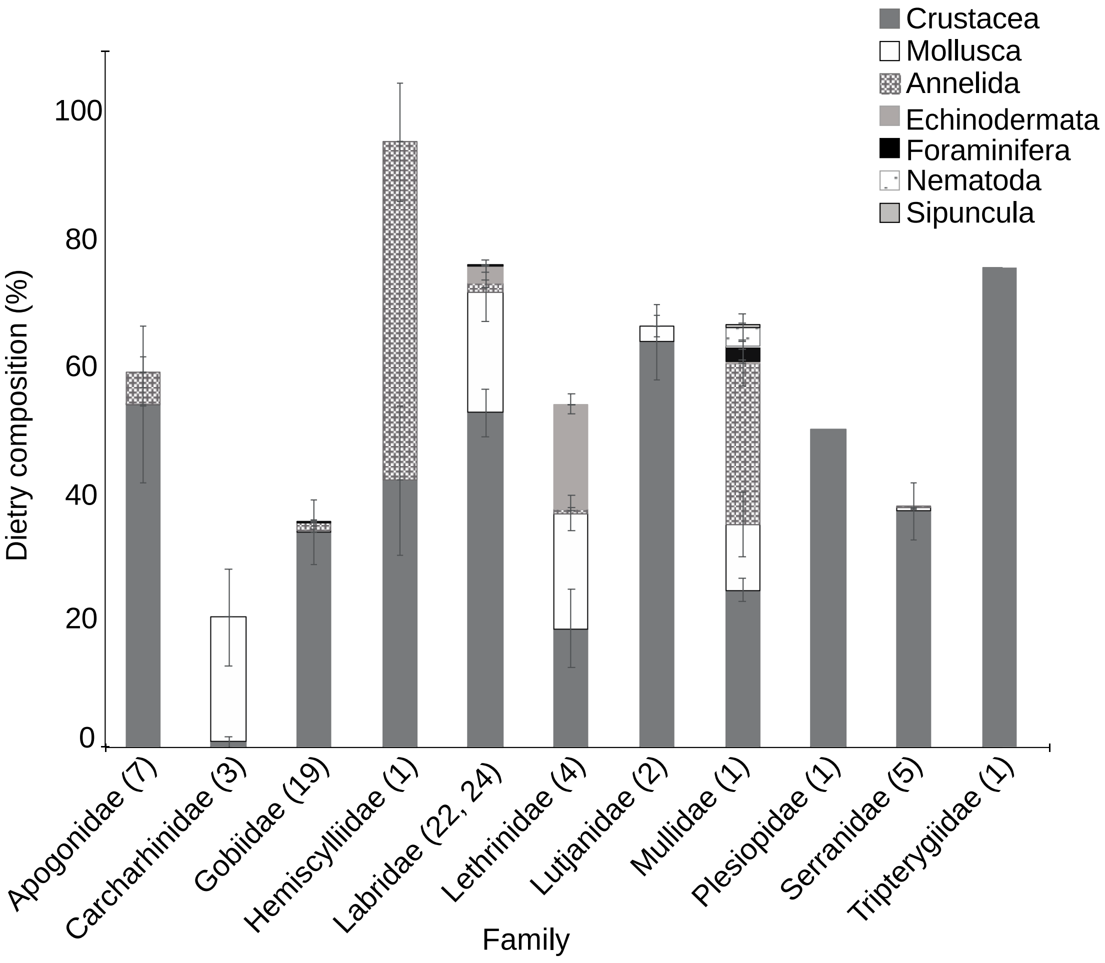

Figure A4.2: Mean proportion (±SE) of invertebrates (by phyla) in the diet of invertivorous fishes (by family). Number of species are indicated in parentheses after family name. For the Labridae data come from 22 species, but the Crustacea component comes from 24 genera where species were not specified and only data for crustaceans were presented (Kramer et al. 2015).

Some invertivorous fishes exhibit highly specialised feeding behaviour. For example, *Labroides dimidiatus* (cleaner wrasse) were found to consume on average 50-90% crustaceans, feeding predominantly on parasitic gnathiid isopods (Grutter 1997a, 2000, Bellwood et al. 2006). Through this specialised mode of invertivory, cleaner wrasses play a functionally important role in parasite removal, which in turn shapes reef fish assemblages (Grutter et al. 2003, Clague et al. 2011, Soares et al. 2011, Waldie et al. 2011, Sun et al. 2015, Binning et al. 2018). Other invertivorous fishes also capitalise on their unique morphologies. *Novaculichthys taeniourus* (rockmover wrasse) are known to move large rocks using their jaws in order to search for benthic prey and are consumers of crabs (Fig. 3, Wainright and Bellwood 2002, Bellwood et al. 2006). The black spot tuskfish, *Choerodon schoenleinii*, which feeds primarily on molluscs (Fig. 3), has learned to use rocks as a tool to break the hard shell of cockles (Jones et al. 2011). Triggerfish (Balistidae) flip sea urchins with their teeth or jets of water to access their lesser protected underside (Randall 1967; Young and Bellwood 2012).

Principal components analysis (PCA) indicated a division between fish species that consume crustaceans and those that consume echinoderms and molluscs (PC1, Fig. 4a). Earlier life-stages and smaller-bodied fishes had a greater propensity to consume crustaceans (Fig. 4a).

In contrast, larger fishes consume a wide variety of prey including large-bodied invertebrates with hard shells (Fig. 4a). This is likely due to a combination of factors, including increases in body size, mouth gape and muscle development (Grutter 2000, Lukoschek and McCormick 2001, Wainright et al. 2004). Bellwood et al. (2006) demonstrated that wrasses with specialised morphologies are not necessarily limited to a narrow diet, but noted that some invertebrate prey have morphologies that protect them and limit the number of predators able to consume them. Structurally defended prey items like sea urchins are known to be consumed by triggerfish (Young and Bellwood 2012), which are also predators of CoTS (Cowan et al. 2017). In a study that measured handling time of tethered sea urchins at Lizard Island, Young and Bellwood (2012) demonstrated that two species of triggerfish, *Balistapus undulatus* and *Balistoides viridescens*, were responsible for over 90% of predation on sea urchins over other predators such as lethrinids. However, we did not find direct dietary information for balistids on the GBR.

The second principle component (PC2) indicated differences between the invertivores that consume worms and foraminifera, and those that consume crustaceans and echinoderms (Fig. 4a). This could be explained by differences in prey defences and/or variable accuracy in identifying worms in gut contents analysis. This may also reflect differences in feeding strategies and trophic space, whereby foraminifera and annelids contribute greater proportions to the diet of bottom-feeders like the Hemiscyllidae (epaulette sharks) and Mullidae (goatfishes) (Fig. 2, 4a, Heupel and Bennett 1998, Lukoschek and McCormick 2001). These two components (PC1 and PC2) explained 60.8% of the total variation. Nematodes and sipunculids were measured in the gut contents of the goatfish, *Parupeneus barberinus* (Mullidae), (Lukoschek and McCormick 2001), but as this was the only species identified to feed on these invertebrates they were not included in the PCA. The diversity of invertebrate taxa in the diet of *P. barberinus* (including many infaunal species) reflects its ability to dig into soft sediments to access prey. Fishes such as labrids and nemipterids forage in association with *P. barberinus*, relying on the abilities of the goatfish to disturb the sediment and expose prey (Lukoschek and McCormick 2001).

Interestingly, there are spatial differences in the contributions of invertebrates detected in the diets of fish species among locations (Kingsford 1992, Connell 1998, Wen et al. 2012) and habitats (Light 1995), and between fished areas and those closed to fishing (Wen et al. 2012). It has been suggested previously that the diets of fishes that consume invertebrates may vary regionally (Fig. 1, Pratchett 2005, Kulbicki et al. 2005). Adult longfin grouper (*Epinephelus quoyanus*) were found to consume ~100% invertebrates in the Keppel Islands region (inshore), in contrast to ~50% at One Tree Island (offshore) (Connell 1998, Wen et al. 2012). *Labroides dimidiatus* consumed less parasitic gnathiid isopods at Heron Island (southern GBR) than at Lizard Island (northern GBR), with suggestions that ectoparasites may be less available at the southern site (Grutter 1997a, 1997b). The invertivorous goby, *Valenciennea muralis*, possesses a high feeding rate that drops off in winter, posited to be due to decreased energetic demands and prey availability (Hernaman et al. 2009). Regional and seasonal variations in diet will be influenced by predator-prey dynamics in terms of distribution, density, morphology, behavioural constraints and prey availability.

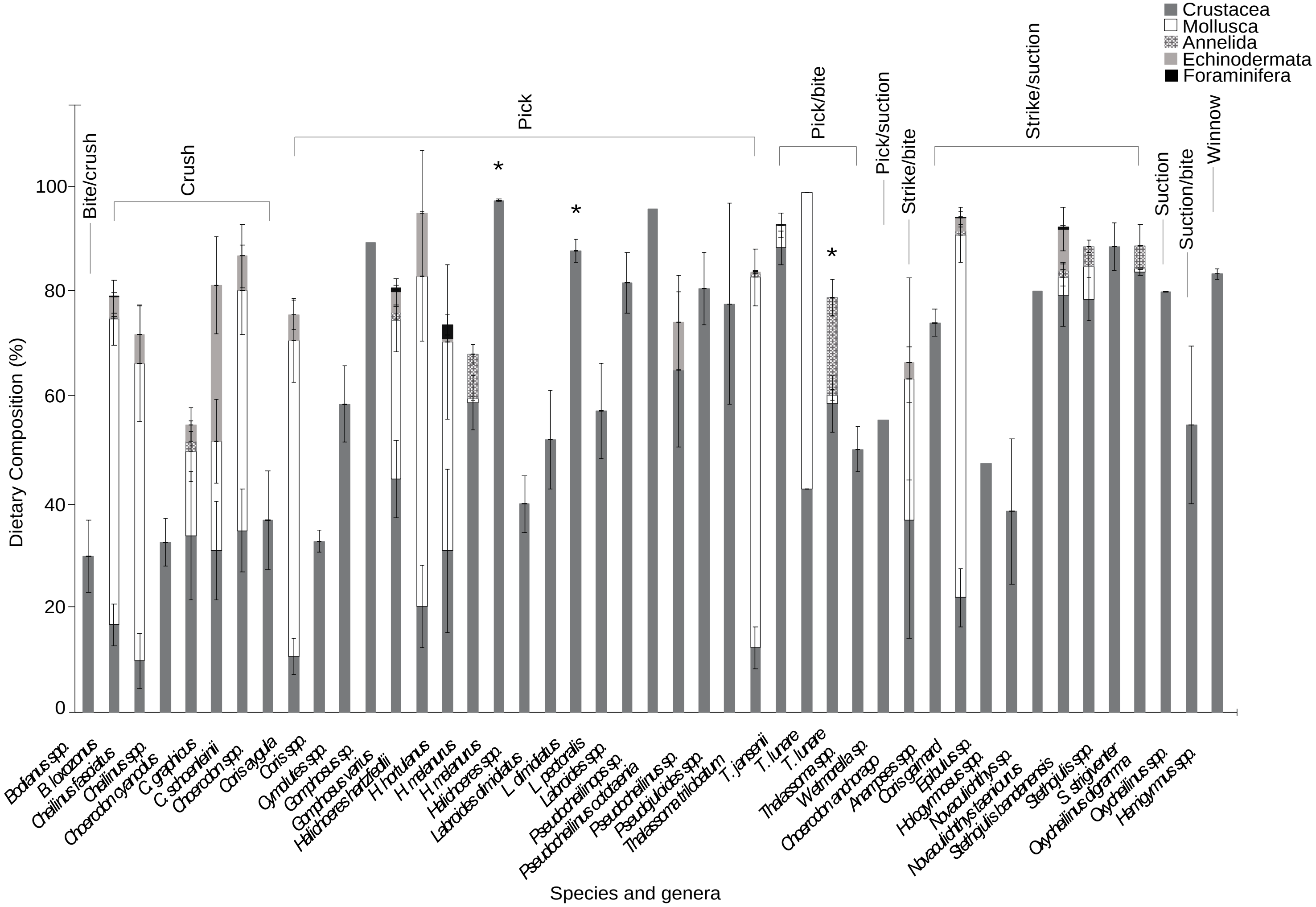

Figure A4.3: Mean proportion (±SE) of invertebrates (by phyla) in the diet of labrids (genera or species) on the Great Barrier Reef. Feeding method is indicated above. Dietary composition (and SE) is presented directly from single studies or averages calculated across multiple studies. Where no error is presented, no error data were available. For genera, only crustacea were measured and values include multiple species (data from Kramer et al. 2015). Asterisks denote data for recruits and juvenile life-stages. Data from: Green 1994, Connell 1998, Grutter 1997a, 2000, Bellwood et al. 2006, Kramer et al. 2013, 2015. Note: data from Bellwood et al. 2006 are estimates and should be treated with caution.

Invertebrate prey on the GBR

Densities of macroinvertebrates on the GBR were dominated by the Echinodermata (Fig. 1c), which is not reflected in the invertivore diet (Fig. 2). The survey data presented aimed to capture large-bodied invertebrates (Fig. 1c, Edgar and Stuart-Smith 2014, 2018b), but the majority of invertebrate taxa are smaller in size and often cryptic in the reef framework. Crustaceans dominate species diversity in coral reefs (Enochs 2012, Stella et al. 2011, Kramer et al. 2014), and many habitat types across the GBR (Fig. 1b). Not surprisingly, crustaceans were the most predominant prey items (43%), followed by molluscs (10.4%), echinoderms (3.7%), polychaetes (3.1%) and foraminifera (2.8%), with occasional records of sipunculids, nemerteans, unspecified arthropods, and nematodes (<1% each). The remaining references to prey items were made up of broader categories of macroinvertebrates (24.7%), microinvertebrates (6.6%) and unspecified invertebrates that were not differentiated (4%).

Due to their disproportionate contributions to invertivore diets (>40%), classes of Crustacea were examined separately (Fig. 4b). Differentiation in predator-prey groupings were apparent with gobies consuming small copepods, apogonids consuming crabs, shrimp and isopods, and serranids and labrids consuming a range of macro- and micro-crustaceans (Fig. 4b). This is likely due to differences in fish size, mouth gape, habitat use and behaviour (Wainwright and Bellwood 2002, Boaden and Kingsford 2012). Kramer et al. (2015) found that crustaceans were a particularly important food source for wrasses (Fig. 3), and found clear divisions between fishes consuming macro- and micro-crustaceans relating to fish size. Wrasses that feed on foraminifera and gnathiid isopods exhibit low morphological variation and specialised feeding (Bellwood et al. 2006), including cleaner wrasses (Grutter 2000). Kramer et al. (2013) emphasised the importance of harpacticoid copepods for small fishes. Here we found 38 fish species including gobies, wrasses, scarids, serranids, blennies and goatfish consumed copepods as recruits or small adults. This likely underestimates consumption of copepods as resolution of prey taxonomy varied between studies. The categories for crustaceans presented here (Fig. 4b) are broad due to variation of detail in the literature, but provide evidence for the importance of predator and prey body size in invertivore trophodynamics.

Macro- and micro-invertebrates are readily available as potential prey on the GBR (Fig. 1b,c), and invertivorous fishes are present across all latitudes (Fig. 1a,d). Habitat type is an important determinant of the composition of invertebrate assemblages with annelid worms and molluscs more available in soft sediment and rubble, and arthropods more available on algae, and live and dead coral (Fig. 1b, Stella et al. 2010, Kramer et al. 2014). Invertebrate diversity and density can change over small spatial scales with crypto-crustacean densities often highest in dead corals and coral rubble (Riddle 1988, Preston and Doherty 1994, Enochs 2012, Enochs and Manzello 2012, Kramer et al. 2014), with specialised coral-associates occupying live coral (Stella et al. 2010, 2011). Considering the invertebrate assemblages found across the GBR, crustaceans are disproportionately represented in the diets of many fish consumers (Fig. 1, Fig. 2, Kramer et al. 2015), reflecting their importance in the cryptofauna. It is interesting that while echinoderms can occur at high densities relative to other macroinvertebrates (Fig. 1c), very few predatory fish species target them. This may be attributed to their protected body forms (e.g. sea urchins) and/or defence and escape mechanisms (e.g. evisceration, regeneration) (Birkeland 1988). In this instance, predator-prey size dynamics are an important consideration, as only large specialised fish can avail of many adult echinoderms, while predation on juveniles is likely a life-history bottleneck (Birkeland 1988, Cowan et al. 2017).

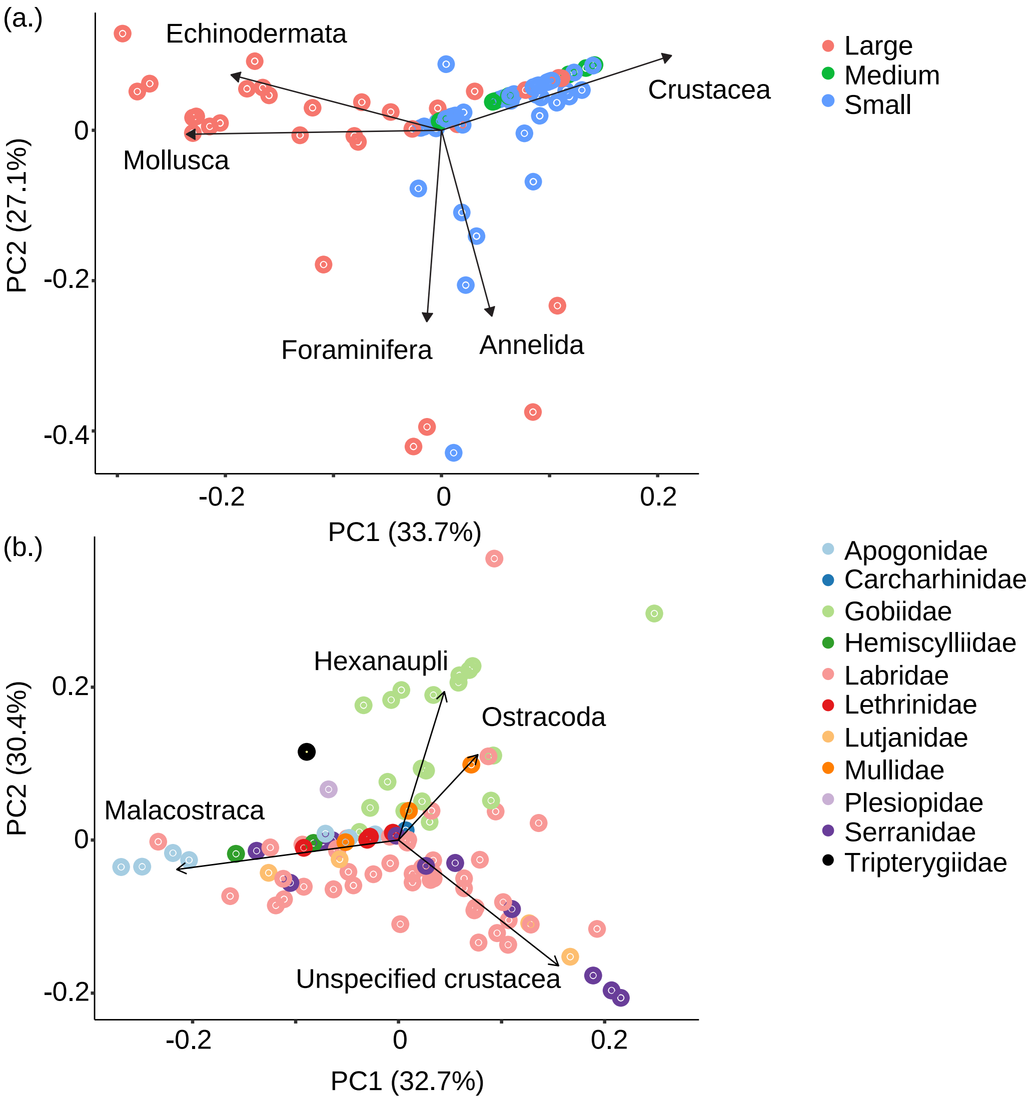

Figure A4.4: Principal components analysis (PCA) of invertebrate prey items of invertivorous fishes on the Great Barrier Reef, indicating groupings of (a) prey items based on size, and (b) crustacean-specific feeding grouped by fish family. For fish size: small<150mm (recruits, juveniles and adults), medium=150-300 (recruits and juveniles), large>300 mm (juveniles and adults, including medium sized adults). Percentages on the axes indicate the amount of variation explained by that component.

Ontogenetic shifts in diet

Changes in fish morphology, behaviour, microhabitat and habitat use are known to influence ontogenetic shifts in diet (Werner and Gilliam 1984). Such shifts were apparent for a range of invertivorous fishes examined here, with representatives from two families documented to transition to piscivory or herbivory as adults. This suggests that many reef fishes – beyond the notional invertivores – depend on invertebrates as a food source. Moreover, this reflects the broad importance of the invertivores across trophic pathways. Herbivorous parrotfishes (Scaridae) are reported to consume micro-crustacea (e.g. copepods, amphipods, ostracods) and foraminifera as recruits and juveniles (Bellwood 1988, Chen 2002). This dietary inclusion of invertebrates during early developmental stages may provide more protein and nutrients to facilitate faster growth through small and vulnerable life-stages, facilitated by changes in the jaw and gut morphology (Werner and Gilliam 1984, Bellwood 1988, Chen 2002).

The early reliance of many coral reef fishes on invertebrate prey spans from herbivores to higher order piscivores that are important fisheries targets on the GBR. As recruits, the carnivore/piscivore *Lutjanus carponotatus* (stripey snapper) consumed ~75% crustaceans compared to 39% as adults (Connell 1998, Wen et al. 2012). The adult diet of this species is not entirely piscivorous but includes crustaceans as well as gobies and blennies (Connell 1998, Wen et al. 2012). The serranids, *Plectropomus leopardus* and *P. maculatus* (coral trout), consumed invertebrates, predominantly decapods, as recruits (~51%) and juveniles (~24%), with *P. leopardus* consuming <10% as adults (St John 1999, 2001, St John et al. 2001, Kingsford 1992, Light 1995, Wen et al. 2012, 2016). In contrast, another serranid, *Epinephelus quoyanus* (longfin grouper), consumed decapods and invertebrates across all life-stages (Connell 1998, Wen et al. 2012). Quantifying these dietary shifts is critical to the characterisation of reef trophodynamics, as the functional role of these species are also likely to change as a result. This is particularly important for determining current and predicting future fisheries productivity on the GBR.

Diets often broaden to encompass a greater diversity and size spectra of prey as fish grow (Fig. 3, Green 1994, Boaden and Kingsford 2012, Kramer et al. 2013). Obligate invertivores such as *Parapeneus barberinus* (goatfish) and *Hemiscyllium ocellatum* (epaulette shark) shift from consuming small crustaceans (ostracods and smaller crabs, respectively) as juveniles to large crabs as adults, but polychaete worms remain an important component of their diets at both life stages (Heupel and Bennett 1998, Lukoschek and McCormick 2001). The cleaner wrasse, *Labroides dimidiatus*, consumes larger and greater quantities of gnathiid isopods as adults than as juveniles (Grutter 2000). The two-lined monocole bream, *Scolopsis bilineata*, moves from diurnal foraging as recruits/juveniles to nocturnal foraging as adults, and invertebrate prey size increases from 1 mm to 6-24 mm diameter respectively (Boaden and Kingsford 2012). These differences are associated with growth, body size and habitat use of the invertivores, shifting their contributions to reef functioning. Ontogenetic shifts were not noted for small-bodied coral reef gobies, which demonstrate minimal change in habitat use over their lifespan (Hernaman et al. 2009).

Where prey selection has been investigated, differences in trophic pathways can be striking. Juvenile *P. barberinus* preferentially consume ostracods despite their low abundance in the associated microhabitat (Lukoschek and McCormick 2001). In a study on *Halichoeres melanurus* (tail-spot wrasse) juveniles, individuals exclusively consumed copepods, despite the availability of many other microcrustaceans, polychaetes, molluscs and nematodes in the reef matrix (Green 1994). However, copepods were the most abundant prey item making it difficult to discern between selection and availability-dependent feeding. Adult *H. melanurus* also consume copepods but their diet expands to include molluscs, ostracods, amphipods and polychaetes (Kramer et al. 2013). Cleaner wrasse preferentially consumes gnathiid isopods despite the prevalence and diversity of parasites on coral reef fish clients (Grutter 1997a, Muñoz et al. 2006). Longfin grouper selectively consume small shrimp and crustaceans as recruits and shift to large crabs as they increase in size (Wen et al. 2012).

Overlooked invertivores and functional roles

Invertivores may often go overlooked in coral reef research, particularly those that are inconspicuous due to their small size (e.g. cryptobenthic fishes) or nocturnal feeding behaviour. Two such families, the Gobiidae (gobies) and the Apogonidae (cardinalfishes), are underrepresented in estimates of abundance on coral reefs, but are essential to marine food webs and trophic pathways (Munday and Jones 1998, Ackerman and Bellwood 2002, Kramer et al. 2012). Species from both families consume large amounts of benthic invertebrates, particularly microcrustaceans (Fig. 2, 5).

Cryptobenthic fishes such as gobies represent around half the total number of reef fishes on the GBR (Depczynski and Bellwood 2003, Brandl et al. 2018). Crustaceans represented 3.6-77.5% of the diet of the species of Gobiidae examined here, while molluscs and worms were only documented as a food source for a few species (Fig. 5). Gobies are a critical step in the transfer of energy from micro-invertebrates within the reef matrix to higher trophic levels in the water column (Fig. 5, Connell 1998, Beukers-Stewart and Jones 2004, Kramer et al. 2013, Brandl et al. 2018). The invertivore *Eviota zebrina* is a highly abundant goby that consumes large quantities of typically hyper-abundant copepods each day, making this cryptic species a particularly important component of reef trophodynamics (Kramer et al. 2013). From a top-down perspective, juvenile *Lutjanus carponatus* (stripey snapper) consume invertebrates but shift to include gobies and blennies as they age (Connell 1998, Wen et al. 2012), while piscivorous coral trout switch to fishes such as apogonids and labrids as adults (Light 1995, Kingsford 1992, St John 1999, 2001, St John et al. 2001).

Nocturnal apogonids are highly abundant on the GBR and have limited morphological variation (Fig. 1d, Bellwood et al. 2006). They are important to reef trophodynamics circulating nutrients within the reef system, with nocturnal spatial partitioning and resource use evident between species (Marnane and Bellwood 2002). Nocturnal communities can be starkly different to daytime assemblages on coral reefs, with many cryptic invertebrates (e.g. ostracods, worms) emerging from the benthos and reef matrix in the cover of night. Our synthesis of data suggests that along with some species of reef shark, epaulette shark, sweetlips, emperors, snapper and goatfish (Table 1), apogonids may be a functionally significant invertivores at night. Apogonids and other nocturnal fishes such *Scolopsis bilineata* (Nemipteridae; Boaden and Kingsford 2012) occupy an important trophic space that is unexploited during the day, and are therefore may be critical to coral reef food webs and function.

The cleaner wrasse, *Labroides dimidiatus*, plays a specific role in the functioning of coral reefs. This specialised fish feeds predominantly on the skin mucus and parasitic isopods (gnathiids) of reef fishes and marine megafauna, which is broadly regarded as a cleaning service. This cleaning process has been documented to reduce stress hormones in the client (Soares et al. 2011), and increase fish abundance, diversity (Grutter et al. 2003), recruitment (Sun et al. 2015), and cognitive performance (Binning et al. 2018) – likely connected to the active removal of deleterious ectoparasites. Cleaner wrasse can improve fish growth rates and/or survivorship (Waldie et al. 2011). On reefs that had cleaner wrasse removed for >8 years, resident reef fishes were 37% less abundant and 23% less diverse compared to control reefs (Waldie et al. 2011). In addition, vagrant fish species were 23% lower in abundance, and species richness decreased by 33% compared to control reefs (Waldie et al. 2011). Visiting

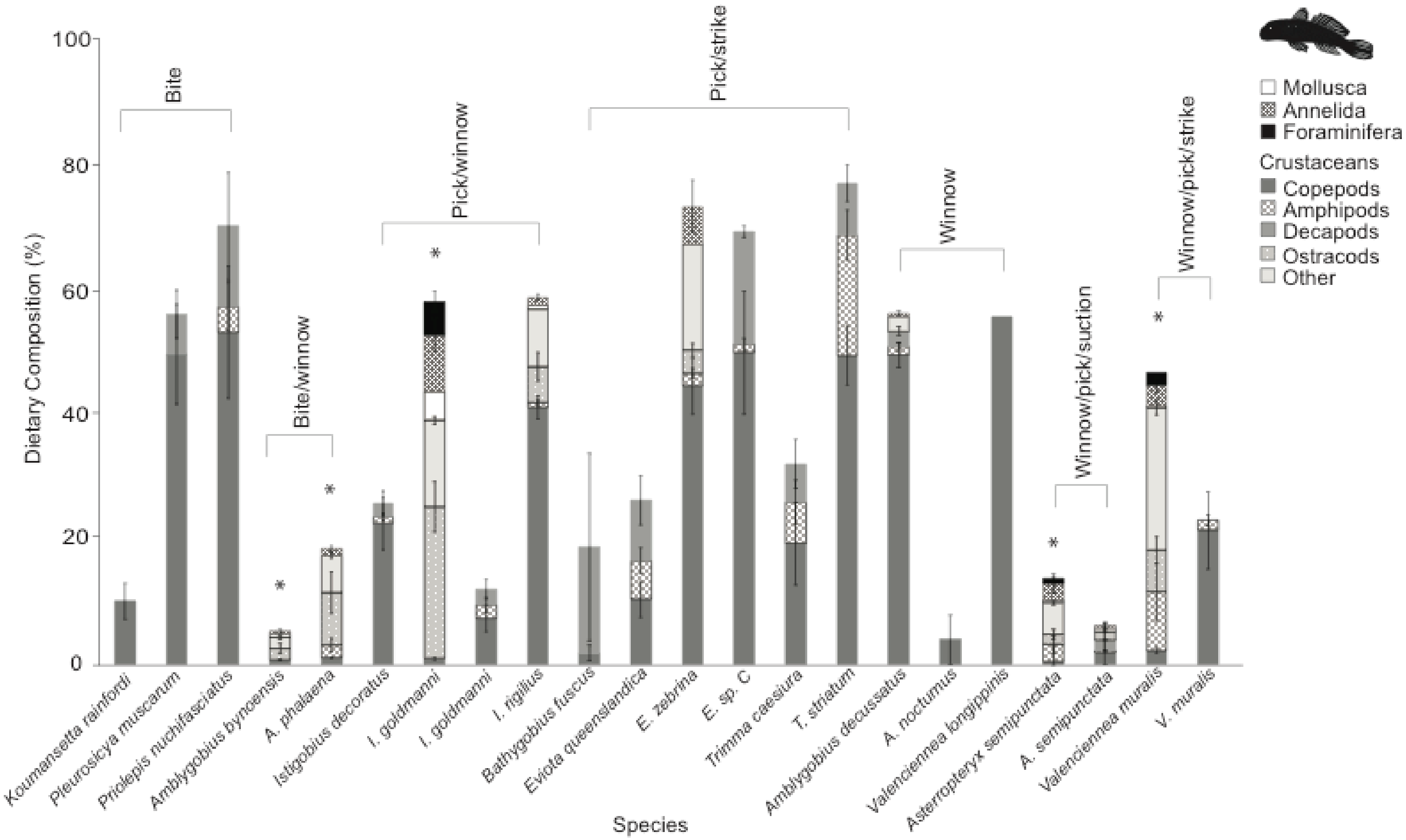

Figure A4.5: Mean proportion (±SE) of invertebrates in the diet of gobies on the Great Barrier Reef. Feeding method is indicated above. Dietary composition (and SE) is presented directly from single studies or averages calculated across multiple studies. Where no error is presented, no error data were available. Asterisk denotes data mixed for juveniles and adults. Data from: St John et al. 1989, Depszynski and Bellwood 2003, Hernamen et al. 2009, Kramer et al. 2013.

herbivores (Acanthuridae; surgeonfishes) were 66% lower in abundance on removal reefs (Waldie et al. 2011). Through its role in invertivory and symbioses, cleaner wrasse can alter reef fish assemblages and shape reef function with little ecological redundancy, making their role particularly critical to understand and maintain.

Potential threats

Invertivorous fish are exposed to a variety of threats, such as overfishing and pollution, but habitat loss via climate change may be the primary threat (Wilson et al 2006; Munday et al 2008; Pratchett et al 2008). Nearly 20% of fish species within the Reef (320 species from 39 families) rely on live coral habitats (Coker et al. 2014). Disturbances that cause even small declines in coral cover (~10%) have caused significant declines in fish abundance (62%) across a range of species (Wilson et al. 2006), sometimes taking years to fully unfold (Graham et al. 2007). Those most reliant upon coral habitat, such as gobies and hawkfishes, are likely to be the most affected habitat loss (Munday et al. 2003, Munday 2004, Coker et al. 2014). A loss of coral-related structural complexity can be associated with a decline in small-bodied fishes, which can include juveniles of ecologically important larger species (Wilson et al. 2010a), as well as fisheries targets (Graham et al. 2007). This would likely have cascading effects on fisheries productivity (Wilson et al. 2010, Rogers et al. 2014, 2018a, 2018b).

A decline in live coral habitat may also impact invertivorous fishes via the loss of invertebrate prey that associate with live coral (Stella et al. 2011). Over 800 coral-associated invertebrate species have been described, with the majority of those found in branching pocilloporid and acroporid corals; these may constitute a significant portion of the diet of some invertivorous fish (Stella et al. 2011). This has been reflected in gut contents for species of wrasse, hawkfish and butterflyfish (Hiatt and Strasburg 1960, Ferry-Graham et al 2001). Dietary importance of coral-associated invertebrates can also very with ontogeny. For example, although adult coral trout and stripey snapper are primarily piscivorous, the diets of recruits are comprised mainly of decapod crustaceans associated with live *Acropora* corals (Wen et al. 2012). The trend of severe declines in coral habitat along the GBR is projected to continue to degrade as climate systems change, putting many fishes at risk (Hughes et al. 2017; Stuart-Smith et al. 2018).

As the structural complexity provided by coral is important in mediating predator-prey interactions, a loss of coral can have a disproportionate effect on certain fish species via an increase in predation (Hixon and Jones 2005). For example, in response to extensive habitat loss due to a cyclone, Brandl et al. (2016a) found that some invertivorous fishes increased in biomass, such as the titan triggerfish (*Balistoides viridescens*), darkspot tuskfish (*Choerodon monostigma*), and sidespot goatfish (*Parupeneus pleurostigma*), suggesting they are able to exploit novel resources “flushed out” of the reef matrix. However, some invertivorous species exhibited a decline in biomass, highlighting species-specific responses to habitat degradation.

In the absence of live coral, habitat structure is still important in shaping benthic marine communities. Degraded habitats have been found to harbour an immense diversity and density of invertebrates, particularly dead coral and coral rubble (Enochs et al. 2011, Enochs and Manzello 2012, Nelson et al. 2016). However, the bioavailability of these species to higher trophic groups remains poorly characterised. Interestingly, dietary shifts in response to habitat degradation (associated with coral bleaching and freshwater flood plumes; Williamson et al. 2014) have been observed in both young (Wen et al. 2016) and adult (Hempson et al. 2017) coral trout. These shifts involved consumption of non-preferred fishes in response to changes in foraging behaviour (Wen et al. 2016) and prey biomass (Hempson et al. 2017). Although dietary adaptive capacity may mitigate short-term impacts of habitat degradation, it can result in shortened and simplified trophic structure and with a longer-term toll on ecosystem function (Graham et al. 2007, Estes et al. 2011, Hempson et al. 2017). Quantification of population productivity of coral reef cryptofauna is imperative to understanding reef trophodynamics, and in predicting potential trophic cascades both within the reef matrix and beyond.

Conclusions and recommendations

In line with the extreme diversity of mobile benthic invertebrates on coral reefs, invertivorous coral reef fishes are both speciose and often highly specialised to target specific prey items. As such, they boast a wide range feeding methods, morphologies and life-stage dependent feeding modes. It has been approximated that ~70% of fishes on the GBR feed predominantly on invertebrates (Kramer et al. 2015). In a more targeted assessment of direct measures of invertivory on the GBR, we identified 174 documented species (and genera) from 20 families that incorporate benthic mobile invertebrates in their diets. This only captures ~10% of the total known number of fish species on the GBR, highlighting the paucity of direct observations and quantification of fish invertivory on the Reef. Our review of the literature emphasises the knowledge gaps regarding invertivorous fishes and ecosystem function in this coral reef.

While the diversity of invertivorous fishes on the GBR exceeds that of other trophic groups, the ecology of invertivorous fishes remains poorly documented and studies are largely biased towards other nominal groups, such as herbivores, corallivores, planktivores and piscivores. Labridae (wrasses) were the most specious invertivores, representing ~35%, in line with expectations from the literature (Williams and Hatcher 1983, Jones et al. 1990, Kramer et al. 2015). Labrids also exhibited the greatest range of feeding mechanisms and niche roles, e.g. blackspot tuskfishes use tools to break open shells (Jones et al. 2011), cleaner wrasses target gnathiid isopods over other parasites (Grutter 1997a), rockmover wrasse overturn the benthos to access cryptic prey (Wainright and Bellwood 2002). Nocturnal fishes (e.g. cardinalfish, reef sharks, threadfin bream) and cryptobenthic fishes (e.g. gobies) occupy important functional spaces (Heupel and Bennett 1998, Depczynski and Bellwood 2003, Hernaman et al. 2009, Boaden and Kingsford et al. 2012, Frisch et al. 2016). These groups provide an important link between invertebrates and meso-predators in reef trophodynamics.

Small to large fishes across their ontogeny rely on benthic invertebrates as a direct food source, including marine worms, foraminifera and molluscs. Crustaceans were present in the diets of all families, and the majority of invertivores consumed more Crustacea than other invertebrates on the GBR. Echinodermata were the most conspicuous macroinvertebrate group across the GBR, but this was not reflected in their contribution to invertivorous fish diets. Better description and quantification of smaller-bodied invertebrate fauna is essential to the characterisation of reef trophodynamic and mapping fisheries productivity beyond herbivores and piscivores. This is particularly true for important fisheries targets such as coral trout and snapper.

The range of feeding strategies, size classes (predators and prey), ontogenetic shifts in diet and habitat utilisation evident in the invertivores suggests broad ecological redundancy in this guild. This is supported by the extreme diversity of their invertebrate prey. In terms of ecosystem function, generalists can be considered more resilient to shifts in ecological states due to a broader redundancy in their roles. Conversely, specialists can occupy ecological niches that are critical and often irreplaceable (Bellwood et al. 2003, 2006, 2017). Thus, niche components of community structures can lay the foundations of ecosystem functions and services, not just the density and diversity of species (Bellwood et al. 2004, Garnier et al. 2015). The specialised morphologies and feeding behaviours of some genera of invertivores (e.g. *Labroides*) may indicate species of particular importance in terms of functioning on the GBR. However, the ecological and functional consequences of losing key invertivores is not yet understood.

The degree of dependency of invertivorous fishes on benthic invertebrates remains unknown for most species, making it hard to predict potential trophic cascades following perturbation. Climate change represents the greatest threat, via the direct effects of increasing sea surface temperatures on invertivorous fish, and the indirect effects of habitat degradation and invertebrate prey losses. Habitat degradation, which results in the loss of structural complexity, may temporarily increase resources available to invertivorous fishes (Enochs et al. 2011, Enochs and Manzello 2012, Nelson et al. 2016), but the bioavailability of these often-cryptic species to higher order consumers is yet to be adequately quantified. Only some species with behaviours and morphologies that avail of cryptic invertebrates (e.g. the rockmover wrasse) may benefit. Conversely, smaller-bodied fishes may be particularly vulnerable to loss of habitat due to increased exposure to predation (Munday 2004; Rogers et al. 2014, 2018a, 2018b). Targeted studies are required to empower our predictions of future reef dynamics involving invertivores and their invertebrate prey on the GBR. Understanding vulnerabilities of invertivorous fishes on the GBR requires better characterisation of their specific morphologies, diets, diel activity, and links in trophic pathways from the reef matrix to the pelagic realm.

Successfully managing impacts on key values in the GBR World Heritage Area is a high priority for GBRMPA, with current management aims focused on building Reef resilience (GBRMPA 2009, 2014, 2017). Identifying critical ecological processes and species that maintain ecosystem function and structure in the face of external stressors is particularly important under a changing climate. This study has enhanced our understanding of the coral reef food web, highlighting a diverse and rarely addressed group of reef fish – the invertivore. A guild of at least 170 species, the majority of which are labrids (wrasses), confers a greater potential for high functional redundancy which may be increasingly important as disturbances increase. Invertivory provides a critical link in the predation process and may be crucial to shaping a healthy and resilient ecosystem. As invertivorous fishes exploit a range of microhabitats, including coral rubble and dead coral, they may be the dominant trophic group in disturbed environments with the potential to fill a bridging role in post-disturbance reef trophodynamics. Information synthesised in this study has allowed us to identify critical risks to invertivores, such as habitat loss. Findings have also highlighted the relative importance and vulnerability of mobile invertebrates as prey items, with emphasis on the crustaceans. For key GBR fishery target species that are invertivores as recruits, such as coral trout and stripey snapper, this could have implications for fisheries management. This study will directly inform the GBR Outlook Report, help to support resilience-based management actions, and influence long-term monitoring such as Reef 2050 Integrated Monitoring and Reporting Program (RIMReP).

Table A4.1: List of fishes and reef sharks that consume invertebrates on the Great Barrier Reef, including their trophic level, life-stage, feeding type and time of foraging activity. Trophic levels (TL): H=herbivore; D=detritivore; Mic=microinvertivore; Mac=macroinvertivore; I=both micro and macroinvertivore; C=carnivore; O=omnivore; Cor=corallivore; Sp=spongivore; P=piscivore; NA=not available. Trophic levels and activity periods are derived from papers included in the review (Appendix 1) as well as Brandl 2016b, Froese and Pauly 2018, and Kingsford (pers comms). Life-stage refers to the stage at which fishes are reported to be feeding on invertebrates. Feeding types are derived from direct measures presented in the literature. Fishes were classed as obligate consumers when diets contained >65% invertebrates and facultative when diets contained <65%.

Family	Species	TL	Life-stage	Feeding type	Activity	Refs
Acanthuridae	*Acanthurus blochii*	D	Adult	Facultative	Diurnal	5
	Acanthurus lineatus	H/D	Adult	Facultative	Diurnal	5
	Acanthurus nigricauda	D	Adult	Facultative	Diurnal	5
	Acanthurus nigrofuscus	D	Adult	Facultative	Diurnal	5
	Acanthurus olivaceus	D	Adult	Facultative	Diurnal	5
	Ctenochaetus striatus	D	Adult	Facultative	Diurnal	5
	Naso unicornis	D	Adult	Facultative	Diurnal	5
	Zebrasoma scopas	H/D	Adult	Facultative	Diurnal	5
	Zebrasoma veliferum	H/D	Adult	Facultative	Diurnal	5
Apogonidae	*Apogon doederleini*	Mac	Juvenile, Adult	Obligate	Nocturnal	24
	Cheilodipterus artus	C	Juvenile, Adult	Facultative	Nocturnal	24
	Cheilodipterus quinquelineatus	C	Juvenile, Adult	Obligate	Nocturnal	24
	Nectamia fusca	Mic	Juvenile, Adult	Facultative	Nocturnal	24
	Ostorhinchus cyanosoma	Mac	Juvenile, Adult	Obligate	Nocturnal	24
	Pristiapogon exostigma	Mac	Juvenile, Adult	Obligate	Nocturnal	24
	Taeniamia leai	Mic	Juvenile, Adult	Facultative	Nocturnal	24
Balistidae	*Balistapus undulatus*	O	Adult		Diurnal	26, 35
	Balistoides viridescens	Mac	Adult		Diurnal	6, 35
	Pseudobalistes flavimarginatus	Mac	Adult		Diurnal	6
	Sufflamen chrysopterum	Mac	Adult		Diurnal	6
Blenniidae	*Salarias patzneri*	D	Adult	Facultative	Diurnal	34
Carcharhinidae	*Carcharhinus amblyrhynchos*	C	Adult	Facultative	Nocturnal	10
	Carcharhinus melanopterus	C	Adult	Facultative	Nocturnal	10
	Triaenodon obesus	C	Adult	Facultative	Nocturnal	10
Chaetodontidae	*Chelmon rostratus*	I	Adult		Diurnal	6, 26
	Heniochus monoceros	O/Mic	Adult		Diurnal	6
Gobiidae	*Amblygobius bynoensis*	H	Juvenile, Adult	Facultative	Diurnal	14
	Amblygobius decussatus	O/Mic	Adult	Facultative	Diurnal	19
	Amblygobius nocturnus	D	Adult	Facultative	Diurnal	9
	Amblygobius phalaena	H	Juvenile, Adult	Facultative	Diurnal	14
	Asterropteryx semipunctata	D	Juvenile, Adult	Facultative	Diurnal	9, 14, 19
	Bathygobius fuscus	D	Adult	Facultative	Diurnal	9
	Eviota sp. C	O/Mic	Adult	Obligate	Diurnal	9
	Eviota queenslandica	O	Adult	Facultative	Diurnal	9
	Eviota zebrina	O/Mic	Adult	Obligate	Diurnal	19
	Istigobius decoratus	D	Adult	Facultative	Diurnal	9
	Istigobius goldmanni	O/D	Juvenile, Adult	Facultative	Diurnal	9, 14
	Istigobius rigilius	O/Mic	Adult	Facultative	Diurnal	19
	Koumansetta rainfordi	H	Adult	Facultative	Diurnal	9
	Paragobiodon sp.	Cor	Adult		Diurnal	21
	Paragobiodons xanthosoma	Cor	Adult		Diurnal	21
	Paragobiodon echinocephalus	Cor	Adult		Diurnal	21
	Paragobiodon lacunicolus	Cor	Adult		Diurnal	21
	Pleurosicya muscarum	C/Mic	Adult	Facultative	Diurnal	9
	Priolepis nuchifasciatus	Mic	Adult	Obligate	Diurnal	9
	Trimma caesiura	O	Adult	Facultative	Diurnal	9
	Trimma striatum	Mic	Adult	Obligate	Diurnal	9
	Valenciennea longipinnis	Mic	Adult	Facultative	Diurnal	27
	Valenciennea muralis	Mic	Juvenile, Adult	Facultative	Diurnal	9, 14
Haemulidae	*Diagramma pictum*	C/Mac	Adult		Nocturnal	6, 17, 26
	Plectorhinchus albovittatus	Mac	Adult		Both**	6
	Plectorhinchus chaetodonoides	C/P	Adult		Both**	26
	Plectorhinchus chrysotaenia	Mac	Adult		Both**	6, 26
	Plectorhinchus gibbosus	Mac	Adult		Both**	26

	Plectorhinchus lineatus	Mac	Adult		Both**	6, 26
Hemiscylliidae	*Hemiscyllium ocellatum*	Mac	Juvenile, Adult	Obligate	Nocturnal	15
Labridae	*Anampses spp.*†	I	Adult		Diurnal	20
	Anampses caeruleopunctatus	I	Adult		Diurnal	2, 6
	Anampses neoguinaicus	I	Adult		Diurnal	2, 6, 26
	Bodianus spp.†	Mac	Adult		Diurnal	20
	Bodianus axillaris	Mac	Adult		Diurnal	6
	Bodianus loxozonus	Mac	Adult	Obligate	Diurnal	2
	Bodianus mesothorax	Mac	Adult		Diurnal	6, 26
	Cheilinus spp.†	Mac	Adult		Diurnal	20
	Cheilinus chlorourus	Mac	Adult		Diurnal	6, 25, 26
	Cheilinus fasciatus	Mac	Adult	Obligate	Diurnal	2, 6, 25, 26
	Cheilinus trilobatus	Mac	Adult		Diurnal	6, 25, 26
	Cheilinus undulatus	C/Mac	Adult		Diurnal	6
	Choerodon spp.†	Mac	Adult		Diurnal	20
	Choerodon anchorago	Mac	Adult	Obligate	Diurnal	2, 26
	Choerodon cephalotes	I	Adult		Diurnal	2
	Choerodon cyanodus	Mac	Adult	Facultative	Diurnal	2
	Choerodon fasciatus	Mac	Adult		Diurnal	6, 26
	Choerodon graphicus	P/Mac	Adult	Obligate	Diurnal	2
	Choerodon monostigma	Mac	Adult		Diurnal	6
	Choerodon schoenleinii	P/Mac	Adult	Obligate	Diurnal	2, 26, 35
	Choerodon sugillatum	I	Adult		Diurnal	2
	Choerodon vitta	I	Adult		Diurnal	2, 6
	Coris spp.†	Mac	Adult		Diurnal	20
	Coris aygula	Mac	Adult	Obligate	Diurnal	2, 6, 26
	Coris batuensis	Mac	Adult		Diurnal	6, 26
	Coris gaimard	Mac	Adult	Obligate	Diurnal	2, 6
	Cymolutes spp.†	NA	Adult		Diurnal	20
	Cymolutes torquatus	Mic	Adult		Diurnal	2
	Epibulus sp.†	C/Mac	Adult		Diurnal	20
	Epibulus insidiator	C/Mac	Adult		Diurnal	6, 25
	Gomphosus sp.†	Mic	Adult		Diurnal	20
	Gomphosus varius	Mic	Adult	Obligate	Diurnal	2, 6, 26
	Halichoeres spp.†	I	Adult		Diurnal	20
	Halichoeres chloropterus	Mac	Adult		Diurnal	6, 26
	Halichoeres hartzfeldii	Mac	Adult	Obligate	Diurnal	2
	Halichoeres hortulanus	Mac	Adult	Obligate	Diurnal	2, 6, 26
	Halichoeres marginatus	Mac	Adult		Diurnal	6, 26
	Halichoeres melanurus	Mic	Recruit, Adult	Obligate	Diurnal	2, 6, 11, 19, 26
	Halichoeres melasmapomus	Mic	Adult		Diurnal	2
	Halichoeres miniatus	Mic	Adult		Diurnal	2
	Halichoeres nebulosus	Mic	Adult		Diurnal	6, 26
	Halichoeres nigrescens	Mic	Adult		Diurnal	6
	Halichoeres prosopeion	Mic	Adult		Diurnal	6
	Halichoeres trimaculatus	Mac	Adult		Diurnal	6
	Hemigymnus spp.†	I	Adult		Diurnal	20
	Hemigymnus fasciatus	I	Juvenile		Diurnal	2, 6, 26
		I	Adult		Diurnal	
	Hemigymnus melapterus	I	Juvenile		Diurnal	2, 6, 26
		I	Adult		Diurnal	
	Hologymnosus spp.†	C/Mac	Adult		Diurnal	20
	Hologymnosus doliatus	C/Mac	Adult		Diurnal	6
	Labroides spp.†	Mic	Adult		Diurnal	20
	Labroides bicolor	Mic	Adult		Diurnal	6
	Labroides dimidiatus	Mic	Juvenile	Obligate	Diurnal	2, 6, 12, 13, 26
		Mic	Adult	Both*	Diurnal	
	Labroides pectoralis	Mic	Adult	Facultative	Diurnal	2
	Labropsis spp.†	Mic	Adult		Diurnal	20
	Macropharyngodon spp.†	Mac	Adult		Diurnal	20
	Macropharyngodon choati	Mac	Adult		Diurnal	2, 6
	Macropharyngodon meleagris	Mac	Adult		Diurnal	6, 26
	Macropharyngodon negrosensis	Mac	Adult		Diurnal	2, 6
	Novaculichthys sp.†	Mac	Adult		Diurnal	20
	Novaculichthys taeniourus	Mac	Adult	Obligate	Diurnal	2, 6
	Oxycheilinus spp.†	C/P	Adult		Diurnal	20

	Oxycheilinus digramma	C/P	Adult	Obligate	Diurnal	8, 25
	Pseudocheilinops sp.†	Mic	Adult		Diurnal	20
	Pseudocheilinus spp.†	Mic	Adult		Diurnal	20
	Pseudocheilinus evanidus	Mic	Adult		Diurnal	2, 26
	Pseudocheilinus hexataenia	Mic	Adult		Diurnal	2, 6
	Pseudocheilinus octotaenia	Mic	Adult	Obligate	Diurnal	2
	Pseudodax sp.†	Mac	Adult		Diurnal	20
	Pseudodax moluccanus	Mac	Adult		Diurnal	6
	Pseudojuloides spp.†	Mac	Adult		Diurnal	20
	Pseudojuloides cerasinus	Mac	Adult		Diurnal	2
	Pteragogus sp.†	Mac	Adult		Diurnal	20
	Stethojulis spp.†	Mic	Adult		Diurnal	20
	Stethojulis bandanensis	Mic	Adult	Obligate	Diurnal	2, 6, 26
	Stethojulis interrupta	Mic	Adult		Diurnal	2, 26
	Stethojulis strigiventer	Mic	Adult	Obligate	Diurnal	2, 6, 19
	Stethojulis trilineata	Mic	Adult		Diurnal	2
	Thalassoma spp.†	Mac	Adult		Diurnal	20
	Thalassoma hardwicke	O/Mac	Adult		Diurnal	6, 26
	Thalassoma jansenii	Mac	Adult	Obligate	Diurnal	2, 6, 26
	Thalassoma lunare	C/P/Mic	Juvenile, Adult	Obligate	Diurnal	8, 19, 26
	Thalassoma lutescens	Mac	Adult		Diurnal	6
	Thalassoma trilobatum	Mac	Adult	Obligate	Diurnal	2
	Wetmorella sp.†	Mac	Adult		Diurnal	20
Lethrinidae	*Gnathodentex aureolineatus*	Mac	Adult		Both**	6
	Gymnocranius microdon	Mac	Adult		Diurnal	6
	Lethrinus atkinsoni	P/C	Adult		Diurnal	31, 35
	Lethrinus erythracanthus	Mac	Adult		Diurnal	31
	Lethrinus harak	P/C	Adult		Diurnal	31
	Lethrinus lentjan	Mac	Adult		Diurnal	6
	Lethrinus miniatus	C/Mac	Juvenile, Adult	Obligate	Diurnal	31
	Lethrinus nebulosus	P/C	Adult	Facultative	Diurnal	17, 31
	Lethrinus obsoletus	Mac	Adult		Diurnal	6, 31
	Lethrinus ornatus	P/C	Adult		Diurnal	31
	Lethrinus reticulatus	Mac	Adult	Facultative	Diurnal	31
	Lethrinus variegatus	Mac	Adult	Facultative	Diurnal	31
	Monotaxis grandoculis	Mac	Adult		Both**	6, 26
	Monotaxis heterodon	Mac	Adult		Both**	6
Lutjanidae	*Lutjanus carponotatus*	C/I	Recruit, Juvenile	Both*	Diurnal	8, 32
		C/I/P	Adult	Facultative	Diurnal	
	Lutjanus fulviflamma	P/C	Adult	Facultative	Nocturnal	32
	Lutjanus kasmira	C/Mac	Adult		Diurnal	6
	Lutjanus quinquelineatus	C/Mac	Adult		Diurnal	6
	Lutjanus russellii	C/Mac	Adult		Diurnal	6
	Lutjanus vitta	C/Mac	Adult		Diurnal	6
Mullidae	*Mulloidichthys flavolineatus*	Mac	Adult		Nocturnal	6, 26
	Parupeneus barberinus	Mac	Juvenile	Facultative	Diurnal	6, 23, 26
		Mac	Adult	Obligate	Diurnal	
	Parupeneus ciliatus	Mac	Adult		Nocturnal	6, 26
	Parupeneus cyclostomus	C/Mac	Adult		Diurnal	6
	Parupeneus indicus	Mac	Adult		Nocturnal	6
	Parupeneus multifasciatus	Mac	Adult		Diurnal	6, 26
	Parupeneus pleurostigma	Mac	Adult		Diurnal	6
	Parupeneus trifasciatus	Mac	Adult		Nocturnal	6
Nemipteridae	*Pentapodus aureofasciatus*	C/Mac	Adult		Diurnal	6
	Pentapodus caninus	C/Mac	Adult		Diurnal	6
	Pentapodus emeryii	C/Mac	Adult		Diurnal	6
	Scolopsis bilineata	Mac	Recruit, Juvenile		Diurnal	4, 6, 26
		Mac	Adult		Nocturnal	
	Scolopsis lineata	C/Mac	Adult		Both**	26
	Scolopsis margaritifera	C/Mac	Adult		Both**	6, 26
	Scolopsis monogramma	C/Mac	Adult		Both**	6, 26
Plesiopidae	*Assessor macneilli*	O	Adult	Facultative	Diurnal	9
Scaridae	*Chlorurus sordidus*	C/O	Recruit		Diurnal	1, 7
	Scarus spp.	C/O	Juvenile		Diurnal	1
	Scarus schlegeli	C/O	Recruit		Diurnal	7
Serranidae	*Cephalopholis boenak*	P/C	Adult	Facultative	Diurnal	3
	Cephalopholis cyanostigma	P/C	Adult	Facultative	Diurnal	3

	Diploprion bifasciatum	C/Mac	Adult		Diurnal	6
	Epinephelus quoyanus	C	Recruit, Juvenile	Both*	Diurnal	8, 32
		P/C	Adult	Facultative	Diurnal	
	Plectropomus leopardus	C	Recruit	Both*	Diurnal	18, 22, 28, 29, 30
		C/P	Juvenile, Adult	Facultative	Diurnal	
	Plectropomus maculatus	C	Recruit	Both*	Diurnal	32, 33
		C	Juvenile	Facultative	Diurnal	
Siganidae	*Siganus argenteus*	H/D	Adult	Facultative	Diurnal	16
	Siganus canaliculatus	H	Adult	Facultative	Diurnal	16
	Siganus corallinus	H/D	Adult	Facultative	Diurnal	16
	Siganus doliatus	H/D	Adult	Facultative	Diurnal	16
	Siganus javus	H	Adult	Facultative	Diurnal	16
	Siganus lineatus	D	Adult	Facultative	Diurnal	16
	Siganus puellus	Sp	Adult	Facultative	Diurnal	16
	Siganus punctatissimus	H/D	Adult	Facultative	Diurnal	16
	Siganus punctatus	H/D	Adult	Facultative	Diurnal	16
	Siganus spinus	H	Adult	Facultative	Diurnal	16
	Siganus vulpinus	H/D	Adult	Facultative	Diurnal	16
Syngnathidae	*Corythoichthys sp.*	Mic	Adult		Diurnal	26
Tripterygiidae	*Enneapterygius tutuilae*	Mic	Adult	Obligate	Diurnal	9

*Differences in feeding types between locations and studies.

**Differences in periods of activity reported in the literature.

† The results of study 20 are not considered in the main text (e.g. when discussing number of species of invertivorous fishes) to avoid bias as only fishes feeding on crustacea were examined. However, this work was incorporated into discussion and analyses (Fig. 4b) of crustacea.

Table A4.2: Invertebrates directly found in the diets of fishes on the Great Barrier Reef.

Phylum	Subphylum	Class	Subclass	Order	Infraorder	Superfamily	Family	Species	Common name
Annelida		Polychaeta							Bristle worms
		Polychaeta	Echiura						Spoon worms
		Polychaeta	Errantia	Amphinomida			Amphinomidae	*Eurythoe complanata*	Fireworms
		Polychaeta	Errantia	Eunicida			Eunicidae		
		Polychaeta	Sedentaria	Terebellida			Terebellidae	*Reteterebella queenslandia*	Spaghetti worms
Arthropoda									
	Crustacea								
	Crustacea	Hexanauplia	Copepoda						Copepods
	Crustacea	Hexanauplia	Copepoda	Cyclopoida					
	Crustacea	Hexanauplia	Copepoda	Harpacticoida					
	Crustacea	Hexanauplia	Copepoda	Siphonostomatoida			Caligidae		Sea louse
	Crustacea	Malacostraca	Eumalacostraca						
	Crustacea	Malacostraca	Eumalacostraca	Amphipoda	Gammarida	Gammaroidea	Gammaridae		Amphipods
	Crustacea	Malacostraca	Eumalacostraca	Cumacea					Hooded shrimp
	Crustacea	Malacostraca	Eumalacostraca	Decapoda					
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Anomura				
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Anomura	Galtheoidea	Galatheidae		Squat lobster
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura				Crabs
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Ocypodoidea	Ocypodidae		Ghost and fiddler crabs
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Portunoidea	Carcinidae	*Carcinus spp.*	European green/shore crab
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Portunoidea	Portunidae		Swimming crabs
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Trapezioidea	Trapeziidae		Coral crabs
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Brachyura	Xanthoidea	Xanthidae		Mud/rubble crabs
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea				Shrimp
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Alpheoidea	Alpheidae		Snapping shrimp

	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Alpheoidea	Hippolytidae	*Saron marmoratus*	Marbled shrimp
	Crustacea	Malacostraca	Eumalacostraca	Decapoda	Caridea	Palaemonoidea			Palaemonoid shrimp
	Crustacea	Malacostraca	Eumalacostraca	Decapoda		Penaeoidea	Penaeidae		Penaeid shrimp
	Crustacea	Malacostraca	Eumalacostraca	Decapoda		Sergestoidea	Sergestidae		Sergestid shrimp
	Crustacea	Malacostraca	Eumalacostraca	Isopoda					Isopods
	Crustacea	Malacostraca	Eumalacostraca	Isopoda		Cymothooidea	Gnathiidae		Gnathiid isopods
	Crustacea	Malacostraca	Eumalacostraca	Mysida					Opossum shrimp
	Crustacea	Malacostraca	Eumalacostraca	Tanaidacea					Tanaids
	Crustacea	Malacostraca	Hoplocarida	Stomatopoda					Mantis shrimp
	Crustacea	Malacostraca	Hoplocarida	Stomatopoda		Gonodactyloidea	Gonodactylidae	*Gonodactylus spp.*	Mantis shrimp
	Crustacea	Malacostraca	Hoplocarida	Stomatopoda		Gonodactyloidea	Pseudosquillidae	*Pseudosquilla ciliata*	Common mantis shrimp
	Crustacea	Malacostraca	Hoplocarida	Stomatopoda		Lysiosquilloidea	Lysiosquillidae	*Lysiosquilla spp.*	Mantis shrimp
	Crustacea	Malacostraca	Hoplocarida	Stomatopoda		Squilloidea	Squillidae		Mantis shrimp
	Crustacea	Ostracoda							Seed shrimp
	Macrocrustacea (>3 mm)								
	Microcrustacea (<3 mm)								
Echinodermata									
	Asterozoa	Asteroidea							Sea stars
	Asterozoa	Ophiuroidea							Brittle stars
	Crinozoa	Crinoidea	Articulata	Comatulida					Feather stars
	Echinozoa	Echinoidea							Sea urchins
	Echinozoa	Echinoidea	Euechinodea	Camarodonta	Echinidea	Odontophora	Echinometridae	*Echinometra mathaei*	Burrowing sea urchin
	Echinozoa	Echinoidea	Euechinoidea	Clypeasteroida					Sand dollars
	Echinozoa	Echinoidea	Euechinodea	Diadematoida			Diadematidae	*Diadema setosum*	Long-spined sea urchin

	Echinozoa	Echinoidea	Euechinodea	Diadematoida			Diadematidae	*Echinothrix calamaris*	Banded sea urchin
	Echinozoa	Holothuroidea							Sea cucumbers
Foraminifera									
Mollusca									
		Bivalvia							
		Bivalvia	Heterodonta	Cardiida		Cardioidea	Cardiidae	*Fragum spp.*	Cockles
		Bivalvia	Heterodonta	Cardiida		Tellinoidea	Tellinidae		
		Bivalvia	Heterodonta	Cardiida		Tellinoidea	Tellinidae	*Cadella obtusalis*	
		Bivalvia	Heterodonta	Cardiida		Tellinoidea	Tellinidae	*Jactellina clathrata*	
		Bivalvia	Heterodonta	Cardiida		Tellinoidea	Tellinidae	*Moerella virgulata*	
		Bivalvia	Heterodonta	Cardiida		Tellinoidea	Tellinidae	*Pinguitellina robusta*	
		Bivalvia	Heterodonta	Cardiida		Tellinoidea	Tellinidae	*Psammacoma myaeformis*	
		Bivalvia	Protobranchia	Solemyida		Solemyoidea	Solemyidae	*Solemya spp.*	Awning clams
		Cephalopoda							
		Cephalopoda		Coleoidea	Octopoda	Octopodoidea	Octopodidae		Octopus
		Cephalopoda	Coleoidea	Myopsida			Loliginidae		Pencil squids
		Cephalopoda	Coleoidea	Sepiida			Sepiidae		Cuttlefish
		Gastropoda							
		Gastropoda	Heterobranchia	Cephalaspidea		Haminoeoidea	Haminoeidae	*Aliculastrum cylindricum*	Bubble snails
		Gastropoda	Heterobranchia	Nudibranchia					Sea slugs
		Gastropoda	Heterobranchia			Acteonoidea	Acteonidae	*Pupa nitidula*	
		Gastropoda	Vetigastropoda	Trochida		Trochoidea	Trochidae	*Ethalia guamensis*	
		Gastropoda	Vetigastropoda	Trochida		Trochoidea	Trochidae	*Mesoclanculus*	
		Gastropoda	Vetigastropoda	Lepetellida			Haliotidae	*Haliotis spp.*	Abalone
		Polyplacophora							Chitons
		Scaphopoda							Tusk shells
Nematoda									Roundworms
Nemertea									Ribbon worms
Sipuncula									Peanut worms

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Appendix

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APPENDIX 5: CARBONATE BUDGET

[Report submitted for Case Study 2]

Calculating the carbonate budget of the GBR: coral cover and coralline growth

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Summary

Increased seawater temperature and acute thermal stress have reduced the abundance of coral populations leading to significant declines in coral carbonate production and collapse in reef carbonate budgets. Declines in the potential of reefs to maintain positive carbonate budgets is a matter of concern as many of the ecological services provided by reefs rest on their ability to maintain their three-dimensional structure. However, there is no baseline data on carbonate budgets for the GBR or information on the extent of damage caused by the recent coral bleaching events. In this study, we calculated carbonate production and bioerosion rates and the carbonate budgets for the GBR before and after the severe coral bleaching in 2016–2017, using the reef surveys data from the long-term monitoring program (LTMP) from the Australian Institute of Marine Science -AIMS.

We found that 94% of reef carbonate production in the GBR was contributed by the hard coral communities and the remaining 6% was produced by crustose coralline algae (CCA). *Acropora* corals showed a strongest positive relationship with carbonate production compared to other carbonate producers (i.e. non-*Acropora* corals and calcareous algae). The mean carbonate production (range 16.5 to 51.5 kg m^{-2} yr^{-1}) and coral cover (13.2 to 30.3%) increased from the North to the South GBR, in contrast to the decline in reef rugosity and calcareous algae cover observed in the same latitudinal gradient. Mean bioerosion rate was similar throughout the GBR at 16.8 kg m^{-2} yr^{-1} and almost entirely driven by 25 species of parrotfish.

There was a strong positive relationship between the total carbonate budget and carbonate production, but a negative relationship with bioerosion rate. A negative carbonate budget was recorded in the North GBR (–1.82 kg m^{-2} yr^{-1}) but increased in the Central (18.31 kg m^{-2} yr^{-1}) and South GBR (34.24 kg m^{-2} yr^{-1}). Our study found that a critical threshold in benthic cover to maintain a positive carbonate budget was ~22.5% cover of the entire calcifying community (i.e. corals and algae combined). It is critical to note that this is a dynamic variable that is **not** to be considered on a per-reef basis, and that carbonate budgets must be refined to resolve the contribution of individual taxa to extrapolate thresholds in coral cover required to maintain a positive carbonate budget.

In the North GBR, the total carbonate budget declines above the average sea surface temperature (SST) of 25.6°C, whereas carbonate budget increased to a maximum level at 28.2°C (Central GBR) and 24.3 °C (South GBR) beyond which budgets declined. During the

study period (2014–2018), the carbonate budget gradually increased between March 2014 and May 2017 but declined in recent years (October 2017–May 2018), suggesting that the impact of the 2016–2017 bleaching events may be delayed and becoming apparent only around a year post-bleaching. The trajectory of carbonate budgets through time following the 2016–2017 coral bleaching indicates that reefs will enter in a critically negative state in which erosive processes overpass carbonate accretion.

Introduction

Coral reef ecosystem services such as the provision of coastal protection, commercial and recreational fishing, tourism, and biodiversity, rest on the ability of reefs to maintain their three-dimensional complexity and framework strength. This requires not only that the production of calcium carbonate (primarily by corals) exceed the rates of carbonate erosion, but also active reef cementation to bind fragments of dead coral and rubble together (primarily by crustose coralline algae – CCA). The balance between the rate at which calcium carbonate is produced by calcifying organisms (e.g. corals, calcareous algae, foraminifera) and reef processes (e.g. cement precipitation), minus the rate at which carbonate is removed by biological, physical and chemical processes (dissolution) determines the capacity of reefs to maintain their complex physical structure and vertical growth potential (Perry et al. 2008).

The calcium carbonate balance (or budget) of a coral reef has been used as a key metric for assessing reef health and to forecast the ability of reefs to cope with projected increases in sea level rise, sea surface temperature and ocean acidification (Perry et al. 2008, Kennedy et al. 2013, Mace et al. 2014, Perry et al. 2018). Despite the critical importance of maintaining positive carbonate budgets for reef status, few studies have estimated the carbonate budget for reefs of the Great Barrier Reef (GBR) (Yamano et al. 2000, Suzuki et al. 2001, Browne et al. 2013, Hamylton et al. 2013, Hamylton et al. 2014, Hamylton et al. 2017). Critically, there is a lack of large-scale assessments of the balance between production and removal of carbonates for the GBR region. Some studies have examined the rates of carbonate production (e.g. Kinsey 1983, Browne et al. 2012, Silverman et al. 2012) and bioerosion from various organisms in the GBR (Kiene & Hutchings 1994, Osorno et al. 2005, Hoey & Bellwood 2008) (Appendix 1). These studies demonstrate the variability in rates of calcification and bioerosion, and add to the body of knowledge showing that reef carbonate budgets are influenced by complex interactions between processes associated with terrestrial influence (e.g. water quality) (Mallela & Perry 2007), reef metabolism (e.g. calcification and dissolution, and photosynthesis and respiration) (Woodroffe et al. 2017), reef topography and hydrodynamics (Vargas-Ángel et al. 2015) and ocean acidification (Kennedy et al. 2013, Shaw et al. 2016). However, it is unclear whether carbonate budgets of the GBR are in a growing or declining trajectory, particularly given the recent impacts of cyclones and coral bleaching. Effective management of the GBR in the face of global warming and ocean acidification requires that the current carbonate balances are known at the reef scale.

The current and projected increase in ocean temperature and in the frequency and magnitude of extreme temperatures events are one of the greatest threats to tropical and temperate marine ecosystems (Hoegh-Guldberg et al. 2007, Wernberg et al. 2016, Hughes et al. 2017). Average sea surface temperature in the GBR is increasing rapidly and is projected to rise by at least 1–3°C over the next 50–100 years (Lough 2007, Frieler et al. 2013), while short-term acute thermal stress and resulting mass coral bleaching events are occurring more frequently (Brown 1997, Hoegh-Guldberg et al. 1997, Anthony et al. 2008, Hughes et al. 2017, Hughes et al. 2018). In 2016 and 2017, the Great Barrier Reef experienced two of the worst coral bleaching events on record. These events were triggered by record-breaking sea-surface temperature (SST) anomalies, where the average SST between February–April 2016 was 1.0 to 1.3 degrees higher than the 1961–1990 average (http://www.gbrmpa.gov.au). Bleaching occurs when the corals expel the symbiotic zooxanthella from their tissue due to environmental stress, which may cause coral mortality. During the 2016 mass bleaching in the GBR, more than 60% of corals bleached in the GBR, and coral mortality was particularly severe in the northern section of the GBR. Overall, such large-scale disturbances cause significant declines in coral cover with subsequent reductions in reef structural complexity (Graham et al. 2006, Alvarez-Filip et al. 2009, Perry & Morgan 2017). The impacts of mass bleaching and other major disturbances such as cyclones on reef community structure have been profound and have led to rapid declines in coral carbonate production and the overall carbonate budgets on reefs (Eakin 1996, Eakin 2001, Perry & Morgan 2017). Despite the significance of coral disturbances to carbonate budgets, there are no detailed studies examining the impacts of bleaching on carbonate budgets in the GBR.

The overall aim of the study was to provide estimates of reef carbonate budgets along a latitudinal gradient in the GBR based on carbonate production by corals and calcareous algae, and bioerosion rates. We also examine the relative contribution of different hard coral species and calcareous algae to carbonate production rates to identify reef building taxa, or groups that are important in carbonate balance estimates. In addition, we estimated the relationship between the abundance (% cover) of carbonate producers and current carbonate budgets across GBR reefs to identify thresholds of % cover of corals and calcareous algae below which reefs enter into a critical negative carbonate budget state. Finally, we investigated the influence of the 2016–2017 coral bleaching event on the carbonate budgets along the GBR to document the potential impact of short-term acute thermal stresses on carbonate budgets and infer their potential impacts for reef functioning. The existing latitudinal gradient along reefs in the GBR allows us to examine the influence of seawater temperature variability on carbonate budgets at a large spatial scale. To accomplish these aims we used data of % cover of major carbonate producers (i.e. hard corals and calcareous algae) from the long-term monitoring program (LTMP) from the Australian Institute of Marine Science (AIMS) collected along reefs in the northern, central and southern sections of the GBR, and literature data on growth rates to calculate carbonate production. Data on the abundance of bioeroders such as parrotfish, sponges and urchins were also obtained from the LTMP while rates of bioerosion from these organisms were gathered from the literature. Rates of carbonate production and bioerosion were then used to estimate carbonate budgets for the GBR. The data used for the study was collected before, during and after the 2016–2017 coral bleaching events in the GBR, and a total of 672 transects in 92 locations were examined.

Methodology

General approach

Calculations of carbonate production and bioerosion rates and carbonate budget followed a modified census-based method described in Perry et al. (2012), as well as further detailed methodologies and spreadsheets for the Indo-Pacific in ReefBudget website (http://www.exeter.ac.uk/ geography/reefbudget). In our study, the estimated total carbonate budget for the GBR is calculated only from the biological processes by marine organisms included in the LTMP data. Our carbonate budget estimates are therefore derived from the rate at which carbonate is produced (or accreted) by hard corals, calcareous algae (i.e. CCA, articulated calcareous red algae, *Halimeda* and *Peyssonnelia*), less the rate at which carbonate is removed by parrotfish and sponge bioerosion. We do not consider other processes that are also important in estimating carbonate accumulation (e.g. cement precipitation), or carbonate disintegration (e.g. dissolution of soft sediments or existing carbonate skeletons and cements).

Study area and sites

The GBR extends for more than 2,300 km along the east coast of Australia and exhibits a clear latitudinal gradient of sea-surface temperature (SST) from north to south, with mean summer SST around 29 °C in the far north section and 24 °C in the southern section of the reef. A total of 92 different reefs and 672 transects distributed along the three major sections of the GBR [northern (12 reefs), central (41), and southern (39)], spanning between 14.52 and 23.89 °S latitude, and 145.5 and 152.5 °E longitude, were selected for the study. Reefs were surveyed by the LTMP between 2014 and 2018 (Fig. 1, Table 1). Reefs included in the surveys are located in the exposed flank of the reefs.

Estimates of abundance (% cover) of benthic calcifying and bioeroder organisms

The percent cover of sessile calcifying and bioeroder organisms (see below) was obtained from permanent photo-transects established as part of the historical monitoring program conducted by AIMS. At each site, photo images are taken at 1 m intervals along each of five 50 m long transects fixed at 6–9 m deep. Forty out of fifty images per transect are selected and the abundance of the organisms is quantified using the photo point intercept method (Jonker et al. 2008): five digitally-overlaid-points are selected and the organism beneath the point is recorded. A total of 200 points per transect and 1,000 points per site are recorded and the % cover represents the proportion of points assigned to the reported taxonomic classification (Jonker et al. 2008). Reef rugosity is estimated by the LTMP for each of the five transects and is presented here as the mean value from the five transects at each site; rugosity is scored on a five-point scale with one being the least complex to five the most complex structure.

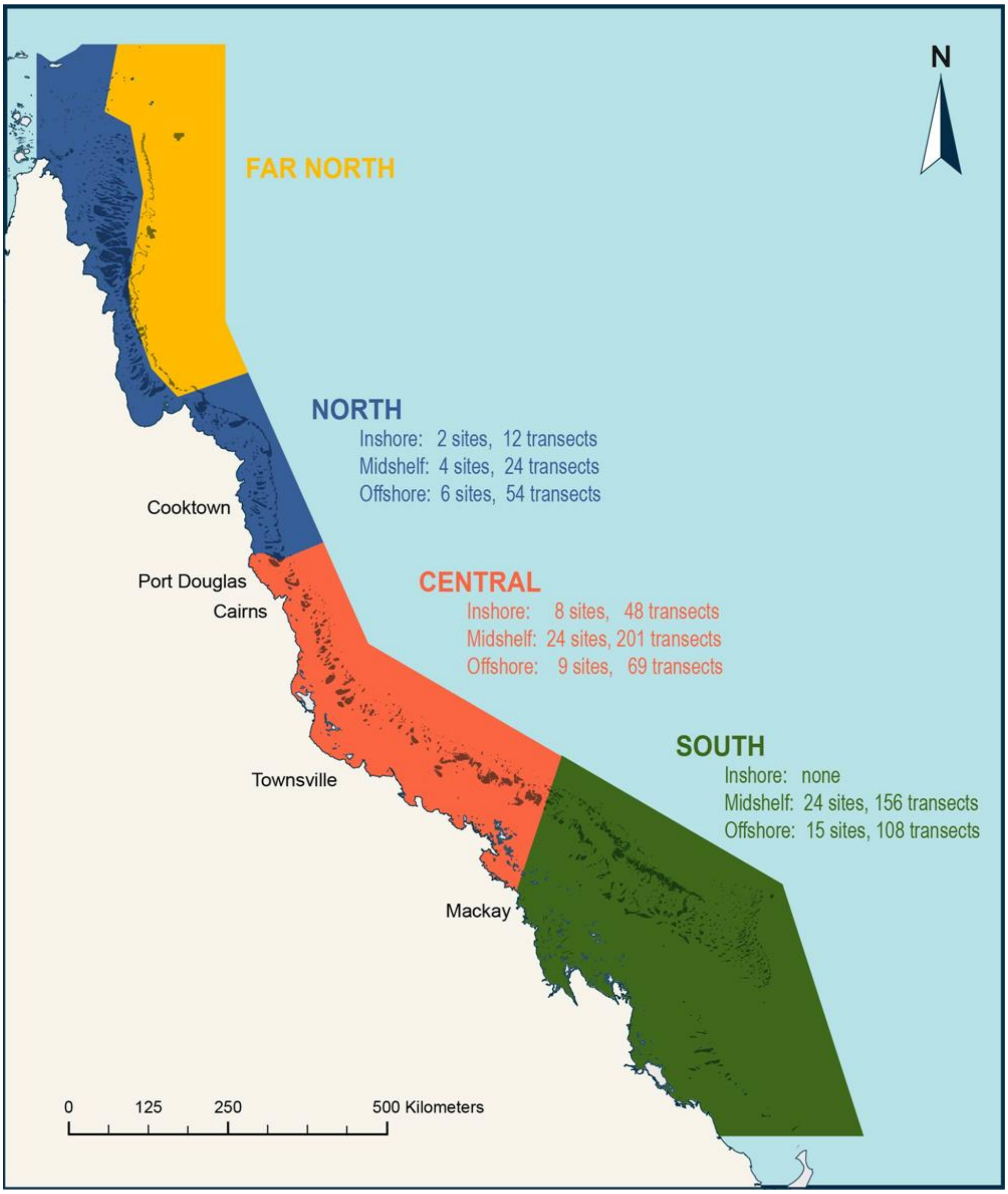

Figure A5.1: The LTMP reef sites and transects in the North, Central and South GBR examined in this study.

Table A5.1: Reef locations surveyed in the LTMP in the GBR, and data from the following surveys (in year and month) were analysed in this study.

						Year and month LTMP surveys were conducted				
Site	Reef Name	GBRMPA sector	Shelf	Latitude	Longitude	2014	2015	2016	2017	2018
1	Linnet Reef	North	Inshore	-14.785	145.355	Dec		Aug		
2	Martin Reef (14123)	North	Inshore	-14.755	145.372	Dec		Sep		
3	Lizard Island	North	Mid shelf	-14.691	145.469	Dec		Dec		
4	Macgillivray Reef	North	Mid shelf	-14.648	145.491	Dec		Sep		
5	North Direction Reef	North	Mid shelf	-14.744	145.516	Dec		Dec		
6	Mackay Reef	North	Mid shelf	-16.043	145.655		Mar	Dec		
7	Carter Reef	North	Offshore	-14.524	145.582	Nov		Sep		
8	No Name Reef	North	Offshore	-14.628	145.645	Nov		Dec		
9	Yonge Reef	North	Offshore	-14.570	145.618	Nov		Sep		
10	Agincourt Reefs (No 1)	North	Offshore	-16.038	145.869	Mar	Mar/Dec	Sep	Dec	
11	Opal (2)	North	Offshore	-16.203	145.906		Apr	Sep		
12	St Crispin Reef	North	Offshore	-16.072	145.845	Mar	Mar/Dec	Sep	Dec	
13	Fitzroy Island Reef	Central	Inshore	-16.923	145.993		Mar	Dec		
14	Green Island Reef	Central	Inshore	-16.775	145.980		Mar	Dec		
15	Low Islands Reef	Central	Inshore	-16.384	145.571		Mar	Sep		
16	Havannah Reef	Central	Inshore	-18.832	146.537		Apr		Apr	
17	Pandora Reef	Central	Inshore	-18.813	146.427		May		Apr	
18	Border Island Reef (No 1)	Central	Inshore	-20.175	149.036		Jan		Mar	
19	Hayman Island Reef	Central	Inshore	-20.057	148.899		Jan		Mar	
20	Langford-Bird Reef	Central	Inshore	-20.078	148.874		Jan		Mar	
21	Arlington Reef	Central	Mid shelf	-16.646	146.111	Mar	Dec	Sep	Dec	
22	Hastings Reef	Central	Mid shelf	-16.499	146.023	Mar	Mar/Dec	Sep	Dec	
23	Michaelmas Reef	Central	Mid shelf	-16.549	146.050		Feb	Dec		
24	Thetford Reef	Central	Mid shelf	-16.799	146.198	Mar	Apr/Dec	Sep	Dec	
25	Mcculloch	Central	Mid shelf	-17.284	146.480		Dec		Dec	
26	Moore Reef	Central	Mid shelf	-16.848	146.236		Dec		Dec	
27	Farquharson Reef (No 1)	Central	Mid shelf	-17.791	146.532		Dec			Feb
28	Feather Reef	Central	Mid shelf	-17.518	146.391	Mar	Dec			Feb
29	Peart Reef	Central	Mid shelf	-17.467	146.403	Mar	Dec			Feb
30	Taylor Reef	Central	Mid shelf	-17.811	146.572		Dec			Feb
31	Centipede Reef	Central	Mid shelf	-18.732	147.554			May		May
32	Davies Reef	Central	Mid shelf	-18.806	147.669		May		May	
33	Fore and Aft Reef	Central	Mid shelf	-18.474	147.055	Apr		May		Apr
34	Grub Reef (18077)	Central	Mid shelf	-18.622	147.433	May		May		Apr
35	Helix Reef	Central	Mid shelf	-18.620	147.298	Mar		May		Feb
36	John Brewer Reef	Central	Mid shelf	-18.619	147.081		Mar		May	
37	Kelso Reef	Central	Mid shelf	-18.422	146.985	Apr		Apr		Feb

38	Little Kelso Reef	Central	Mid shelf	-18.461	146.998	Apr		May		Apr
39	Lynchs Reef	Central	Mid shelf	-18.732	147.722			May		Apr
40	Rib Reef	Central	Mid shelf	-18.472	146.879	Mar	Mar	May	Apr	Feb
41	Roxburgh Reef	Central	Mid shelf	-18.428	147.059	Apr		May		Feb
42	19131s	Central	Mid shelf	-19.766	149.380		Jan		Feb	
43	19138s	Central	Mid shelf	-19.807	149.430		Jan		Mar	
44	20104s	Central	Mid shelf	-20.029	149.695		Jan		Feb	
45	Hedley Reef	Central	Offshore	-17.225	146.479		Dec			Feb
46	Chicken Reef	Central	Offshore	-18.652	147.722	May	May	May	May	Apr
47	Dip Reef	Central	Offshore	-18.400	147.452		May		May	
48	Fork Reef	Central	Offshore	-18.605	147.570	May		May		Apr
49	Knife Reef	Central	Offshore	-18.571	147.577	May		May		Apr
50	Myrmidon Reef	Central	Offshore	-18.257	147.381		May		May	
51	Hyde Reef	Central	Offshore	-19.739	150.081		Jan		Feb	
52	Rebe Reef	Central	Offshore	-19.792	150.161		Jan		Feb	
53	Slate Reef	Central	Offshore	-19.663	149.915		Jan		Feb	
54	20353s	South	Mid shelf	-20.960	150.927			Mar		Mar
55	21060s	South	Mid shelf	-21.007	150.595	Apr		Mar		Mar
56	21062s	South	Mid shelf	-21.027	150.854			Mar		Mar
57	21064s	South	Mid shelf	-21.051	150.784			Mar		Mar
58	21591s	South	Mid shelf	-21.027	150.381	Apr		Mar		Mar
59	Penrith Reef	South	Mid shelf	-21.003	149.888	Apr		Mar		Mar
60	Pompey Reef (No 1)	South	Mid shelf	-20.920	150.558	Apr		Mar		Mar
61	Tern Reef (20309)	South	Mid shelf	-20.899	150.029	Apr		Mar		Mar
62	Pompey Reef (No 2)	South	Mid shelf	-20.991	150.539	Apr				May
63	20348s	South	Mid shelf	-20.883	150.939					Mar
64	21139s	South	Mid shelf	-21.455	151.465			Jan		Mar
65	21187s	South	Mid shelf	-21.405	151.638			Mar		Mar
66	21529s	South	Mid shelf	-21.863	152.187	Aug			Jan	
67	21550s	South	Mid shelf	-21.961	152.317			Jan		Jan
68	22084s	South	Mid shelf	-22.000	152.471			Jan		Jan
69	Chinaman Reef (22102)	South	Mid shelf	-21.998	152.669		Jan	Jan	Jan	Feb
70	Gannett Cay Reef	South	Mid shelf	-21.976	152.480	Aug			Jan	
71	Horseshoe	South	Mid shelf	-22.023	152.619		Jan		Jan	
72	Jenkins Reef	South	Mid shelf	-21.950	152.615			Jan		Jan
73	Small Lagoon Reef	South	Mid shelf	-21.867	152.526			Jan		Jan
74	Snake (22088)	South	Mid shelf	-22.024	152.196	Aug			Jan	
75	Wade Reef	South	Mid shelf	-21.985	152.659			Jan		Jan
76	21245s	South	Mid shelf	-21.296	152.442			Jan		
77	21278s	South	Mid shelf	-21.109	152.550			Jan		
78	Boult Reef	South	Offshore	-23.745	152.275		Oct		Oct	

79	Broomfield Reef	South	Offshore	-23.250	151.943	Aug	Oct		Jan/oct	
80	Erskine Reef	South	Offshore	-23.498	151.775		Oct		Oct	
81	Fairfax Islands Reef	South	Offshore	-23.848	152.372		Oct		Oct	
82	Hoskyn Islands Reef	South	Offshore	-23.796	152.297		Oct		Oct	
83	Lady Musgrave Reef	South	Offshore	-23.884	152.420	Aug	Oct		Jan/Oct	
84	Mast Head Reef	South	Offshore	-23.534	151.750		Oct		Oct	
85	North Reef (North)	South	Offshore	-23.175	151.909		Oct		Oct	
86	One Tree Reef	South	Offshore	-23.484	152.089	Aug			Jan	
87	Wreck Island Reef	South	Offshore	-23.317	151.976	Aug			Jan	
88	21296s	South	Offshore	-21.328	152.566			Jan		Jan
89	21302s	South	Offshore	-21.424	152.582			Jan		Jan
90	21558s	South	Offshore	-21.540	152.547			Jan		Jan
91	East Cay Reef	South	Offshore	-21.470	152.567	Aug		Jan	Jan	Jan
92	Turner Reef	South	Offshore	-21.703	152.560	Aug			Jan	

Sixty-three groups of hard corals (of at least 56 taxa) and four groups of calcareous algae including crustose coralline algae (CCA), articulated calcareous red macroalgae (*Amphiroa* and *Jania*), *Halimeda*, and *Peyssonnelia* were reported in the LTMP data and included in the calculation of reef carbonate production (Appendix 2). The % cover of two groups of sponges (*Cliona* and "non-*Cliona*") was recorded by the LTMP, however only data of *Cliona* was included in the analyses due to the limited data available on bioerosion rates for non-clionid species (e.g. Achlatis et al. 2017, Fang et al. 2017, Ramsby et al. 2017). Urchin densities were extremely low in the LTMP surveys, therefore were excluded from further analyses.

Estimates of abundance (density) of parrotfish

The feeding activity of excavator/scraper parrotfish is the most important process contributing to the external bioerosion in many tropical reefs (Hutchings 1986, Kiene 1988, Bellwood 1995b); we therefore used the estimates of parrotfish abundance collected by the LTMP in our estimates of bioerosion rates. Parrotfish were counted along a 5 m wide transect along the same line used in the coral and algae surveys. The LTMP data listed the abundance (individuals m^{-2}) of 25 species of bioeroder parrotfish belonging to five genera: *Bolbometopon*, *Cetoscarus*, *Chlorurus*, *Hipposcarus* and *Scarus* (see Appendix 3 for the species list of bioeroder parrotfish).

Estimates of rates of carbonate production

Carbonate production for each transect was obtained by multiplying the % cover of each coral and calcareous algal species or group with their estimated calcification rate (kg m^{-2} yr^{-1}) and rugosity of the transect for each coral by the area that it occupied in the zone (m^2) following Perry et al. (2012).

Carbonate production (kg m^{-2} yr^{-1}) =

$$\Sigma_i \left(R \times ((X_i/100) \times ((D_i \times G_i \times 10{,}000)/1{,}000))\right) \qquad \text{(hard corals)}$$

$$\Sigma_i \left(R \times ((X_i/100) \times ((C_i \times 10{,}000)/1{,}000))\right) \qquad \text{(calcareous algae)}$$

R = Rugosity of transect
X_i = Mean % cover of ith species
D_i = Density (g cm^{-3}) of the ith species
G_i = Linear extension rate (cm yr^{-1}) of the ith species
C_i = Calcification rate (g cm^{-2} yr^{-1})

Hard corals: Calcification rates of hard corals were taken from recent publications in the GBR (Pratchett et al. 2015, Anderson et al. 2017, Razak et al. 2017), and the Indo-Pacific datasets listed on the ReefBudget website (https://geography.exeter.ac.uk/reefbudget/indopacific/). Due to the limited data availability from the GBR, we included data from Western Australia, as well as from the northern parts of the equator at a similar latitudinal range with the GBR (14–23 °N latitude) listed in the ReefBudget datasets (Appendix 4). When calcification rates of certain coral taxa were not known, such as *Barabattoia*, *Catalaphyllia*, *Lobophyllia*, and *Paraclavarina* (see Appendix 2 for details), we used available rates from closely related taxa or other taxa with similar morphology. Information for taxa similarity was obtained from Darling et al. (2012), the World Register of Marine Species (WoRMS) (http://www.marinespecies.org/) and Corals of the World (http://www.coralsoftheworld.org) websites.

Calcareous algae: Calcification rates of crustose coralline algae (CCA) were obtained from the study by Kennedy and Diaz-Pulido (in prep) who estimated calcification rates for the CCA *Porolithon cf. onkodes* (a dominant species in shallow reefs of the GBR) in the North, Central and Southern sections of GBR using the procedure described by Lewis et al. (2017) (see Appendix 2). Rates of calcification for upright calcareous red macroalgae used data from *Amphiroa* from McCormack (2014), while for the green macroalgae *Halimeda* we used data from Drew (1983). There are no estimates of calcification rates for *Peyssonnelia* in the literature therefore we used expert opinion and estimated that rates for this alga may be half of those of CCA as their encrusting tissues are only partially calcified. Other calcareous macroalgae such as *Liagora, Galaxaura* or *Padina* were rarely recorded by the LTMP and were excluded from the analyses.

Bioerosion rates

Bioerosion rates considered in this study included those caused by the parrotfish feeding activities and the excavation by clinoid sponges. Parrotfish bioerosion rates were estimated by multiplying the LTMP parrotfish densities from each surveyed transect (as detailed earlier) by their estimated mean erosion rate (7.84 kg m^{-2} yr^{-1}, see below). Parrotfish body size is important when estimating bioerosion rates by this group (Peyrot-Clausade et al. 2000, Mallela & Perry 2007, Perry et al. 2012), however, the LTMP fish surveys only determined density (individuals per m^{-2}) with no estimates of body size. To address this limitation, we made the assumption that the parrotfish recorded in the LTMP surveys were in mature stage and we used the average erosion rate from adult parrotfish reported for the GBR by Bellwood (1995a, 1996) and Hoey and Bellwood (2008). Based on these three studies, the average erosion rate by parrotfish was 7.84 kg m^{-2} yr^{-1} for the average fish density of 0.02 individuals m^{-2} (Appendix 5).

Bioerosion rates from *Cliona* sponges were defined by multiplying their % cover of *Cliona* (%) from each LTMP transect by their estimated erosion rate (kg m^{-2} yr^{-1}) as shown in Perry et al. (2012). We utilized published datasets for *Cliona* erosion rate in the GBR including those from inshore (0.08 kg m^{-2} yr^{-1}; Osorno et al. 2005), mid-shelf (0.30 kg m^{-2} yr^{-1}; Musso 1994, Osorno et al. 2005) and offshore reefs (0.03 kg m^{-2} yr^{-1}; Osorno et al. 2005).

Sea surface temperature

To explore the influence of SST variability, SST anomaly, and Degree Heating Weeks (DHW) on the estimated carbonate budgets for reefs along the latitudinal gradient of the GBR we obtained data of these variables from the NOAA's Coral Reef Watch (CRW) (https://coralreefwatch.noaa.gov/ satellite/vs/greatbarrierreef.php). NOAA CRW provides averaged SST data from 15 locations along the GBR, and we used available data from the closest CRW location for our 92 study locations. The CRW near-real-time SST and SST anomaly are a twice-weekly composite at 0.5° resolution (50 km). CRW's SST anomaly is produced by subtracting the long-term mean SST (for that location in that time of year) from the current value. DHW is the accumulation of thermal stress that coral reefs have experienced where the SST is greater than 1°C over a 12- week window. SST, SST anomaly and DHW data from the periods when the LTMP surveys were conducted were included in the analyses.

Statistical analyses

Generalized additive mixed models (GAMMs) (Woods et al. 2006) were used to determine:

(i) the significance of the contribution of the different groups of carbonate producers to the overall carbonate production in the GBR;
(ii) the relationship between carbonate budget vs. carbonate production and bioerosion rates in the GBR;
(iii) thresholds levels for % coral cover which are critical for maintaining positive carbonate budgets in the GBR;
(iv) the relationships between carbonate producers and seawater temperature in the North, Central and South GBR; and
(v) temporal changes in carbonate budget.

The GAMMs modelling approach incorporates the possibility of non-linear relationships between the response and predictive variables. Models for reef carbonate budget, as response variable, included predictors '% cover coral' (point i and iii above), 'accretion' and 'erosion' rates (ii); 'SST', 'SST anomaly', and 'DHW' (iv); and 'year' (v), and individual survey 'transect' as a random effect.

Results and Discussion

Trends in the abundance of dominant benthic calcifiers, parrotfish and rugosity (2014–2018)

The abundance of the major reef carbonate producers vary along the latitudinal gradient in the GBR. Calcareous algae were more abundant in the north (20.5 ± 17.8%, of which 20.1% corresponded to CCA) and gradually declined towards the Central (11.1 ± 7.8%) and South (8.5 ± 6.9%) sections of GBR (Table 2). The abundance of hard corals, in contrast, was lowest in the North GBR (13.2 ± 6.8%, mean ± SD) and increased towards the Central (23.3 ± 14.2%) and the South GBR (30.3 ± 18.5%). Similar pattern was observed in *Cliona* populations, but the mean percent cover was very low in all three regions (< 0.1%). As for bioeroder parrotfish, the mean density was similar throughout the GBR at 0.05 ± 0.04 individual per m^2, which is comparable to previous reports by Bellwood (1995a, 1996) and Hoey and Bellwood (2008) for the North and South GBR. The mean rugosity of the reef was highest in the North section (3.34 ± 0.62, mean ± SD, *n* = 90) and gradually declined to the southern section, with 3.27 ± 0.60 in the Central GBR (*n* = 318) and 2.77 ± 0.67 in the South GBR (*n* = 264).

Table A5.2. Mean values (± SD) of % cover of benthic calcifying and bioeroder organisms, abundance of bioeroder parrotfish, and rugosity in the North, Central and South GBR.

	North	Central	South
Calcareous algae (%)	**20.50 ± 17.78**	**11.08 ± 7.82**	**8.52 ± 6.94**
CCA (%)	20.14 ± 17.54	10.26 ± 7.96	8.08 ± 6.57
Calcareous red macroalgae (%)	0.16 ± 0.24	0.16 ± 0.23	0.05 ± 0.14
Halimeda (%)	0.19 ± 0.34	0.64 ± 1.72	0.37 ± 1.01
Peyssonnelia (%)	0.01 ± 0.04	0.02 ± 0.07	0.02 ± 0.07
Hard corals (%)	**13.24 ± 6.83**	**23.30 ± 14.22**	**30.31 ± 18.46**
Acropora (%)	7.67 ± 7.85	3.59 ± 4.36	16.70 ± 17.43
Non-*Acropora* (%)	9.65 ± 4.42	15.63 ± 10.31	13.61 ± 8.80

Bioeroders			
Parrotfish (ind m^{-2})	0.053 ± 0.048	0.046 ± 0.034	0.050 ± 0.036
Cliona (%)	0.002 ± 0.015	0.035 ± 0.121	0.084 ± 0.366
Rugosity	3.34 ± 0.62	3.27 ± 0.60	2.77 ± 0.67

Trends in the rates of carbonate production along the latitudinal gradient

Rates of carbonate production from corals along the GBR followed a similar pattern to that observed in % cover of hard corals (Fig. 2, Table 3). The lowest average rate of carbonate production from corals was observed in the North (16.5 ± 11.7 kg m^{-2} yr^{-1}), followed by the Central GBR (34.3 ± 30.0 kg m^{-2} yr^{-1}) while the highest production rates were found in the South (51.5 ± 52.5 kg m^{-2} yr^{-1}) (Table 3). To summarise this section, hard corals (combined *Acropora* and non *Acropora*) are the main contributor to carbonate production, accounted for 94.0 ± 8.1% of the total carbonate production in the GBR, while calcareous algae only accounted for 6.0 ± 8.1% of the total carbonate production.

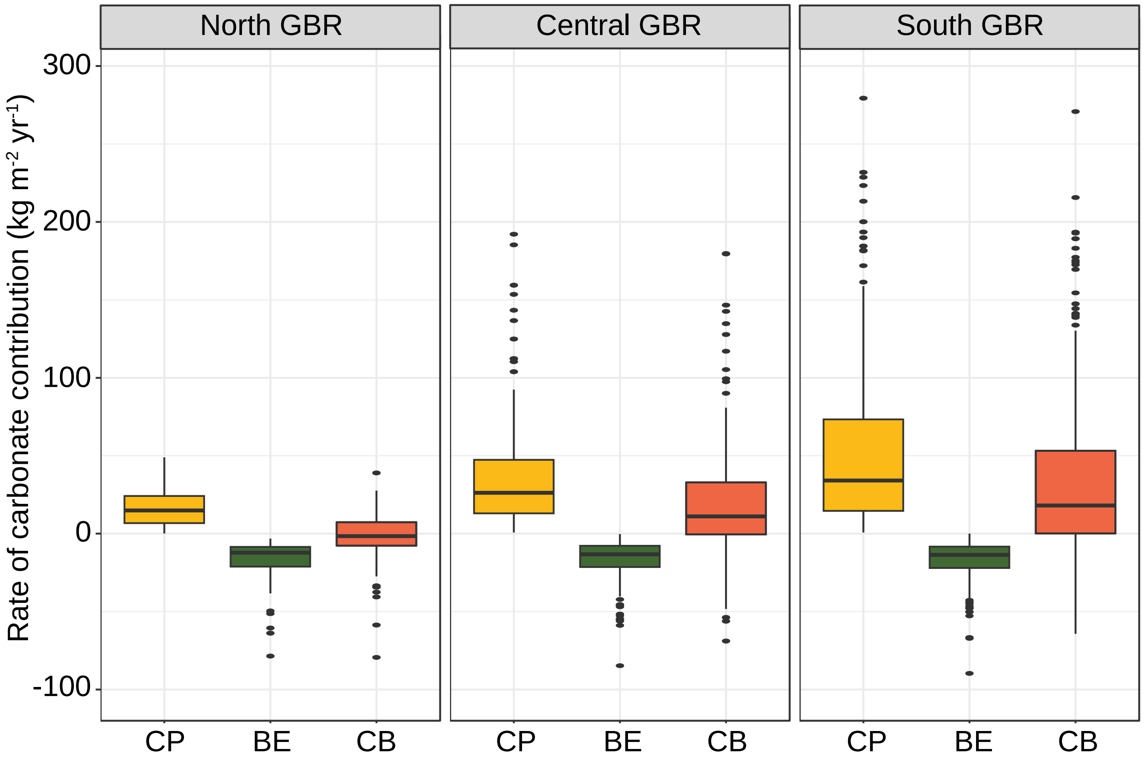

Figure A5.2: Trends in the rates of carbonate production (CP, *yellow*), bioerosion rate (BE, *dark green*) and carbonate budget (CB, *orange*) along the latitudinal gradient in the GBR.

Table A5.3: Mean values (± SD) of carbonate production, bioerosion rate and carbonate budget (kg m^{-2} yr^{1}) in the North, Central and South GBR.

	North	**Central**	**South**
Carbonate production (total)	**16.51 ± 11.74**	**34.29 ± 30.02**	**51.51 ± 52.47**
Calcareous algae	1.59 ± 1.39	1.00 ± 0.72	0.83 ± 0.67
Hard corals	14.91 ± 10.88	33.29 ± 30.09	50.68 ± 52.37
Bioerosion rate (total)	**18.32 ± 16.75**	**15.98 ± 11.74**	**17.27 ± 12.47**
Parrotfish	18.32 ± 16.75	15.97 ± 11.74	17.26± 12.47
Cliona sponge	0.0004 ± 0.003	0.010 ± 0.035	0.010 ± 0.033
Carbonate budget	**–1.82 ± 18.54**	**18.31 ± 33.17**	**34.24 ± 53.13**

Relationship between rates of carbonate production and % cover

As expected, there was a significant positive linear relationship between the total carbonate production and percent cover of all producers (hard corals and calcareous algae) ($p < 0.001$, $r^2 = 0.68$), but the strongest positive relationship was observed with *Acropora* cover ($p < 0.001$, $r^2 = 0.87$; Fig. 3). Non *Acropora* corals and CCA showed a weak non-linear relationship with carbonate production (both $r^2 = 0.05$; Fig. 3). The remaining three groups of calcareous algae (articulated red algae, *Halimeda* and *Peyssonnelia*), however, did not significantly contribute to the total carbonate production in the GBR.

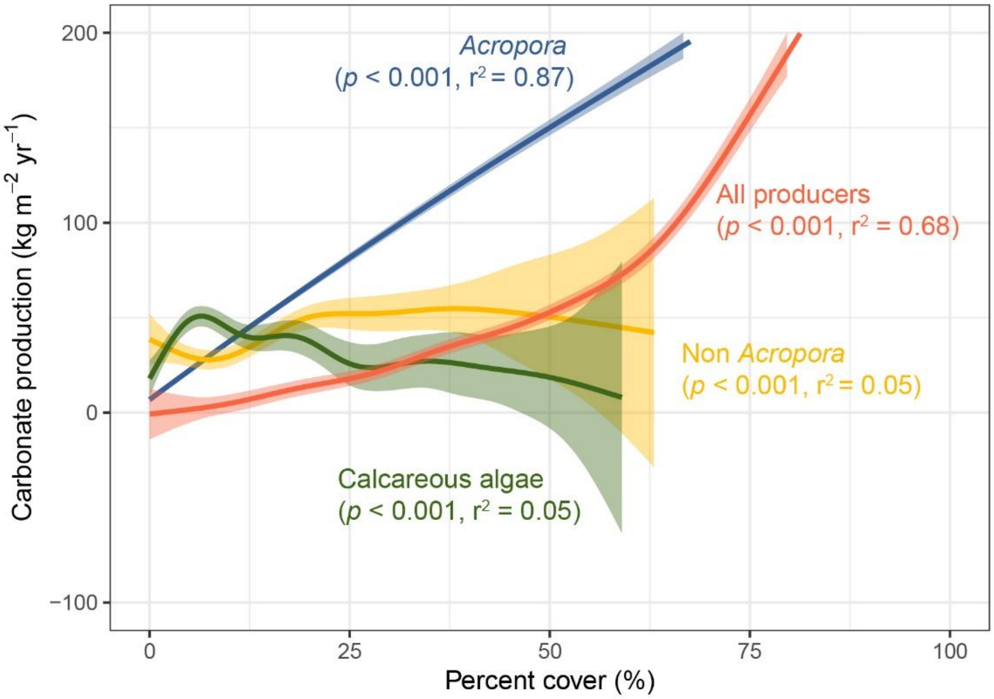

Figure A5.3: Relationship between the abundance of major reef calcifiers and carbonate production in the GBR. All reef sections (north, central, and south) were combined.

Bioerosion rates

Reef bioerosion in the GBR was entirely dominated by parrotfish grazing at 16.8 ± 12.8 kg m^{-2} yr^{-1} (*n* = 672), and there was no difference in the mean parrotfish bioerosion rate across our study sites (Fig. 2, Table 3). The mean bioerosion rate of *Cliona* was almost negligible at 0.01 ± 0.03 kg m^{-2} yr^{-1} (*n* = 672).

Carbonate budget

We found that reefs in the North section of the GBR are currently in a negative state of carbonate accumulation, with bioerosion processes exceeding carbonate production rates (Fig. 2, Table 3). The carbonate budget in the North section is –1.82 (± 18.54) kg m^{-2} yr^{-1}, and gradually increase southwards, with a value of 18.31 (± 33.17) kg m^{-2} yr^{-1}, and 34.24 ± 53.13 kg m^{-2} yr^{-1}in the Central and South sections of the GBR, respectively.

The carbonate budgets in the GBR showed a strong and positive linear relationship with carbonate production ($p < 0.001$, $r^2 = 0.91$; Fig. 4), but demonstrated a weak negative relationship with bioerosion rate ($r^2 = 0.05$; Fig. 4). We found that carbonate budget is strongly related to percent cover of carbonate producers ($p < 0.001$; Fig. 5). This significant relationship shows threshold levels of benthic cover to maintain positive carbonate budgets in the GBR. Benthic cover threshold levels were >2.5% for *Acropora* only cover, >13% for hard corals (*Acropora* and non *Acropora*), and >22.5% for combined hard corals and calcareous algae cover (Fig. 5). It is essential to note that these are dynamic thresholds that are **not** to be considered on a per-reef basis. These values are not transferable to any reef or location; for example, we do not suggest that any reef with 2.5% cover of *Acropora* will have a positive carbonate budget, or that any reef with <22.5% cover of calcifiers will be in a state of net erosion. Carbonate budgets must be refined to resolve the contribution of individual taxa to extrapolate thresholds in coral cover required to maintain a positive carbonate budget.

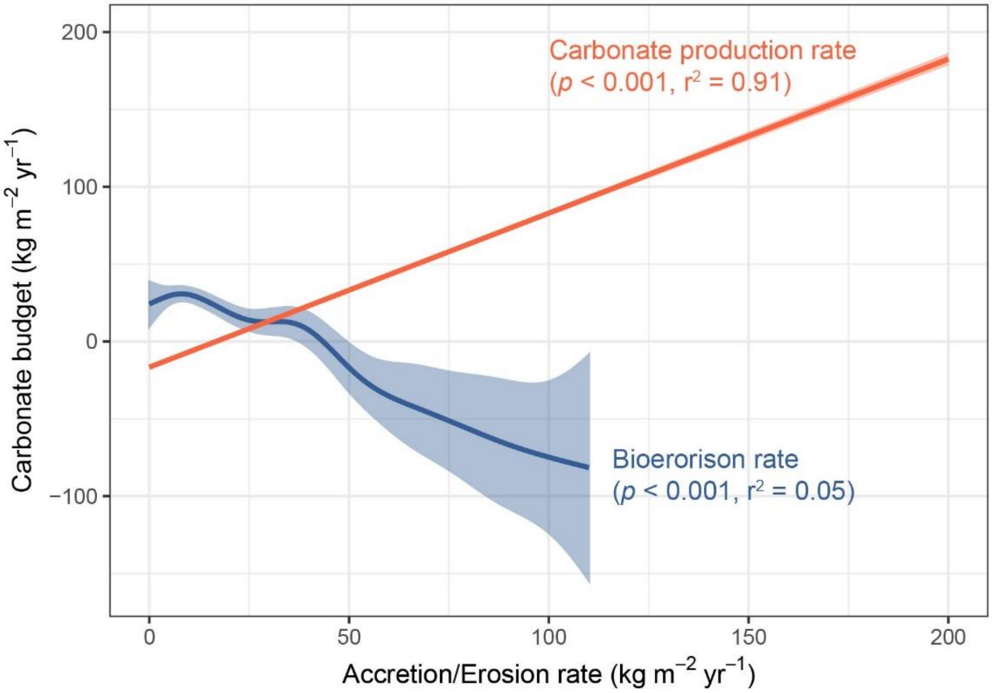

Figure A5.4: The contribution of carbonate production and bioerosion rates to the total carbonate budget in the GBR.

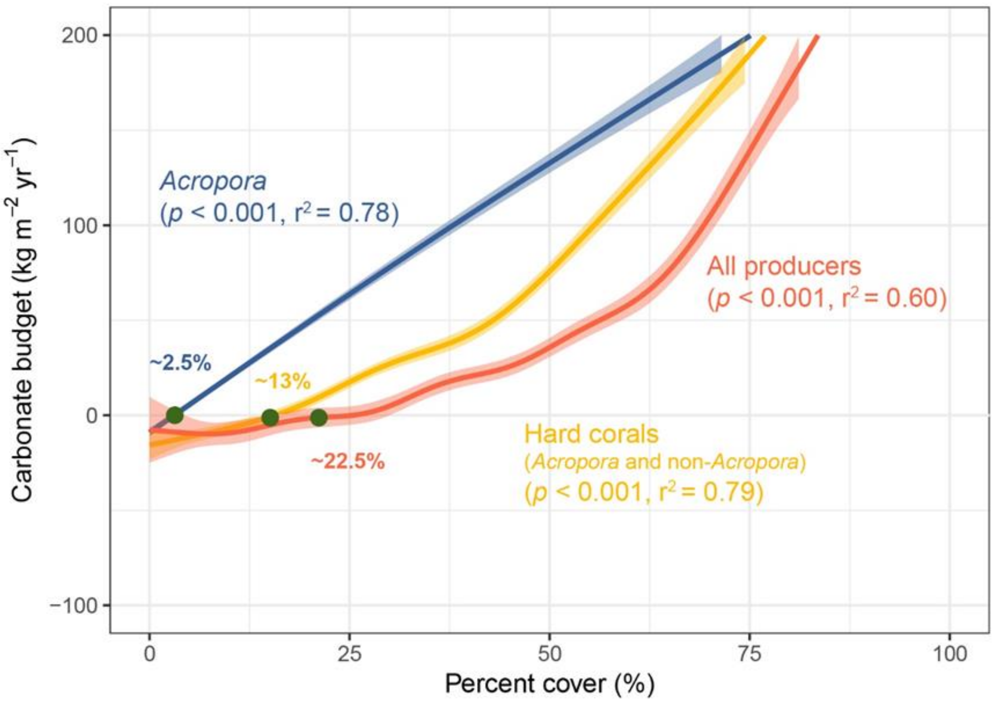

Figure A5.5: The relationships between percent cover of carbonate producers and total carbonate budget. Points and values denote thresholds for positive carbonate budget levels.

Carbonate budget and seawater temperature

To gain insights into the relationship between carbonate budgets and the latitudinal gradient along the GBR we tested the significance of the relationship between the carbonate budgets and temperature variability. SST was significantly related with carbonate budgets ($p < 0.001$; Fig. 6), but the direction and magnitude of the relationship varied along the different GBR sections. Carbonate budget showed a weak but significant negative relationship with SST in the North GBR ($p < 0.001$, $r^2 = 0.05$), in which the carbonate budget declines above 25.6°C. A significant but non-linear relationship was observed both in the Central ($p < 0.001$, $r^2 = 0.04$) and South sections ($p < 0.001$, $r^2 = 0.13$). In the Central, carbonate budgets were highest at 28.2°C and declined at lower and warmer temperatures, whereas for the South, a lower thermal optimum was noted, peaking at 24.3 °C and declining at higher temperatures. Neither SST anomaly nor DHW showed any significant relationship with the total carbonate budget in the GBR.

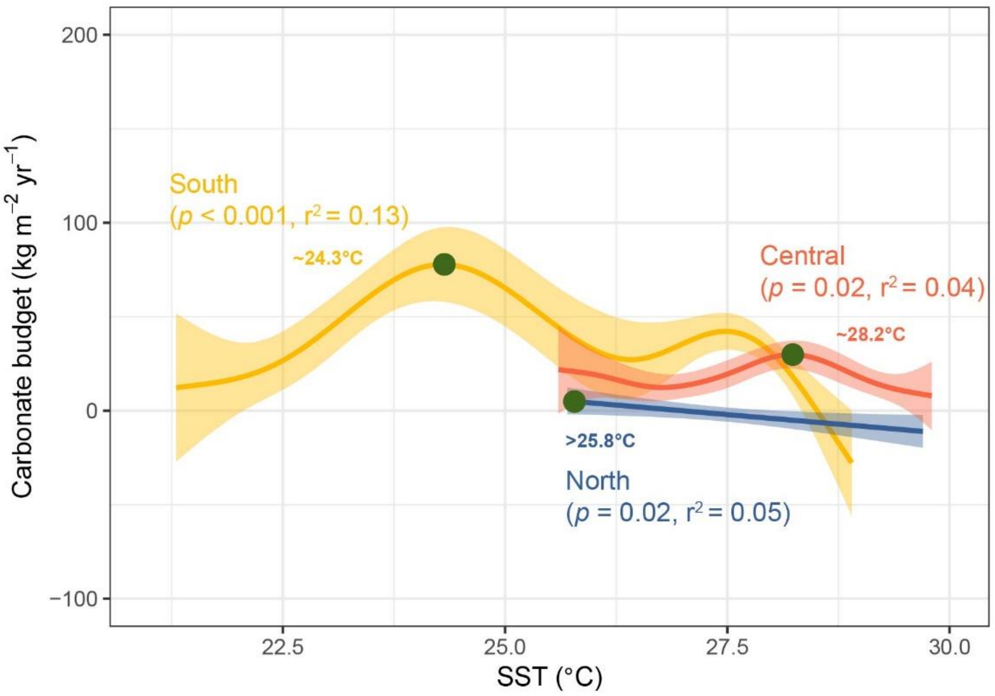

Figure A5.6: The relationships between carbonate budget and seawater surface temperature in the North, Central and South GBR.

Influence of the 2016–2017 coral bleaching events on carbonate budgets

To examine the influence of the 2016–2017 coral bleaching events, we calculated the carbonate budgets for reefs before, during and after these major events. Between 2014 and 2018, the total carbonate budget in the GBR varied nonlinearly ($p < 0.001$, $r^2 = 0.10$; Fig. 7), with a gradual increase between March 2014 and May 2017, and a decline following October 2017 until the end of the sampling period in May 2018. The decline on the total carbonate budget in later years suggests that the impact of the 2016–2017 bleaching events are not immediately observed, but rather becomes apparent approximately one year post-bleaching. The trajectory of carbonate budgets through time following the 2016–2017 coral bleaching indicates that reefs will enter in a critically negative state in which erosive processes overpass carbonate accretion.

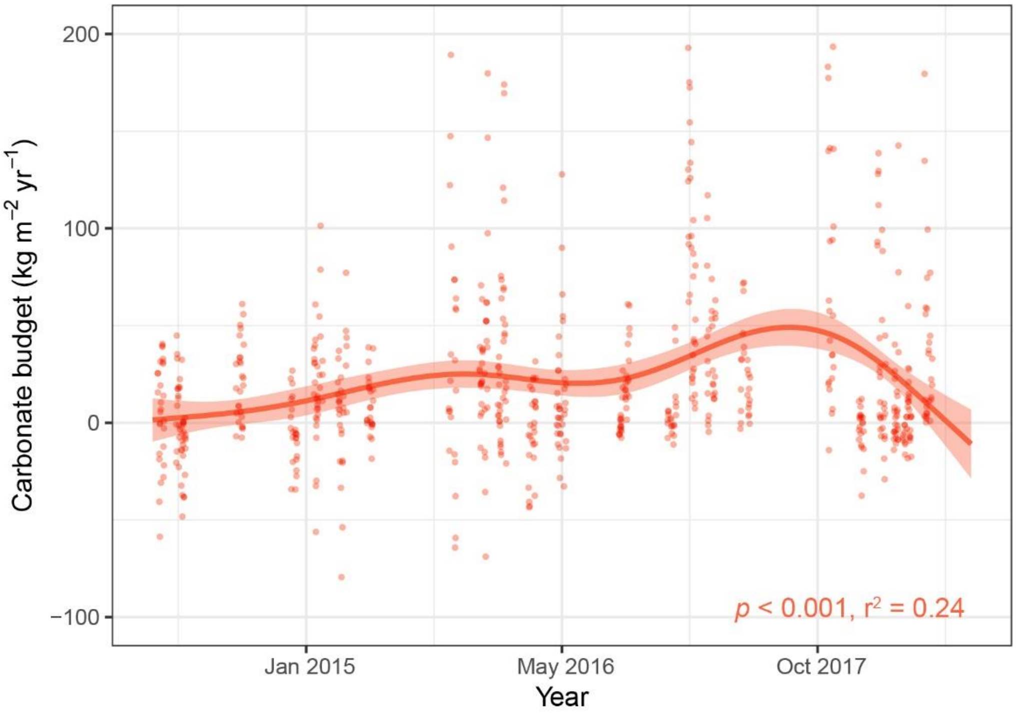

Figure A5.7: Temporal changes in the total carbonate budget in the GBR between March 2014 and May 2018.

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APPENDIX 6: MICROBES

[Report submitted for Case Study 3]

Microbial communities on the GBR: links to water quality parameters that indicate healthy reef systems

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Abstract/ Introduction

Microorganisms are fundamental drivers of biogeochemical cycling within coral reef ecosystems (Gast et al. 1998; Bourne and Webster 2013), and critical to the health of keystone marine invertebrates including corals (Bourne et al. 2016). However, their contribution to reef resilience is poorly understood (Dinsdale et al. 2008). Faced with the growing impacts of rapid climate change which lowers the resilience of the Great Barrier Reef (GBR) (Hughes et al. 2017a), identification of microbial taxa and functions that contribute to a healthy reef is critical. Here, we synthesise current information that characterises the pelagic microbial communities within GBR regions to identify: a) how communities are influenced by input of riverine floodwaters and plumes on inshore reefs (Angly et al. 2016), b) how changes in benthic composition (macroalgal versus coral cover) and health of the reef influence the pelagic microbes (Glasl et al. in review), and c) how microbial communities change along inshore to offshore gradients (Alongi et al. 2015).

Our meta-analysis indicates that pelagic microbial communities across the GBR respond in a deterministic way to environmental fluctuations and drivers. Therefore, microbial community dynamics can be modeled to better understand how ecosystem functions predict changes to reef health and redress knowledge gaps that may guide future interventions aimed at mitigating environmental stressors. Additional work is required to identify microbial indicators of reef health and use these indicators to inform stakeholders about ecological tipping points. However, in this synthesis, we identify planktonic microbial taxa that are indicators for certain environmental conditions within individual reef systems of the GBR. Specifically, the Prochlorococcaceae:Synechococcaceae relative abundance ratio provides an indicator of the contribution of nutrient enrichment in GBR waters that seems to be sensitive both at spatial and temporal scales. From other coral reef systems it is known that whereas Prochlorococcaceae is common in oligotrophic waters, Synechococcaceae becomes increasingly dominant in higher nutrient rich coral reef waters (Dinsdale et al. 2008), as these two photo-autotrophic bacterial families have different capacities to use low amounts of organic nitrogen (Scanlan and West 2002; Zubkov et al. 2003). Another indicator example is the ratio between Pelagibacteraceae and SAR86, which correlates negatively with increasing nutrient levels. Alternatively, comparison of broader trophic groups may also prove valuable indicators of ecosystem health and/or function.

For example, levels of typical copiotrophs such as families OCS155, Flavobacteraceae, Cryomorphaceae and Rhodobacteraceae, can in the future be modelled against levels of oligotrophs such as Pelagibacteraceae and SAR86 to generate new indices indicative of eutrophication (e.g., Haas et al. 2016). Typical opportunistic bacteria, such as those exhibiting virulence towards benthic organisms (e.g., in the families Rhodospirillaceae, Rhodobacteraceae and Vibrionaceae), could also be used as indicators of reef health and or degradation. In addition, a recent study on inshore reefs highlighted the diagnostic value of microorganisms to characterise seasonality, confirming the potential for microorganisms to enhance current reef monitoring efforts (Glasl et al. in review). The application of microbial based monitoring and diagnostics is in its infancy, however once established, these approaches will increase our understanding of the biological response of all trophic levels to impacts affecting coral reefs.

Currently a lack of available microbial data collected at sufficient spatial and temporal resolution hinders our capacity to identify the contribution microbes make to a functioning coral reef ecosystem. Establishment of microbial baselines through a network of microbial observatories spanning key habitats along inshore to offshore gradients in the Northern, Central and Southern GBR would enable a robust assessment of the microbial contribution to reef function and health. Microbial baselines could be used to assess impacts from coastal eutrophication, anthropogenic disturbance and climate change. While other reefs metrics provide this information, inclusion of microorganisms is critical, as microorganisms represent the first responders to environmental change and may mitigate or exacerbate the impacts of disturbance for higher trophic levels.

Review of the literature

Coral reef ecosystems are under increasing anthropogenic pressure leading to concerning declines globally (Hughes et al. 2017a). Local pressures such as overfishing, pollution, declining water quality, disease and outbreaks of coral predating crown-of-thorns starfish (De'ath et al. 2012), in combination with global disturbances such as rising seawater temperatures (Hoegh-Guldberg et al. 2007) are driving these declines (Lam et al. 2018). Despite being considered among the best-managed marine areas, the GBR is also threatened by nutrient, sediment and pollutant inputs from land-based sources (Brodie et al. 2007; Schaffelke et al. 2012). The GBR was also recently impacted by back-to-back bleaching events resulting in the loss of one-third of all its shallow-water corals (Hughes et al. 2017b). As a means to counteract reef loss and protect the socio-economic and ecological value of coral reefs, there is the need to better understand the functioning of coral reefs inclusive of the GBR.

Microorganisms are fundamental drivers of biogeochemical cycling on coral reef waters (Gast et al. 1998; Bourne and Webster 2013). They are also a crucial component of the coral holobiont (Bourne et al. 2016) and contribute significantly to the resilience of the ecosystem (Dinsdale et al. 2008). However, their contribution to a functioning reef is not fully understood. Recently, shifts in the compositional and functional diversity of both coral-associated (Ziegler et al. 2016) and free-living planktonic microbial communities (Dinsdale et al. 2008) have been linked to changes in water quality and varying levels of anthropogenic impact. Chronic nutrient exposure has been correlated to increase in coral disease prevalence and severity in other reef systems (Vega Thurber et al. 2014). Protection from fishing has been shown to lead to greater reef health by promoting high microbial diversity as opposed to the growth and rapid development of opportunistic microbial pathogens in unprotected reefs (Bruce et al. 2012). Also, recently, these findings have been validated in a field experiment simulating overfishing and nutrient pollution, which were shown to interact with sea surface temperatures to cause changes in coral microbiomes leading to coral mortality (Zaneveld et al. 2016).

Positive feedback loops implicating a role for macroalgae-derived labile dissolved organic carbon in supporting copiotrophic and potentially pathogenic bacterial communities have been shown to increase in microbial abundances on algal-dominated reefs worldwide, a phenomenon coined microbialization of coral reefs (Haas et al. 2016). This mechanism illustrates how two different pressures, overfishing and nutrient pollution, can ultimately lead to similar phase-shifts in coral reef ecosystems. Microbialization is suggested to trigger a switch from autotrophic to heterotrophic or copiotrophic microbial communities (Haas et al. 2016). A few studies have reported on shifts in particular microbial lineages as a response to water quality gradients in non-GBR reef systems. For instance, across the Line Island atolls (Dinsdale et al. 2008), microbial abundances became ten-fold higher and were dominated by heterotrophs, including a large percentage of potential pathogens, on the atoll with water chemistry characteristic of a near-shore environment (highest coral disease, lowest coral cover, highest nitrogen and phosphate). Types of bacterial autotrophs changed on the atolls from *Prochlorococcus*-dominated in the most pristine atolls, to *Synechococcus*-dominated when nitrogen and phosphate concentrations increase towards the most human-influenced atolls. In another study including samples from 60 coral reefs across three different ocean basins (Haas et al. 2016), algal-dominated sites were enriched in copiotrophic taxa, including Gammaproteobacterial families (Enterobacteriaceae, Vibrionaceae, Shewanellacaeae and Pasteurellaceae) and Bacteriodetes (Cytophagaceae and Flavobacteriaceae), whereas coral-dominated reefs were enriched in oligotrophic Alphaproteobacteria families (Caulobacteriaceae, Sphingomonadaceae, Hyphomonadaceae, Bradyrhizobiaceae, Acetobacteriaceae, Phyllobacteriaceae, Rhodospirillaceae, Pelagibacteraceae, Rhizobiaceae, Rhodobacteriaceae) and from other phyla (Clostridiaceae, Bacillaceae), all known to be widespread in oceanic waters and coral exudates. Finally, between protected and unprotected reefs in Brazil, photoautotrophs were found to be more abundant in protected reefs, whereas rapidly growing heterotrophic bacteria, including potential pathogens (Bacteroidetes, *Pseudoalteromonas*, and *Alteromonas macleodii*), were more abundant in unprotected reefs (Bruce et al. 2012).

However, the drivers of bacterioplankton community change have rarely been investigated within the GBR. In a study on the Tully River region (Northern GBR), microbial communities have been shown to follow seasonal dynamics and respond to riverine inputs onto coral reef waters (Angly et al. 2016). Rainfall, water quality index, salinity and temperature were implicated as drivers of bacterial community composition. Bacterial orders Sphingobacteriales, Burkholderiales, and Xanthomonadales dominated the riverine site, whereas euryarchaeal Thermoplasmata order E2 and bacterial orders Rickettsiales and Synechococcales (including *Synechococcus* and *Prochlorococcus* genera) were prevalent at the plume and marine sites. Further south, a study covering across-shelf gradients (Alongi et al. 2015) has shown that bacterioplankton numbers correlate with dissolved organic carbon and particular carbon, nitrogen and phosphorus.

Pelagibacter spp. and *Alteromonas* spp. dominated the bacterioplankton community. A recent study focusing on inshore reefs in the Burdekin region (Glasl et al. in review) aimed at quantifying the potential of the seawater microbiome to be used as a predictive parameter for environmental perturbations affecting the reef. The compositional variability of the seawater microbial community was significantly explained by sampling date, season (summer versus winter), average hours of daylight, and water quality parameters such as average seawater temperature, total suspended solids, particulate organic carbon or chlorophyll concentrations. Perhaps surprisingly, microbial community data provided a 92% accurate prediction of seawater temperature registered during the sampling period, highlighting the diagnostic value of microorganisms and exemplifying how assessments of microbial communities in seawater could be incorporated into monitoring initiatives (Glasl et al. 2018). Furthermore, the authors were able to identify microbial indicator taxa for high and low chlorophyll, total suspended solids and particulate organic carbon levels (Glasl et al. in review). Microbial indicators in the bacterial phyla Proteobacteria, Bacteroidetes, Cyanobacteria, Actinobacteria and Planctomycetes were pinpointed for low and high seawater temperatures. High temperatures were indicated by an increase of sequence variants belonging to the bacterial families Rhodobacteraceae, Cryomorphaceae, Synechococcaeae, Vibrionaceae and Flavobacteraceae, whereas lineages in the family Pelagibacteriaceae and the genus *Prochlorococcus* were indicative for low seawater temperatures. Altogether, the phyla Proteobacteria, Bacteroidetes and Cyanobacteria had the greatest number of indicator lineages across all water quality parameters. Flavobacteriaceae were significant indicators for temperature, chlorophyll, total suspended solids and particulate organic carbon. Halomonadaceae significantly associated with high chlorophyll and total suspended solids, and lineages within the phylum Verrucomicrobia were significant indicators for high levels of total suspended solids (Glasl et al. in review).

These studies show that, although the use of free-living microbiomes for diagnosing environmental perturbation on coral reefs is still at its infancy, this field is progressing fast. The main limitation to further understand the role of microbes in the functioning of the coral reef ecosystem is really the lack of available microbial data collected at a sufficient spatial and temporal resolution, backed up by a comprehensive suite of contextual parameters (Bourne et al. 2016).

Methodology

To deliver putative taxonomic and functional groups of reef microbes across known abiotic gradients for the Great Barrier Reef (GBR), we undertook an assessment of the available literature (summarized in Table 1). Studies establishing robust links between physical-chemical conditions and the microbial communities inhabiting the reef water column are scarce, particularly for regions of the GBR. This limited availability of relevant microbial data contrasts with the broad contextual data for water quality parameters across the GBR, an extensive reef system with large longitudinal temperature gradients and a water quality gradient mostly defined by distance to shore. In assessing the relevant information available for the study, we took advantage of the few existing detailed microbial datasets for the GBR as case studies to characterize the pelagic microbiome in response to:

a) input of riverine floodwaters and plumes on inshore reefs,
b) changes in benthic composition (macroalgal versus coral cover) and health of the reef, and
c) increasing distance from shore along an inshore to offshore gradient.

From the synthesis of this information we draw conclusions about the dominant microbial communities within pelagic reef water and the physico-chemical and biological drivers that influence the community structure. We also identify regions that need further study to achieve a more complete representation of microbial variation across the GBR, and propose specific hypothesis for further testing.

The core datasets identified as GBR case studies are spatially restricted, covering Heron Island in the south GBR, localised sites in the Mackay, Burdekin and Tully regions as well as several off-shore sites in the Coral Sea (Fig. 1). However, despite the limited spatial coverage, these studied demonstrate:

1. robust evidence for seasonal effects on microbial community composition in shallow pelagic environments affected by seasonal riverine input along an offshore gradient from the Tully river mouth (Angly et al. 2016),
2. community structure differences between shallow inshore waters when compared with oceanic waters flushing onto the reef matrix within the Mackay (Alongi et al. 2015) region,
3. community structure differences between healthy and degraded reef sites at inshore Orpheus Island and Magnetic Island reefs (Glasl et al. in review).

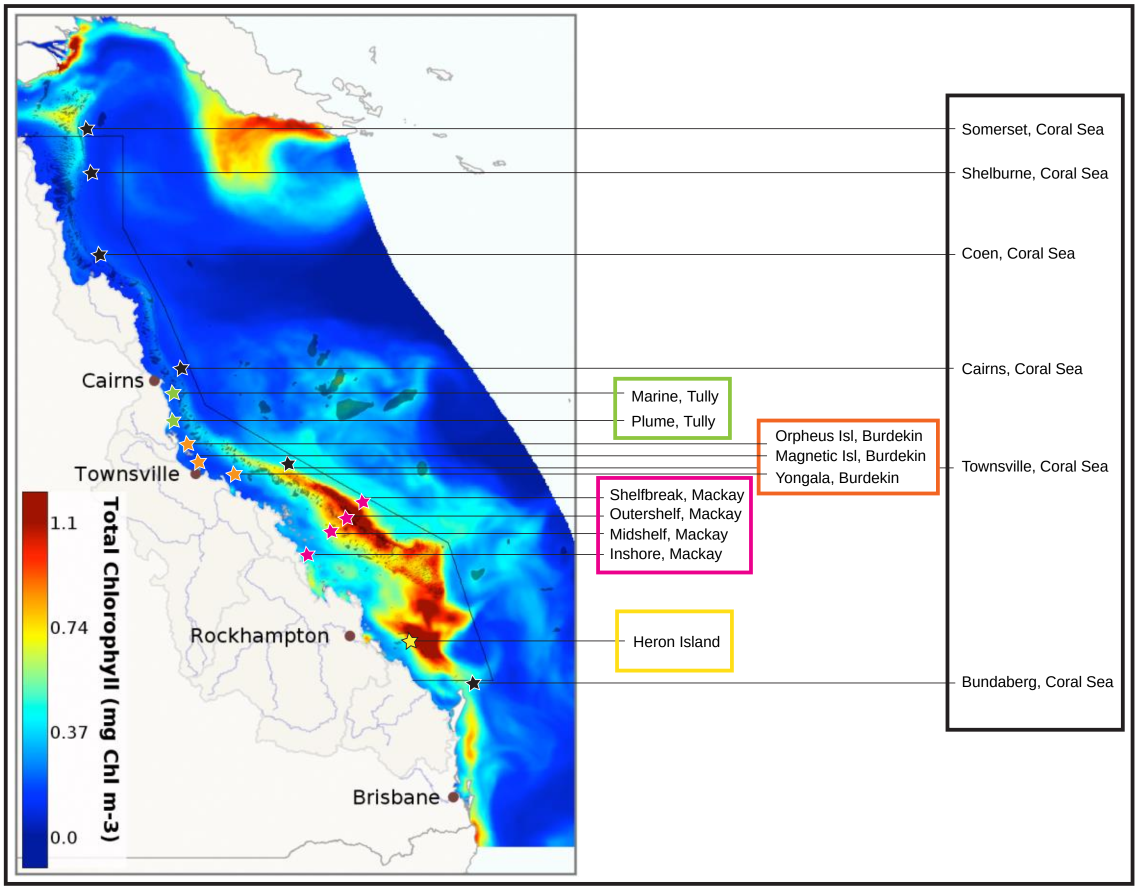

Figure A6.1: Map of the Great Barrier Reef with sampling groups included in the meta-analysis marked as stars and their respective affiliation into regions (or case-studies) represented by distinct colours. Data depicted on background was obtained from eReefs CSIRO GBR4 Hydrodynamic Model v2.0, with online map generation by AIMS. Colour of GBR and Coral Sea waters represents average concentration of total chlorophyll during the month of June in 2016. Licensing: CC-BY 4.0 Aust. Note that a particular sampling group may represent an individual location (e.g., for the Coral Sea region) or include several locations (e.g., for the Tully region).

Additional datasets available through unpublished studies were also incorporated into our meta-analysis (Fig. 1), including the Yongala and Coral Sea sites within the Integrated Marine Observing Systems (IMOS) National Reference Station (NRS) Network (Brown et al. in review) and Heron Island in the southern GBR (Epstein et al. in review), for which we included data on pelagic shallow microbial communities for the reef flat and reef slope habitats.

Microbial community data originating from the different GBR case studies was obtained in the form of “species versus samples”, or tables of operational taxonomic units (OTUs) for which microbial taxonomy had previously been assigned using 16S rRNA phylogenetic marker genes. OTU tables contained relative abundances of the 16S rRNA gene sequences affiliated with each microbial lineage across sampling locations. Limitations of this metadata approach are that methodologies differed amongst case studies (Table 1), including: i) different primer sets to amplify the 16S rRNA gene ii) different reference databases to infer taxonomic affiliation of the

16S reads, ii) different taxonomic resolution, and iv) different sampling depths, such that only the 2-5 m depth was used unless specified otherwise.

Table A6.1: Summary of published and unpublished microbial 16S rRNA datasets used in the meta-analysis, with respective study and region of origin, number of samples and locations included, primers used, and other methodological details. Note that the Yongala dataset is part of the Burdekin region (see Fig. 1), but was also analysed separately.

Study	Region	Nr samples	Nr locations	Rarefaction depth	Sequencing platform	Taxonomic assignment	Primer pair and refs
Angly et al 2016	Tully	78	7	250	454	SILVA and Greengenes	pyroLSSU926F/ pyroLSSU1392R
Glasl et al in review	Burdekin	48	3	25,000	Illumina Miseq 2x300	SILVA	27F/519R
BPA unpublished	Coral Sea	9	6	100,000	Illumina Miseq 2x300	SILVA	27F/519R
BPA unpublished	Yongala (Burdekin)	97	1	30,000	Illumina Miseq 2x300	SILVA	27F/519R
Epstein et al in review	Heron Island	16	4	50,000	Illumina Miseq 2x300	SILVA	515F/806Rb
Alongi et al 2014	Mackay	8	4	1,350	454	GreenGenes	63F/533R

Although these limitations provide a cautionary note when inferring trends across studies, they still represent robust and comprehensive datasets and this approach is commonly used to interpret patterns in microbial community structure within any given environment. Nevertheless, here we focus primarily on changes in microbial community captured within each of the individual case studies rather than inferring responses between datasets.

All OTUs derived from cellular plastids (mitochondrial and chloroplast) were removed from the analyses and, because Archaea were only reported for the Tully region (Angly et al. 2016), our analyses are mostly restricted to the domain Bacteria (unless specified). OTUs with one single occurrence (singletons) were removed to avoid including spurious data originating from sequencing errors. All data has been rarefied, both for within-study comparisons (see Table 1), as well as through an overall cut-off sequencing depth (of 1,000 reads) to allow for comparisons across studies. All microbial data has been transformed into relative abundance data and figures in this report summarize the most abundant microbial taxa in each case. For all data generated by BioPlatforms Australia (BPA) (Burdekin, Yongala and Coral Sea datasets), further documentation outlining the standard operating procedures for generating and processing sequencing amplicons is available at https://data.bioplatforms.com/organization/pages/bpa-marine-microbes/methods. Otherwise, all pre-processing data analyses steps are detailed in the respective publications for each of the GBR regions: Tully (Angly et al. 2016), Burdekin (Glasl et al. in review), Mackay (Alongi et al. 2015) and Heron Island (Epstein et al. in review). The microbial data here summarized originates from 256 samples collected from shallow pelagic habitats across 25 locations that fall into 5 different groups within our meta-analysis.

Environmental parameters and nutrient concentrations were acquired from the BPA website (https://data.bioplatforms.com/) for the Burdekin, Yongala and Coral Sea regions, from the NCBI SRA website (accession nr PRJNA276058) for the Tully region, and from the Water Quality Particulate and Dissolved Nutrient Data repository (Australian Institute of Marine Science (AIMS) 2017) for the Mackay region. No metadata was available for the Heron Island study. All environmental parameters are reported as averages ± SD. All meta-analyses of available microbial community composition and contextual environmental data were performed in R version 3.4.3 (R Development Core Team 2015) using packages ggplot2 (Wickham 2009) and phyloseq (McMurdie and Holmes 2013).

Results / Discussion

Overall bacterial patterns on the GBR

Pelagic microbiomes in the GBR are dominated by bacterial phyla Proteobacteria, Cyanobacteria, Bacteroidetes and Actinobacteria (Fig. 2). The most dominant bacterial families across the entire GBR (Fig. 3) are the autotrophic cyanobacterial Prochlorococcaceae and Synechococcaceae and the oligotrophic Pelagibacteraceae and copiotrophic Alteromonadaceae, both within the Alphaproteobacteria. These bacterial groups are known for their high abundance in the ocean with Pelagibacteraceae (formerly SAR11 clade) accounting for up to a third of all cells present in the oceans' surface waters (Morris et al. 2002). Prochlorococcaceae and Synechococcaceae, represent the main photosynthetic bacteria in the ocean (Partensky et al. 1999; Scanlan and West 2002).

Bacterial community shifts from inshore to offshore

A comparison of microbiome community structure was conducted between inshore (Geoffrey Bay on Magnetic Island, plus Pioneer Bay and a channel site on Orpheus Island), lagoon (Yongala National Reference Station) and Coral Sea pelagic environments for the Burdekin region (Fig. 4). The three inshore reef locations were dominated by the family Synechococcaceae, followed by Pelagibacteraceae, Flavobacteraceae (Bacteroidetes), Rhodobacteraceae (Proteobacteria), family OCS155 (Actinobacteria), Cryomorphaceae (Bacteroidetes), Halomonadaceae (Proteobacteria) and the poorly described SAR406 clade. The cyanobacterial family Prochlorococcaceae was only present at inshore sites at relatively low abundance. At the mid-lagoon site (Yongala) and the open ocean Coral Sea area however, the bacterial community was dominated by Pelagibacteraceae, with Prochlorococcaceae being more abundant than the Synechococcaceae, potentially linked to changes in the water chemistry across the reef shelf (Fig. 5).

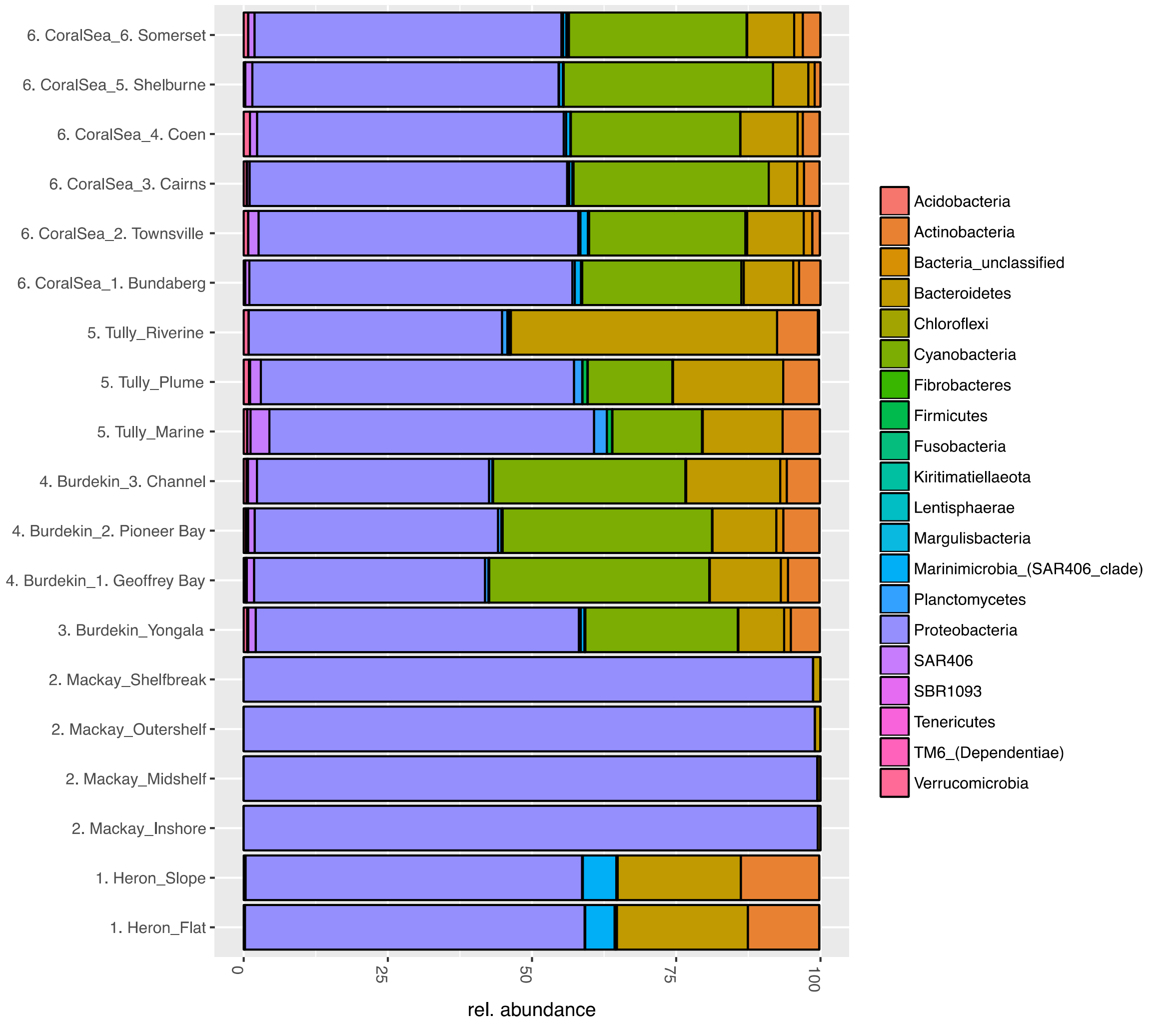

Figure A6.2: Phylum-level bacterial community composition (relative abundance) across all regions, sampling groups and seasons. For simplicity, only the most abundant bacterial phyla across all samples are shown.

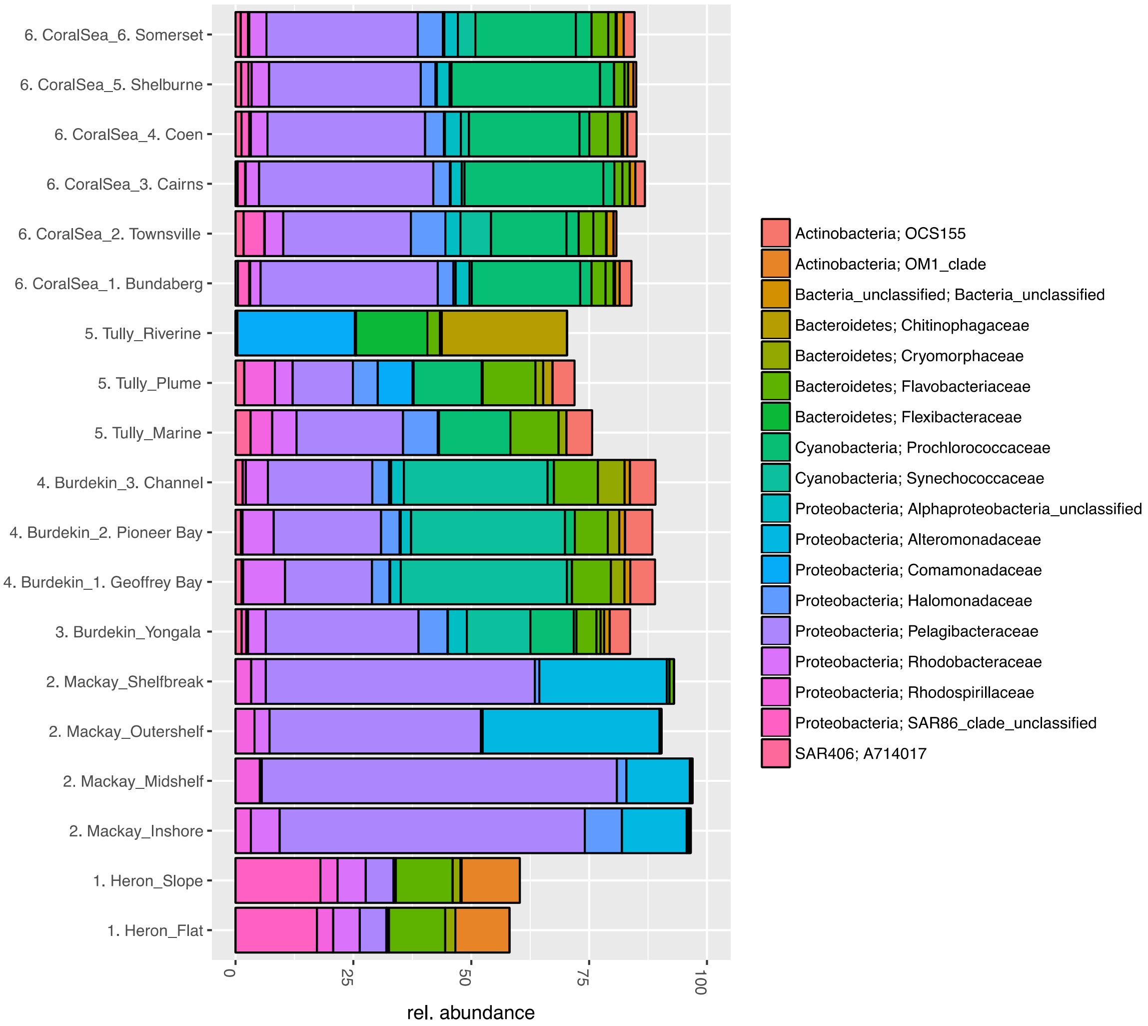

Figure A6.3: Family-level bacterial community composition (relative abundance) across all regions, sampling groups and seasons. For simplicity, only the most abundant bacterial families across all samples are shown.

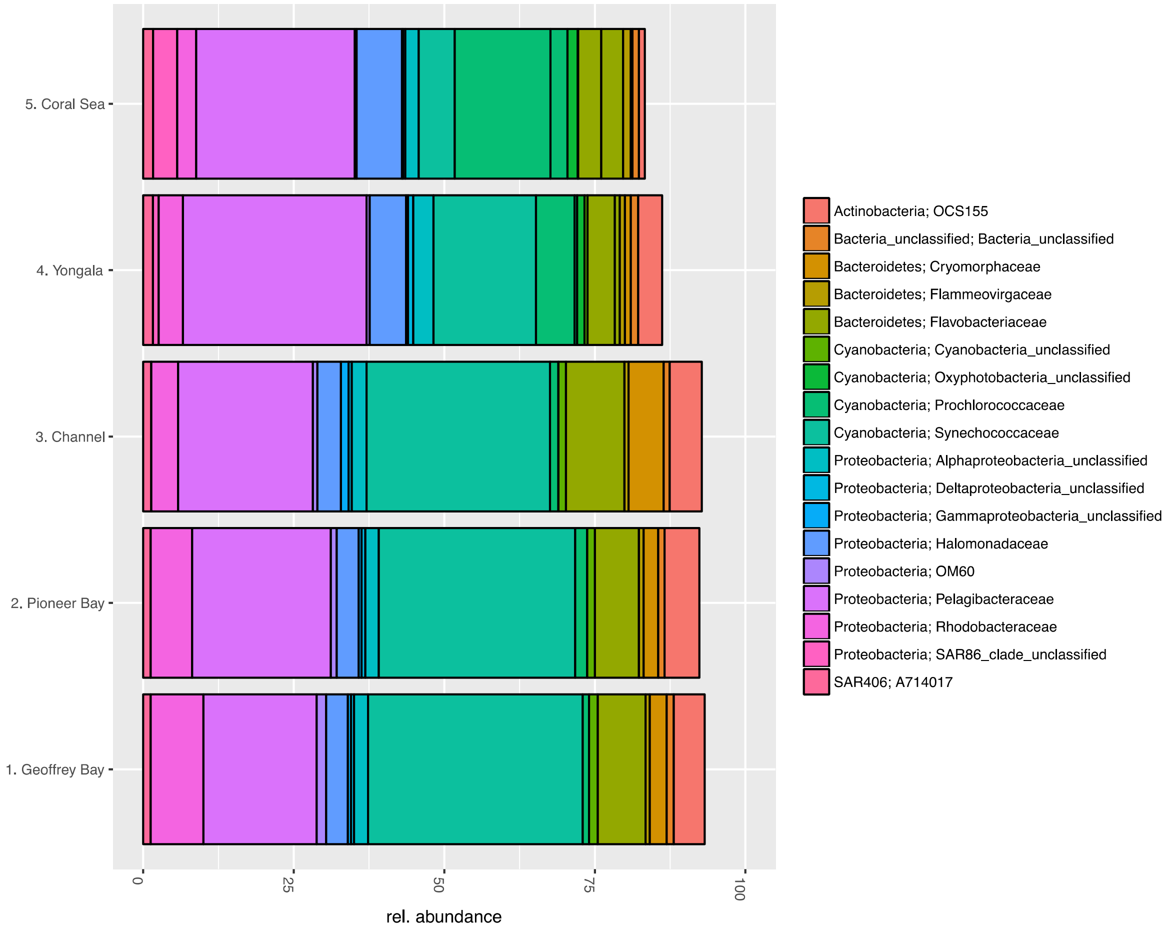

Figure A6.4: Family-level bacterial community composition (relative abundance) for the Burdekin (including three inshore reef locations and the Yongala lagoon site) and Coral Sea regions, across all seasons. For simplicity, only the most abundant bacterial families across all samples are shown.

The inshore reefs of Orpheus and Magnetic Island have typically higher nutrient levels than the Yongala lagoon and the Coral Sea locations. For instance, during the dry season, chlorophyll *a*, ammonia and dissolved phosphorus all show decreasing concentrations as the sites shift from inshore, to lagoon and the open ocean (Fig. 5). Chlorophyll *a* concentrations were 0.33±0.17 and 0.26±0.11 µg/L at the Magnetic and Orpheus Island, respectively, 0.09±0.03 µg/L at the lagoon Yongala site and 0.18±0.10 µg/L in the Coral Sea. Total dissolved phosphorus varied from ~ 0.09±0.05 at inshore Magnetic and Orpheus Island sites to ~0.07±0.03 µM at the lagoon Yongala and Coral Sea sites. Ammonium concentrations went from 0.21±0.05 and 0.24±0.05 µM at the Magnetic and Orpheus Island, respectively, to 0.04±0.05 µM at the lagoon Yongala site and 0.03±0.04 µM in the Coral Sea. The same trend is apparent during the wet season between inshore reefs and lagoon (Fig. 5), but Coral Sea measurements are not available for the wet season.

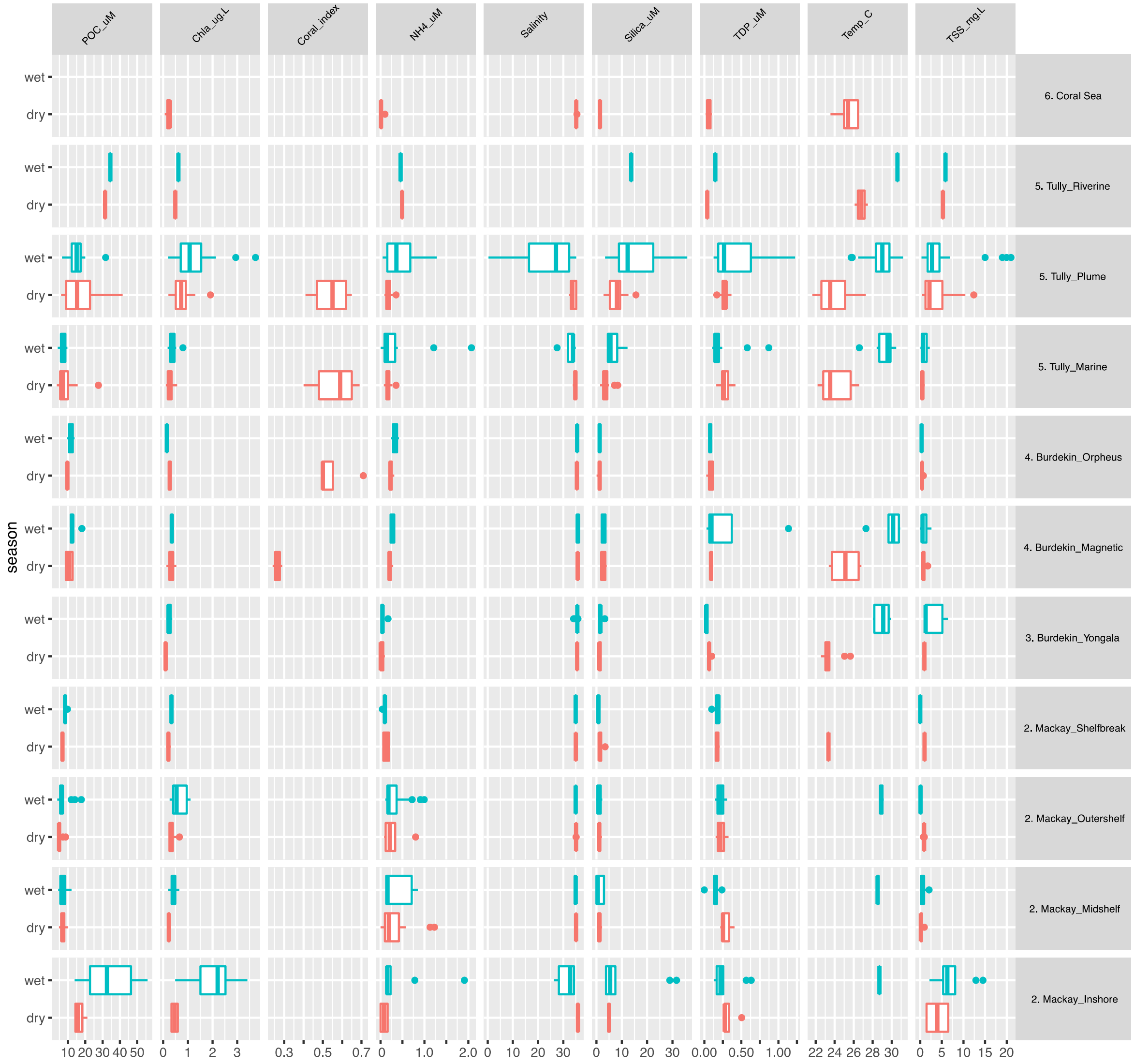

Figure A6.5: Most representative contextual environmental parameters across all regions, sampling groups and seasons. Season category includes the peak of the season: Dec-Feb for wet season and Jul-Sep for dry season. Note that no contextual data was available for the Heron Island dataset. Parameter codes are as follows: POC, particulate organic carbon (µM); Chla, chlorophyll a (µg/L); coral index represents the health of the reef according to Thompson et al. (2018); NH4, ammonium (µM); TDP, total dissolved phosphorus (µM); Temp, temperature (°C); and TSS, total suspended solids (mg/L).

Prochlorococcus is commonly reported from oligotrophic waters, due to its capacity to take up low levels of organic nitrogen, whereas *Synechococcus* becomes increasingly dominant in nutrient rich waters (Scanlan and West 2002; Zubkov et al. 2003). These patterns have also been observed for pristine versus human-influenced reefs atolls, with a four-fold increase in nitrogen and phosphate concentrations driving *Synechococcus* dominance from 9-15% to 64-66% of the cyanobacterial population (Dinsdale et al. 2008). Comparison of sites across the inshore to offshore gradient also revealed lower relative abundance of families OCS155 (Actinobacteria), Flavobacteraceae, Cryomorphaceae and Rhodobacteraceae. The typically halophilic family Halomonadaceae and an unclassified family in clade SAR86 show the opposite trend, increasing for sites further distanced from the shore. The increase in Pelagibacteraceae and SAR86, two abundant marine bacterial lineages which exhibit metabolic streamlining (Dupont et al. 2012), is consistent with the oligotrophic conditions found in the GBR lagoon and Coral Sea. Nutrient levels measured in these habitats were the lowest found across all parameters and throughout all datasets included in our meta-analysis (see Fig. 6 for carbon and phosphorus parameters and Fig. 7 for nitrogen parameters).

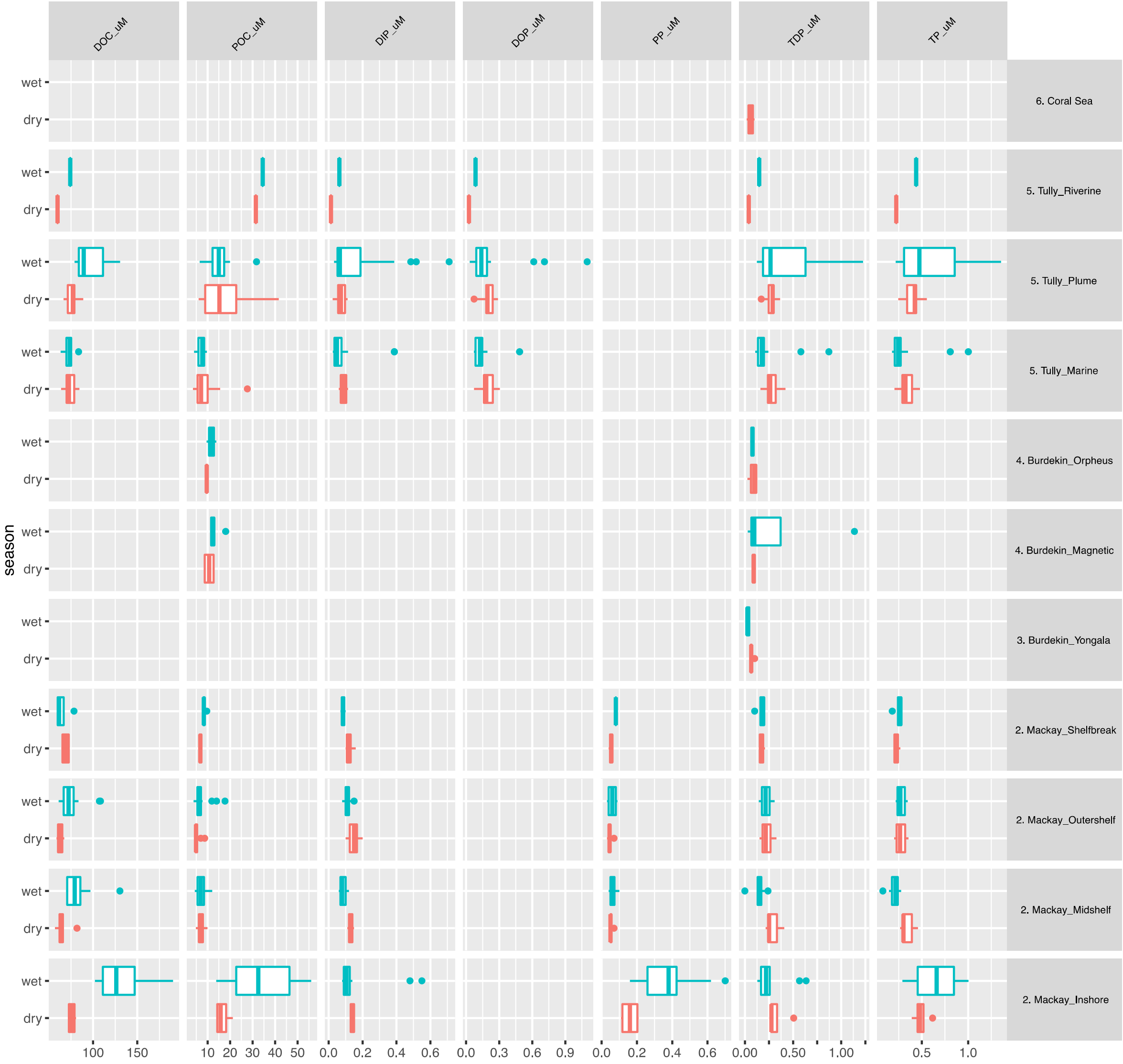

Figure A6.6. Contextual environmental carbon and phosphorus parameters across all regions, sampling groups and seasons. Season category includes the peak of the season: Dec-Feb for wet season and Jul-Sep for dry season. Note that no contextual data was available for the Heron Island dataset. Parameter codes are as follows: DOC, dissolved organic carbon (μM); POC, particulate organic carbon (μM); DIP, dissolved inorganic phosphorus (μM); DOP, dissolved organic phosphorus (μM); PP, particulate phosphorus (μM); TDP, total dissolved phosphorus (μM); and TP, total phosphorus (μM).

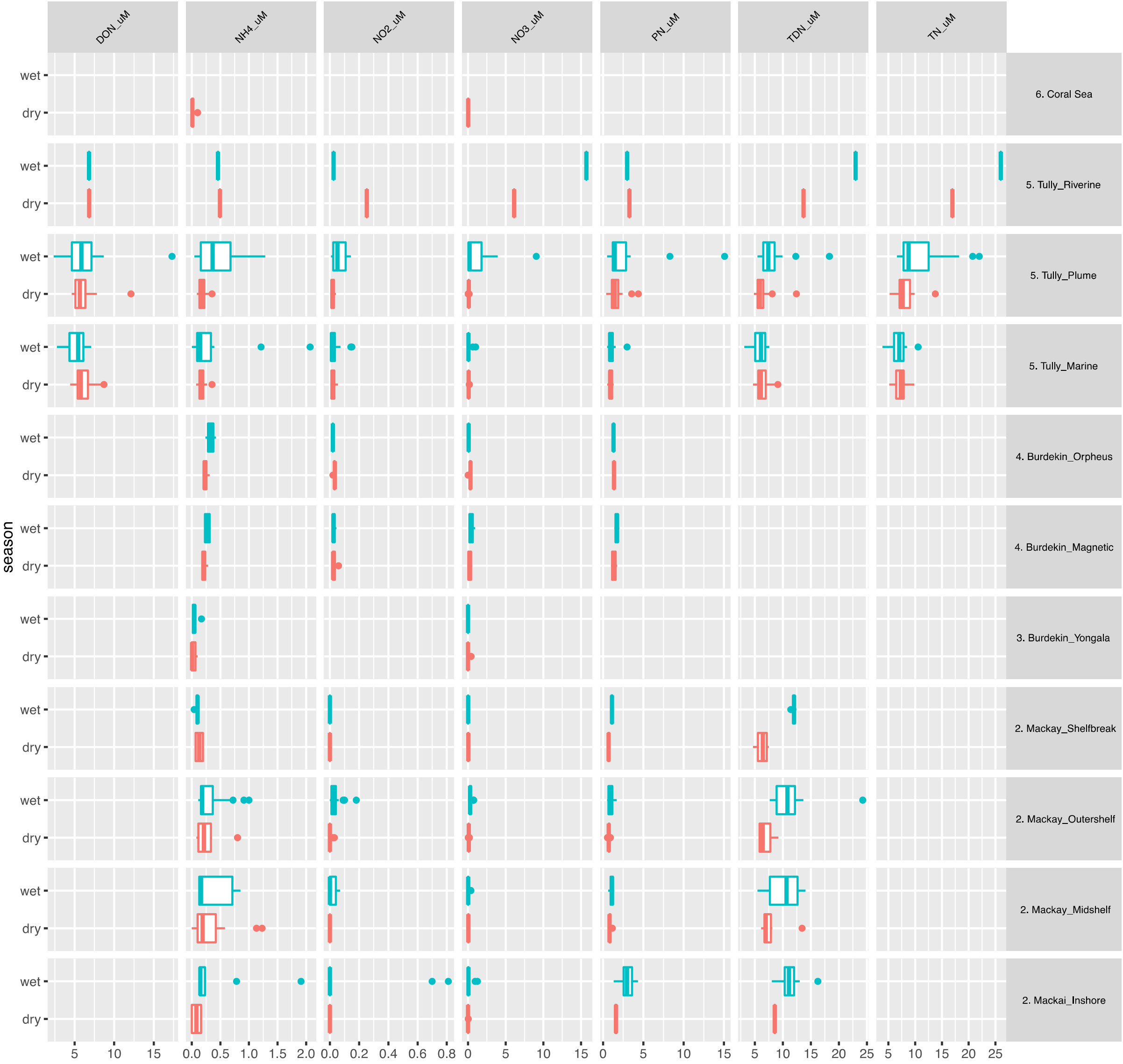

Figure A6.7. Contextual environmental nitrogen parameters across all regions, sampling groups and seasons. Season category includes the peak of the season: Dec-Feb for wet season and Jul-Sep for dry season. Note that no contextual data was available for the Heron Island dataset. Parameter codes are as follows: DON, dissolved organic nitrogen (µM); NH4, ammonium (µM); NO2, nitrite (µM); NO3, nitrate (µM); PN, particulate nitrogen (µM); TDN, total dissolved nitrogen (µM); and TN, total nitrogen (µM).

Bacterial community structure is stable at oceanic sites

Irrespective of sampling location, the microbial community patterns from all Coral Sea locations were similar in terms of composition and relative abundance (Fig. 8). There was however, a strong signal of Synechococcaceae and the SAR86 clade in the Townsville section of the Coral Sea (described above; Fig. 4) that was not apparent in the other Coral Sea samples. This may be a signature of anthropogenic impact within the Burdekin region as intense agricultural practices may drive infusion of nutrients further offshore (Thompson et al. 2018) and regular dredging (and sediment disposal) of the Townsville shipping channel (14 Km long and 92 m wide) may also contribute to the outflow of suspended sediments (McCook et al. 2015). However, it is also possible that upwelling processes contribute to shaping this offshore community. An increase in nutrients would cause SAR86 and Synechococcaceae to occupy habitats that are generally characterized by other members of their respective trophic groups, respectively SAR11 in the case of oligotrophs and Prochlorococcaceae in the case of photoautotrophs. Scarce water quality data for these locations in the Coral Sea prevent assigning microbial diversity patterns to nutrient levels, however, this location had some of the highest phosphate concentrations (0.09 μM, against 0.05±0.03 μM of all other sites; data not shown) and the shallowest bottom depth (129 m depth against 1113±670 m depth for all other Coral Sea sites), such that it could be influenced by environmental pressures shaped by vertical processes occurring in the water column. We recommend that future studies have comparable Coral Sea samples collected offshore from other human-impacted regions as well as in areas known to be under the influence of upwelling for direct comparison of water quality data and microbial community structure. Overall, stable and consistent patterns in microbial community structure were observed in Coral Sea locations and the microbiome shifts closer to shore are likely driven by processes of community dynamics taking place within the GBR lagoon.

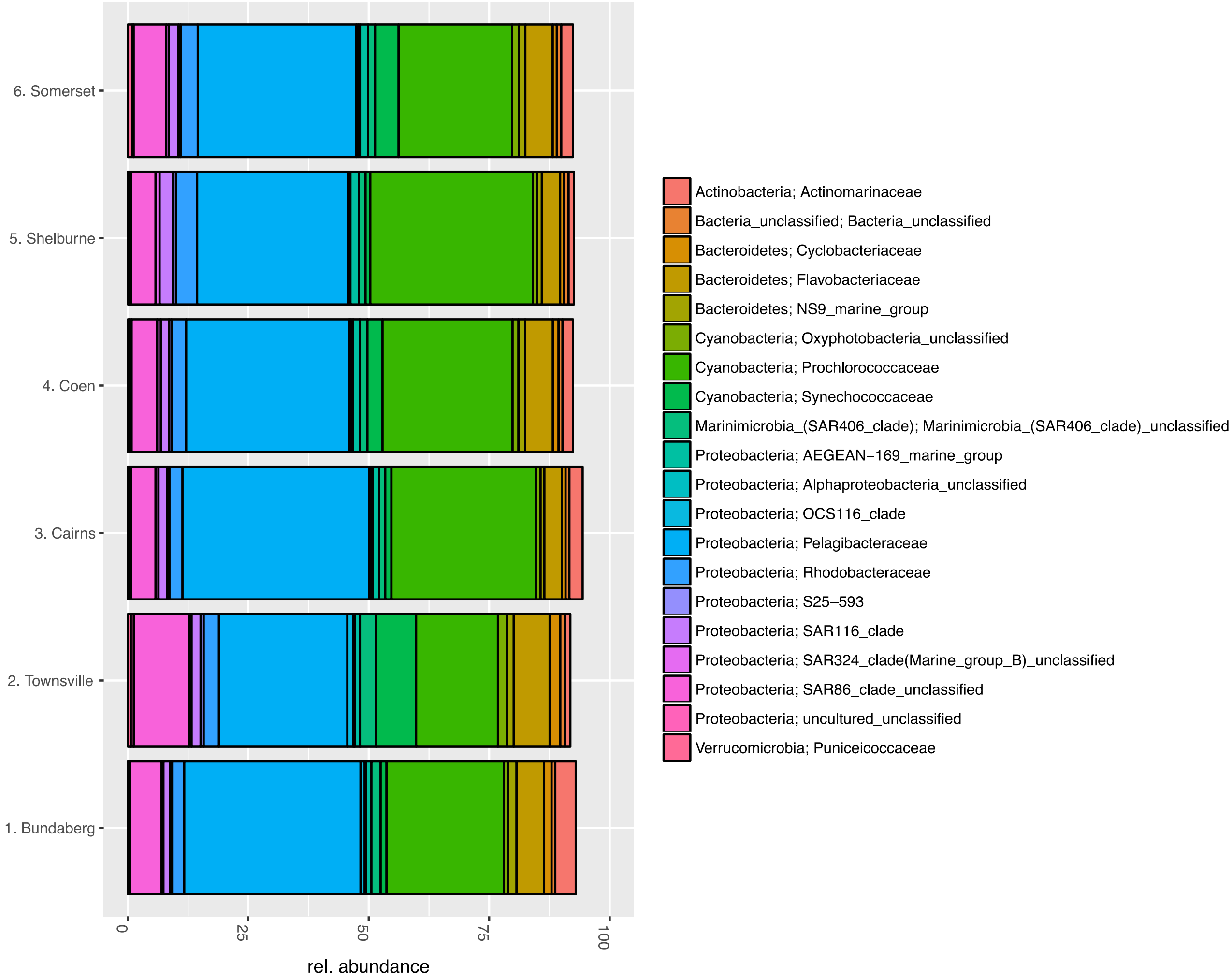

Figure A6.8: Family-level bacterial community composition (relative abundance) for the Coral Sea region, for the dry season only (no data available for the wet season). For simplicity, only the most abundant bacterial families across all samples are shown.

Bacterial community structure of inshore reefs is influenced by terrestrial run-off and/or macrobenthic primary producers

Microbial community patterns between inshore sites within the Burdekin region were relatively similar (sites across almost 100 Km from Orpheus Island to Magnetic Island; see Fig. 4). A high relative abundance of Synechococcaceae, Rhodobacteraceae and the proteobacterial family OM60 was evident in samples from Geoffrey Bay (located on Magnetic Island) particularly compared to the two sites at Orpheus Island (Channel and Pioneer Bay). An increase in Pelagibacteraceae and Prochlorococcaceae was observed at Orpheus Island compared to Magnetic Island. These patterns are consistent (though less pronounced) with the inshore-offshore gradient and could reflect the higher contribution of the GBR lagoon to microbial processes taking place on Orpheus than on Magnetic Island. Magnetic Island is located in the shallow Cleveland Bay area and is under higher influence of terrestrial run-off and higher nutrient loads as seen throughout the years by higher wet season chlorophyll concentrations than Orpheus (Thompson et al. 2018). This was also captured by our meta-analysis, with chlorophyll *a* concentrations of 0.36±0.05 and 0.15±0.02 µg/L during the wet season on Magnetic and Orpheus Island, respectively. Total dissolved phosphorus was 0.34±0.5 µM on Magnetic Island and 0.08±0.03 µM and Orpheus Island (Fig. 5).

A non-mutually exclusive alternative explanation for these patterns could be variability in benthic cover and associated availability of labile organic matter released by dominant benthic primary producers (Nelson et al. 2013). Orpheus Island has a much higher coral cover and coral index (Fig. 5) than Magnetic Island (Thompson et al. 2018), whereas macroalgal cover is much higher at Magnetic Island following a coral-algal phase-shift (Ceccarelli et al. 2018). A reduced dominance of Pelagibacteraceae, and the reduced Prochlorococcaceae:Synechococcaceae ratio at Magnetic Island could be related to the increasing contribution of organic carbon of macroalgae origin. While the cause/effect pathway has not been demonstrated, Magnetic Island is likely affected by feedback loops through which microbial coral-algal interactions related to increased macroalgae cover promote more advanced states of macroalgae domination (Roach et al. 2017; Ceccarelli et al. 2018). Rhodobacteraceae, for instance, are often characterized as opportunistic microbes correlated with poor reef health (Zaneveld et al. 2016) and commonly enriched in diseased corals (Roder et al. 2014). OM60 is an oligotrophic gammaproteobacterial family known to encompass diverse metabolisms including aerobic anoxygenic phototrophs (Jang et al. 2011) and which is known to be more abundant in marine coastal zones than in open-ocean surface waters (Yan et al. 2009). Both these lineages were found at higher relative abundances on the more degraded reefs of Magnetic Island as compared to Orpheus Island.

Bacterial response to riverine and seasonal influences on inshore reefs

In contrast to the Burdekin, the Tully region displayed dominance of the Prochlorococcaceae taxa as opposed to Synechococcaceae (see Fig. 3), in addition to an overall reduction in Cyanobacteria and an increase in the relative abundance of Rhodospirillaceae. Inshore reefs in the Tully region show a coral health index similar to that of Orpheus Island and higher than that of Magnetic Island (Fig. 5; Thompson et al. 2018). It is likely that this pattern is attributed to primer bias (different primer sets were used between studies) that excluded amplification of

Synechococcaceae.

The importance of the Tully region microbiome dataset (Angly et al. 2016) is that it encompasses both the spatial dynamics generated by the outflow of the Tully river onto the inshore reef, as well as the superimposed temporal dynamics established between dry and wet seasons. Riverine outflows are a major impact to the health of inshore reefs as they carry organic and inorganic nutrients of terrestrial origin (such as agricultural fertilizers) onto the reef systems (Brodie et al. 2007; De'ath et al. 2012). The Tully river plume, impacts directly Dunk Island, located approximately 15 Km from the river mouth. Locations under the influence of the river plume (i.e. Tully Mouth, Mission Beach and Dunk Island), display a microbial community characterized by an abundance of the bacterial taxa Bacteroidetes, Chitinophagaceae, Comamonadaceae, Proteobacteria and Oxalobacteraceae. Bacteroidetes have been used as fecal indicators and have some potential to be a reservoir of resistance genes for other more pathogenic bacterial strains (Lofmark et al. 2006). On the spatial gradient from the mouth of the river to the reefs around Dunk Island there is a decreasing influence of the river plume, which is reflected in the microbial community patterns by an increase in Pelagibacteraceae and Halomonadaceae taxa. Further offshore and away from the mouth of the Tully River, microbial communities are consistent with inshore Burdekin sites, dominated by Pelagibacteraceae and Cyanobacteria, Flavobacteraceae (Bacteroidetes), Rhodobacteraceae (Proteobacteria), family OCS155 (Actinobacteria), Cryomorphaceae (Bacteroidetes), Halomonadaceae (Proteobacteria), the poorly described SAR406, and also Rhodospirillaceae (Proteobacteria). This profile is typical of pelagic microbial communities throughout the inshore reef locations studied.

Seasonal dynamics also influence the microbial profiles in the Tully Region (Fig. 9). Variability in bacterial community structure among inshore sites located away from the Tully river plume (i.e., Tully Offshore, Russel Island and Fitzroy Island) is lower during the dry season than during the wet season. However, the microbial community of the river plume-impacted sites (i.e., Tully Mouth, Mission Beach and Dunk Island) is homogenous during the wet season, indicative of the influence that fresh water flows have on these inshore sites and reflecting the environmental forcing brought about by stronger river discharge. For the Tully Offshore, Russel Island and Fitzroy Island sites during the wet season, each display a different microbial signature, likely related to unique oceanographic conditions and exposure to the effects of terrestrial run-off and river plumes. For example, at Russel Island, which is in proximity to the mouth of the Russel River and therefore also influenced by riverine discharge, microbial communities during the wet season exhibit a reduction in Pelagibacteraceae and an increase in Vibrionaceae and Rhodospirillaceae, with these taxa commonly reported from compromised coral tissues. Hence, proximity to river mouths can drive microbial community dynamics which increase taxa in the surrounding waters that have been implicated as causing corals diseases (Zaneveld et al. 2016).

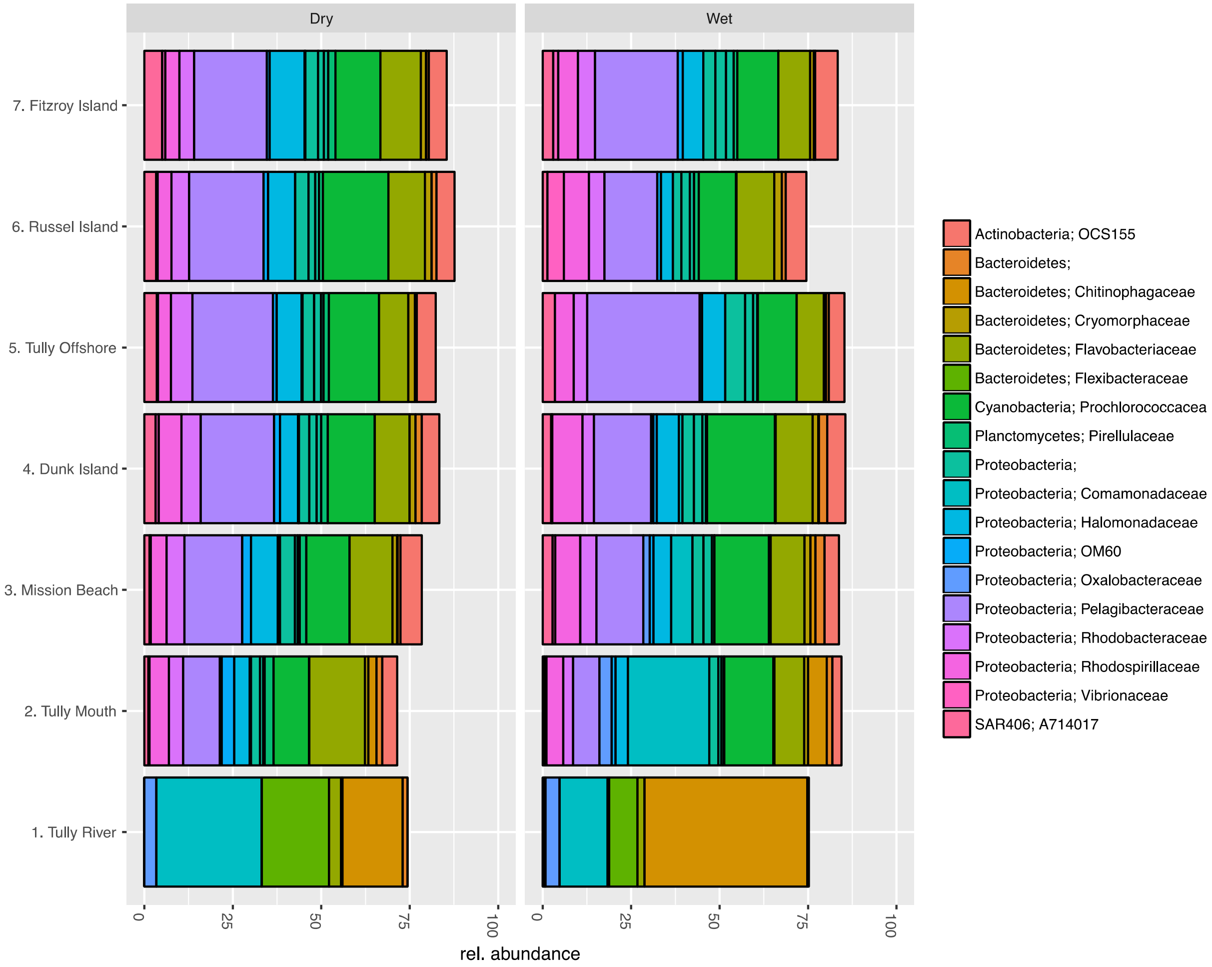

Figure A6.9: Family-level bacterial community composition (relative abundance) for the Tully region, with seasonal resolution. Locations include the Tully River, three locations under the influence of the river plume (2-4), and three marine locations out of the plume (5-7). For simplicity, only the most abundant bacterial families across all samples are shown.

Marine Group II Euryarchaeota were also more abundant during the wet season (Angly et al. 2016). These motile residents of the photic zone that have a photo-heterotrophic lifestyle through which they degrade protein and lipids, are also known to display great seasonal and spatial variation elsewhere (Iverson et al. 2012; Zhang et al. 2015). Most likely there are also important numbers of Archaea across the abovementioned inshore to offshore gradient, as well as within each of the regions here characterized. Archaea have not been characterized widely and their importance for coral reef functioning is far from being understood.

Seasonal influences on lagoon bacterial communities

Sites located away from river sources have the highest microbial stability across seasons. For example, the Fitzroy Island, Tully Offshore and Yongala sites all show relatively stable microbial profiles across seasonal sampling. (Figs. 9-10). This stability seems to reflect lower variation in nutrient levels at these sites (Figs. 5-7). For the Yongala site, the most conspicuous microbial community shift observed was a decrease in the Prochlorococcaceae:Synechococcaceae relative abundance ratio during the wet season (Fig. 10). Apart from temperature, the parameter exhibiting the strongest seasonal signal was total suspended solids, varying from 0.95±0.00 mg/L in the dry season to 2.98±2.56 mg/L in the wet season (Fig. 5). Interestingly, the microbial community at the Yongala site was consistent across the sampling depth profile (Fig. 10), suggesting that the water column is well-mixed vertically in the lagoon waters throughout both summer and winter. Once again the nutrient data is consistent with the microbial patterns, with little to no variation across depths (data not shown).

Although we could not access samples collected in the Coral Sea during the wet season, differences between seasons are probably low in the open ocean, due to being relatively well buffered from terrestrial influence. However, differences caused by other seasonal processes, such as varying seawater temperature or influx of nutrients due to cold-water upwelling along the shelf edge of the GBR cannot be excluded.

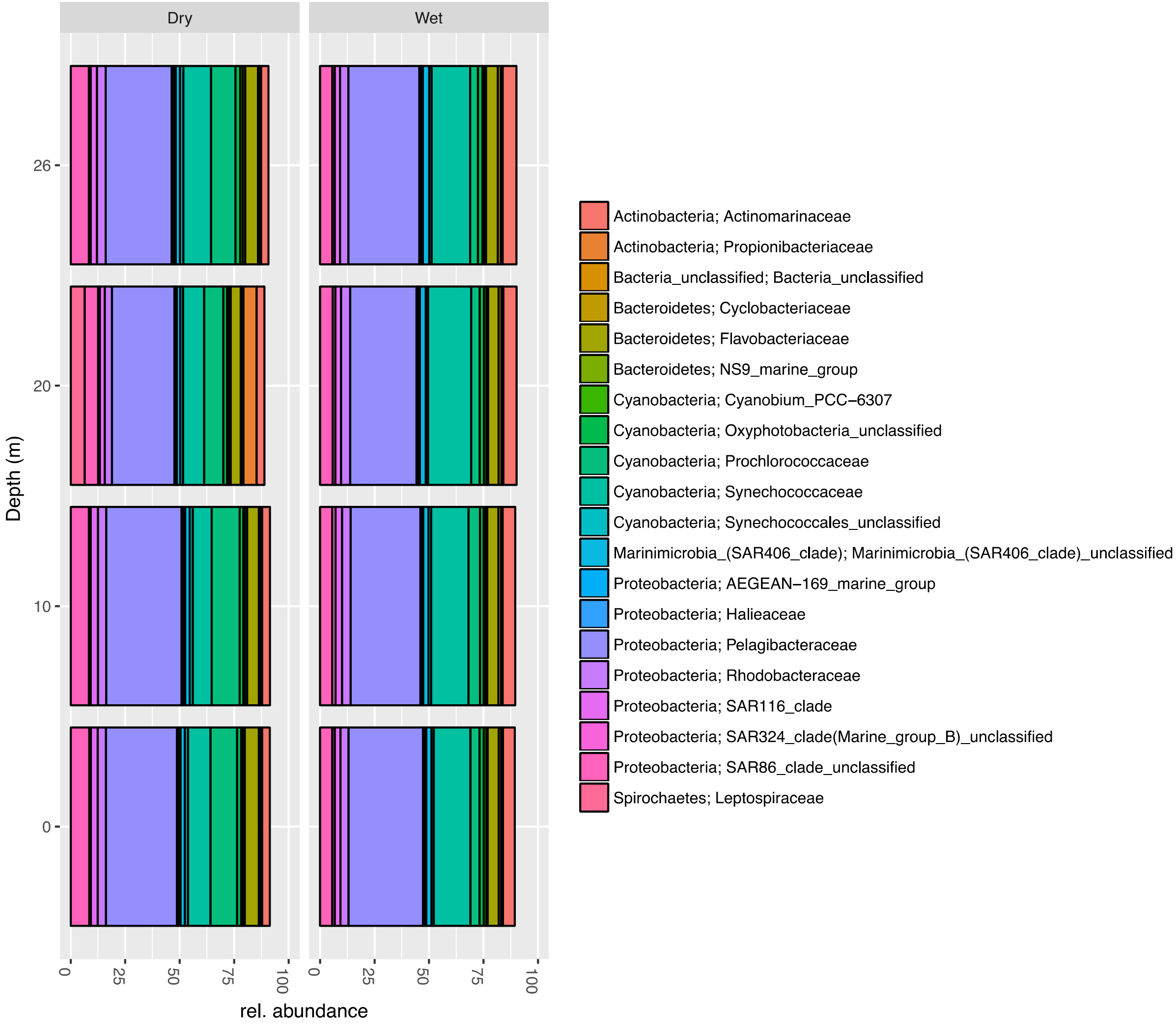

Figure A6.10: Family-level bacterial community composition (relative abundance) for the Yongala (Burdekin) region, with seasonal resolution. Note that all other comparisons include only the Yongala data from 10 m depth. For simplicity, only the most abundant bacterial families across all samples are shown.

Shelf edge effects on bacterial community profiles.

The dataset derived from the Mackay region (Alongi et al. 2015), allows investigation of the influence of coastal distance and reef shelf on microbial community structure (Fig. 3). From the inshore and midshelf to the outershelf and shelfbreak there is large increase in relative abundance of Alteromonadaceae and a concomitant decrease in Pelagibacteraceae and the Halomonadaceae. However, when seasonal parameters are overlaid (Fig. 11), it becomes apparent that the major differences in community composition between the different locations studied across the GBR shelf occur during the dry season. This is inconsistent with patterns observed in the Burdekin and Tully regions, where terrestrial run-off increased during the wet season and correlated with shifts in the pelagic microbial communities of the inshore reef locations, but not of the lagoon locations. Whereas the seasonal effects for Tully region are likely related to terrestrial run-off and riverine incursion into marine communities along the inshore reefs (Angly et al. 2016; Thompson et al. 2018), seasonal drivers in the Mackay region could be of oceanic origin. The region is highly productive due to upwelling along the shelf (see Fig. 1 for regional chlorophyll *a* levels in August 2016), bringing nutrients and cold water from the deep and therefore contributing to shaping the microbial communities of outer reefs. However, the upwelling regime in that area is restricted to the summer wet months (Berkelmans et al. 2010), but the nutrient data does not support a hypothesis of upwelling as a driver of changing microbial community structure (Fig. 5). This may be related to the very restricted temporal window during which samples were taken in the region. One important characteristic of the GBR in this region is the extensive distance of the outer reef from shore. This and the prevalent upwelling system that is active during the wet season could contribute to differences seen in community composition. Alteromonadaceae are recognized as copiotrophs that can grow rapidly when organic nutrients are available in the environment (McCarren et al. 2010; Bruce et al. 2012).

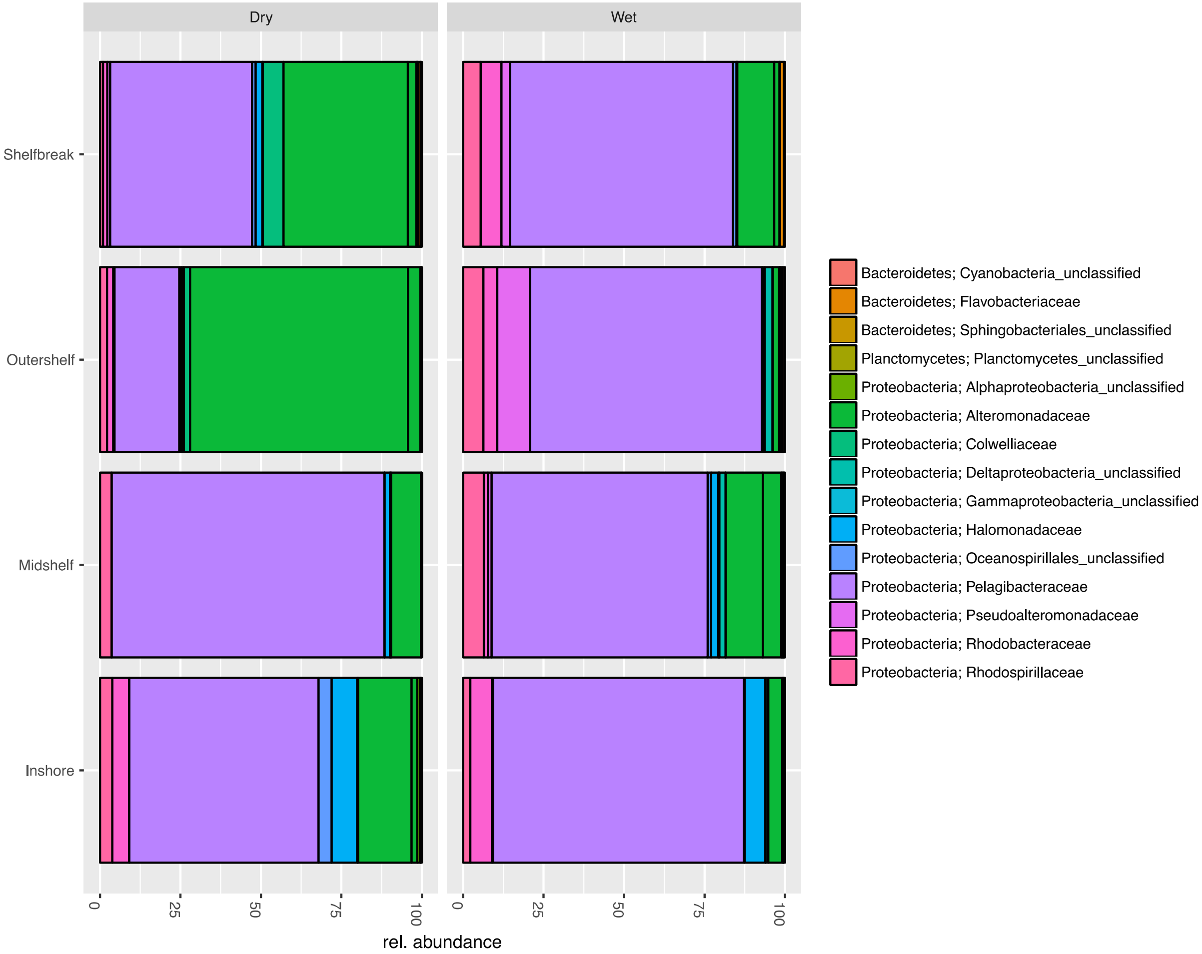

Figure A6.11: Family-level bacterial community composition (relative abundance) for the Mackay region, with seasonal resolution. Each sampling group (or reef group) summarizes a number of locations. For simplicity, only the most abundant bacterial families across all samples are shown.

Bacterial community patterns in the southern GBR

The final data set included in this report is derived from Heron Island and presents a different microbial community compared to the more Northern regions (see Fig. 3). Methodological biases likely contributed to these differences, which are reflected mainly by an absence of Cyanobacteria. This site however is dominated by similar groups identified for the Burdekin lagoon and Coral Sea regions. For example, Pelagibacteraceae, SAR86 (now very dominant), SAR406, Rhodobacteraceae and Rhodospirillaceae, and Cryomorphaceae are abundant taxa. Other dominant groups include the SAR116, the Bacteroidetes NS9 and Flavobacteraceae, as well as OM1 clade in the Actinobacteria. It is interesting to note that community assemblages are almost identical between the reef flat and reef slope (2 and 6 m depth, respectively; see Fig. 12) at this site. The increase in the proteobacterial clades SAR86 and SAR116 as well in OM1 clade (Actinobacteria), all known for their streamlined genomes (Mizuno et al. 2015), likely reflect the oligotrophic conditions in the system. However dominance of Flavobacteraceae, may suggest an increased abundance of opportunistic bacteria that may affect coral health (Bruce et al. 2012; Haas et al. 2016).

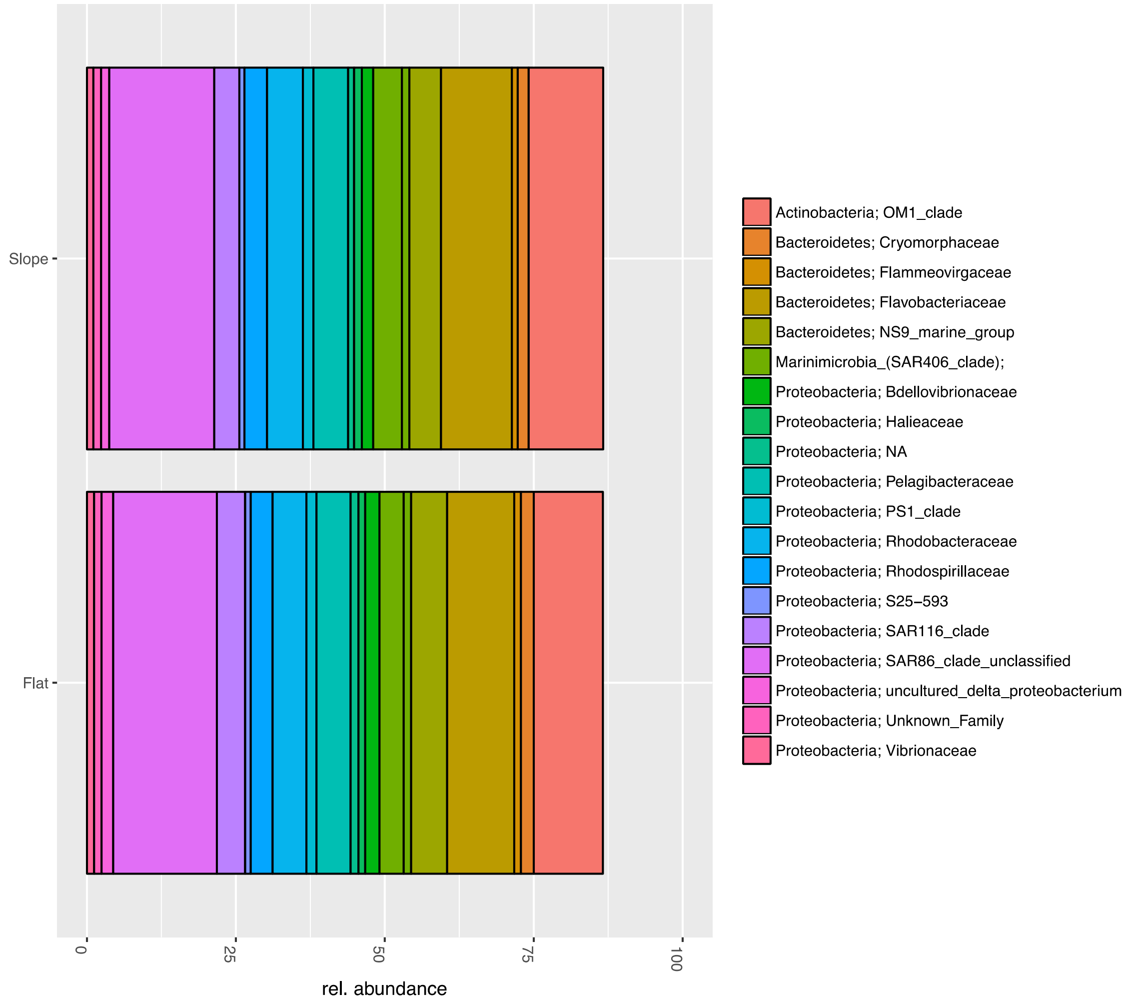

Figure A6.12: Family-level bacterial community composition (relative abundance) for the Heron Island region, for the dry season only (no data available for the wet season). Each reef habitat consists of two different locations. For simplicity, only the most abundant bacterial families across all samples are shown.

Caveats of this meta-analysis

The datasets originating from the Burdekin region, including the Yongala lagoon site, plus the Coral Sea dataset were obtained with the same primer set and processed through the same analysis pipeline of BPA (Brown et al. in review; Glasl et al. in review). This allowed for a fairly robust comparison across sites. The very low abundance of Cyanobacteria in the Heron Island dataset, and the unaccompanied dominance of Proteobacteria in the Mackay dataset are surprising outliers, since other studies using the same primer sets (515F-806b for the Heron study and 63F-533R for the Mackay study) did retrieve large numbers of cyanobacterial reads from marine samples collected in the Red Sea (Apprill et al. 2015) and GBR (Bourne et al. 2013), respectively. Still, primer bias or biases in DNA extraction are potential explanations for such differences in community composition at the phyla level, and this again highlights the need for caution when making comparisons across datasets. We also note that the Coral Sea dataset covers only a few locations and microbial community composition can be affected by site-specific upwelling and other processes (Berkelmans et al. 2010). In context of this sparse availability of microbial community data, it is virtually impossible to disentangle the contribution of various biotic and abiotic factors to microbial community composition. For example, Russel Island (in the Tully region), is subjected to a higher influence of terrestrial run-off than the neighboring Fitzroy Island (Angly et al. 2016), but also has a lower coral cover (Thompson et al. 2018), making it challenging to assign cause/effect pathways for microbial dynamics.

Further data synthesis and interpretation will complement this report prior to the end of 2018. In particular, eReefs data available for the locations (and respective time points) targeted in our case studies will be extracted and used to cross-validate abiotic data measured in these studies. We will also attempt to overlap eReefs derived seasonal variability (winter versus summer) for representative GBR reef groups or regions exhibiting relatively homogeneous abiotic conditions (following unpublished clustering analyses available from the Australian Institute of Marine Science). Microbial data available from reef systems other than the GBR will be used as proxy for reef groups not yet characterized by GBR case studies. This will be achieved using similarity in variability of environmental conditions between each GBR reef group and the different studies available. A strategy for modelling microbial data in the context of available environmental metadata for incorporation into the eReefs platform will also be developed. This will facilitate identification of relationships between pelagic microbiomes and the environments they are exposed to, which will provide the foundation for further funding applications.

Contribution to a functioning reef

From the limited number of microbial studies focused on the GBR system that include contextual metadata on environmental conditions, all indicate that communities respond in a deterministic way to environmental fluctuations and drivers. Therefore microbial community dynamics can be modeled to better understand how the ecosystem functions. These conclusions are supported by the patterns observed during the dry season from inshore to lagoon and then from the lagoon to the offshore Coral Sea locations which presented robust and consistent community patterns resulting from terrestrial and oceanic influences (see Fig. 13 for overall summary). Microbial communities were deterministic of the spatial habitat and surrounding nutrient dynamics, at least at broad geographical scales and at the coarse taxonomic level considered. On top of spatial variation, temporal microbial responses can also be modeled, since microbial communities have fast response times to their surrounding environment and as such their community composition was related to these abiotic conditions. For example, The Tully River study demonstrates that seasonal variation and a spatial-temporal lag of riverine influence over a local and regional scale can be modeled. Environmental parameters (nutrients, temperature, etc.) drive the spatial distribution and temporal dynamics of pelagic microorganisms across different habitats of the GBR. These microbes can therefore be used to develop systems for assessing cumulative stress associated with altered environmental conditions.

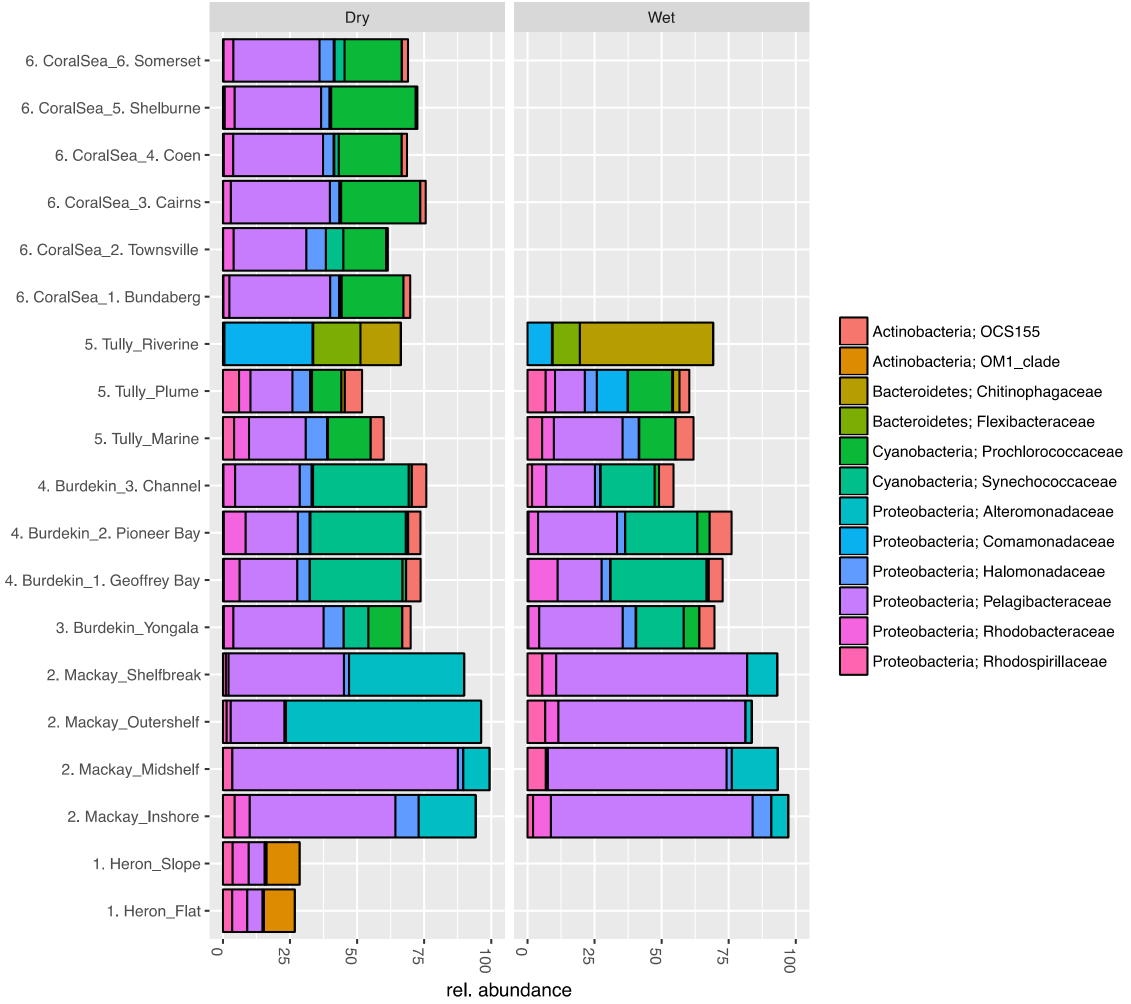

Figure A6.13: Family-level bacterial community composition (relative abundance) across all regions, sampling groups and seasons. For simplicity, only the most abundant bacterial families across all samples are shown.

Identification of microbial taxa and functions that contribute to a functioning reef or to disturbed reef states is a major objective of this work, though further analyses are required to identify potential microbial indicators of reef health, degraded environments and tipping points. The present meta-analysis identified microbial taxa that are indicative of particular conditions on the reef, either because they contribute to the processes underlying reef health, or because they occur as a consequence of those underlying processes. We propose the Prochlorococcaceae:Synechococcaceae relative abundance ratio as an indicator of the contribution of nutrient enrichment in coral reef waters as these two photo-autotrophs have different capacities to use low amounts of organic nitrogen. Whereas *Prochlorococcus* is common in oligotrophic waters, *Synechococcus* is known to become increasingly dominant in increasingly nutrient rich waters. We therefore hypothesize that an index could be established that categorizes this ratio into levels that correlate with the availability of nutrients in the system and therefore with either the contribution of terrestrial run-off or of benthic primary producers in the case of macroalgae-dominated reef habitats. Other indices can also be generated to monitor eutrophication of GBR waters. This includes comparing particular lineages with different substrate affinities (such as the Prochlorococcaceae:Synechococcaceae ratio). Another such example is the ratio between Pelagibacteraceae and SAR86, which at least for the inshore reefs in the Burdekin region, appear to correlate negatively with increasing nutrient levels. Alternatively, comparison of broader trophic groups may also prove valuable indicators of ecosystem health and/or function. For example, levels of typical copiotrophs such as families OCS155, Flavobacteraceae, Cryomorphaceae and Rhodobacteraceae, can be modelled against levels of oligotrophs such as Pelagibacteraceae and SAR86 to generate another index indicative of eutrophication that can complement existing ones (e.g., Haas et al. 2016). Typical opportunistic bacteria, such as those exhibiting virulence towards benthic organisms, could also be used as indicators of reef health and or degradation. Such families include, Rhodospirillaceae, Rhodobacteraceae and Vibrionaceae.

Because individual lineages within a particular microbial family are likely to respond differently to the environment, it is important to assign the highest taxonomic resolution to the microbial taxa. Recent and as yet unpublished research, has shown that even within a particular bacterial genus or species, there can be different lineages (i.e., 16S rRNA sequence variants) that are statistically associated with distinct environmental conditions (Glasl et al. in review). Such indicator taxa probably consist of specialised lineages that have diversified to occupy a particular niche (Ngugi et al. 2016), allowing prediction of the surrounding environment with fairly high confidence. Theoretically, this same indicator approach can be extended to microbial functions, measured either as abundances (or ratios) of particular genes, gene transcripts or even of the proteins they code for.

Future approaches

Microbial baselines, achieved through a series of microbial observatories spanning key habitats of the GBR, would greatly assist reef-monitoring efforts. These observatories should cover representative areas of the Northern, Central and Southern GBR, spanning the inshore, mid- and outer shelf reefs for each sector. One proposed approach would be the establishment of several parallel cross-shelf transects running from the coast to the GBR shelf edge, with frequent sampling to capture seasonal peaks of the wet and dry season as well as the dynamics established in-between these peaks. This would complement projects already underway for Australia, such as the Australian Microbiome (AM) initiative, which aims to develop an Australian microbial genomics resource for management and monitoring applications. Opportunistic sampling undertaken by scientists, managers or stakeholders that visit particular areas of the reef would complement this approach (e.g., the IMOS program Ships of Opportunity). A microbial observatory should be incorporated into current monitoring efforts for a more effective understanding of how coastal eutrophication or climate driven changes impact the different biological trophic levels on reef ecosystems.

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APPENDIX 7: SPEARFISHING

[Report submitted for Case Study 4]

Spatial patterns and functional impacts of recreational spearfishing on the Great Barrier Reef

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Key words: Spearfishing, recreational fisheries, coral reef, ecosystem function, herbivory

Abstract

Recreational fishing practices can have significant impacts on marine ecosystems but their catch dynamics are often difficult to quantify, particularly for recreational spearfishing. On coral reefs, the impacts of recreational spearfishing are often considered to be negligible compared to other practices, but the highly selective method adopted by spearfishers can result in specific ecological consequences. Here we investigated the spatial patterns and catch dynamics of recreational spearfishers on the Great Barrier Reef using an online survey (n=141 participants) targeted at spearfishers active along the coastline of Queensland. Observations from within the Queensland spearfishing community were also used to explore perceived changes in catches of three primary spearing targets. Spatial use and catch composition varied among major coastal cities ranging from Bundaberg (south) to Cooktown (north). The piscivorous coral trout, *Plectropomus leopardus*, was the most heavily targeted species comprising 34% (±1.5) of the catch composition. Variations in spearing targets across the Reef were primarily driven by the parrotfishes, *Chlorurus microrhinos* and *Scarus ghobban*, and invertivorous tuskfishes, *Choerodon schoenleinii* and *Cho. venustus*. Proximity of spearfishing activity to the coastline (coastal diving, inshore reefs, offshore reefs) significantly influenced the proportional catch of herbivores, invertivores and piscivores, with herbivore compositions being twice as high in coastal regions than offshore. Spearfishers perceived a variety of changes in catch composition over time, which varied geographically. Action brought about by spearfisher concerns has been highly effective in the past and spearfishers have the potential to address their concerns if organised appropriately.

Introduction

Coral reefs are increasingly exposed to a range of anthropogenic and environmental stressors that threaten the long-term viability of these coral dominated communities[1]. Of particular concern are recent changes in global climate, including on the Great Barrier Reef (GBR), Australia, which has experienced sequential mass-bleaching events over recent years and extreme declines in live coral cover[2]. In light of such global climatic stress, it is becoming more apparent that the impacts of local issues, such as fisheries, must be better understood and managed to facilitate reef resilience in a future ocean[3,4,5,6,7,8].

Overfishing is considered one of the greatest local threats to coral reefs[8,9,10,11,12]. On the GBR, the total annual value of commercial fisheries and aquaculture production is estimated at ca. $200 million, while recreational fishing activities are predicted to generate ca. $70 million p.a.[13]. Fishing is also one of the foremost recreational activities in Australia[14,15,16], with an estimated 3.8 million fishing trips taking place on the GBR alone in 2015–16[13]. Despite the relative importance of recreational fisheries both socially and economically[16], both line-fishing and spearfishing practices are notoriously difficult to monitor and quantify, and their impacts on the GBR (and elsewhere) are little understood[15,17,18].

Of the recreational fishing methods, spearfishing is a small but sometimes contentious component [16,19]. Given the well-documented impacts of line-fishing from discarded pollution, catch-and-release effects, lost gear, the requirement of bait and frequent levels of bycatch[17,20,21], spearfishing may be considered the more sustainable practice. Spearfishing is a highly selective method where participants can target specific individuals based on species and size, with limited impacts on non-target species[17,22,23,24,25]. In a comparison between line-fishers and spearfishers on the GBR, despite a similar catch composition and catching fewer fish overall, the mean size of target fish caught by spearfishers was significantly larger than that caught by line-fishers[17]. While the spearfishing technique may have a seemingly smaller impact on the marine environment, selectivity towards large individuals (that are likely fecund) and trophy species with low reproduction potential (e.g. wrasses, coral trout, sharks) may result in negative impacts to the viable breeding stock of spearfishing targets[17,19,26,27,28,29]. Therefore, recreational line-fishing and spearfishing have the potential to have broadly equivalent impacts on the marine environment[17].

Recent advances in boating technologies have increased spearfishers' access to offshore regions and consequently allow greater penetration of the GBR Marine Park (GBRMP)[16]. The development of powerful spear guns and snorkelling gear has also increased spearfisher's catch per unit effort and overall success[16,17]. As a result, there has been a substantial shift in target species within the spearfishing community over the past 60 years from coastal fishes to coral reef and pelagic species[16], with potential negative ecological impacts. Just three years after the introduction of spearfishing on an inshore reef on the GBR, vast decreases in the number (54%) and size (27%) of *Plectropomus leoparus* (coral trout) –the primary fisheries target on the GBR[34]– were recorded[29]. The general lack of information on spearfishing often causes it to be seldom considered in the development of fisheries management plans[18,30,31]. Due to the growing popularity and success of spearfishers, it is critical to understand their catch composition and preferences in order to inform management[16,18,29]. Note that this does not necessarily imply future restrictions, but rather to facilitate a balanced consideration of spearfisher values and preferences against fisheries impacts.

Here, we characterised the sport of spearfishing on the GBR using an online survey. Surveys targeted spearfishers currently operating along the coastline of Queensland, Australia, from Bundaberg (south) to Cooktown (north), directly adjacent to the GBRMP. Survey questions were developed to quantify (1) spatial differences in intensity of spearfishing across the Reef and Marine Park, (2) the composition of spearfishing catches on the GBR, and (3) the perceived changes in catch dynamics on the GBR over time. Coral reef fishes were selected for their contribution to fisheries catches on the GBR[17,32,33,34] (Pannach 2016 pers. comm.) and/or importance to ecosystem functioning on coral reefs[25,35]. It was predicted that spearfishers target offshore regions of the GBR owing to advances in spearing methods and technologies[16] and potential for larger catch sizes[32], particularly in northern regions where the Reef is significantly closer to mainland (i.e. Cairns, Cooktown). It was also predicted that *P. leopardus* would be the primary target species, as previously documented[17,32]. In light of recent changes in the population dynamics of *P. leopardus* on the GBR[36], in some cases related to spearfishing[29], we aimed to characterise the diversification of spearfishing catches predicting a greater representation of herbivores and invertivores. Effectively incorporating the impacts of spearfishing into fisheries management is reliant on the identification of target species and the potential ecological and social outcomes of this selective fishing method.

Methods

Location and study species

Spearfishers were surveyed from Bundaberg to Cooktown (Figure 1). Participants were grouped based on where they reside (and therefore frequently spearfish), forming seven distinct groups based on location (Figure 1). As these locations are among the most populous cities directly adjacent to the GBRMP, this survey method likely captured those whom most regularly partake in the sport of spearfishing.

Twenty-two common coral reef fish species were selected to examine spearfishing catches (Table 1). These species were selected because of their contribution to the catch of spearfishers operating on the GBR, established through preliminary observations of the prominent Queensland spearfishing online noticeboard “Northern Freediver”[37] and conversations with the Australian Underwater Federation Spearfishing Commissioner for Queensland, Michael Pannach (Pannach 2016 Pers. Comm.). Species were also chosen based on their ecological[25,27,35] or commercial[34] importance. Eight notionally ‘herbivorous’ species were chosen for their ecological importance, wide distribution range and population sizes and/or popularity within the spearfishing community[27,33,35,38]. We note that the true nutritional source of some of these species comprise a combination of microorganisms and detritus[39]. Eleven piscivorous species were chosen for their contribution to spearfishing catches and broad distributions across the GBR (Table 1). This included the coral trout, *P. leopardus*, the most heavily fished finfish species[17,34,36]. Three obligatory invertivorous fishes were chosen, including two tuskfish species (*Choerodon* spp.) (Table 1).

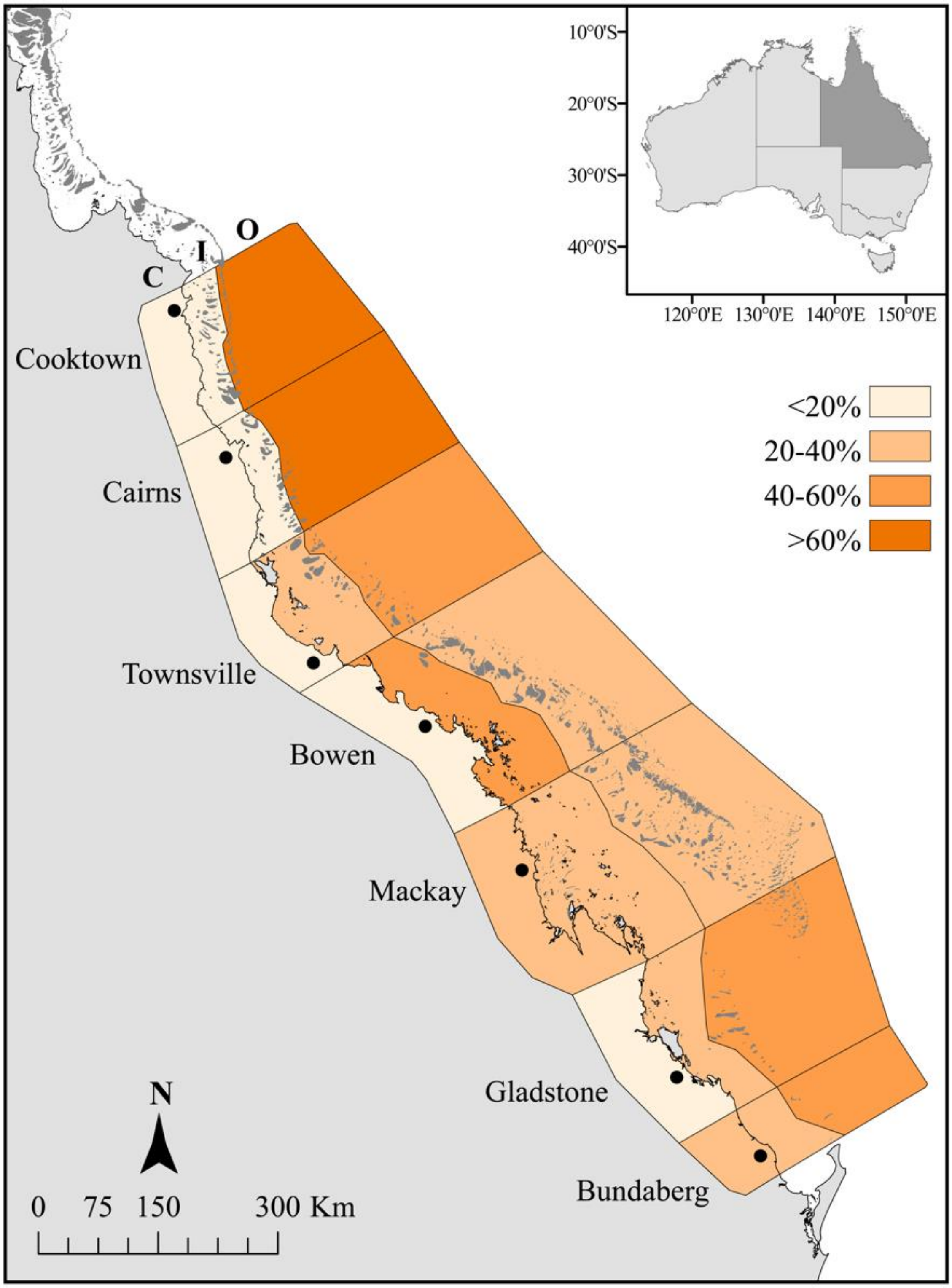

Figure A7.1: Major cities along the Queensland coast and Great Barrier Reef, where active spearfishers were surveyed. Colours reflect the percentage of time participants spent spearfishing on coastal (C), inshore (I) and offshore (O) reefs.

Table A7.1: List of species included in surveys of spearfishers operating on the Great Barrier Reef, Australia. Data was obtained from the online FishBase resource, unless otherwise stated. H (herbivore); I (invertivore); P (piscivore); LC (least concern); V (vulnerable); NT (near threatened); N/A (data not available).

Family	Species	Common names	Guild	IUCN listing	Size at maturity (cm)	Max size (cm)	Legal catch size (cm)	Legal bag limit	References
Acanthuridae	*Acanthurus dussumieri*	Eyestripe surgeonfish	H	LC	N/A	54	25	5	
	Naso unicornis	Bluespine unicornfish	H	LC	30-35	70	25	5	DeMartini et al 2014
Scaridae	*Bolbometopon muricatum*	Green humphead parrotfish	H	V	65	130	25	5	Chan et al. 2012
	Cetoscarus bicolor	Bicolour parrotfish	H	LC	30	50	25	5	
	Chlorurus bleekeri	Bleeker's parrotfish	H	LC	N/A	49	N/A	N/A	
	“ *microrhinos*	Steephead parrotfish	H	LC	37	70	N/A	N/A	Barba 2010
	Scarus ghobban	Blue-barred parrotfish	H	LC	41	90	25	5	Mellin et al 2007
Siganidae	*Siganus lineatus*	Goldlined rabbitfish	H	LC	19-24	43	N/A	N/A	Longenecker et al. 2014
Labridae	*Choerodon schoenleinii*	Black-spot tuskfish	I	NT	25	100	30	6	Fairclough & Nakazono 2004
	“ *venustus*	Venus tuskfish	I	LC	24	65	30	6	Platten et al. 2005
Lethrinidae	*Monotaxis grandoculis*	Bigeye seabream	I	LC	27.5	60	25	5	
	Lethrinus miniatus	Redthroat emperor	P	LC	36.1	90	38	8	
	“ *xanthochilus*	Yellowlip emperor	P	LC	42.4	70	25	5	Carpenter et al. 2016
Lutjanidae	*Aprion virescens*	Green jobfish	P	LC	44.9	112	38	5	
	Lutjanus argentimaculatus	Mangrove jack	P	LC	57	150	35	5	
	“ *johnii*	Golden snapper	P	LC	44	97	35	5	Kamali et al. 2006
	“ *rivulatus*	Maori seaperch	P	LC	40	80	25	5	Longenecker et al 2014
	“ *sebae*	Red emperor	P	LC	54.2	116	55	5	
	Macolor niger	Black and white snapper	P	LC	38	75	25	5	Longenecker et al. 2014
Serranidae	*Epinephelus cyanopodus*	Purple cod (Blue Maori)	P	LC	31-35	122	38	5	Lau & Parry-Jones 1999
	Plectropomus leopardus	Coral trout	P	NT	32-17	120	38	7	Longenecker et al. 2014
Rachycentridae	*Rachycentron canadum*	Cobia	P	LC	75	200	70	2	Babatunde et al. 2018

Survey description

An online survey was constructed based on preliminary assessments of spearfishers from the above online noticeboard[37] and an interview with the Queensland Spearfishing Commissioner (Pannach 2016 Pers. comm.). The anonymous survey was approved by the University of Queensland Institutional Human Research Ethics Approval board and participants gave written consent before partaking. A total of 149 surveys were completed between November 2016 and February 2017, of which 141 contained sufficient information to be used in analyses. Spearfishers were approached to complete the survey using the foremost Queensland spearfishing online noticeboard; the “Northern Freediver” spearfishing forum[37]. All surveys were completed online to ensure anonymity of participants. Primary questions within the survey were developed to quantify (1) the proportion of time spearfishers spent in different regions of the Reef and Marine Park, (2) the contribution of functionally important coral reef fish species to spearfisher’s catches, annually, and (3) the perceived changes in catch dynamics of three target species (representing each functional guild) on the GBR. Further details on these primary aims are outlined below.

Spearfisher experience and spatial dynamics on the GBR

Spearfishers were asked to estimate the amount of time spent spearfishing, in terms of hours per week and the number of spearfishing trips in an average month. These were used to approximate the amount of time each participant spent spearfishing per annum. This metric was used as a proxy for the experience for each spearfisher, under the assumption that more time performing a set task correlates with a greater skill level[40,41]. Participants were also asked whether they participate in spearfishing competitively and this was used as an additional measure of experience.

To identify regional differences in spearfishing dynamics across the GBR participants were grouped latitudinally in one of the seven major cities along the Queensland coastline (Figure 1). Spatial preferences of spearfishers were further examined longitudinally within each location, measured as the proportion of time each participant spent spearfishing on coastal, inshore or offshore reefs (Figure 1). Coastal regions were defined as areas accessible from the shore without the need of a vessel. Inshore sites (reefs and islands) were defined as regions that could be accessed by private boat with minimal effort (<2 hours) or commercial ferry. Such coastal and inshore regions were generally inside the GBRMP with varying levels of protection. Offshore sites were defined as reefs or islands that required a private boat for access and were either part of the structure of the GBR and Marine Park, or east into the Coral Sea. The average amount of time spearfishers spent in each region (coastal, inshore, offshore) was calculated for each location (Bundaberg–Cooktown).

Catch Composition

Survey participants were asked to estimate the proportional contribution of the twenty-two coral reef fish species (Table 1) to their average annual catch. Participants were presented with images and species common names to ensure accuracy of identification during surveys. An additional category (‘other predatory reef fishes’) was included to determine the potential contribution of alternate fish species to the annual catch of spearfishers. This category, however, was not further analysed at the species level as contributing species were not identified. The average proportional contribution of each study species to the annual catch of spearfishers was calculated for each location (Bundaberg–Cooktown) and region (coastal, inshore, offshore). Averages were also calculated within each functional group (herbivory, invertivory, piscivory) for each location and region.

Perceived changes in catch dynamics

Spearfishers were asked their opinion of changes in catch levels (increases, no change or decreases) over time. While the question was expected to reflect broad changes within the spearfisher community, responses likely reflect the personal catch dynamics of each participant. Three functionally-different and easily recognisable genera/families were targeted for this part of the survey; coral trout (Plectropomus spp., a piscivore), tuskfish (Choerodon spp., an invertivore) and parrotfish (Scaridae, notional 'herbivores'). Average perceptions of catch dynamics over time (increased, decreased, no change) were calculated for each location (Bundaberg–Cooktown).

Statistical analyses

Data on the proportion of time participants spent spearfishing were analysed by permutational multivariate analysis of variance (PERMANOVA) using 999 permutations[42]. Location (Bundaberg–Cooktown) and preferred region (coastal, inshore, offshore) were used as fixed factors. The covariates of experience through competition participation and experience through annual time spent spearfishing were originally included in the PERMANOVA design, but were removed from the analysis because of non-significant effects[42]. Pairwise and SIMPER tests were used to explore significant values between factors.

Species' contributions to the annual catch of spearfishers were analysed in several ways. Overall contribution of each species to catch were analysed using a one-way analysis of variance (ANOVA) in JMP 9[43], with species as the factor and percent contribution as the response. All percent data was log10 transformed before analysis. Spatial differences in catch were examined using PERMANOVA and SIMPER functions, as above. Analyses were completed first for all 22 coral reef fishes included in the survey, and second, for total contributions within each functional group (herbivory, invertivory, piscivory). Covariates (as above) were removed from the analyses because of their insignificant effects[41]. All PERMANOVAs and SIMPER tests were completed in PRIMER v7[42,44].

Pearson Chi-squared tests were used to test for differences in the perceived changes in spearfishing catch dynamics of coral trout, tuskfish and parrotfish. Separate analyses were performed for each species within each location (Bundaberg–Cooktown). Chi-squared comparisons were conducted in R-Studio[45].

Results

Survey summary statistics

A total of 141 responses from spearfishers active on the GBR were used in survey analyses. Participant sample size varied by location; Bundaberg (n=12), Gladstone (n=33), Mackay (n=13), Bowen (n=8), Townsville (n=26), Cairns (n=40), Cooktown (n=9). Participants ranged from 18 to over 60 years old, but gender was not determined. The experience of each spearfisher (competitive spearing or time spent spearing) did not have a significant effect on the proportion of time spent in each region or catch composition.

Spatial patterns of spearfishing

Those surveyed were estimated to spend between 48 and 2,688 h spearfishing on and adjacent to the GBRMP each year (mean = 329 h p.a.). The intensity of spearfishing (time spent) in coastal, inshore and offshore regions differed significantly among locations (Bundaberg–Cooktown) (Figure 1,S1; Tables S1,S2). Pairwise analysis (PERMANOVA) showed that spearfishers from Mackay operated differently to those from Gladstone (t=1.67, p=0.05), Townsville (t=1.85, p=0.029), Cairns (t=2.44, p=0.004) and Cooktown (t=2.27, p=0.009) (Figure 1,S1, Table S2,S3). On average, Cairns (68 ± 3.9%) and Cooktown (73 ± 9.5%) had the greatest proportion of spearfishers preferring to operate offshore (Figure 1,S1). Those from Mackay represented the greatest proportion operating from the coastline (32 ± 6.6%) (Figure 1,S1). Inshore and coastal regions were preferred by spearfishers from Bowen compared to those from Cairns (t=2.45, p=0.001) and Cooktown (t=2.04, p=0.035) (Figure 1,S1; Table S2,S3).

Catch composition by species

Species contributed differently to spearfisher catch composition (df=22, p<0.001) (Figure 2,S2; Table S4). *P. leopardus*, was consistently selected as the primary target for spearfishers regardless of location, representing 34% (±1.5) of catches (Tukey's HSD tests, Figure 2,S2; Table S4). Reef species listed as "other" represented the second highest proportion in the total catch of spearfishers (Figure S2; Table S4) but the species concerned are unknown. The blackspot tuskfish, *Cho. schoenleinii*, was a significant component overall (8 ± 0.6%) (Figure 2,S2; Table S4). Large piscivorous species, particularly those of the families Lethrinidae (e.g. *Lethrinius miniatus*) and Lutjanidae (e.g. *Lutjanus argentimaculatus*), were also important targets (Figure 2, S2; Table 1, S4). The most intensively speared herbivores were *Chlorurus microrhinos* (3 ± 0.6%) and *Scarus ghobban* (3 ± 0.5%), but herbivores comprised an overall small portion of spearfisher catches (Figure 2, S2; Table S4).

Overall, species specific catch composition varied significantly by location (Bundaberg–Cooktown) (df=6, p=0.004), but not by position across the reef (coastal, inshore, offshore) (Figure 2; Table S1). Pairwise analyses revealed that the composition of catch in Cairns was significantly different to that in Townsville (t=1.38, p=0.039), Mackay (t=1.54, p=0.01) and Cooktown (t=1.58, p=0.008), and catch compositions from Mackay were significantly different to Townsville (t=1.31, p=0.043) and Gladstone (t=1.44, p=0.01) (Figure 2; Table S5). The two tuskfish species, *Cho. schoenleinii* and *Cho. venustus*, represented the greatest differences in catch components of spearfishers operating from Cairns, with significantly fewer speared from Townsville, Mackay and Cooktown (Figure 2; Table S6). For Townsville, significant differences in catch composition were largely driven by the presence of *Sc. ghobban* and *Ch. microrhinos* compared to spearfishers from Mackay and Cairns (Figure 2; Table S6). Similarly, *Sc. ghobban* represented a greater proportion of spearfisher's catch from Mackay than in Cairns and Gladstone (Figure 2; Table S6). Despite its overall high contribution to spearing catches on the GRB (Figures 2, S2), *P. leopardus* did not drive significant differences between locations (Table S6).

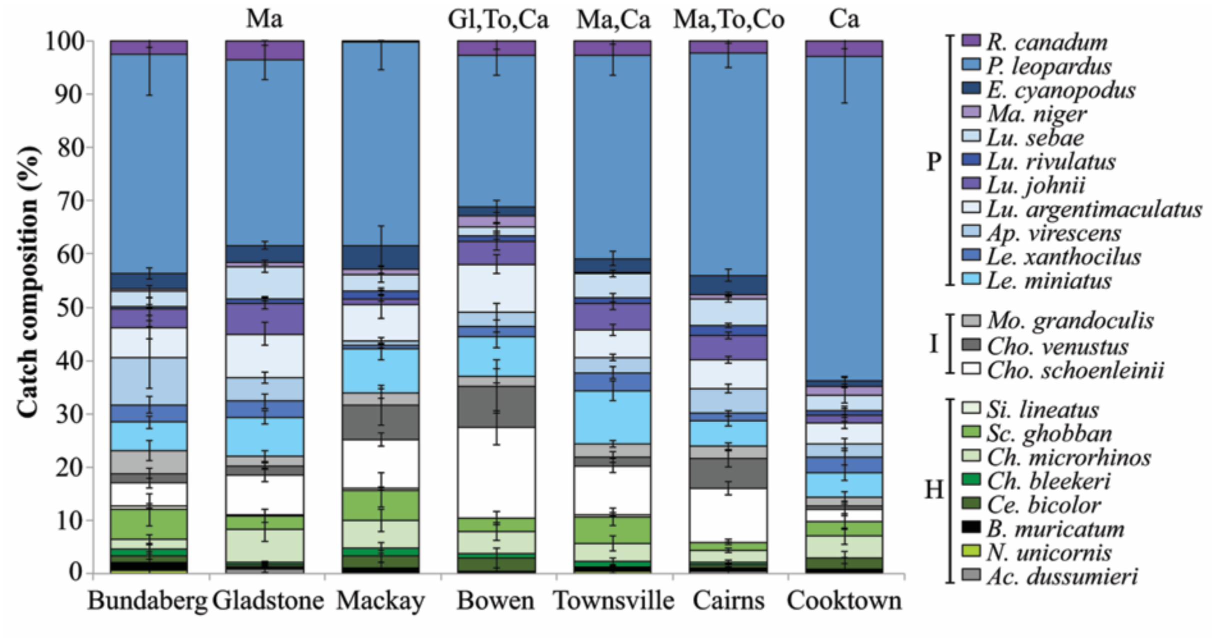

Figure A7.2: Mean proportion of study species in spearfishing catches across seven locations on the Great Barrier Reef, Australia. Species are grouped by functional guild (notional herbivores = greens; invertivores = greys; piscivores = blues). SIMPER tests: locations listed above bars are significantly different to the respective bar (Gladstone (Gl); Mackay (Ma); Townsville (To); Cairns (Ca); Cooktown (Co)). A full species list is available in Table 1.

Catch composition by functional guild

By functional group (herbivores, invertivores, piscivores), the catch composition of spearfishers differed significantly among locations (Bundaberg–Cooktown) (df=6, p=0.001) and across the shelf (coastal, inshore, offshore) (F=2.73, df=2, p=0.028) (Figure 3; Table S1). The interaction between these two factors was not significant (Table S1), nor were measures of spearfisher experience. Pairwise analysis revealed that the contribution of functional groups to the total catch of spearfishers operating from Cooktown was significantly different to those from Bundaberg (t=1.81, p=0.045), Mackay (t=2.99, p=0.001), Bowen (t=3.32, p=0.002), Townsville (t=2.36, p=0.01) and Cairns (t=2.81, p=0.001) (Figure 3, Table S7). Herbivores and invertivores were important drivers of the difference among catches, accounting for 34–65% of the significant differences between Cooktown and Bundaberg, Mackay, Bowen, Townsville and Cairns (SIMPER) (Figure 3; Table S8). In Cooktown, herbivores were preferentially targeted, making up almost twice the proportion of invertivores in the catch composition (Figure 3). Conversely, a greater proportion of invertivores contributed to the catch of spearfishers operating from Bundaberg, Mackay, Bowen, Townsville and Cairns (Figure 3). The catch composition of spearfishers from Gladstone contained a significantly greater proportion of invertivores compared to those operating from Cairns (SIMPER; Table S8). Despite their high contribution to the catch of spearfishers overall (77–81%; Figure 3), in no cases were significant differences in catch compositions driven by piscivorous species. This functional group only accounted for <1% of the differences between significantly different locations (SIMPER; Table S8).

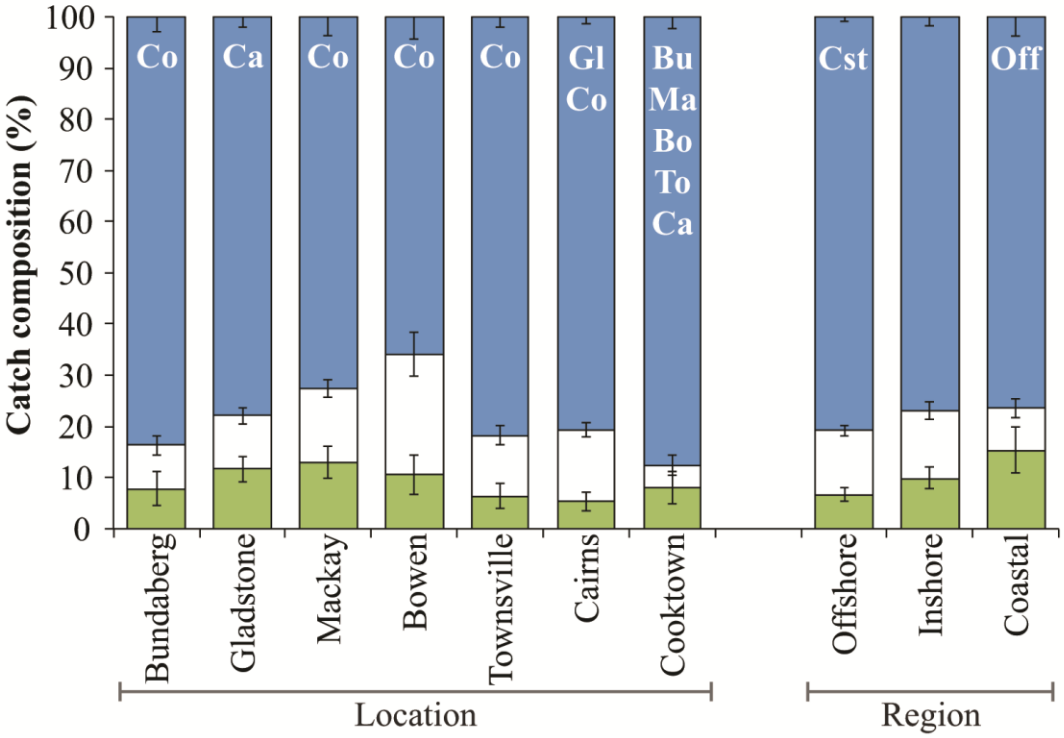

Figure A7.3: Mean contribution of herbivores (green bars), invertivores (white bars) and piscivores (blue bars) to the percent catch of spearfishers on the Great Barrier Reef, Australia. *Location* and *region* had significant effects on catch composition, but not their interaction. SIMPER tests: locations and regions listed on bars are significantly different to the respective bar (Bundaberg (Bu); Gladstone (Gl); Mackay (Ma); Bowen (Bo); Townsville (To); Cairns (Ca); Cooktown (Co); Offshore (Off); Coastal (Cst)).

Pairwise analyses revealed a significant difference between coastal and offshore regions (t=2.03, p=0.02), driven by differences in the catch of herbivores and invertivores (Figure 3; Table S7,S8). Preference towards spearing herbivores was twice as high in coastal regions compared to reefs offshore, while invertivores contributed more to spearfisher catches offshore (Figure 3). Piscivores accounted for ~1% of the difference between coastal and offshore regions (SIMPER; Table S8).

Perceived changes in catch

Significant differences in the perceived changes in catch of coral trout, tuskfish and parrotfish were evident across locations (Bundaberg–Cooktown) (Pearson Chi-squared tests, Figure 4; Table S9). Spearfishers generally noted an increase or no change in the catch of coral trout (Figure 4; Table S9). A perceived decrease in catch of coral trout was greatest in Mackay, with 39% of survey participants suggesting so (Figure 4). No spearfishers from Bundaberg or Bowen perceived a decrease in coral trout catches (Figure 4; Table S9). The greatest perceived increases in coral trout catches were documented for Bundaberg and Cooktown, as suggested by 50% and 56% of participants, respectively (Figure 4). Similarly, most spearfishers recorded an increase or no change in the catch of tuskfish, with no decrease reported in Mackay or Cooktown (Figure 4; Table S9). Participants from Bundaberg considered that tuskfish catches had dropped more severely than suggested at other locations (17% of participants), while those from Mackay noted the greatest perceived increase (62% of participants) (Figure 4; Table S9). Catches of parrotfish varied largely with latitude. Spearfishers from Bundaberg (south) suggested the smallest decrease in parrotfish catches over time (8.3% of participants), with an incremental number of survey participants suggesting a decrease in parrotfish catches northwards to Cooktown (56% of participants) (Figure 4; Table S9). Mackay was the exception, with the greatest perceived decrease in parrotfish catches over time (62% of participants) (Figure 4). Overall, few spearfishers stated that parrotfish catch numbers had increased (0–18%) (Figure 4).

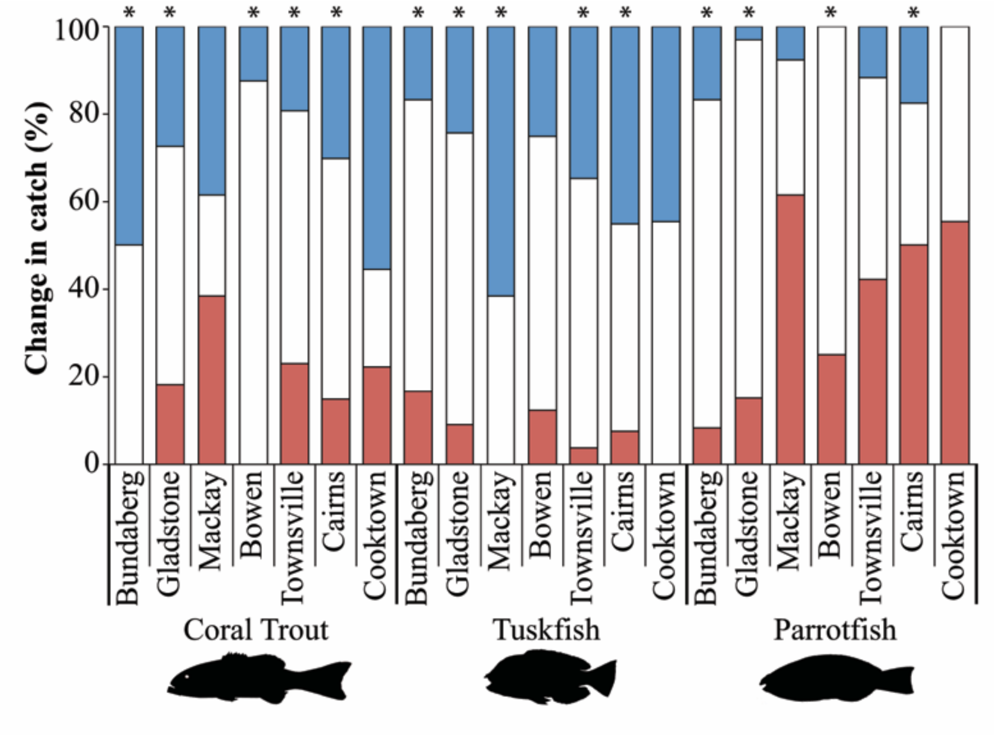

Figure A7.4: Total perception of changes in catch (decrease = red bars, no change = white bars, increase = blue bars) of coral trout (*Plectropomus* spp.), tuskfish (*Choerodon* spp.) and parrotfish (Scaridae spp.) from surveys taken by spearfishers along the Great Barrier Reef, Australia.

Discussion

The activities, preferences and perceptions of 141 spearfishers were evaluated along the coast of the GBR. We document significant differences among regions (coastal, inshore, offshore) and species that spearfishers target based on their location (Bundaberg–Cooktown). *Plectropomus leopardus* dominated catch composition, which is also the primary target species in recreational line-based and commercial fisheries of the GBR[34,36]. Together, piscivores and invertivores dominated catch composition while herbivorous fishes were seldom targeted. Interestingly, spatial differences were driven by variations in the catch of herbivorous and invertivorous fishes (i.e. *Sc. ghobban*, *Cho. schoenleinii*). Perceived changes in catch within the spearfishing community also varied spatially, most interestingly for herbivores, which were broadly suggested to have decreased following a parrotfish-centric education campaign targeted at spearfishers[46].

Spatial selectivity in spearfishing practices, as shown here, can result in regionally specific ecological consequences. The opening of the Palm Archipelago (an inshore reef network near Townsville) to spearfishing in 2004 resulted in a 54% reduction in abundance and a 27% reduction in mean size of the target population (*P. leopardus*) in just three years[29]. This is clear evidence that the intensive and selective nature of recreational spearfishing can have significant impacts on the population dynamics of coral reef fishes. The incremental level of spearfishing pressure from coastal (14%) to inshore (32%) to offshore (54%) regions from Townsville may reflect historical patterns of overfishing on near-shore reefs[29], such that there is increased necessity to travel offshore in search of a successful catch[32]. Unfortunately, the survey method used here does not provide detailed information on the specific reefs most heavily targeted by spearfishers. More broadly, we outline spearfishing hotspots for each location (Bundaberg–Cooktown), and thus regions where the potential impacts of spearfishing may be heightened along the GBR.

P. leopardus is the most commonly fished finfish species on the GBR, both commercially and recreationally[34]. An estimated 749 tonnes are harvested from the GBR each year by the commercial industry, with an additional 103,000 individuals harvested by recreational spear- and line-fishers[34]. Preference for this species by spearfishers was evident here (34 ± 1.5% total catch), as previously shown[17,29]. Although *P. leopardus* is a Near Threatened species[47], its fishery on the GBR is well monitored and managed[34]. However, as it is a protogenic hermaphroditic species[48,49], the sex ratio of adult *P. leopardus* could potentially be impacted by intensive fishing[50,51,52]. The rapid decrease in *P. leopardus* size and abundance in the Palm Archipelago owing to spearfishing[29] indicates the potential ecological impacts of the selective and targeted methods of spearfishers on the GBR and elsewhere. The disproportionate contribution of this species to the catch composition of spearfishers argues for an evaluation of total harvest from spearfishing with a concomitant consideration of impacts on stocks.

Other large predatory coral reef fishes such as snappers and emperors (Lethrinidae, Lutjanidae) were also commonly speared across all locations, but the demographic impacts of such fishing are unknown. The slow growth, great longevity, and large age at maturity of many snappers and emperors[53,54,55] indicate their potential vulnerability to the selectivity of spearfishing, especially in regions where primary targets (i.e. *P. leopardus*) become increasingly sparse[56].

Spearfishing preferences were largely weighted towards piscivorous species (77–81%), but herbivore and invertivore contributions varied significantly. *Choerodon schoenleinii*, a large invertivorous tuskfish, was the second most intensively speared species across all locations (8 ± 0.6% total catch). Our data show that *Choerodon* spp. were often the primary drivers of the variation among locations and were most favoured by spearfishers operating from Bowen and Cairns. The drivers of such spatial differences in tuskfish preferences are unknown, especially given the broad distribution of *Cho. schoenleinii* and *Cho. venustus* across the GBR[57,58]. As a Near Threatened and monandric protogynous hermaphrotidic species with males only occurring in the largest size bracket[57], *Cho. schoenleinii* may be particularly vulnerable to the selectivity of spearfishing. The reproductive biology of this species has resulted in rapid population declines on other coral reefs attributed to overfishing[57,59,60], highlighting the importance of monitoring catch trends of *Cho. schoenleinii* and other tuskfish within the spearfishing community, perhaps most importantly in Bowen and Cairns.

Although herbivorous coral reef fishes were rarely included in the catches of spearfishers, two species were particularly important. The steephead parrotfish, *Chlorurus microrhinos*, and the blue-barred parrotfish, *Scarus ghobban*, represented 3% (±0.6%) and 3% (±0.5%) of the catch composition, respectively. *Ch. microrhinos* is likely speared because of its high abundance across the Reef[61], although the cause of the higher proportion of *Sc. ghobban* was not confirmed. Both species are broadly distributed[62], but vary in their ecological and functional significance[38]. *Ch. microrhinos* is a particularly important species on midshelf reefs, while *Scarus* spp. are more functionally important inshore[35,38,53]. Our data shows that parrotfishes were more heavily targeted by spearfishers on coastal and inshore regions, where their functional importance might be relatively high[37,53]. Despite their relatively low contribution to the total catch of spearfishers across the reef, the selectivity of spearfishing towards some inshore herbivores could drive significant alterations to the ecological functioning of inshore reefs, particularly given the propensity for algal growth on inshore reefs[64,65]. Interestingly, the region with the greatest reported catch composition of herbivores (Mackay) also perceived the greatest decrease in herbivores in their catch over time. A demographic analysis of fishery impacts on parrotfishes would be desirable, as has been done elsewhere[7].

Species preferences of spearfishers are likely driven by species' availability and perceived prestige from within the spearfishing community[36,66]. The high proportion of *Sc. ghobban* and *Ch. microrhinos* in overall annual catch compared to other herbivorous species could render these species particularly vulnerable to spearfishing selectivity with potential impacts on population biology (though we note that smaller-bodied parrotfishes are generally highly resilient). The IUCN-listed Vulnerable green humphead parrotfish, *Bolbometopon muricatum* was seemingly unpopular to spearfishers operating on the GBR (0.5 ± 0.1% total catch p.a.). While there is no immediate threat to this species on the GBR, its biology renders it highly susceptible to fishing and spearfishing activities, as documented for other coral reefs where it is often targeted at night[22,25,67,68].

Unlike line-based fishing practices, spearfishers can provide critical information on fish population dynamics through direct underwater observations[18], with a potentially broader understanding of the marine community. Views of survey participants provide anecdotal evidence on the catch and population dynamics of coral trout, tuskfish and parrotfish along the Queensland coastline (Bundaberg–Cooktown). Trends in the decreases of parrotfish landings, were likely strongly influenced by the (then) newly implemented Coral Reef Recovery Program[46], which included a fisheries education campaign targeting spearfishers to limit herbivore catches[30,63]. The Australian spearfishing community is considered to be sufficient at self-regulating the catch of target species and sizes, and in detecting and acting on early warning signs of decreases in species populations[69]. For example, the Queensland and New South Wales spearfishing communities were responsible for reporting the dramatic decrease in populations of the grey nurse shark, *Charcharias taurus*–a once popular spearfishing target and now a recovered abundant species along the Australian east coast[69]. Furthermore, in a temperate region of Australia, the exclusion of spearfishing using a marine protected area had a significantly positive effect on the previously overfished populations of two target species; red morwong (*Cheilodactylus fuscus*) and yellow-fin bream (*Acanthopagrus australis*)[70].

Despite their reported decrease in population numbers and sizes following increased spearfishing[29], catches of P. leopardus were generally noted to have increased or remained stable across all locations, Townsville inclusive. Regardless of the target species, the fact that many fishers perceived significant changes in catch composition over time suggests that the sport is changing, with potentially deleterious impacts on the fishery. Due to the highly selective nature of spearfishing methods towards larger individuals[17,22,23,24], it would be appropriate to monitor populations of new target and trophy species in order to reduce their susceptibility to overharvest. Moreover, that fisher perceptions varied among locations lends credibility to their sensitivity. The Queensland spearfishing community has been highly responsive to previous campaigns and issues[46] and self-regulatory and monitoring approaches have been highly successful in the past[69]. Spearfishers might consider holding local discussions to review their perceptions and consider whether management actions are warranted. This may become increasingly important if Australia's fish stocks deteriorate in a changing climate31.

Acknowledgements

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Supplementary Material

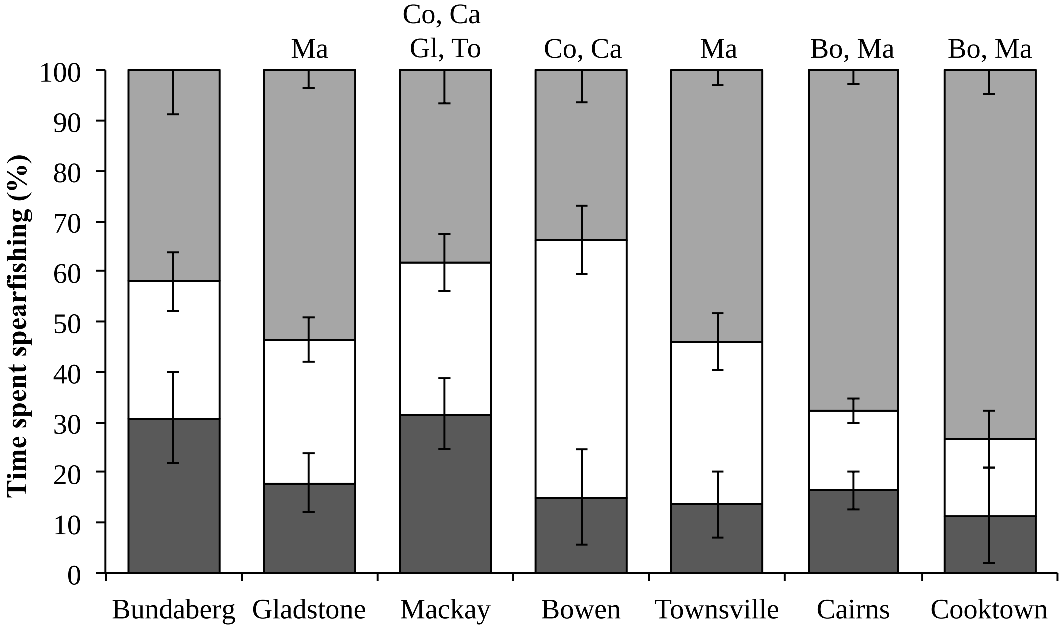


Figure A7.S1: Mean proportion of time participants spent spearfishing in coastal (dark bars), inshore (white bars) and offshore (grey bars) reefs in seven locations across the Great Barrier Reef, Australia. SIMPER tests: locations listed above bars are significantly different to the respective bar (Gladstone (Gl); Mackay (Ma); Bowen (Bo); Townsville (To); Cairns (Ca); Cooktown (Co)).

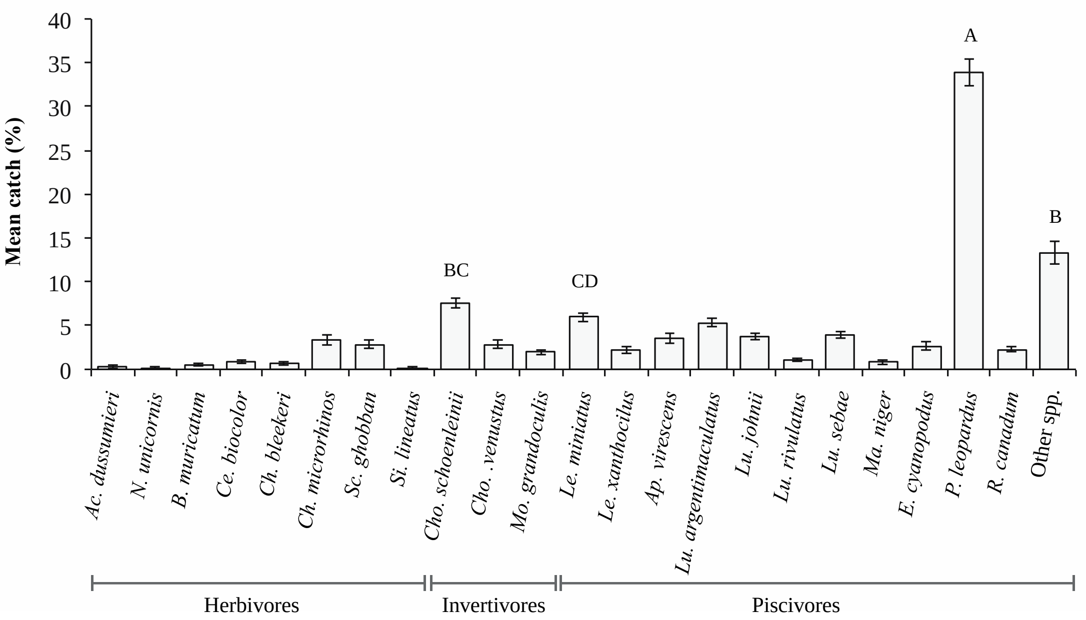


Figure A7.S2: Mean proportion of study species in total catch of spearfishers on the Great Barrier Reef, Australia. Tukey's HSD test: letters that differ are significantly different (see Table S4 for more detail).

Table A7.S1: PERMANOVA results on the (A.) proportion of time participants spent spearfishing in each location (Bundaberg–Cooktown); (B.) percent contribution of target coral reef fishes to the catch of spearfishers in each location (Bundaberg–Cooktown); and (C.) percent contribution of coral reef fish functional groups (herbivores, invertivores, piscivores) to spearfisher catches by location (Bundaberg–Cooktown) and region (coastal, inshore, offshore). Significant values in bold.

Source	df	SS	MS	*p* value	Unique perms
A. *Proportion of time spent spearfishing*					
Location	6	91.2	15.2	**0.019**	999
Res	134	949.1	7.08		
Total	140	1040.3			
B. *Percent contribution of target species*					
Location	6	154.2	25.7	**0.004**	997
Res	134	2357.8	17.6		
Total	140	2512.1			
C. *Percent contribution of functional groups*					
Location	6	49.0	8.17	**0.001**	999
Region	2	15.1	7.56	**0.028**	998
Interaction	10	38.8	3.88	0.108	997
Res	122	388.3	2.77		
Total	140	441.3			

Table A7.S2: Pairwise test (PERMANOVA) results on the proportion of time spearfishers spent fishing in each location (Bundaberg–Cooktown) on the Great Barrier Reef, Australia. Significant values in bold.

Location	df	t	*p* value	Unique perms
Bowen, Bundaberg	18	1.29	0.206	960
Bowen, Cairns	46	2.45	**0.001**	946
Bowen, Cooktown	15	2.04	**0.035**	757
Bowen, Gladstone	39	1.42	0.124	983
Bowen, Mackay	19	1.66	0.051	966
Bowen, Townsville	32	1.39	0.143	957
Bundaberg, Cairns	50	1.67	0.059	997
Bundaberg, Cooktown	19	1.53	0.086	946
Bundaberg, Gladstone	43	0.98	0.411	998
Bundaberg, Mackay	23	0.58	0.775	997
Bundaberg, Townsville	36	1.16	0.273	998
Cairns, Cooktown	47	0.53	0.754	894
Cairns, Gladstone	71	1.28	0.175	998
Cairns, Mackay	51	2.44	**0.004**	997
Cairns, Townsville	64	1.35	0.179	998
Cooktown, Gladstone	40	0.95	0.403	975
Cooktown, Mackay	20	2.27	**0.009**	943
Cooktown, Townsville	33	0.96	0.363	958
Gladstone, Mackay	44	1.67	**0.05**	998
Gladstone, Townsville	57	0.32	0.948	997
Mackay, Townsville	37	1.85	**0.029**	999

Table A7.S3: SIMPER test results on the proportion of time spearfishers spent fishing in each location (Bundaberg–Cooktown) on the Great Barrier Reef, Australia. Locations in bold represent significant values identified in PERMANOVA tests (see Table S2).

Location	Region	Av.Value		Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Bowen	Inshore	3.89		0.177	0.54	2.66	2.66
	Offshore	2.8		3.16	0.53	47.52	50.19
	Coastline	1.69		3.31	0.62	49.81	100
Bundaberg	Offshore	3.18		2.45	0.45	30.58	30.58
	Inshore	2.67		2.68	0.51	33.48	64.07
	Coastline	2.67		2.87	0.52	35.93	100
Cairns	Offshore	4.1		0.553	0.2	8.95	8.95
	Inshore	1.91		2.79	0.57	45.1	54.04
	Coastline	1.92		2.84	0.57	45.96	100
Cooktown	Offshore	4.22		0.217	0.48	3.47	3.47
	Coastline	1.46		2.99	0.61	47.76	51.23
	Inshore	1.82		3.06	0.61	48.77	100
Gladstone	Offshore	3.52		2	0.38	23.55	23.55
	Coastline	1.8		3.23	0.58	38.08	61.63
	Inshore	2.47		3.25	0.55	38.37	100
Mackay	Coastline	3.18		1.11	0.33	21.52	21.52
	Inshore	2.97		1.88	0.42	36.59	58.11
	Offshore	3.16		2.16	0.43	41.89	100
Townsville	Offshore	3.64		1.45	0.34	19.06	19.06
	Coastline	1.65		2.87	0.59	37.67	56.73
	Inshore	2.61		3.29	0.54	43.27	100
Location	**Region**	**Av.Value 1**	**Av.Value 2**	**Av.Sq.Dist**	**Sq.Dist/SD**	**Contrib%**	**Cum.%**
Bowen, Bundaberg	Coastline	1.69	2.67	6.5	0.96	41.31	41.31
	Offshore	2.8	3.18	5.15	0.73	32.7	74
	Inshore	3.89	2.67	4.09	0.61	26	100
Bowen, Cairns	Inshore	3.89	1.91	6.79	0.9	38.82	38.82
	Coastline	1.69	1.92	5.72	0.98	32.71	71.53
	Offshore	2.8	4.1	4.98	0.65	28.47	100
Bowen, Cooktown	Coastline	2.67	1.92	5.97	0.91	38.89	38.89
	Inshore	2.67	1.91	5.75	0.92	37.46	76.35
	Offshore	3.18	4.1	3.63	0.54	23.65	100
Bowen, Gladstone	Inshore	3.89	1.82	7.15	0.94	40.28	40.28
	Coastline	1.69	1.46	5.61	0.98	31.65	71.93
	Offshore	2.8	4.22	4.98	0.64	28.07	100
Bowen, Mackay	Coastline	2.67	1.46	6.77	1	41.8	41.8

	Inshore	2.67	1.82	5.89	0.94	36.38	78.17
	Offshore	3.18	4.22	3.54	0.53	21.83	100
Bowen, Townsville	Coastline	1.92	1.46	5.64	1	47.68	47.68
	Inshore	1.91	1.82	5.44	0.97	45.99	93.67
	Coastline	1.69	1.8	6.04	0.98	36.43	36.43
Bundaberg, Cairns	Inshore	3.89	2.47	5.32	0.73	32.09	68.53
	Offshore	2.8	3.52	5.22	0.71	31.47	100
	Coastline	2.67	1.8	6.51	0.95	39.57	39.57
Bundaberg, Cooktown	Inshore	2.67	2.47	5.65	0.85	34.32	73.88
	Offshore	3.18	3.52	4.3	0.63	26.12	100
	Inshore	1.91	2.47	6.18	0.95	41.5	41.5
Bundaberg, Gladstone	Coastline	1.92	1.8	5.91	0.98	39.68	81.18
	Offshore	4.1	3.52	2.8	0.46	18.82	100
	Inshore	1.82	2.47	6.29	0.96	42.43	42.43
Bundaberg, Mackay	Coastline	1.46	1.8	5.91	0.98	39.89	82.32
	Offshore	4.22	3.52	2.62	0.44	17.68	100
	Coastline	1.69	3.18	6.15	0.97	44.66	44.66
Bundaberg, Townsville	Offshore	2.8	3.16	4.89	0.72	35.52	80.18
	Inshore	3.89	2.97	2.73	0.5	19.82	100
	Inshore	2.67	2.97	4.29	0.71	34.48	34.48
Cairns, Cooktown	Offshore	3.18	3.16	4.23	0.65	34.05	68.52
	Coastline	2.67	3.18	3.91	0.69	31.48	100
	Inshore	1.91	2.97	5.6	0.9	38.91	38.91
Cairns, Gladstone	Coastline	1.92	3.18	5.38	0.87	37.43	76.35
	Offshore	4.1	3.16	3.4	0.52	23.65	100
	Coastline	1.46	3.18	6.65	1.05	42.22	42.22
Cairns, Mackay	Inshore	1.82	2.97	5.79	0.92	36.76	78.99
	Offshore	4.22	3.16	3.31	0.51	21.01	100
	Coastline	1.8	3.18	6.04	0.95	39.6	39.6
Cairns, Townsville	Inshore	2.47	2.97	5.15	0.81	33.79	73.39
	Offshore	3.52	3.16	4.06	0.61	26.61	100
	Coastline	1.69	1.65	5.66	0.98	36.58	36.58
Cooktown, Gladstone	Inshore	3.89	2.61	4.95	0.7	32.02	68.61
	Offshore	2.8	3.64	4.86	0.68	31.39	100
	Coastline	2.67	1.65	6.43	0.96	40.43	40.43
Cooktown, Mackay	Inshore	2.67	2.61	5.62	0.83	35.36	75.8
	Offshore	3.18	3.64	3.85	0.59	24.2	100
	Coastline	1.91	2.61	6.38	0.94	45.16	45.16

Cooktown, Townsville	Coastline	1.92	1.65	5.6	0.98	39.64	84.8
	Offshore	4.1	3.64	2.15	0.42	15.2	100
	Inshore	1.82	2.61	6.51	0.95	46.83	46.83
Gladstone, Mackay	Coastline	1.46	1.65	5.45	0.99	39.26	86.08
	Offshore	4.22	3.64	1.93	0.4	13.92	100
	Inshore	2.47	2.61	6.34	0.88	40.66	40.66
Gladstone, Townsville	Coastline	1.8	1.65	5.91	0.98	37.9	78.56
	Offshore	3.52	3.64	3.34	0.54	21.44	100
	Inshore	3.18	1.65	6.11	0.97	41.4	41.4
Mackay, Townsville	Inshore	2.97	2.61	5.04	0.79	34.14	75.55
	Offshore	3.16	3.64	3.61	0.57	24.45	100
	Coastline	1.69	2.67	6.5	0.96	41.31	41.31

Table A7.S4: One-way ANOVA results on the percent contribution of target coral reef fish species to the total catch of spearfishers across the Great Barrier Reef, Australia. Significant values in bold; Tukey's HSD tests: letters that differ are significantly different.

Source	df	SS	MS	*p* value
Species	22	347.8	15.8	**<0.001**
Res	3220	481.5	0.15	
Total	3242	829.2		

Post-*hoc* Tukey's HSD												
P. leopardus	A											
Other spp.		B										
Cho. schoenleinii		B	C									
Le. miniatus			C	D								
Lu. argentimaculatus			C	D	E							
Lu. sebae				D	E	F						
Lu. johnii					E	F	G					
Ap. virescens						F	G	H				
Ch. microrhinos						F	G	H	I			
R. canadum							G	H	I			
E. cyanopodus							G	H	I			
Sc .ghobban								H	I	J		
Cho. venustus								H	I	J		
Mo. grandoculis								H	I	J		
Le. xanthocilus								H	I	J	K	
Lu. rivulatus									I	J	K	L
Ce. bicolor										J	K	L
Ma. niger											K	L
Ch. bleekeri											K	L
B. muricatum											K	L
Si. lineatus												L
Ac. dussumieri												L
N. unicornis												L

Table A7.S5: Pairwise test (PERMANOVA) results on the percent contribution of target coral reef fish to the catch of spearfishers by location (Bundaberg–Cooktown) on the Great Barrier Reef, Australia. Significant values in bold.

Location	df	t	*p* value	Unique perms
Bundaberg, Gladstone	43	1.015	0.43	997
Bundaberg, Mackay	23	0.93833	0.58	999
Bundaberg, Bowen	18	1.0833	0.29	991
Bundaberg, Townsville	36	0.88166	0.70	998
Bundaberg, Cooktown	19	0.79936	0.85	997
Gladstone, Mackay	44	1.4417	**0.010**	998
Gladstone, Bowen	39	1.1069	0.25	999
Gladstone, Cooktown	40	1.1939	0.13	997
Mackay, Bowen	19	0.87299	0.71	997
Mackay, Cooktown	20	1.194	0.15	997
Townsville, Gladstone	57	0.98304	0.50	998
Townsville, Mackay	37	1.314	**0.043**	997
Townsville, Bowen	32	1.1179	0.24	998
Townsville, Cooktown	33	1.3385	0.054	998
Cairns, Bundaberg	50	1.2579	0.067	997
Cairns, Gladstone	71	1.0991	0.25	998
Cairns, Mackay	51	1.5378	**0.010**	998
Cairns, Bowen	46	1.1242	0.22	998
Cairns, Townsville	64	1.3797	**0.039**	999
Cairns, Cooktown	47	1.5802	**0.008**	999
Cooktown, Bowen	15	1.3767	0.055	981

Table A7.S6: SIMPER test results on the percent contribution of target coral reef fish to the catch of spearfishers by location (Bundaberg–Cooktown) on the Great Barrier Reef, Australia. Results only shown for the three highest contributing species. Locations in bold represent significant values identified in PERMANOVA tests (see Table S5).

Location	Species	Av.Value		Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Bundaberg	*Lu. argentimaculatus*	1.18		1.67	0.57	7.79	80.93
	Sc. ghobban	0.875		1.89	0.5	8.8	89.73
	Ap. virescens	1.11		2.21	0.5	10.27	100
Gladstone	*Ap. virescens*	1.03		1.4	0.56	7.26	74.54
	Le. miniatus	1.55		1.45	0.54	7.52	82.06
	Cho. schoenleinii	1.58		1.57	0.55	8.13	90.19
Mackay	*Ch. microrhinos*	0.977		1.78	0.56	9.52	80.26
	Sc. ghobban	0.937		1.78	0.5	9.56	89.82
	Cho. venustus	0.99		1.9	0.5	10.18	100
Bowen	*Le. miniatus*	1.73		1.27	0.54	7.3	78.49
	Ch. microrhinos	1.08		1.4	0.61	8.01	86.5
	Cho. venustus	1.05		2.35	0.54	13.5	100
Townsville	*Lu. argentimaculatus*	1.34		1.15	0.55	6.86	74.99
	Ch. microrhinos	0.699		1.25	0.47	7.44	82.43
	Le. miniatus	1.89		1.39	0.5	8.28	90.71
Cairns	*Ap. virescens*	1.23		1.17	0.55	7.52	81.48
	Le. miniatus	1.2		1.25	0.54	8	89.48
	Cho. venustus	1.01		1.64	0.51	10.52	100
Cooktown	*Lu. sebae*	0.743		1.26	0.56	7.59	76.05
	R. canadum	0.758		1.3	0.57	7.88	83.92
	Le. xanthocilus	0.758		1.3	0.57	7.88	91.8
Location	**Species**	**Av.Value 1**	**Av.Value 2**	**Av.Sq.Dist**	**Sq.Dist/SD**	**Contrib%**	**Cum.%**
Bundaberg, Gladstone	*Ap. virescens*	1.11	1.03	3.38	0.79	8.32	8.32
	Lu. johnii	0.62	1.35	3.13	0.99	7.68	16
	Lu. argentimaculatus	1.18	1.65	3.05	0.88	7.5	23.5
Bundaberg, Mackay	*Sc. ghobban*	0.88	0.94	3.38	0.77	8.51	8.51
	Ap. virescens	1.11	0.29	3.15	0.65	7.94	16.45
	Lu. argentimaculatus	1.18	1.39	3.06	0.88	7.69	24.14
Bundaberg, Bowen	*Cho. venustus*	0.53	1.05	3.16	0.73	7.95	7.95
	Ap. virescens	1.11	0.75	3.16	0.72	7.93	15.88
	Cho. schoenleinii	1.40	2.80	2.85	0.85	7.16	23.04

Bundaberg, Townsville	*Sc. ghobban*	0.88	1.00	3.25	0.82	8.65	8.65
	Ap. virescens	1.11	0.98	2.9	0.76	7.73	16.37
	Lu. johnii	0.62	1.32	2.85	0.97	7.58	23.95
Bundaberg, Cooktown	*Ap. virescens*	1.11	0.69	3.16	0.71	8.57	8.57
	Sc. ghobban	0.88	0.72	2.82	0.77	7.67	16.24
	Le. xanthocilus	0.77	0.76	2.39	0.85	6.49	22.73
Gladstone, Mackay	*Ch. microrhinos*	0.85	0.98	3.49	0.8	8.68	8.68
	Sc. ghobban	0.41	0.94	2.9	0.69	7.22	15.9
	Lu. argentimaculatus	1.65	1.39	2.85	0.84	7.1	23.01
Gladstone, Bowen	*Cho. venustus*	0.45	1.05	3.18	0.72	8.48	8.48
	Cho. schoenleinii	1.58	2.80	3.18	0.8	8.47	16.95
	Ch. microrhinos	0.85	1.08	3.1	0.85	8.27	25.22
Gladstone, Cooktown	*Cho. schoenleinii*	1.58	0.69	3.26	1.02	8.78	8.78
	Ch. microrhinos	0.85	1.13	3.01	0.87	8.1	16.88
	Lu. johnii	1.35	0.44	2.89	0.99	7.77	24.65
Mackay, Bowen	*Cho. venustus*	0.99	1.05	3.82	0.79	10.82	10.82
	Ch. microrhinos	0.98	1.08	2.87	0.93	8.14	18.95
	Sc. ghobban	0.94	0.75	2.63	0.76	7.47	26.42
Mackay, Cooktown	*Cho. schoenleinii*	2.15	0.69	3.61	1.24	9.83	9.83
	Sc. ghobban	0.94	0.72	2.76	0.76	7.52	17.36
	Ch. microrhinos	0.98	1.13	2.76	0.95	7.52	24.88
Townsville, Gladstone	*Ch. microrhinos*	0.70	0.85	3.06	0.71	8.48	8.48
	Le. miniatus	1.89	1.55	2.86	0.85	7.93	16.41
	Sc. ghobban	1.00	0.41	2.82	0.78	7.83	24.24
Townsville, Mackay	*Sc. ghobban*	1.00	0.94	3.15	0.81	8.56	8.56
	Ch. microrhinos	0.70	0.98	2.92	0.82	7.92	16.48
	Cho. venustus	0.35	0.99	2.88	0.68	7.81	24.29
Townsville, Bowen	*Cho. venustus*	0.35	1.05	3.26	0.7	9.36	9.36
	Ch. microrhinos	0.70	1.08	2.56	0.89	7.35	16.72
	Sc. ghobban	1.00	0.75	2.51	0.84	7.21	23.93
Townsville, Cooktown	*Cho. schoenleinii*	1.96	0.69	3.63	1.14	10.27	10.27
	Le. miniatus	1.89	1.22	3	0.88	8.48	18.75
	Sc. ghobban	1.00	0.72	2.65	0.84	7.49	26.24
Cairns, Bundaberg	*Ap. virescens*	1.23	1.11	3.18	0.83	8.42	8.42
	Lu. johnii	1.35	0.62	2.75	1.09	7.28	15.7

	Cho. venustus	1.01	0.53	2.66	0.76	7.05	22.75
Cairns, Gladstone	*Le. miniatus*	1.20	1.55	2.75	0.91	7.84	7.84
	Cho. schoenleinii	2.05	1.58	2.72	0.83	7.78	15.62
	Cho. venustus	1.01	0.45	2.68	0.75	7.64	23.26
Cairns, Mackay	*Cho. venustus*	1.01	0.99	3.35	0.79	9.22	9.22
	Sc. ghobban	0.46	0.94	2.61	0.69	7.18	16.4
	Le. miniatus	1.20	1.87	2.58	0.88	7.1	23.5
Cairns, Bowen	*Cho. venustus*	1.01	1.05	3.66	0.81	10.94	10.94
	Le. miniatus	1.20	1.73	2.61	0.94	7.81	18.75
	Ap. virescens	1.23	0.75	2.38	0.94	7.13	25.87
Cairns, Townsville	*Le. miniatus*	1.20	1.89	3.03	0.9	9.12	9.12
	Cho. venustus	1.01	0.35	2.75	0.72	8.26	17.38
	Sc. ghobban	0.46	1.00	2.53	0.79	7.59	24.97
Cairns, Cooktown	*Cho. schoenleinii*	2.05	0.69	3.79	1.11	10.76	10.76
	Cho. venustus	1.01	0.23	2.62	0.71	7.43	18.19
	Lu. johnii	1.35	0.44	2.51	1.12	7.13	25.32
Cooktown, Bowen	*Cho. schoenleinii*	0.69	2.80	5.58	1.39	14.85	14.85
	Cho. venustus	0.23	1.05	3.14	0.68	8.37	23.22
	Le. miniatus	1.22	1.73	2.58	0.92	6.87	30.09

Table A7.S7: Pairwise test (PERMANOVA) results on the effect of location (Bundaberg–Cooktown) and region (coastal, inshore, offshore) on the percent contribution of coral reef fish functional groups (herbivores, invertivores, piscivores) to spearfisher catches on the Great Barrier Reef, Australia. Significant values in bold.

Location	**df**	**t**	***p* value**		**Unique perms**
Cairns, Bundaberg	48	0.73	0.599		999
Cairns, Townsville	62	1.13	0.288		999
Cairns, Gladstone	69	1.76	**0.049**		999
Cairns, Mackay	49	1.27	0.196		999
Cairns, Cooktown	45	2.81	**0.001**		998
Cairns, Bowen	44	0.96	0.390		998
Bundaberg, Townsville	34	0.49	0.782		999
Bundaberg, Gladstone	41	0.56	0.724		997
Bundaberg, Mackay	21	1.76	0.063		999
Bundaberg, Cooktown	17	1.81	**0.045**		997
Bundaberg, Bowen	16	0.87	0.461		999
Townsville, Gladstone	55	1.44	0.138		998
Townsville, Mackay	35	1.76	0.055		998
Townsville, Cooktown	31	2.36	**0.010**		998
Townsville, Bowen	30	1.65	0.085		999
Gladstone, Mackay	42	1.44	0.135		999
Gladstone, Cooktown	38	1.37	0.177		999
Gladstone, Bowen	37	1.67	0.058		999
Mackay, Cooktown	18	2.90	**0.001**		998
Mackay, Bowen	17	1.20	0.254		998
Cooktown, Bowen	14	3.32	**0.002**		999
Region					
Offshore, Inshore	118	1.2488	0.201		999
Offshore, Coastal	95	2.0283	**0.020**		999
Inshore, Coastal	45	1.3322	0.183		999

Table A7.S8: SIMPER test results on the effect of location (Bundaberg–Cooktown) and region (coastal, inshore, offshore) on the percent contribution of coral reef fish functional groups (herbivores (H); invertivores (I); piscivores (P)) to spearfisher catches on the Great Barrier Reef, Australia. Locations in bold represent significant values identified in PERMANOVA tests (see Table S7).

Location	**Functional group**	**Av.Value**		**Av.Sq.Dist**	**Sq.Dist/SD**	**Contrib%**	**Cum.%**
Cooktown	P	4.48		0.015	0.46	0.51	0.51
	H	1.8		1.37	0.54	45.82	46.33
	I	1.02		1.61	0.6	53.67	100
Cairns	P	4.39		0.026	0.38	1.07	1.07
	I	2.45		0.84	0.39	34.11	35.18
	H	1.06		1.59	0.51	64.82	100
Townsville	P	4.4		0.016	0.37	0.62	0.62
	I	2.21		1.00	0.45	38.76	39.38
	H	1.01		1.57	0.49	60.62	100
Mackay	P	4.29		0.023	0.46	2.04	2.04
	I	2.66		0.067	0.45	5.94	7.98
	H	2.1		1.03	0.43	92.02	100
Bowen	P	4.19		0.022	0.49	3.53	3.53
	I	3.09		0.26	0.6	41.95	45.47
	H	1.69		0.34	0.53	54.53	100
Gladstone	P	4.35		0.031	0.52	0.73	0.73
	I	1.85		1.67	0.52	40.13	40.86
	H	1.65		2.46	0.58	59.14	100
Bundaberg	P	4.43		0.023	0.48	0.86	0.86
	I	1.89		0.33	0.49	12.29	13.15
	H	1.43		2.32	0.62	86.85	100
Region	**Functional group**	**Av.Value**		**Av.Sq.Dist**	**Sq.Dist/SD**	**Contrib%**	**Cum.%**
Offshore	P	4.39		0.02	0.4	0.93	0.93
	I	2.24		0.97	0.41	36.26	37.18
	H	1.16		1.69	0.51	62.82	100
Inshore	P	4.34		0.02	0.47	0.66	0.66
	I	2.2		1.44	0.49	39.31	39.97
	H	1.62		2.20	0.56	60.03	100
Coastal	P	4.32		0.06	0.63	2.15	2.15
	I	1.82		0.61	0.45	23.84	25.99
	H	2.19		1.89	0.54	74.01	100
Location	**Functional group**	**Av.Value 1**	**Av.Value 2**	**Av.Sq.Dist**	**Sq.Dist/SD**	**Contrib%**	**Cum.%**
Cairns, Bundaberg	H	1.06	1.43	3.72	0.95	77.48	77.48
	I	2.45	1.89	1.04	0.55	21.65	99.13
	P	4.39	4.43	0.04	0.6	0.87	100

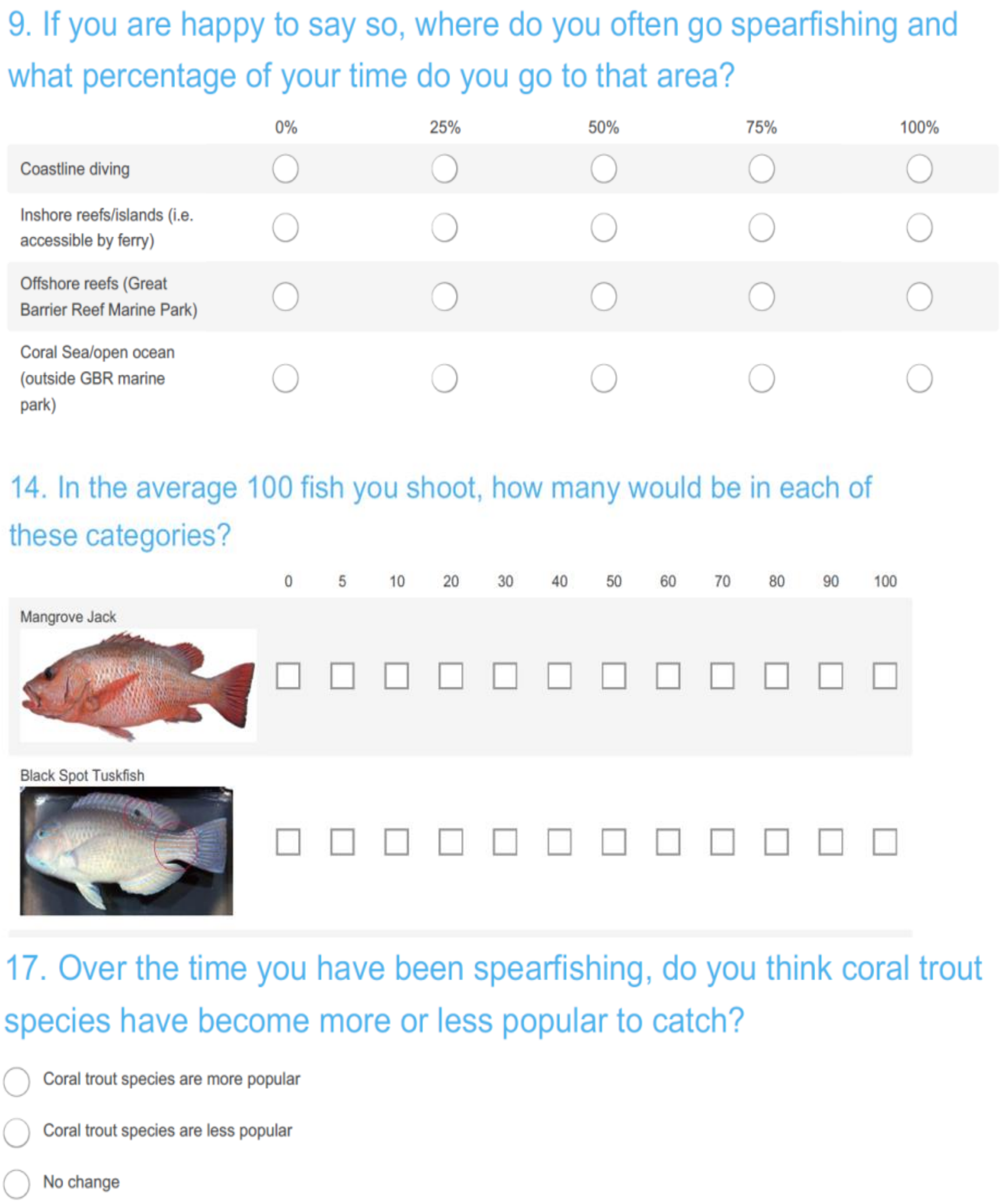
Cairns, Townsville	H	1.06	1.01	2.84	0.77	60.62	60.62
	I	2.45	2.21	1.80	0.65	38.48	99.11
	P	4.39	4.4	0.04	0.51	0.89	100
Cairns, Gladstone	H	1.43	1.01	3.84	0.98	72.46	72.46
	I	1.89	2.21	1.42	0.6	26.77	99.24
	P	4.43	4.4	0.04	0.6	0.76	100
Cairns, Mackay	H	1.06	1.65	4.59	1.01	64.93	64.93
	I	2.45	1.85	2.42	0.7	34.19	99.12
	P	4.39	4.35	0.06	0.83	0.88	100
Cairns, Cooktown	H	1.43	1.65	4.04	0.96	65.21	65.21
	I	1.89	1.85	2.11	0.74	33.98	99.19
	P	4.43	4.35	0.05	0.77	0.81	100
Cairns, Bowen	H	1.01	1.65	4.84	1.01	63	63
	I	2.21	1.85	2.78	0.79	36.14	99.13
	P	4.4	4.35	0.07	0.82	0.87	100
Bundaberg, Townsville	H	1.06	2.1	2.48	1.06	67.93	67.93
	I	2.45	2.66	1.13	0.47	31.04	98.97
	P	4.39	4.29	0.04	0.71	1.03	100
Bundaberg, Gladstone	H	1.43	2.1	3.54	0.93	72.63	72.63
	I	1.89	2.66	1.27	0.7	26.08	98.7
	P	4.43	4.29	0.06	0.63	1.3	100
Bundaberg, Mackay	H	1.01	2.1	3.16	0.96	65.2	65.2
	I	2.21	2.66	1.64	0.61	33.91	99.11
	P	4.4	4.29	0.04	0.89	0.89	100
Bundaberg, Cooktown	H	1.65	2.1	3.64	0.95	60.35	60.35
	I	1.85	2.66	2.34	0.67	38.8	99.14
	P	4.35	4.29	0.05	0.78	0.86	100
Bundaberg, Bowen	I	2.45	1.02	3.86	1	53.04	53.04
	H	1.06	1.8	3.38	1.02	46.35	99.39
	P	4.39	4.48	0.04	0.54	0.61	100
Townsville, Gladstone	I	1.89	1.02	3.28	1.06	51.85	51.85
	H	1.43	1.8	3.01	0.9	47.63	99.48
	P	4.43	4.48	0.03	0.74	0.52	100
Townsville, Mackay	H	1.01	1.8	3.69	1.14	52.81	52.81
	I	2.21	1.02	3.28	0.97	46.84	99.65
	P	4.4	4.48	0.02	0.56	0.35	100
Townsville, Cooktown	I	1.85	1.02	3.83	0.99	51.59	51.59
	H	1.65	1.8	3.52	0.97	47.5	99.09
	P	4.35	4.48	0.07	0.93	0.91	100

Townsville, Bowen	I	2.66	1.02	4.91	1.16	71.94	71.94
	H	2.1	1.8	1.88	0.84	27.48	99.42
	P	4.29	4.48	0.04	0.96	0.58	100
Gladstone, Mackay	H	1.06	1.69	2.40	0.65	59.34	59.34
	I	2.45	3.09	1.57	0.53	38.78	98.12
	P	4.39	4.19	0.08	0.8	1.88	100
Gladstone, Cooktown	H	1.43	1.69	3.68	0.89	80.58	80.58
	I	1.89	3.09	0.82	0.85	17.88	98.46
	P	4.43	4.19	0.07	0.98	1.54	100
Gladstone, Bowen	H	1.01	1.69	2.98	0.75	57.49	57.49
	I	2.21	3.09	2.13	0.64	40.97	98.45
	P	4.4	4.19	0.08	0.89	1.55	100
Mackay, Cooktown	H	1.65	1.69	5.17	1.1	58.41	58.41
	I	1.85	3.09	3.60	0.78	40.63	99.03
	P	4.35	4.19	0.09	0.9	0.97	100
Mackay, Bowen	H	2.1	1.69	2.89	0.98	85.28	85.28
	I	2.66	3.09	0.45	0.75	13.29	98.57
	P	4.29	4.19	0.05	0.75	1.43	100
Cooktown, Bowen	I	1.02	3.09	6.72	1.3	64.89	64.89
	H	1.8	1.69	3.54	1.06	34.15	99.04
	P	4.48	4.19	0.10	0.9	0.96	100

Region	Functional group	Av.Value 1	Av.Value 2	Av.Sq.Dist	Sq.Dist/SD	Contrib%	Cum.%
Offshore, Inshore	H	1.16	1.62	4.10	0.95	63.25	63.25
	I	2.24	2.2	2.33	0.69	35.93	99.18
	P	4.39	4.34	0.05	0.69	0.82	100
Offshore, Coastal	H	1.16	2.19	4.33	0.99	68.84	68.84
	I	2.24	1.82	1.88	0.68	29.84	98.68
	P	4.39	4.32	0.08	0.94	1.32	100
Inshore, Coastal	H	1.62	2.19	4.20	0.89	64.89	64.89
	I	2.2	1.82	2.20	0.73	34.04	98.93
	P	4.34	4.32	0.07	0.87	1.07	100

Table A7.S9: Pearson Chi-square test results of the perceived changes in catch dynamics for each location (Bundaberg–Cooktown), focusing on three commonly caught species on the Great Barrier Reef, Australia; coral trout (*Plectropomus* spp.), tuskfish (*Choerodon* spp.) and parrotfish (Scaridae). Significant values in bold.

Genera	Location	df	X-squared	*p* value
Coral trout	*Bundaberg*	2	6	**0.049**
	Gladstone	2	7.0909	**0.029**
	Mackay	2	0.61538	0.735
	Bowen	2	10.75	**0.005**
	Townsville	2	7	**0.030**
	Cairns	2	9.8	**0.007**
	Cooktown	2	2	0.368
Tuskfish	*Bundaberg*	2	6	**0.049**
	Gladstone	2	17.636	**<0.001**
	Mackay	2	7.5385	**0.023**
	Bowen	2	3.25	0.197
	Townsville	2	13	**0.001**
	Cairns	2	12.05	**0.002**
	Cooktown	2	3.7143	0.156
Parrotfish	*Bundaberg*	2	9.5	**0.009**
	Gladstone	2	35.636	**<0.001**
	Mackay	2	5.6923	0.058
	Bowen	2	7	**0.030**
	Townsville	2	5.6154	0.060
	Cairns	2	6.35	**0.042**
	Cooktown	2	3.7143	0.156



9. If you are happy to say so, where do you often go spearfishing and what percentage of your time do you go to that area?

	0%	25%	50%	75%	100%
Coastline diving	○	○	○	○	○
Inshore reefs/islands (i.e. accessible by ferry)	○	○	○	○	○
Offshore reefs (Great Barrier Reef Marine Park)	○	○	○	○	○
Coral Sea/open ocean (outside GBR marine park)	○	○	○	○	○

14. In the average 100 fish you shoot, how many would be in each of these categories?

	0	5	10	20	30	40	50	60	70	80	90	100
Mangrove Jack	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐
Black Spot Tuskfish	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐	☐

17. Over the time you have been spearfishing, do you think coral trout species have become more or less popular to catch?

○ Coral trout species are more popular

○ Coral trout species are less popular

○ No change

Figure A7.S3: Sample questions from the survey of Queensland spearfishers, pertaining to each of the major aims.

APPENDIX 8: COTS JUVENILES

[Report submitted for Case Study 5]

Juvenile CoTS 'in waiting': the missing link in population and connectivity models

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Abstract

Survival of the herbivorous juveniles into the corallivorous adult stage is required for a population outbreak of Crown of Thorns starfish (COTS) to arise. The biology of this juvenile stage remains largely unknown due to their highly cryptic nature, yet is key to understand the success of COTS that poses such a severe threat to the health of the Great Barrier Reef. We sought to determine if juveniles were able to be sustained on foods which are abundant in nature in addition to crustose coralline algae (CCA) that they are known to feed on. Juveniles were raised on three diets: CCA, *Amphiroa sp*, and biofilm and their growth rates were measured over 4.5 months (139 days). Juveniles fed CCA grew at the same rate as those fed *Amphiroa sp* until 43 days when CCA juveniles began to grow at a faster rate. Juveniles were able to consume and survive on biofilm, although their growth was minimal. When juveniles were offered a choice between the three diets, they selected either CCA or *Amphiroa sp* over biofilm indicating that they can identify preferred food. COTS may have a greater diet range than previously recognised. Their ability to be maintained on biofilm alone suggests that juvenile COTS may be able to survive for extended periods of time in coral rubble prior to the switch to coral food. This may create a time lag across the larval settlement, juvenile and outbreak stages of COTS.

Introduction

Starfish are important ecosystem engineers. Their feeding activities have long been recognised to play a major role in structuring marine benthic communities including rocky shores, sandy floor, seagrass and coral reefs (Paine 1974; Sloan 1980; Martinez *et al.* 2017). The size, mobility and abundance of the starfish, their feeding mechanism and ability to detect food determines the rate of consumption on their prey and the extent to which they alter community composition (Pratchett *et al.* 2014; Martinez *et al.* 2017).

Crown of Thorns starfish (COTS, *Acanthaster sp*) are endemic throughout the Indo-Pacific region from Panama to the Red Sea (Branham *et al.* 1971; Vine 1973; Vogler *et al.* 2008; Houk and Raubani 2010). They begin their benthic life as herbivorous juveniles but are best known for their corallivorous stage when they transition to adulthood (Yamaguchi 1974; Pratchett *et al.* 2014). Juvenile COTS evert their stomach and secrete digestive enzymes to externally digest crustose coralline algae (CCA) and later coral to avail of the wax esters for energy (Benson *et al.* 1975; Brahimi-Horn *et al.* 1989). In non-outbreak, stable populations (<1 starfish per hectare), COTS have minimal impact on the coral community (Branham *et al.* 1971) and in some cases have been suggested to promote coral diversity by eating fast growing coral species and creating space for new colonisers (Done et al. 2012). However, spikes in abundance with >10-15 starfish/ha (up to 1000 starfish/ha) have caused widespread coral loss (Moran and De'ath 1992; Pratchett *et al.* 2014). Although outbreaks of other coral predators such as *Drupella* gastropods have been found to impact local coral abundance (Cumming 2009), the voracious consumption of COTS can substantially, if not completely, reduce coral cover during outbreaks (Chesher 1969; De'ath *et al.* 2012; Kayal *et al.* 2012). Their fast growth and large body size, rapid consumption of coral and their dietary flexibility make COTS the most destructive coral predator on the reef.

Causes of population outbreaks

COTS outbreaks have caused widespread reef damage and have been one of the leading causes of coral loss in the GBR since 1985 (Carpenter 1997; Rotjan and Lewis 2008; De'ath *et al.* 2012). Since the 1960's, the frequency of outbreaks on the Great Barrier Reef (GBR) has increased from once every 50-80 years to repeat at <15 year intervals (Fabricius *et al.* 2010). *Acanthaster cf. solaris* is the single most important species influencing the health of the Great Barrier Reef (GBR) alongside global warning (eg bleaching) and severe tropical storms (De'ath *et al.* 2012; Pratchett *et al.* 2017a).

The disproportionate success of the early life history stages of COTS appears to be unique among tropical asteroids but is also a feature of temperate boom and bust starfish species which have periodic outbreaks (Uthicke *et al.* 2009). The larval and juvenile stage of broadcast spawning marine invertebrates are typically considered to be the vulnerable bottlenecks tempering population growth as the stages experiencing high rates of mortality (Gosselin (Gosselin and Qian 1997; Hunt and Scheibling 1997). As COTS are highly fecund, releasing up to 100 million eggs per individual female (Babcock *et al.* 2016), larval success together with enhanced survival in post-settlement stages may lead to substantial increases in recruitment and population replenishment (Keesing and Halford 1992).

It is becoming more apparent that the ecological success of COTS is due to their natural biological traits that enable them to capitalise on anthropogenic disturbances to reef systems and make them so resilient to perturbation. The drivers of their boom/bust life history are considered in several conflicting hypotheses. It has been suggested that outbreaks are caused by a release of top-down control throughout their life cycle (*predator-removal hypothesis*). Extensive overfishing of COTS predators such as the Giant Triton snail (*Charonia tritonis*, Endean 1969) and fish (Sweatman 2008; Cowan *et al.* 2017) occurred in the 1960s and since this time outbreaks have been occurring at shorter time intervals (Fabricius *et al.* 2010) providing indirect evidence for the *predator-removal* hypothesis. It has also been found that outbreaks occur less frequently in protected marine park areas that support larger fish assemblages (Sweatman 2008). This hypothesis is also supported by the evidence of sublethal predation on COTS (Messmer *et al.* 2017) as well as the morphological and behavioural adaptions they have evolved to counter predation with their toxic spines and eggs (Lucas *et al.* 1979), ability to camouflage, and larvae that avoid settling in areas where predators are more abundant (Cowan *et al.* 2016).

The hypothesis that has received the most traction to explain COTS outbreaks is that temporal pulses in larval success are driven by an increase in the phytoplankton food source for the larvae (*terrestrial run-off, enhanced-nutrients or larval-success hypothesis*, Pratchett *et al.* 2014). Nutrient runoff from terrestrial systems following rainfall or localised upwelling away from coastal areas leads to eutrophication promoting phytoplankton blooms that are proposed to enhance larval growth, survival and subsequently recruitment (Birkeland 1982; Fabricius *et al.* 2010). The *enhanced-nutrients* hypothesis also implies that the low-nutrient conditions typical of coral reefs substantially reduce COTS larval survival due to starvation. However, COTS larvae typically experience low nutrient conditions in the tropical environment that they have evolved in (Wolfe *et al.* 2017) and outbreaks can occur kilometers from eutrophic events (Roche *et al.* 2015). Thus, COTS larvae are likely to be more tolerant of low food abundance than the nutrient-runoff hypothesis would posit. Their resilience in low food conditions may allow them to thrive in the oligotrophic waters of the GBR (*larval-resilience hypothesis*, Olson 1985, 1987). This is likely also associated with many inherent traits of COTS including high levels of maternal provisioning in their unusually large eggs for a species with planktotrophic larvae (Caballes *et al.* 2016), as well as phenotypic plasticity of larval feeding structures (Wolfe *et al.* 2015a), and potentially symbiotic phototrophic bacteria (Carrier *et al.* 2018).

These hypotheses form a framework to advise and design management strategies to mitigate future COTS outbreaks. The *larval-success* and *larval-resilience hypothesis* reflect the opportunistic nature of COTS and encompass multiple interacting factors that may contribute to outbreaks. However, aside from the *predator-removal hypothesis*, none of the hypotheses considers the potential vulnerability or resilience of the early post-larval and herbivorous juvenile life history stages.

COTS juvenile stage

Resilience of COTS juveniles is likely to be critical in generating outbreak populations. Compared with other life history stages, however, little is known about COTS juveniles due to their highly cryptic nature. Two days after COTS larvae settle out of the water column into coral rubble habitat, they metamorphose into 5-armed juveniles, 0.3-0.7 mm in diameter (Henderson 1971, second ref). They add arms as they grow and emerge from the rubble when they are large enough to feed on coral (laboratory: 8-10 mm, Yamaguchi 1974; field: 30-120 mm diameter, Zann *et al.* 1987). Despite extensive sampling efforts, their small size, complex habitat, ability to camouflage and night time foraging behaviour make the early COTS juveniles notoriously difficult to find in nature (Yamaguchi 1973; Johnson *et al.* 1992; De'ath and Moran 1998). It has also been suggested that juveniles settle in deeper waters where their preferred CCA species grow making it difficult to predict an outbreak until adults walk up the reef slope into shallower waters (Endean and Stablum 1973; Black and Moran 1991; Johnson *et al.* 1991).

Mortality rates of juvenile COTS can be very high and vary with size (Lucas 1984; Zann *et al.* 1987; Sweatman 1995; Cowan *et al.* 2017; Keesing *et al.* 2018). In Fiji, disease and, to a lesser extent, predation and water turbulence were suggested to cause ~99% mortality in juveniles aged 8-23 months (Zann *et al.* 1987). Daily mortality rates have been documented to be 7.8% per day in a field-based study (Keesing *et al.* 1996). A similar experiment found that mortality of starfish 3 mm in diameter was 2.55% per day of which 73% was attributed to predation compared to 0.82% per day for 13 mm in diameter (Keesing *et al.* 2018). As starfish emerge from the rubble to forage for coral, sublethal predation from visual predators (fish) increase from <25% at <10 mm to 80% at 11-20 mm diameter (Rivera-Posada *et al.* 2014) although the threat of lethal predation by benthic invertebrates is likely to decrease (Wilmes *et al.* 2018). Eight invertebrates and six fish species have been observed to consume COTS juveniles (Cowan *et al.* 2017).

Older juveniles are more mobile in their search of food (Pratchett *et al.* 2017b) and less susceptible to lethal predation (Wilmes *et al.* 2018). As vulnerability is likely to be size-dependent, growth rates influence post-settlement mortality. Thus, food availability and diet are likely to play a significant role in the ability of a juvenile to develop into reproductively mature, corallivores adult (Yamaguchi 1974).

Juvenile feeding ecology

In laboratory studies, the herbivorous juvenile COTS consume CCA until 4-6 months post settlement when they begin feeding on coral (Yamaguchi 1974; Moran 1986; Johansson *et al.* 2016; Kamya *et al.* 2018). This ontogenetic switch from herbivory to carnivory occurs in at least 11 other predatory starfish (Martinez *et al.* 2017). Like COTS, *Stichaster australis* consumes encrusting coralline algae before they switch to prey on juvenile mussels at 15-28 months post-settlement (Baker et al. 1979). This obligatory herbivorous stage of predatory starfish is required to undergo the morphological and physiological changes that allow them to consume and digest coral (Martinez et al. 2017), withstand being stung by coral polyps (Yamaguchi 1973) and be large enough to avoid predation (Zann *et al.* 1987, Wilmes *et al.* 2018).

The timing of the herbivory-corallivory ontogenetic switch of COTS is likely to vary in the field as resource availability, predation pressure and competition from adults may prevent juveniles venturing out from the protection of this rubble habitat to search for more exposed coral. Zann *et al.* (1987) observed that juvenile COTS began feeding on corals at 13-15 months of age (ages may be overestimated by 0.5-1.5 months, see Wilmes *et al.* 2017) in a field-based study on Suva reef, Fiji. Another study that modelled juvenile age through extensive field sampling of 64 reefs in the GBR found that juvenile growth varied as they aged and attributed this to different diets (Wilmes *et al.* 2017). Individuals that switch to coral sooner have been shown to grow faster than those that remain feeding on CCA (Lucas 1984). Thus, the variation in estimated growth rates increased with diet and age (Wilmes *et al.* 2017).

We do not know how the success of the juvenile relates to their algal food source. So far, studies on juvenile COTS have only tested their one known food source: CCA. CCA is an encrusting, calcareous algae that is distributed throughout the GBR. It is greater in abundance in the mid and outer GBR with reduced sedimentation (Fabricius and De'ath 2001). Starfish consume the top layer of tissue rather than the whole algae leaving light orange or white feeding scars (Figure 1A,C). White feeding scars are also left on coral by both young and adult starfish and can help to locate them in the field, although similar marks are left by other corallivores such as *Drupella* (Johnson *et al.* 1992).

Chemical cues emanating from CCA and their thick biofilm is considered to promote settlement for COTS larvae (Johnson *et al.* 1991). However, COTS larvae can also settle in the absence of a specific CCA cue or possibly in response to other biofilms (Wolfe *et al.* 2015b). Conspecific cues are also suggested to promote settlement (Chesher 1969; Black and Moran 1991; Cowan *et al.* 2016). Variation in settlement behaviour is typical among echinoderms (Pawlik 1992; Bishop *et al.* 2006).

If COTS are able to settle without CCA, this begs the question: are COTS able to survive when CCA is unavailable? The specificity of a starfish to a particular diet is restricted by their feeding structures and digestive enzymes (Martinez *et al.* 2017). It has been mentioned that juvenile COTS eat diatoms (Keesing *et al.* 1996) although this has not yet been investigated. In a review on starfish feeding behaviour, 44 of 57 species (17/29 omnivorous species) were determined to eat biofilms (Martinez *et al.* 2017). Biofilms are considered to be a cost-effective food source for starfish because the single celled diatoms, bacteria and algal are more readily digested than multicellular algae (Martinez *et al.* 2017) such as CCA. It is likely the COTS observed to be eating CCA area also are consuming biofilms and other epiphytes. It is unknown if COTS juveniles feed on other types of algae although adults can consume calcareous turfs, filamentous and foliose algae when coral is scarce (De'ath and Moran 1998).

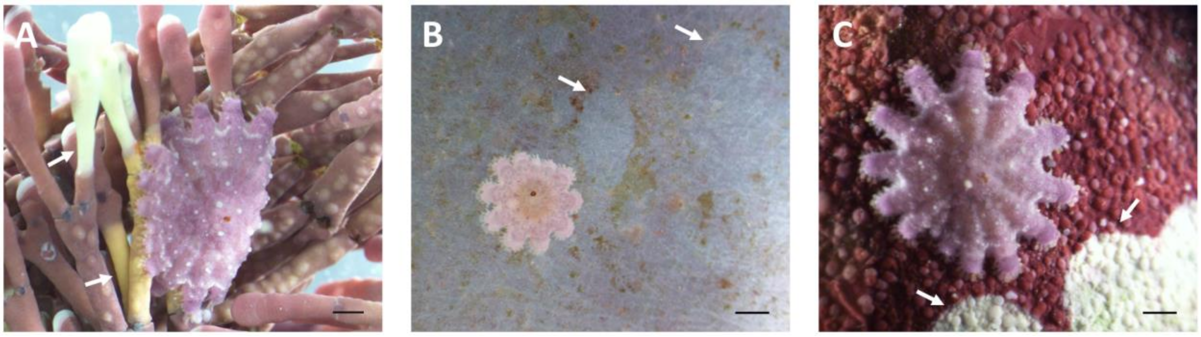

Figure A8.1: Juvenile starfish in different diet treatments: A) *Amphiroa sp* (104 days in treatment) B) Biofilm (139 days in treatment). The juvenile has a green stomach indicating that the starfish is feeding. C) CCA (76 days in treatment). Arrows indicate orange and white feeding scars (A, C) and where algae have been eaten off the biofilm plate (B). Scale bar = 1 mm.

Juvenile COTS prey on a range of coral species in their corallivorous stage (Collins 1975; Keesing and Halford 1992; Johansson *et al.* 2016). In a feeding choice experiment, juveniles were found to prefer *Acropora tenuis* over *A. millepora*, *A. pormosa*, *Pavona cactus* and *Pocillopora damicornis* (Johansson *et al.* 2016). They did not prefer, although still consumed, *Stylophora pistillata* and only ate *Echinopora lamellosa* and *Porites lutea* when no other corals were presented. This suggests that the juveniles, as for the adults (Pratchett 2007), have some dietary flexibility. Thus, ease of access and food availability are likely to play a large role in diet.

In situations of coral scarcity such as in the aftermath of cyclones, the passage of COTS outbreaks and bleaching events (Halford *et al.* 2004; Kayal *et al.* 2012), juveniles may have to depend on algae for a prolonged period, delaying the ontogenetic switch to coral. This study explores the potential of these juveniles to form reserve populations in the reef infrastructure as a potential source of outbreaks.

Project aims

The juveniles stage is a highly vulnerable and likely to be a weak link in the life cycle of COTS although there is potential that they can remain as juveniles for years, a key consideration when identifying the sources of outbreaks. The biology and ecology of the juvenile life stage is a black box in our understanding of COTS, a knowledge gap addressed in this project on the nutritional biology of juveniles and how this influences their performance.

This study explores the resilience of juvenile COTS to scarcity of CCA, their preferred food source. We investigated diet flexibility during the herbivorous phase and determined the effect of different algal diets on their diet preferences and growth rates. Firstly, we compared the growth rates of juvenile COTS on three diets: CCA, a biofilm and *Amphiroa sp. Amphiroa sp* is a calcifying geniculate algae that occurs throughout the Great Barrier Reef and more commonly in the outer reef (Diaz-Pulido 2008). We then sought to test diet preferences of COTS juveniles by offering the starfish all three food options concurrently to determine 1) the ability of the starfish to recognise food, 2) if CCA is in fact preferred over biofilm and *Amphiroa sp* and, 3) if diet history affects their choice of diet.

Methods

In November 2017, COTS were collected near Cairns, North Queensland (16°550'S, 145°460'E) and transported to the Southern Cross National Marine Science Centre (NMSC) in Coffs Harbour, NSW where they were maintained in flow through aquaria at 26-27˚C. Within days of arrival, two male and two female starfish were spawned. The ovaries were removed, rinsed and placed in 1-MA for 45 minutes and checked for quality and maturation. The testes were removed and the sperm were collected dry. Equal amounts of eggs or sperm were pooled between the males and the females and then the eggs and sperm were fertilised ensuring at least 95% success.

Larvae were raised in two 300 L cylindro-conical tanks at 26˚C in UV-filtered seawater that was changed every 1-2 days. They were fed daily with 25–40 $\times 10^3$ cells ml^{-1} of the tropical microalga *Proteomonas sulcata* once the gut was formed (~48 h post fertilisation) and when larvae reached the brachiolaria stage (>16 days old), CCA sheets were placed into the tanks to induce settlement. The two tanks were treated as two separate populations.

Juvenile feeding experiment

When the juveniles were ~7-8 mm in diameter they were randomly distributed into individual pots (~4 cm diameter). There was no significant difference in the size (area) of the starfish between food treatments ($F_{2,54} = 0.287$, $p = 0.751$) although there was a significant difference between the two populations ($F_{1,54} = 14.697$, $p < 0.0001$, average area ± SE of population A: 2.27 mm^2 ± 0.10, population B: 3.01 mm^2 ± 0.15, n = 30 per population). Pots were haphazardly distributed in a flow through system that was designed to deliver 1 µm-UV filtered fresh sea water through an individual dripper into each pot. Drippers were manually adjusted to maintain ~26˚C. Temperature was monitored daily using a Hach® HQ40d multi-controller with a Hach® PHC101 temperature adjusted pH probe and HOBO loggers in place throughout the experiment with readings at 30 min intervals. The average temperature throughout the experiment was 25.94 ± 0.02˚C (n=99).

The juveniles were fed three diets: biofilm, CCA and *Amphiroa sp*. Biofilm was grown on plastic sheets in tanks at NMSC for >2 years. CCA was cultured on plastic sheets and small pebbles in the aquarium at ~26˚C. The sheets were cut into 2 x 3 cm pieces and placed into each individual container. *Amphiroa sp* was collected at low tide from Charlesworth Bay, Coffs Harbour, (30°16'S, 153°8'E) and washed in freshwater to remove any benthic predators. Food was replaced every two weeks or as necessary to ensure that the starfish were fed *ad libitum*. The pots were also replaced and cleaned every two weeks to prevent biofilm build-up.

The starfish were photographed using Cellsens imaging program after two weeks and then at monthly intervals using an Olympus camera mounted to a dissecting microscope. The number of any visually distinguishable arms were counted and the 2D-area of the juvenile was measured using ImageJ (Schneider *et al.* 2012) by manually adjusting the image threshold to fit the area of the starfish (Fig. 2). As time points were approximately one month apart, the growth rates of the juveniles were calculated per week at 0.5, 1.5, 2.5, 3.5 and 4.5 months since the experiment commenced. Growth rates $\left(= \frac{\text{Area}_{\text{final}} - \text{Area}_{\text{initial}}}{\text{time (weeks)}}\right)$ were calculated as the change in area divided by the number of weeks (W) that had passed since the previous time point ($\text{time} = \text{W}_{\text{x}+1} - \text{W}_{\text{x}}$) where one week = 7 days.

Diet choice experiment

After ~3.5 months (105 days) in treatment, each individual starfish was placed in the centre of a Petri-dish and offered a ~1 x 1.5 cm sample of each diet (*Amphiroa sp*, biofilm, CCA) that were spaced ~2 cm apart. The starfish was then left to select a food source. A "choice" was recorded if the starfish arrived on the sample and stopped moving for >5 minutes. It was not counted if the starfish walked over and off the sample.

The diet choice experiment was also carried out for a separate population of juveniles that were raised in flow through FSW on a "mixed diet" of low quality CCA and biofilm (2.5 – 7.2 mm diameter). These juveniles were from the same cohort as the other juveniles but were not selected for the controlled feeding experiment. In a second diet choice experiment, the juveniles in the "mixed diet" population were allowed to select and feed for 72 hours on either *Amphiroa sp*, biofilm and CCA. Starfish were observed every hour for five hours and at 22, 30, 48 and 72 hours. The longer experiment is yet to be completed for the starfish in experimental treatments.

Statistical analysis

All analyses were performed in R (version 3.4.3) using RStudio (RStudio Team 2018). Data on the number of arms, the area and growth rates of each juvenile were analysed using a repeated measures linear mixed model with time (days), diet (*Amphiroa sp*, biofilm and CCA) and population (A and B) as fixed factors and individual juvenile starfish nested within time (lme4 package, Bates *et al.* 2015). The models were tested using a type III analysis of deviance and post-hoc analysis were computed for significant main effects and interactions using Tukey distances (lsmeans package, Lenth *et al.* 2016). Homoscedasticity was checked, as was the normal distribution of data by visually inspecting the distribution of residuals on a qqplot. Diet choice data was analysed using a Fishers Exact test. The time taken for each individual to choose a food was analysed using a one-way ANOVA. Graphs were made using ggplot2 (Wickham *et al.* 2018).

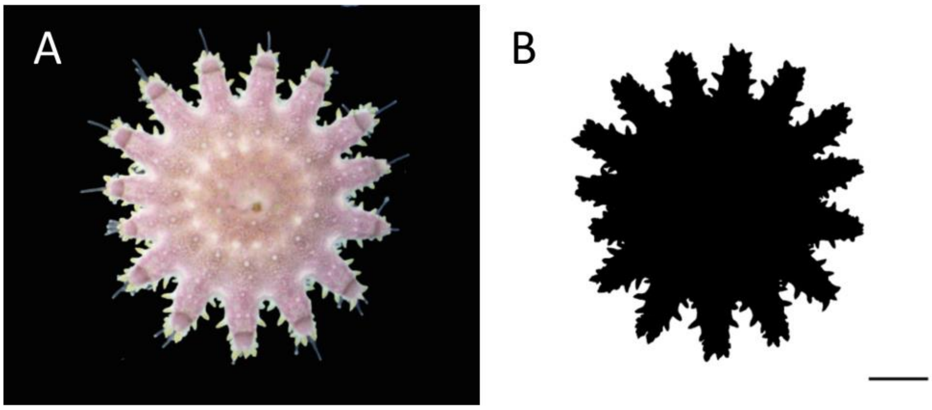

Figure A8.2: (A) Juvenile starfish after 3.5 months (104 days) on a diet of CCA; (B) The stencil of the same juvenile (excluding tube feet) created using image thresholding on imageJ to measure its 2D surface area. Scale bar = 2 mm.

Results

Feeding scars were present on *Amphiroa sp*, CCA and were rarely identified on biofilm plates although the starfish had green stomachs indicating that they were feeding (Fig.1). The stomachs of juveniles in the other two treatments were pink/cream. The juveniles on the *Amphiroa sp.* diet were able to wrap themselves around the articulations to feed. Few juveniles died over the course of the experiment and mortality was not specific to a treatment or population (Figure 1B).

The position of the juveniles were noted on four separate days. In the experimental pots, the juveniles fed biofilm (n=68, 17 juveniles) were often found on the mesh (25%,) or walls (64.7%) and more rarely on their food (10.29%). The juveniles in the CCA and *Amphiroa sp* treatment (n= 72 each, 18 juveniles) were almost always on their food (88.8% and 97.22%, respectively) and were otherwise on the walls of the pot, not on the mesh. A number of juveniles walked up the pot and began floating on the surface of the water (n=20).

Growth in the different treatments

Growth rates differed between diet treatments and changed over time ($\mathcal{X}^2$ = 209.67, df = 8, p < 0.0001, Fig. 4). There was no difference in growth rates throughout the experiment for the *Amphiroa sp* treatment and the growth rates of the juveniles fed CCA increased over time and plateaued after 76 days. In the biofilm treatment, growth rates decreased until 139 days where there is a slight increase.

There was a significant diet x time interaction for arm number ($\mathcal{X}^2$ = 408.27, df = 10, p < 0.0001). Post-hoc analysis showed than from day 76 onwards, the juveniles in the *Amphiroa sp* and CCA treatment did not differ in arm number but had significantly more arms than the juveniles in the biofilm treatment (Fig. 3A, Supp. Mat. 1). Juveniles in the biofilm treatment had significantly more arms from 43 to 139 days than at the start of the experiment.

There was also a significant diet x time interaction for area ($\mathcal{X}^2$ = 3767.28, df = 10, p < 0.0001). The juveniles in the *Amphiroa sp* and CCA treatment were significantly larger than the biofilm treatment at day 43 and by day 104 the juveniles fed CCA were larger than the *Amphiroa sp* treatment (Fig. 3B, Supp. Mat. 1). On average, the juveniles in the biofilm treatment grew slightly over time but did not significantly differ from the start of the experiment. Three starfish fed biofilm that decreased in size between time points recovered. Two juveniles decreased in size between day 76 to 104 (3.92%, 7.28%) and another decreased in area by 31.42% between day 43 and 76 but by the next time point it had began to recover with only a 14.17% decrease in area from day 43 and was 86.9% larger by day 139. Two more juveniles decreased in size between day 104 and 189 (9.5%, 15.3%).

There was no significant difference in the size of the juveniles (area) between the two populations although there was a significant population x time interaction for arm number between population A and B ($\mathcal{X}^2$ = 15.16, df = 5, p = 0.010). Population B had significantly more arms that population A until 104 days when the mean number of arms was equal (Fig. 3B, Supp. Mat. 1).

Diet choice experiment

In the immediate diet choice experiment, all starfish selected a food when concurrently offered biofilm, CCA and *Amphiroa sp*. The diet of the starfish did not influence their choice and no single food option was chosen significantly more times than the other two ($p>0.05$) although the statistical power is likely to be limited by our low sample size ($n \leq 22$ per treatment). However, *Amphiroa sp* and CCA were almost always chosen with the exception of three juveniles raised in the *Amphiroa sp* treatment that selected biofilm (Fig. 5). Some juveniles walked over and then off the biofilm (n=13) and *Amphiroa sp* (n=4) before selecting a different food.

There was no significant difference in the time taken to select a food between diet treatments ($F_{3,71}$ = 1.906, p = 0.136). On average, the juveniles in the CCA, *Amphiroa sp*, and biofilm treatments chose a food after 11.69 ± 1.87 minutes (n=18), 15.16 ± 3.48 minutes (n=18), and 17.82 ± 3.26 minutes (n=17), respectively. The mixed diet treatment took slightly longer to make a choice (25.31 ± 6.29 minutes, n=21).

In the 72 h diet choice experiment using the juveniles from the mixed diet population, more juveniles immediately chose *Amphiroa sp* (68.1%) than CCA (22.7%) or were not on a food option (no choice, 9.1%, Fig 5). Biofilm was not selected. After making a choice, 21 of the 22 juveniles remained on their first choice and began feeding (as evident by feeding scars) for at least five hours. By 22 h, two juveniles had switched from *Amphiroa sp* to CCA and after 30 h, three juveniles had switched from CCA to *Amphiroa sp* after they had completely consumed the available CCA. For the duration of the experiment, 77.3% of juveniles only fed on one of CCA or *Amphiroa sp*.

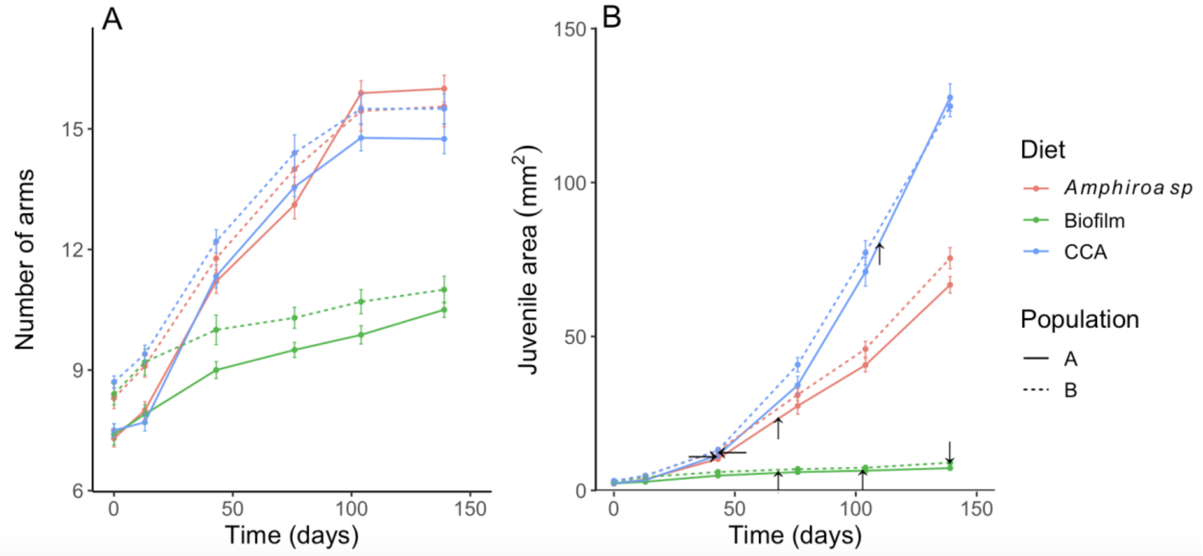

Figure A8.3: The mean (±SE) A) number of arms and B) area (mm^2) of juveniles in three diet treatments from two populations. Arrows indicate when a juvenile died.

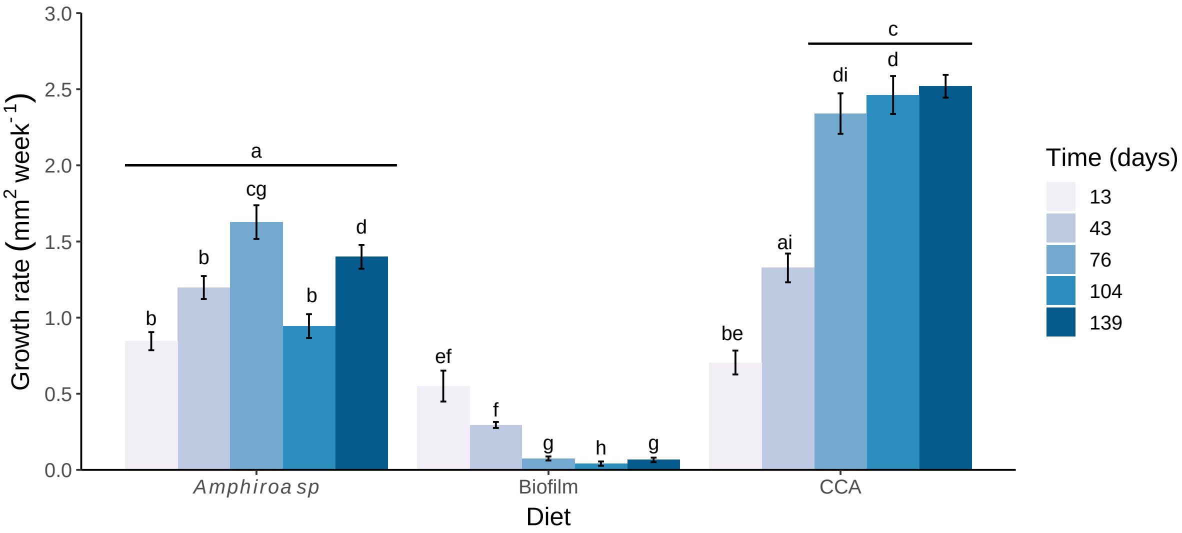

Figure A8.4: Weekly growth rates (mean ± SE) of juveniles in three diet treatments at five measurement time points (days in diet treatment). The same letters (with or without bars) represent no significant difference.

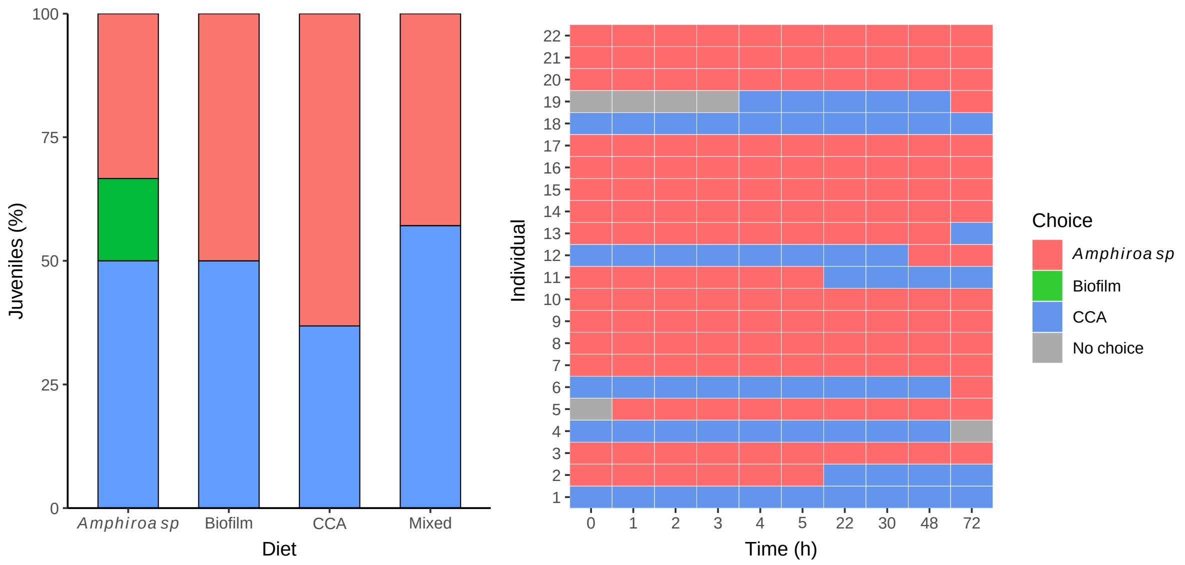

Figure A8.5: The food choice by juveniles offered *Amphiroa sp*, biofilm, CCA. Left: percentage choice of juveniles that were fed *Amphiroa sp*, biofilm, CCA or a mixed diet for ~3.5 months. A choice was typically made in <1h (short diet experiment). Right: The selection made by each individual starfish in the mixed diet treatment over 72 h (long diet experiment).

Discussion

Juvenile COTS do not require encrusting CCA for nutrition and can consume and grow, albeit at different rates, on the geniculate coralline algae, *Amphiroa sp*, and biofilm. The juveniles fed CCA grew more than those fed *Amphiroa sp* and there was minimal growth for the juveniles fed biofilm. However, these juveniles did consume biofilm and increased in arm number over time, although more slowly than those on the other diets. Our results suggest that the diet of COTS juveniles may be more flexible in their diet than previously understood grazing on a range of coralline algae and biofilms in addition to CCA. The juveniles may be able to survive for months if CCA is not available, albeit growing more slowly on other diets.

Diet and growth

The size and growth rates of juveniles fed *Amphiroa sp* were similar to those fed CCA until 2.5 months (76 days). Thereafter, the juveniles in the CCA treatment grew faster than those in the *Amphiroa sp* although they had the same number of arms. With the juveniles in the *Amphiroa sp* treatment may become stunted. Lucas (1984) fed COTS different food (coral and scallop) for four years after a juvenile diet of CCA. Although the growth rates were similar, the size of the scallop-fed starfish plateaued at a smaller maximum size than the coral-fed starfish. An adult COTS that was offered coral at two years of age was smaller than the starfish (n=2-3) offered coral at one year old. Stress and starvation as a young immature adult starfish was also found to result in a dwarfed adult form (Yamaguchi 1974). A prolonged study where juveniles fed different diets are then transitioned to coral will be needed to determine if the juvenile diet also influences their final adult size and potentially their reproductive output.

Although the juveniles in the biofilm treatment grew slowly, they were able to survive for months without feeding on coralline algae. These juveniles increased in area, albeit not significantly, but did show a significant increase in arm number. Furthermore, their green stomachs indicated that they were feeding. Biofilm is consumed by a number of starfish species at the juvenile stage (Sloan 1980, Martinez *et al.* 2017) and may be sufficient to maintain physiological processes for COTS. They can have high, yet variable, nutritional quality (protein, carbohydrate and calorific value) for juvenile starfish depending on the species of cyanobacteria present (Nagarkar *et al.* 2004; Martinez *et al.* 2017). The composition of biofilms are likely to vary at small spatial scales in nature and be of variable nutritional value for juveniles.

As biofilms are ubiquitous in nature, starvation driven mortality of COTS juveniles may be rare. The results of the present study indicate that juveniles may be resistant to starvation for long periods of time. In a study by Yamaguchi (1974), one juvenile (~90 mm diameter) decreased in size by 10% when it was starved for three months. This starfish was able to feed and start growing again when it was re-introduced to coral. In our study, three starfish in the biofilm treatment exhibited shrinkage indicating that they may have stopped feeding for periods of time. However, by the next time point they had recovered and had continued growing. Due to their small size, it is unlikely that the juveniles fed biofilm will be able to switch to coral without first feeding on coralline algae for 3-4 months (Yamaguchi 1974; Kamya *et al.* 2018) . However, as smaller juveniles are more vulnerable to predation (Zann *et al.* 1987; Keesing *et al.* 2018; Wilmes *et al.* 2018), juveniles that cannot access CCA and depend on biofilm may suffer greater predator driven mortality rates.

Variable palatability, digestibility, nutritional content and energetic value of different foods affect juvenile growth rates (Johansson *et al.* 2016; Martinez *et al.* 2017). It was not possible to measure feeding rate given the nature of each food source. The CCA was grown on irregularly shaped rocks and shells, some with small crevices and grazing on biofilm was seldom distinguishable and was usually not identified. The yellowing of *Amphiroa sp* as it aged looked similar to feeding scars and a single feeding scar would stretch across multiple thin branches as the juveniles would wrap around them to feed.

Wilmes *et al.* (2017) approximated the age of juveniles collected through extensive field sampling based on their size and estimated month of settlement. By modelling juvenile age, they found that variability in size increased as the starfish became older and attributed this to different diets as individuals that switch to coral grow faster than juveniles that remain feeding on CCA (Lucas 1984). We have shown that this variability may also be driven by different herbivorous diets. As growth rates depend on diet, it may be difficult to gauge a size-age relationship of juveniles in nature if they have a mixed diet.

Diet selection

In the diet choice experiment, food choice was not related to diet history. All juveniles except three from the *Amphiroa sp* treatment chose CCA or *Amphiroa sp* over biofilm. However, we did not find a significant difference between the foods chosen. This result is likely to be due to our low sample size and so this work is being repeated. Most starfish that explored the biofilm option walked over and off the plate showing a clear disinterest. It was also observed that the biofilm-fed juveniles were typically on the walls of the experimental pots and mesh covering the outflow rather than on the biofilm plate, whereas the CCA and *Amphiroa sp* treatments were always on their food. This suggests that they spent much less time feeding than the other treatments and that biofilm appears to be the Hobson's choice for juveniles. While they are able to consume it when there is no other alternative available, biofilm appears to be a poor food and if given a chance they seek out more preferable algae.

A preference for coralline algae suggests that juveniles are able to recognise and detect their food based on sight and/or chemoattraction. Even though *Amphiroa sp* may not be as nutritious or palatable as CCA (reflected by the differences in growth rates), it is a more complex habitat and may provide a better shelter from benthic and fish predators. Juveniles are able to hide within the algae and wrap themselves around the branches. The diet choice experiment disturbed the juveniles and thus this experiment reflects both the juvenile's reaction to the threat of predation as well as diet preference. However, once the juvenile had selected CCA or *Amphiroa sp* in the longer choice experiment, they remained there and began feeding. A longer choice experiment that does not disturb the juveniles is required to more fully understand food preferences.

Juvenile behaviour changed in response to disturbance. During sampling or when the pots were moved, some starfish would climb up the walls, and use the water tension to float oral-side up and oscillate their tube feet which may help keep them afloat, take grip when they come into contact with a surface and to potentially help them to disperse. Floating may be a potential escape mechanism and this behaviour was exhibited by a large size range of juveniles from 1 mm^2 to 60 mm^2 area. This has also been observed in juvenile *Parvulastra exigua* and was suggested to be a possible mechanism for dispersal (Byrne 1995). Therefore, the larval stage may not be the only time COTS can disperse if the juveniles are able to climb structures that break through the surface at low tide and go into suspension.

Conclusions and significance

Food availability is likely to play a major role in the success and survivorship of the COTS juvenile. We have established the resilience and opportunistic nature of the juvenile and demonstrated their capacity to consume alternative food to CCA. If juveniles settle where CCA is absent or if the quantity of accessible CCA and other calcifying coralline algae is limited, they may be able to survive on biofilm and remain in the coral rubble for extended periods of time until finding a more nutritious food source. Additionally, as susceptibility to predation is influenced by juvenile size (Zann et al. 2987, Keesing and Halford, Wilmes et al. 2018), mortality rates are likely to be associated with diet-dependent growth rates. Juveniles that grow faster would spend less time at this vulnerable stage and are more likely to develop into mature, coralivorous adults.

The time lag from larvae to adulthood is unknown and complicates our ability to understand the bottom-up processes that drive population outbreaks. Rather than temporal pulses of enhanced larval survival leading to increased recruitment (the *terrestrial-runoff* hypothesis), the juvenile stage is likely to be the rate determining factor governing recruitment into the adult population, as suggested by other studies on post-settlement mortality and survival (Keesing and Halford 1992). Variable growth rates may also complicate the ability to age adult COTS by counting the pigment bands on COTS spines (Stump and Lucas 1990; Stump 1996) if the time to reach maturity (~2 years, supposed time of initial band formation, MacNeil *et al.* 2017) is delayed. Although this is a useful method to determine the demography and age structure of the population, it may not be possible to reliably estimate age or be used to draw conclusions as to the spawning year the COTS originated from, but rather time since maturity.

The next step to understand the biology of the COTS juvenile is to establish how long the ontogenetic switch from herbivory to corallivory can be delayed if coral is unavailable (Halford *et al.* 2004; Kayal *et al.* 2012). Juveniles that can continue to persist during food scarcity may form reserve populations in the reef infrastructure that give rise to outbreaks.

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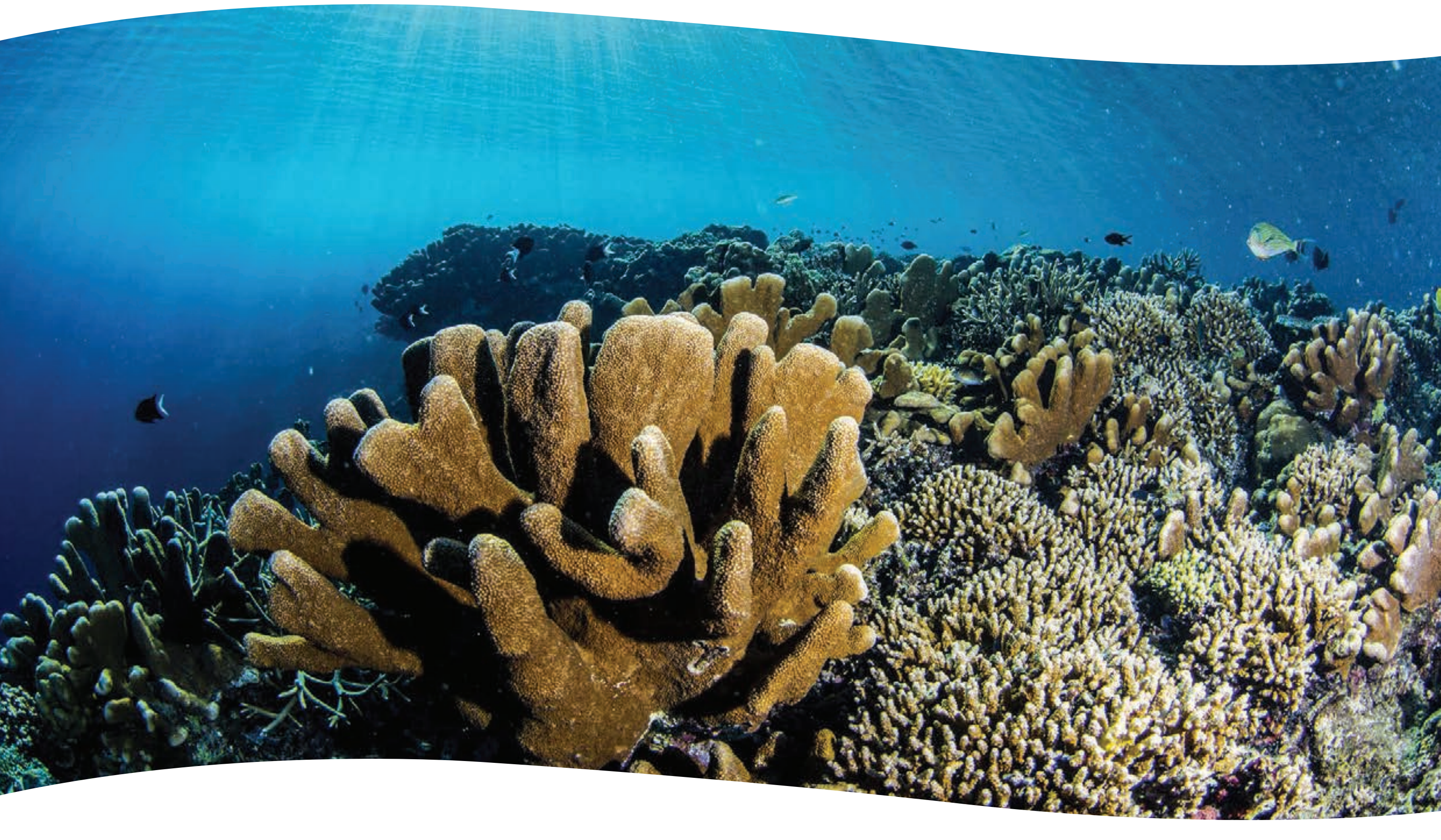
Supplementary Material 1: Post-hoc pairwise comparisons for main effects and interactions of the change in arm number and area of juvenile starfish over time with time (days), diet and population (A and B) as factors.

	Post hoc results: Interactions	
Arm number	*Time × diet*	
	Biofilm: 0=13<13=43<43=76=104=139	0: Biofilm = *Amphiroa sp* = CCA
	Amphiroa sp: 0=13<43<76<104=139	13: Biofilm = *Amphiroa sp* = CCA
	CCA: 0=13<43<76<104=139	43: Biofilm < *Amphiroa sp* = CCA
		76: Biofilm < *Amphiroa sp* = CCA
		104: Biofilm < *Amphiroa sp* = CCA
		139: Biofilm < *Amphiroa sp* = CCA
	Time × population	
	A: 0=13<43<76<104=139	0-76: B<A
	B: 0<13<43<76<104=139	104-139: A=B
Area	*Time × diet*	
	Biofilm: 0 = 13 = 43 = 76 = 104 = 139	0: Biofilm = *Amphiroa sp* = CCA
	Amphiroa sp: 0 = 13 < 43 < 76 < 104 < 139	13: Biofilm = *Amphiroa sp* = CCA
	CCA: 0 = 13 < 43 < 76 < 104 <139	43: Biofilm < *Amphiroa sp* = CCA
		76: Biofilm < *Amphiroa sp* < CCA
		104: Biofilm < *Amphiroa sp* < CCA
		139: Biofilm < *Amphiroa sp* < CCA



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