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Chapter 5

Priority Species to Support the Functional Integrity of Coral Reefs

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PRIORITY SPECIES TO SUPPORT THE FUNCTIONAL INTEGRITY OF CORAL REEFS

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Abstract Ecosystem-based management on coral reefs has historically focussed on biodiversity conservation through the establishment of marine reserves, but it is increasingly recognised that a subset of species can be key to the maintenance of ecosystem processes and functioning. Specific provisions for these key taxa are essential to biodiversity conservation and resilience-based adaptive management. While a wealth of literature addresses ecosystem functioning on coral reefs, available information covers only a subset of specific taxa, ecological processes and environmental stressors. What is lacking is a comparative assessment across the diverse range of coral reef species to synthesise available knowledge to inform science and management. Here we employed expert elicitation coupled with a literature review to generate the first comprehensive assessment of 70 taxonomically diverse and functionally distinct coral reef species from microbes to top predators to summarise reef functioning. Although our synthesis is largely through the lens of the Great Barrier Reef, Australia, a particularly data-rich system, it is relevant to coral reefs in general. We use this assessment to evaluate which taxa drive processes that maintain a healthy reef and whether management of these taxa is considered a priority (i.e. are they vulnerable?) or is feasible (i.e. can they be managed?). Scientific certainty was scored to weight our recommendations, particularly when certainty was low. We use five case studies to highlight critical gaps in knowledge that limit our understanding of ecosystem functioning. To inform the development of novel management strategies and research objectives, we identify taxa that support positive interactions and enhance ecosystem performance, including those where these roles are currently underappreciated. We conclude that current initiatives effectively capture many priority taxa but that there is significant room to increase opportunities for underappreciated taxa in both science and management to maximally safeguard coral reef functioning.

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. 2019a, b), reef recovery and persistence will be variable at local and global scales (Guzman & 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 & Halpern 2005, Ferrigno et al. 2016, McWilliam et al. 2018). Species-poor ecosystems, in contrast, 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 processes 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, 2018a, Mora et al. 2016, Harborne et al. 2017, Mumby 2017, Clements & Hay 2019).

Coral reefs are complex ecosystems with a great diversity of players, including microbes, algae, sponges, corals, other 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 & Silliman 2017, Renzi et al. 2019), their broad distributions and high abundances or high degree of specialisation with limited functional redundancy (Power et al. 1996, Piraino et al. 2002, 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, 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 & Bellwood 2003, Kramer et al. 2015, Brandl et al. 2018, 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, 2014, Hoey & Bellwood 2009, 2010b, Loffler et al. 2015a) and predatory fishes can alter reef community structure (Almany & Webster 2004, Rizzari et al. 2014, Stier & White 2014, Palacios et al. 2016b, Stier et al. 2017). As biodiversity conservation is often based on broad-scale habitat protection through marine reserves (Maynard et al. 2016, Mellin et al. 2016), ensuring that specific provisions for key species are incorporated could enhance effectiveness of management strategies (Halpern et al. 2007, Naeem et al. 2012, Shaver & Silliman 2017, Richards & Day 2018).

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 & Choat 1990, Bellwood et al. 2004, 2017, 2019, Munday et al. 2009b, Stuart-Smith et al. 2013, McClanahan et al. 2014, Pratchett et al. 2015, Bourne et al. 2016, Konow et al. 2017, Bierwagen et al. 2018, Brandl et al. 2018, McWilliam et al. 2018), 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 & 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 & 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 & McCormick 2000), cleaning symbioses (Cote 2000, Vaughan et al. 2017) and certain modes of predation like corallivory (Cole et al. 2008, Rotjan & 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 & Cuet 2008, Baker et al. 2008, Pratchett et al. 2008b, Przeslawski et al. 2008, Graham et al. 2011b, Harley et al. 2012, Andersson & 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 & Johnston 2010, Brodie et al. 2012, Browne et al. 2012, Erftemeijer et al. 2012, Wear & Thurber 2015, Hairsine 2017) and anthropogenic stressors more generally (Wilkinson 1999, Brodie & Waterhouse 2012, Ban et al. 2014b, Uthicke et al. 2016, Harborne et al. 2017, Richards & Day 2018). However, the majority of these studies are still focussed on corals and fishes.

While a wealth of empirical data and literature reviews address ecosystem functioning on coral reefs, they are typically targeted at specific taxa, processes and/or stressors. What is lacking 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 key species that support ecosystem functioning 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, He et al. 2013, Shaver & Silliman 2017, Thomsen et al. 2018, Renzi et al. 2019, Zhang & Silliman 2019). Identifying and protecting species of particular 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 & 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 focussed on the Great Barrier Reef (GBR), Australia, but is relevant for coral reefs globally. We assessed taxa based on their contributions to ecosystem processes and functioning and examined 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 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, functioning and stressors. 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. Case study themes were nominated by our expert panel during workshop discussions, and consensus decisions were made to reflect the multidisciplinary expert assemblage, 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 priority species regarding ecosystem functioning on coral reefs using a framework that can be expanded to guide future integrated and holistic management.

Defining ‘key’ species

There is some confusion and debate regarding the definition of ‘key’ versus ‘keystone’ species (Piraino & Fanelli 1999, Valls et al. 2015). Keystone species (Paine 1969) are those that have a large, disproportionate effect on their community relative to their abundance (Power et al. 1996). The ‘keystone’ archetype was applied to an intertidal marine predator that shaped community assemblages despite their low relative abundance (Paine 1969) but is not exclusive to top-down processes (Mills et al. 1993). Yet notably, species that drive ecosystem processes, energy flows and/or functioning can be abundant and dominant and thus should not be included in the ‘keystone’ typology (Paine 1995, Piraino & Fanelli 1999). Here, we refer to ‘key’ species as those with explicit roles in ecosystem functioning regardless of their relative abundance This facilitated our analysis across a diverse range of coral reef species at various levels of taxonomy and functioning, whether comparatively rare or abundant. This is particularly important given the challenges associated with identifying key species and quantifying their roles in high-diversity ecosystems (Gotelli et al. 2011, Pigot et al. 2016), including coral reefs (Maire et al. 2018). Critically, species’ roles in ecosystem functioning are dynamic, and species and their interactions have variable inputs and outputs over space and time (Piraino et al. 2002, Bellwood et al. 2019, Williams & Graham 2019).

Ecosystem functioning on coral reefs

Ecosystem functioning (Jax 2005) refers to the range of natural processes and components that contribute to the production and exchange of energy and materials (Srivastava & Vellend 2005, Pacala & 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 functioning 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 & 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 focussed 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) functioning (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 & 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 functioning encapsulate the most important goods and services provided by coral reefs, scaling up to benefit coastal protection and fisheries production (Moberg & Folke 1999, Harborne et al. 2017). They are fundamental 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).

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

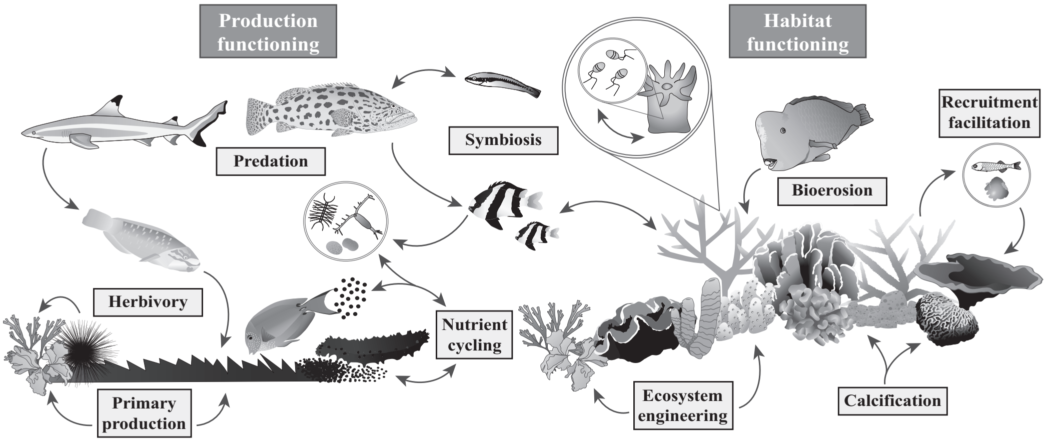

Figure 1 Simplistic representation of the nine key ecological processes considered here in support of habitat and production functioning on coral reefs.

and production functioning (De'ath et al. 2012, Cinner et al. 2016, 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 impact reef community composition, reef accretion and the net carbonate budget (Silverman et al. 2012, 2014, De'ath et al. 2013, Dove et al. 2013, DeCarlo et al. 2015, Albright et al. 2016b, 2018, Perry & Harborne 2016, Manzello et al. 2017, Schönberg et al. 2017, 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 & Hay 2010, Cheal et al. 2010, Hoey & 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 & Diaz-Pulido 2013, Hughes et al. 2019a) and 4) antagonistic population outbreaks of predatory species with impacts on live coral cover (Endean 1982, Brodie & Waterhouse 2012, De'ath et al. 2012, Baird et al. 2013, Pratchett et al. 2014, Hoey et al. 2016b). Such shifts in the coral reef archetype will continue to have serious repercussions on ecosystem resilience and recovery and in how we shape current and future management practises (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.

Methods

Expert elicitation

Quantifying the importance of species to ecosystem functioning is challenging and complex, especially for high-diversity ecosystems like rainforests and coral reefs. A number of studies have addressed this at specific levels of taxonomy and functioning, including for lichen assemblages within soil ecosystems (Gotelli et al. 2011), avian traits regarding plant-frugivore interactions (Pigot et al. 2016) and the influence of coral reef fishes on live coral cover and socio-environmental services (Maire et al. 2018). Yet for coral reefs, functional ecology lacks a clear definition and empirical evidence on the assumed links between reef taxa and processes (Williams & Graham 2019). Further, knowledge of reef functioning is largely weighted towards certain taxonomic and functional groups (e.g. corals and fishes; Bellwood et al. 2004, 2017, 2019, Stuart-Smith et al. 2013, Bierwagen et al. 2018, McWilliam et al. 2018). Given the breadth of our analysis, we employed expert elicitation to facilitate a comparative assessment of the ecological roles of a diverse array of coral reef taxa – from microbes to top predators – and broad spectrum of ecosystem processes and functioning.

Expert elicitation can provide valuable insight and data 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). 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, Australia. Using a snowball approach, experts were invited to participate in the project, ensuring a multidisciplinary assemblage with expertise across taxonomic groups, levels of ecosystem functioning and environmental stressors. A total of 18 experts were directly involved in project development, scientific workshops and/or the elicitation process. This size pool is within the lower ($n = 3$; Clemen & Winkler 1999) and upper ($n = 60$; de Franca Doria et al. 2009) ranges for the expert elicitation process (Ban et al. 2014b). Given the level of involvement and knowledge provided through the elicitation process, experts were included as co-authors.

Our expert elicitation process conformed to the Investigate, Discuss, Estimate, Aggregate (IDEA) protocol, which was designed to improve the accuracy of expert judgement (Burgman 2016, Hemming et al. 2018). In short, in a two-day workshop, we convened our panel of GBR experts, where they were first asked to *Investigate* knowledge and information on key coral reef taxa across a range of processes, functioning and threats. Attempts at compiling and formulating this information into questions and evidence were then open to feedback. Experts were encouraged to *Discuss* interpretations and results to promote critical thinking and reduce ambiguity. These two stages provided the framework of further project and survey development before experts completed an official independent *Estimate* scoring stage. Expert responses and scores were then *Aggregated* to produce mean data across responses. Specific details on project and survey development, and data handling and aggregation, can be found in the following sections.

Project and survey development

In the two-day workshop with our expert panel, 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 high-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 & 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,b, Marshall et al. 2018, Curnock et al. 2019). The exclusion of these species does not devalue their contributions to a functioning ecosystem (e.g. Graham et al. 2018, Savage 2019, Tavares et al. 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, dynamics (McCook et al. 2010, Day 2016) and governance (Day 2002, Brodie & 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, 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, interreefal areas) (GBRMPA 2004, 2014b,c, van de Koppel et al. 2015, Sievers et al. 2019), 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.

A methodology to assess functionally important species was developed by our scientific panel during the workshop (Figure 3; Table 1) in a series of stages framed by the IDEA protocol for expert elicitation (as previously) (Burgman 2016, Hemming et al. 2018). 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 functioning.
   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 the context of biological functioning.
   Question: Is management feasible for important species?

Figure 2 Taxonomic and functional groups partitioned in this assessment with 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).

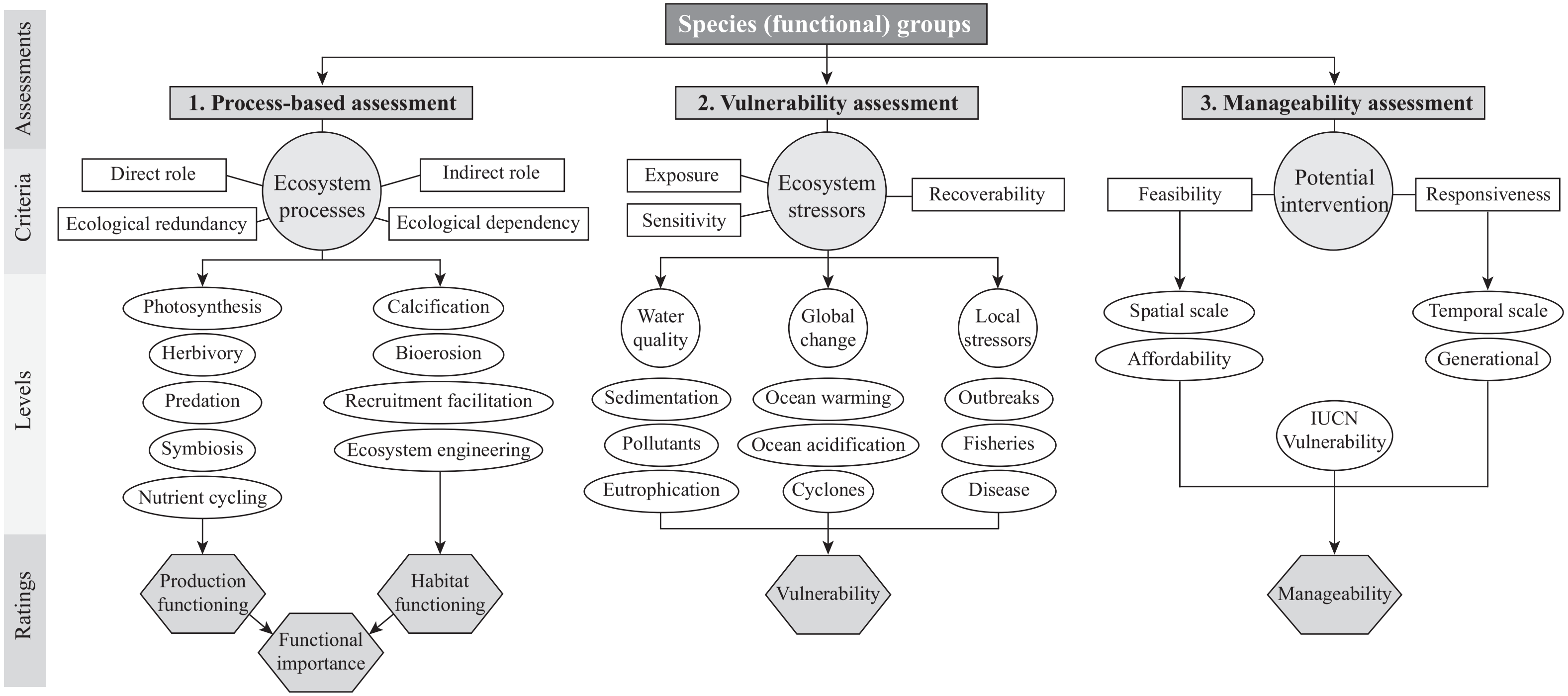

Figure 3 Framework outlining the assessment criteria employed to identify and rank priority species in support of ecosystem functioning based on their 1) functional importance (process-based assessment), 2) vulnerability and 3) manageability.

Table 1 Criteria used to score 70 functional groups on their (A) functional importance, (B) vulnerability and (C) manageability on the GBR.

Dynamic	Category	Score	Notes
A. Functional importance			
Direct contribution	None	0	No direct role performing the process
	Low	1	Directly contributes to the 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 the 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 performing the process or in mediating it
	Low	1	Some level of replaceability, similar species performing the process
	High	2	Replaceable in its role performing the process
Dependency	None	0	Self-sufficient in performing the process
	Low	1	Some level of dependence to perform the process
	High	2	Reliant on other organisms to complete the 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
B. Vulnerability			
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
C. Manageability			
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

Surveys to address these criteria were developed online using the Surveymonkey platform and 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 Table 1), 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, which is outlined as a critical elicitation process to ensure expert knowledge is accurately captured and interpreted (Martin et al. 2012, Hemming et al. 2018). 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. This proved particularly effective during the *Discuss* stage of the IDEA framework (Hemming et al. 2018). Scoring criteria are explicitly outlined for each assessment (Figure 3; Table 1).

Extensive literature searches were conducted by the primary author between March 2018 and June 2019 using online databases, including Web of Science and Google Scholar. Experts involved in the elicitation process had the opportunity to recommend relevant literature through the IDEA framework, but the review process remained largely independent of the expert panel. Peer-reviewed research and review articles pertaining to the 70 species groups and various levels of ecosystem processes, functioning and/or environmental stressors, as addressed in this review, were of focus. As a particularly data-rich system, literature explicitly related to the GBR was targeted, although we included relevant information for coral reefs more generally. Particular attention was given to species groups that scored highly at specific levels of ecosystem processes, functioning and/or stressors to benchmark results against peer-reviewed literature. This process aided in the interpretation of expert results and response accuracy (Hemming et al. 2018). We outline discrepancies between expert responses and the literature when evident, particularly for groups that scored highly despite receiving comparatively marginal representation in the literature. Independent literature searches were also conducted for each of the five case studies integrated in this review.

Scoring criteria

Functional importance: A process-based assessment

Contributions of organisms to ecosystem processes (e.g. calcification, bioerosion, herbivory, predation; Figure 1) drive and support ecosystem functioning (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 (Figures 1 and 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 functioning, 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 ecosystem processes were considered equally important to ensure that all were represented at their highest levels; that is, no process was weighted as more important to a functioning ecosystem.

Species groups were scored based on their direct and indirect contributions to each process (Figure 3; Table 1A). 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 process (e.g. algae to herbivory), as indirect effects are fundamental to the complexity of ecosystem functioning and to conservation outcomes (Wootton 1994, 2002, Dulvy et al. 2004, Jordán et al. 2008, Bergstrom et al. 2009, Ritchie & Johnson 2009). Species groups were also scored based on their ecological redundancy and dependency on a per-process basis (Figure 3; Table 1A), as species interactions and functional diversity can highlight critically important taxa (Petchey & Gaston 2002, Mouillot et al. 2013, 2014). Expert scores were compiled and average scores calculated for each functional group–ecosystem process combination. Finally, experts were elicited to rate the level of confidence (i.e. certainty; Table 1A) in their scores for each functional group. These scores 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:

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

This equation worked under the assumption that direct and indirect effects were equally important to ecosystem processes and functioning. 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 2). For magnitude, the top and bottom 33rd percentile of scores were classed as 'high' and 'low', respectively, with the remaining scores classed as 'intermediate' (Table 2). 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 importance of species groups; that is, how much they contribute (directly or indirectly) to the process outweighed their ecological redundancy and/or dependency (Table 2). 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 2), 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 2). 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 2), 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 2), as their ecological performance requires inclusion of other species with implications for management efficacy.

Table 2 Ranking scheme for functional groups based on their magnitude, redundancy and dependency in the context of nine key ecosystem processes on the GBR

Rank	Magnitude	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

Abbreviations: H, high; M, intermediate; L, low.

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 groups (i.e. $x = 1$) received higher final scores, and that those ranked highly for just one process were recognised. This also ensured that no species scored a complete zero (i.e. when $x = 12$). Final values for FI were square root transformed to normalise data. FI was calculated in the same manner for habitat and production functioning 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.

Assessing the vulnerability of coral reef species

Ecosystems are considered healthy if they are able to maintain (or recover) structure and functioning in the face of external pressures (Costanza & 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 (Figure 3). Parallel to scoring functional importance, experts were elicited to score the 70 functional groups (Figure 2) based on their vulnerability to nine critical stressors (Figure 3) in line with previous projects, elicitation processes and reviews (Ban et al. 2014a,b, Uthicke et al. 2016, Harborne et al. 2017). The Intergovernmental Panel on Climate Change (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 3; Table 1B).

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 1B), 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 & Brodie 2005, Wooldridge et al. 2006, Brodie & 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–functional group combination, using the equation:

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

This calculation assumes that sensitive groups that are not exposed 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:

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

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 1B), 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:

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

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.

Assessing the manageability of coral reef species

Each functional group was assessed in context of its relative manageability on the GBR. This assessment was in context of the biological roles 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 1C). Conservation status (e.g. IUCN Red List species) was also considered *post hoc* to address 'at risk' populations (Richards & Day 2018) (Figure 3).

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 (Figure 3). Groups were categorised as a high priority for management if they were in the top 66th percentile of scores for Mg, while those in the bottom 33rd 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.

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) (Table 1A, B). 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.

Knowledge gaps in ecosystem functioning on the Great Barrier Reef

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 previously, critical knowledge gaps in our understanding of reef functioning were made evident by our expert panel. Consensus decisions on the most logical, feasible and important knowledge gap themes were made, which were developed into five subprojects that reflect our multidisciplinary expert assemblage across taxonomic groups, levels of ecosystem functioning and environmental stressors on the GBR. 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;

1. Invertivory on the GBR: a poorly understood link in the trophic chain.
2. Addressing the carbonate budget for the GBR.
3. Microbial communities as indicators of water quality on the GBR.
4. Functional impacts of recreational spearfishing on the GBR.
5. Juvenile CoTS 'in waiting': the missing link in population and connectivity models.

Results and discussion

Species of particular functional importance on the GBR are outlined subsequently using an ecosystem process-based assessment for 70 distinct groups (Figure 2). Rankings for functional importance are provided at various levels of ecosystem functioning, 1) for each ecosystem process, 2) for habitat and production functioning and 3) combined overall (Figure 3). Additional rankings are outlined for species groups based on their perceived vulnerability to nine key environmental stressors on the GBR and for their relative manageability (Figure 3). Final scores are presented across these three components and weighted to scientific certainty. Note that all levels of ecosystem processes were considered equally important to a functioning reef to reflect all species and processes at their highest level of functioning.

Process-based assessment

Top-ranked species groups within each process are outlined in Table 3. Scores are discussed, interpreted and/or supported in the following sections through case-specific reviews of the literature available for coral reefs, primarily the GBR, at various levels of ecosystem processes and

Table 3 Functional importance (FI) rankings for 70 functional groups per process on the GBR

Taxa	Functional group	Primary production	Herbivory	Predation	Nutrient cycling	Symbiosis	Calcification	Bioerosion	Ecosystem engineering	Recruitment facilitation
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

(*Continued*)

Table 3 (*Continued*) Functional importance (FI) rankings for 70 functional groups per process on the GBR

Taxa	Functional group	Primary production	Herbivory	Predation	Nutrient cycling	Symbiosis	Calcification	Bioerosion	Ecosystem engineering	Recruitment facilitation
	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	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

(*Continued*)

Table 3 ***(Continued)*** Functional importance (FI) rankings for 70 functional groups per process on the GBR

Taxa	Functional group	Primary production	Herbivory	Predation	Nutrient cycling	Symbiosis	Calcification	Bioerosion	Ecosystem engineering	Recruitment facilitation
	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

Note: Shading denotes highest scores; 1st = dark, 2nd = mid, 3rd = light.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

functioning. Results met expectations in many cases, but due to our assessment of both direct and indirect effects, and ecological redundancy and dependency, we highlight novel and sometimes unexpected players. This interpretation was supported through the evaluation of peer-reviewed literature, outlined for groups that received high scores despite comparatively marginal attention in the literature.

Primary production

Algal turfs, phytoplankton, CCA and host-associated phototrophic microbes were the top-ranked groups for primary production (Table 3). Approximately 70% of the carbon fixed by primary producers on the GBR originates from phytoplankton (Furnas & Mitchell 1987, 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 & 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 are critical primary producers in oligotrophic coral reef waters, exhibiting high mass-specific rates of productivity (Adey & 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). Although they have a relatively low biomass per unit area and typically only reach heights of ~1 cm, algal turfs have a rapid turnover and can shape coral reef communities from cryptic species diversity (Carpenter 1985, 1986, Klumpp et al. 1988, Klumpp & McKinnon 1989, Klumpp & Pulfrich 1989, Enochs 2012, Enochs & Manzello 2012) to herbivore assemblages on reef flats (Bellwood 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 & McKinnon 1992, Russ 2003), lower than estimates for fleshy macroalgae (e.g. *Sargassum*; 1000 $g.C.m^{-2}.yr^{-1}$) (Schaffelke & Klumpp 1997). Turfs often persist as constant grazing by herbivores prevents overgrowth by larger, fleshy seaweeds (e.g. *Sargassum*) (Diaz-Pulido & 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 & Hoey 2018). 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.

Primary production by CCA is similar to that by turf algae (Chisholm 2003, Diaz-Pulido & McCook 2008, Lewis et al. 2017). Despite lower direct contributions to primary production, 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 & McKinnon 1992, Russ 2003, Littler & Littler 2007, Arnold et al. 2010), and recruitment dynamics (Doropoulos et al. 2017a,b).

Interestingly, no group scored the top ranking (FI = 1; Table 3), 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;

Symbiodiniaceae, 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.

Herbivory

Farming (e.g. damselfishes) and excavating (e.g. parrotfishes) fishes were the highest-rated groups for herbivory (FI = 2; Table 3). Farming damselfishes are well recognised for their role regulating the growth and composition of algal assemblages within their territories (Ceccarelli et al. 2001, 2011, Hata & Kato 2004, Hoey & Bellwood 2010c), 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 & Robertson 1994, Madin et al. 2011, Downie et al. 2013, Ollivier et al. 2018), particularly for species that are closely associated with reef refugia, including 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 & 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 & 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 3) 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. 2006a, Hoey & Bellwood 2009, Wismer et al. 2009, Johansson et al. 2013, Loffler et al. 2015a, Streit et al. 2015, Loffler & Hoey 2018). Caution must be taken when assuming functional redundancy among herbivorous fishes, particularly when generalising within the common nominal feeding modes (Bejarano et al. 2017).

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 3). As scored by experts, this may be an artefact of the low functional redundancy of detritivores, which are outlined in the literature 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, 2005, Wilson et al. 2003, 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 by experts as particularly important. This is supported in the literature, which describes the active role of *C. striatus* in removing sediment and detritus from the EAM, indirectly facilitating herbivory by other species (Goatley & Bellwood 2010, Marshell & 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 & McCormick 2000, Crossman et al. 2001, Goatley & Bellwood 2010, Marshell & 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 & Galzin 1993, Choat et al. 2002, 2004, Clements et al. 2009, 2017, Hernaman et al. 2009, Kramer et al. 2013). Notably, diet partitioning and selectivity are currently underestimated for many nominal detritovores and herbivores (Choat & 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. This was not captured in expert responses 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, 2015). Zooplankton, and a range of other invertebrates (sea urchins, decapods, gastropods, seastars), scored highly for herbivory (FI = 3; Table 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 in the oligotrophic waters of the GBR (McKinnon & 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 & Adey 1981, Klumpp & 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 & 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 documented in the Caribbean (Carpenter 1990, Mumby 2006, Mumby et al. 2006b). Some sea urchin species are also outplanted as biocontrol (e.g. *Tripneustes*) to maintain invasive algal growth on some reefs (Conklin & 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, particularly in the cryptic reef framework, limiting algal growth and facilitating coral recruitment in refugia from higher order grazers (Brawley & Adey 1981, Coen 1988, Klumpp & Pulfrich 1989, Doropoulos et al. 2012b, 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.

Predation

Somewhat unexpectedly, the top-ranked groups for the predation process were triton snails and cephalopods (FI = 1; Table 3). 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). Expert scores for triton snails are likely a reflection of this niche role in predation, especially as CoTS population control is a prime management focus on the GBR (Pratchett et al. 2014, Babcock et al. 2016a, Hoey et al. 2016b). CoTS population outbreaks have been attributed 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 & Endean 1969). Regardless, their ranking here reflects this important predatory niche, which has been addressed for the GBR in depth 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 3), 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*) (Jones et al. 2011), cleaner wrasses (*Labroides*) (Grutter 1997) and rockmover wrasses (*Novaculichthys*) (Wainwright et al. 2002). The lack of consideration of invertivores by experts here may reflect the broad ecological redundancy of this group at this level of functioning and, importantly, the data gaps regarding empirical observations of invertivory on the GBR (Case Study 1).

Cephalopods also received the top score for the predation process (FI = 1), despite the literature being largely restricted to their taxonomy and diversity (Roper & Hochberg 1987, Norman 1992, Norman & Finn 2001, Rosa et al. 2019). Surprisingly little information exists on their functional ecology on the GBR and in general (Ponder et al. 2002). The ecological importance of cephalopods is perhaps mostly presumed from their fast growth rates (Pecl & Jackson 2008), broad cross-shelf distributions occupying cryptobenthic to pelagic habitats (Moltschaniwskyj & Doherty 1995) and their contributions to fisheries productivity as both predators and prey (Connell 1998, Beukers-Stewart & Jones 2004, Taylor & 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 & Essington 2008). Changes to predatory-prey dynamics of cephalopods could have ecosystem-level implications (Pecl & Jackson 2008, Spady et al. 2014, 2018, Rosa et al. 2019). 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 the predation process by experts here (FI = 5). Overall, trophic interactions in cryptic habitats are difficult to quantify and are poorly characterised.

Cryptobenthic fishes, which also occupy the reef matrix, rated highly for predation (FI = 3), despite the lack of empirical information on their taxonomy and ecological 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 & 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 in the reef framework (Goatley et al. 2017), particularly of microcrustaceans (e.g. copepods) (Case Study 1).

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 & 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 & Thorrold 1993, McKinnon et al. 2005, 2007). Zooplankton scored high within the predation process (FI = 3), given their fundamental contribution to reef trophodynamics. 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.

CASE STUDY 1: INVERTIVORY ON THE GREAT BARRIER REEF: A POORLY UNDERSTOOD LINK IN THE TROPHIC CHAIN

Hannah Sheppard-Brennand, Maria Byrne, Jessica Stella, Kennedy Wolfe

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 this case-specific 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 1), ~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). 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). Targeted research is imperative to quantify predator-prey dynamics for invertivores on the GBR, including a focus on quantifying direct measures of invertivory, prey availability and trophic transfers from the benthos to higher order taxa to enhance production functioning.

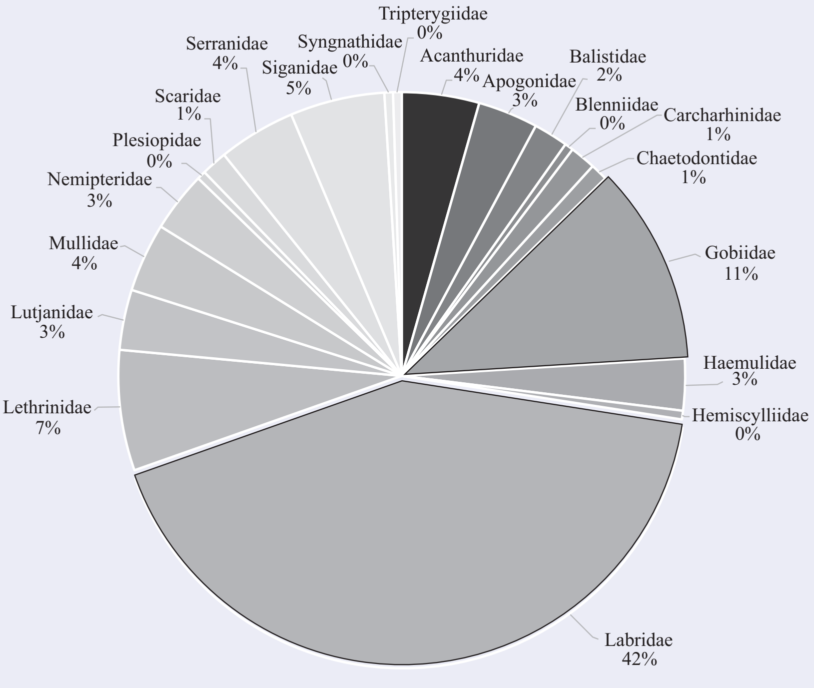

Figure CS1.1 Proportion of coral reef fishes and sharks (by family) that are reported to consume benthic mobile invertebrates on the GBR.

The greatest diversity of 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 & Hatcher 1983, Bellwood et al. 2006b, Kramer et al. 2015). While this may suggest high functional redundancy (Bellwood et al. 2006b), labrids exhibit the greatest range of specialised feeding mechanisms and species with key roles; for example, 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) 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 & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 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 & Bellwood 2002, Boaden & Kingsford 2012).

For species where invertivory was quantified (Figure CS1.2), ~40% were obligate consumers of invertebrates. 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: *Cheilodipterus quinquelineatus* and *Carcharhinus melanopterus*, >35% of stomach contents; herbivores and detritivores: *Amblygobius phalaena* and *Bathygobius fuscus*, >15%; carnivores/piscivores: *Lethrinus nebulosus*, >50%) (Appendix 1). 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).

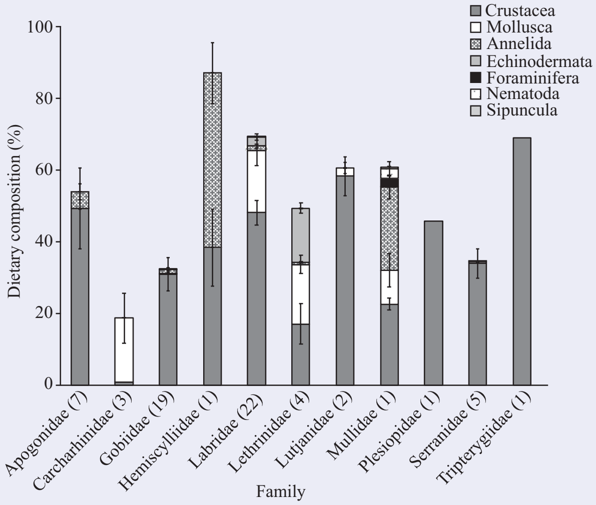

Figure CS1.2 Mean proportion (±SE) of invertebrates (by phyla) in the diet of nominally invertivorous fishes (by Family). Number of species are indicated in parentheses after family name. Note only 11 of 18 families are presented as other data were not comparable.

Notably, the zooplankton group also comprises the macro- and mega-plankton, which includes the larger-bodied (>200 mm) cnidarian and ctenophoran jellyfishes. This group has 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 & Arai 2001). Jellyfish blooms are increasingly documented around the world, including on the GBR, with impacts on ecosystem stability and functioning (Hutchings et al. 2019). Cubozoans (box jellyfish and *Irukandji*) are a particularly important group on the GBR resulting from their socioeconomic impacts on inshore reefs through their sometimes fatal envenomation (Huynh et al. 2003, Kingsford et al. 2012, Gershwin et al. 2014).

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, 2007, Johansen & 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 & 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, including the planktivores and invertivores. Similarly, 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 & 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).

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 cryptopredators 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 (*Odontodactylus*) (deVries et al. 2016, Goatley et al. 2017) and cone snails (*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 the juvenile life stage 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 & Stier 2010), and sponge-feeding nudibranchs sequester chemical defences that can alter fish feeding behaviour (Proksch 1994, Becerro et al. 1998, Ritson-Williams & 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 3), 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 & 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 & Krupp 1986). A recent (but rare) outbreak of *Culcita schmideliana* in the Maldives was associated with 24% mortality of juvenile acroporid and pocilloporid corals, hindering postbleaching reef recovery (Bruckner & Coward 2019). The boom-and-bust population characteristic typical of echinoderms attributes to the ephemeral nature of their ecological roles and impacts (Birkeland 1989, Uthicke et al. 2009). Even the nominally herbivorous sea star, *Linckia* *laevigata*, is reported to feed on live coral, but this behaviour is rare, with little documented impact as their stomachs are relatively small (Laxton 1974b).

Large predatory reef fishes (transients and residents) were among the highest scoring fishes within the predation process but were rated lower by experts than a range of other taxa (Table 3). This is in line with suggestions in the literature 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 & Almany 2002, Almany 2004b, Almany & Webster 2004, Rizzari et al. 2014, Palacios et al. 2016a,b), 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 coral 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). As reflected in expert scores, this may be associated with the dependency of resident predators on habitat refugia (Rogers et al. 2014, 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 & Carr 1997, Almany 2004a).

Nutrient cycling

Detritivorous fishes were the highest-ranked group regarding nutrient cycling (FI = 1; Table 3). They are outlined in the literature as fundamental components of nutrient pathways transferring energy from the EAM (i.e. algal turfs) to secondary consumers (Crossman et al. 2001, 2005, Wilson et al. 2003, Bellwood et al. 2014) and in the export of nutrients and detritus from sand patches across the calcified reef structure (Lukoschek & McCormick 2000, Crossman et al. 2001, Goatley & Bellwood 2010, Marshell & Mumby 2012). 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 and highly productive and provide direct links from the hidden and largely inaccessible reef matrix to higher consumers (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018). The small size (<50 mm length) and rapid population turnover of cryptobenthic fishes reflect their niche roles in top-down trophodynamics within the reef matrix and bottom-up pathways that support fisheries productivity (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 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 & Mitchell 1987, 1988, Klumpp & McKinnon 1992, Russ 2003, Littler & 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 & Gilmartin 1982, Revelante et al. 1982, Furnas 1992). Similarly, turf algae are particularly important in the fixation of nitrogen on coral reefs. 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). 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 nominally 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, 2018a). Impressively, host-associated microbes (the 'coral microbiome') (FI = 2) can provide >90% of a coral's nutritional requirements (Muscatine & Porter 1977, Bourne et al. 2016). While the ecological 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).

Tabular corals (FI = 2) were ranked higher than the remaining coral groups (FI = 4–8) by our expert panel. Based on the literature, this is likely a result of the broader importance of tabular corals regarding rapid reef growth and post disturbance recovery (Connolly & Muko 2003, Ortiz et al. 2014, 2018). In the context of nutrient cycling, 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). A range of coral species, including some acroporids and pocilloporids, exhibit higher rates of heterotrophy in turbid environments near shore compared to the same species in oligotrophic waters offshore (Anthony 2000, Anthony & Fabricius 2000). Soft corals tend to dominate the turbid waters typical of nearshore reefs on the GBR, suggesting regional specificity in functional importance between coral taxa (Fabricius 1997, Fabricius & 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 & De'ath 2008).

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 & Steneck 2018). This discrepancy between expert scores and peer-reviewed evidence is important to note. This may be a result of the lack of information available for sponges (particularly cryptic species) on Pacific reefs, as most information on the trophic ecology of sponges is derived from the Caribbean (Wilkinson 1983, 1987, Mumby & Steneck 2018).

The highest-scoring mobile invertebrates to nutrient cycling were the zooplankton (FI = 2; Table 3), which include 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 taxa, 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 & Greenwood 1994, Marnane & Bellwood 2002, Holzman & Genin 2003, Holzman 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). There are also demersal zooplankton that migrate between the benthos and water column daily with important roles in nocturnal trophodynamics (Jacoby & Greenwood 1988). Zooplankton can be highly abundant with distinct cross-shelf community assemblages (Sammarco & Crenshaw 1984, Williams et al. 1988, McKinnon & 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 & 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 & 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 3). As reflected by expert scores here, these groups are commonly underappreciated in their roles compared to reef fishes and corals. Sea cucumbers have been coined the 'vacuum cleaners' of the reef (Samyn & 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 & Klumpp 1998, Uthicke 1999, 2001, Wolkenhauer et al. 2010, Schneider et al. 2011, 2013, Purcell et al. 2016a, Lee et al. 2017, Wolfe & 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.

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) functional groups for symbiosis were microbes (host-associated phototrophic), corals (tabular, massive, soft), decapods (coral-associated) and fishes (cleaner wrasse) (Table 3). The coral microbiome (i.e. coral-associated microbes) can exist at densities exceeding one million cells per cm^2 of host tissue (Garren & Azam 2012a), with diversities in the thousands in some host species (Mouchka et al. 2010, Blackall et al. 2015, Bourne et al. 2016). The best-known coral symbionts are photosynthetic dinoflagellates within the Symbiodiniaceae, which can reach densities $>10^6$ cm^{-2} of host tissue (Garren & Azam 2012a, 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, 2018b, Ramsby et al. 2018b). 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 & Porter 1977, Bourne et al. 2016), including up to 100% of their carbon requirements (Falkowski et al. 1993, Palardy et al. 2008). The relative abundance of particular *Symbiodinium* cells (e.g. Clade D) can increase thermal tolerance in their coral hosts (Howells et al. 2012, 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*, *Tetralia*, *Trapezia*) (Glynn 1980, 1983, Pratchett 2001, Stella et al. 2011b, Pollock et al. 2013). Christmas tree worms (*Spirobranchus*) 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 & 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 individual's 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), which may reflect the coral-centric interpretation of symbioses in expert scores.

For the reef fishes, cleaner wrasses (*Labroides*) scored highest (FI = 2). 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 & Poulin 1998, Bshary &

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, 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.

Calcification

Microbes (host-associated phototrophic), calcifying algae (CCA, calcareous species) and corals (tabular) scored highest for their roles in calcification (Table 3). The influence of the coral microbiome on coral health and functioning is widely appreciated in the literature (Egan et al. 2013, Blackall et al. 2015, Bourne et al. 2016, Glasl et al. 2016, 2018b), and their functional ranks by experts here even outweighed some coral species. 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). 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, 2018), including those on turbid inshore reefs (Thompson & 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). In addition, the redundancy of key tabular corals could be considered relatively low, with just three species considered common on the GBR: *Acropora hyacinthus*, *A. cytherea* and *A. clathrata*.

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 & 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 & 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 interreefal space. Overall, hard scleractinian corals are calculated to be responsible for ~95% of carbonate production on the GBR, with CCA accounting for the remaining 5% (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 programme, and/or their contributions are often comparatively marginal. 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, 2015, Wilson & Vecsei 2005, Sarkar et al. 2016, Schmitt & Gischler 2017). Large benthic foraminiferans (e.g. *Marginopora*, *Baculogypsina*) can be the single most important contributors to mass sediment production on

CASE STUDY 2: ADDRESSING THE CARBONATE BUDGET OF THE GREAT BARRIER REEF

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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 forecast the ability of reefs to cope with environmental change (Perry et al. 2008, 2018, Kennedy et al. 2013, Mace et al. 2014). Some studies have quantified the rates of carbonate production (e.g. Kinsey 1983, Browne et al. 2012, Silverman et al. 2012) and bioerosion (Kiene & Hutchings 1994, Osorno et al. 2005, Hoey & 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 & 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, 2014, 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.

Carbonate production and bioerosion rates were calculated from coral cover reported for 37 reefs across the southern GBR between 2017 and 2019 using the long-term monitoring programme (LTMP) data provided by the Australian Institute of Marine Science (AIMS) (Jonker et al., 2008). Southern reefs were selected as this analysis spanned a period of time when coral cover was in serious decline on the northern GBR (Hughes et al., 2017b, 2018b). This is an important consideration with regard to spatial and temporal changes in the carbonate budget of the GBR in future work. Data for coral cover were combined with published extension, production or erosion rates sourced from the ReefBudget website (http://www.exeter.ac.uk/geography/reefbudget) and other publications for the GBR (Drew, 1983; Musso, 1994; Osorno et al., 2005; Hoey & Bellwood, 2008; Pratchett et al., 2015; Anderson et al., 2017; Razak et al., 2017; Rocker et al., 2017). Total carbonate production of each reef was calculated with a model derived from geometric growth forms of corals. Estimates were derived from rates of carbonate production (or accretion) by hard corals and calcareous algae (CCA, articulated calcareous red algae, *Halimeda* and *Peyssonnelia*). Carbonate removal (bioerosion) by parrotfishes (*Bolbometopon*, *Cetoscarus*, *Chlorurus*, *Hipposcarus* and *Scarus*) was calculated using density and size records in the AIMS LTMP fish transect dataset. Secondary bioerosion by micro- and macro-borers (including polychaetes, sipunculans, sponges [e.g. *Cliona*] and molluscs) was estimated using experimental data from the GBR (Kiene & Hutchings, 1994; Osorno et al., 2005; Chazottes et al., 2017).

Hard coral assemblages contributed to approximately 95.5% of the total reef carbonate production (calcification) across all reefs on the GBR, with the remaining 4.5% contributed by calcareous algae, including CCA, *Halimeda* spp., *Peyssonnelia* spp. and calcareous red algae

Table CS2.1 Mean rates (±SE) of carbonate production, bioerosion and carbonate budget in the southern GBR

		$kg\ m^{-2}\ yr^{-1}$
Production	Primary (corals)	6.36 ± 0.52
	Secondary (algae)	0.30 ± 0.03
	Total	6.66 ± 0.54
Bioerosion	Primary (parrotfish)	−4.18 ± 0.53
	Secondary (micro/macroborers)	−0.42 ± 0.02
	Total	−4.60 ± 0.53
Carbonate budget		2.07 ± 0.77

(Table CS2.1). *Acropora* species exhibit the greatest calcification rates on the GBR compared to other carbonate producers (i.e. non-*Acropora* corals and calcareous algae) (Figure CS2.1). Total carbonate production ranged between 0.49 and 12.97 kg m^{-2} yr^{-1} in the southern GBR (Table CS2.1). Mean bioerosion rates, driven almost entirely by grazing parrotfishes (Figure CS2.1), ranged between 0.69 and 19.0 kg m^{-2} yr^{-1}) (Table CS2.1). Overall, the total carbonate budget ranged from –14.9 to 12.05 kg m^{-2} yr^{-1} with a mean of 2.1 ± 0.8 kg m^{-2} yr^{-1}, suggesting a positive carbonate budget in the southern GBR (Table CS2.1). 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.

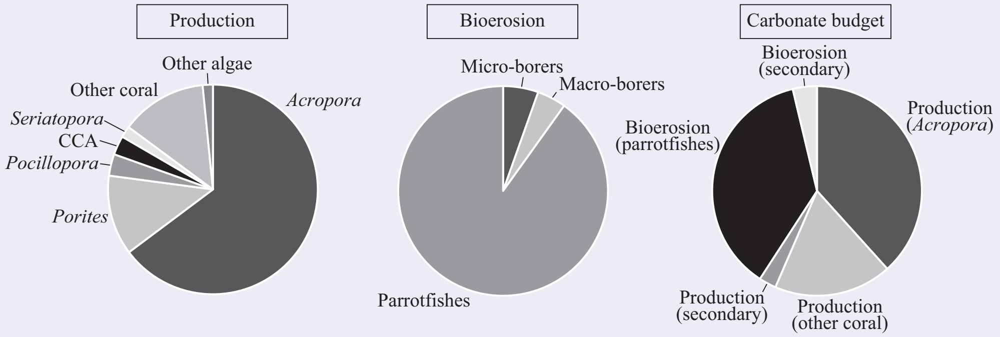

Figure CS2.1 Proportional mean rates of production (calcification), bioerosion and the total carbonate budget by key groups in the southern GBR between 2017 and 2019 (AIMS LTMP).

the GBR where they can make up >60% of biogenic sediment (Yamano et al. 2000, Dawson & 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), 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, which facilitate coral calcification, upregulated coral associates within this process compared to other crustaceans.

Molluscs generally scored highly (FI = 3), but as for crustaceans, they have lower direct contributions to calcification compared to corals. Calcification in Mollusca is perhaps greatest for giant clams (Tridacnidae), with some species reaching >120 cm across and weighing >200 kg (Rosewater 1965). Calcifying 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). Corallivorous molluscs (e.g. *Drupella*) have indirect impacts on calcification through coral predation (Cumming 1999, 2009, Glynn & 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 antillarum* can be derived from living scleractinian corals (Carpenter 1981), an unsuspected coral predator.

Bioerosion

No group received the top ranking for bioerosion, reflecting the high redundancy within this process (Table 3). 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, 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 & 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 & 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 & Golubic 2005). However, the contributions of microborers to net reef erosion are difficult to quantify, and large knowledge gaps remain (Case Study 2) (Hutchings 1986, Glynn & 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 undersaturation) 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 & Manzello 2015). Around 2%–3% of the carbonate skeleton is dissolved in this process, with the remainder passed on as sediments (Glynn & 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 dataset, as densities of other cryptic bioeroding invertebrate species are hard to quantify. The lack of spatially explicit data on these groups makes it difficult to upscale their contributions to bioerosion and reef carbonate budgets (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 & 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 biological and ecological 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 & Hutchings 1983). *Spirobranchus* (Serpulidae) scored highly among the other worm groups, but, importantly, they do not bore into live coral directly. Instead, these worms stimulate corals to grow around their thinly calcified tubes, 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 3). 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, 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 & 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 & 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 muricatum*) (Bonaldo et al. 2014). Parrotfishes are generally the greatest contributors to bioerosion on coral reefs 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 in the southern GBR. Excavating parrotfishes (*Bolbometopon* and *Chlorurus* spp.) are typically the most significant external bioeroders on coral reefs, contributing to erosion rates over 32 kg $CaCO_3$ m^{-2} yr^{-1} on the GBR (Hoey & Bellwood 2008), with significant contributions to sediment production (Bellwood & Choat 1990, Bellwood et al. 2003). *Bolbometopon muricatum* 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 & Bellwood 2008).

Ecosystem engineering

Bolbometopon scored highest by experts regarding ecosystem engineering (FI = 1; Table 3). This was influenced by the low redundancy of this species, which is supported in the literature, given its functionally explicit role as a mass excavator of live and dead coral, particularly on outer-shelf reefs (Hoey & 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 & Bellwood 2008) and has the potential to drive a negative carbonate budget (Case Study 2), especially following disturbance 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, 2011, Hata & Kato 2004, Ceccarelli 2007, 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, 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 & Menge 1991, Cheal et al. 2008, Harborne et al. 2012, Rogers et al. 2014, 2018a,b). Different coral species support different fish communities (Holbrook et al. 2008, 2015, Messmer et al. 2011), 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 scales up to support fisheries productivity (Pratchett et al. 2008a, Kerry & Bellwood 2012, 2015a,b, 2016, 2017). However, tabular and branching corals typically have ephemeral life history traits (Tanner et al. 1996), and the loss of particular coral species can 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 & Muko 2003, Ortiz et al. 2014, 2018, Yadav et al. 2016). 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, 2018, Yadav et al. 2016). 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), brooding *Pocillopora* (grouped here within ‘other branching corals’) replaced broadcast spawning acroporids as the predominant recruitment taxon for the first time recorded (Hughes et al. 2019a) and may emerge as key features in the current reef recovery trajectory owing to transgenerational plasticity and adaptation through local retention of brooding reproductive modes (Torda et al. 2013a,b, 2017).

Sponges also scored highly for ecosystem engineering, particularly larger conspicuous groups (heterotrophs, phototrophs) (Table 3). 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 & Taylor 2012, Taylor et al. 2013). It is not surprising that all microbe groups also scored highly (FI ≥ 4). Although scoring lower for ecosystem engineering than other sponge groups (Table 3), the role of cryptic and boring sponges to reef and rubble consolidation is well appreciated (Wulff & 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 & 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.

Recruitment facilitation

Parrotfishes scored highest for recruitment facilitation (FI ≥ 3; Table 3). As previously, 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 & Choat 1990, Bonaldo & Bellwood 2009, Bonaldo et al. 2014). This may also be true for grazing invertebrates like sea urchins (Dart 1972). 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 & Negri 1999, Harrington et al. 2004, Birrell et al. 2008b, Arnold et al. 2010, Doropoulos et al. 2012a, 2013, Brooker et al. 2016b). While turf and macroalgal growth can impair the recruitment of coral reef species (Birrell et al. 2008a, Diaz-Pulido & 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 such as 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 & 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 & 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, other invertebrates) (Baird & 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 & Buss 1979, Fox et al. 2003, Fox & 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 & Jones 1998, Lecchini et al. 2007, Cabaitan et al. 2008, Neo et al. 2015). Shell and ‘bed’ construction by giant clams and other bivalves offers structural complexity to the reef that provides substrate for colonisation by a diversity of holobionts, epibionts, commensal and ectoparasitic organisms (Neo et al. 2017). 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. Further, the functional roles of bed-forming species are likely to be greater in intertidal and estuarine habitats (e.g. oysters), beyond the target habitat explored here.

Functional importance rankings

In this section, we provide a ranking across our 70 functionally and taxonomically distinct groups, creating a hierarchy of species in terms of their total functional importance from our ecosystem process-based assessment. Using the scores elicited by experts on a per-process basis (as previously), we produced three sets of ranks for each group’s relative importance to: 1) production functioning (i.e. primary production, herbivory, predation, nutrient cycling and symbioses), 2) habitat functioning (i.e. calcification, bioerosion, ecosystem engineering and recruitment facilitation) and 3) total ecosystem functioning (i.e. all nine processes combined) (greater detail can be found in the methods). These ranks are presented in Table 4.

Table 4 Functional importance (FI) rankings for functional groups on the GBR, calculated for production and habitat functioning and overall

Taxa	Functional group	Production functioning	Habitat functioning	Total functioning
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	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

(*Continued*)

Table 4 (*Continued*) Functional importance (FI) rankings for functional groups on the GBR, calculated for production and habitat functioning and overall

Taxa	Functional group	Production functioning	Habitat functioning	Total functioning
	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

Note: Shading denotes ranks; 1st = dark, 2nd = mid, 3rd = light.
Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

Species that scored highly within just one ecosystem process were not necessarily ranked highly in terms of total functional importance (e.g. cephalopods) (Table 4). Similarly, species that scored well within either production or habitat functioning separately may not have ranked highly overall (e.g. zooplankton, cryptobenthic fishes, detritivorous fishes) (Table 4). Only those that scored highly across multiple processes, and those contributing to both production and habitat functioning, would achieve a high final rank (Table 4). For specific details within each process with support from the literature, refer to the sections previously.

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 5). Inner-reef regions were assessed separately, as exposure to some stressors (particularly those related to water quality) is most significant inshore (Devlin & Brodie 2005, Wooldridge et al. 2006, Brodie & 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). Thus, we specifically contrast results for water quality stressors between inshore and offshore regions (Table 6). Vulnerabilities to each of our nine key stressors were considered equal, 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. 2018).

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 5). 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, 2018b,c), with alterations to reef community assemblage and structure (Stuart-Smith et al. 2018), trophodynamics (Hempson et al. 2018a,b), 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). Rates of change in ocean chemistry are also 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). Further, 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).

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 & Munday 2018, Wolfe et al. 2020). Transgenerational plasticity may enable some marine organisms to acclimatise over several generations, enhancing adaptive responses, poleward migration and reef resilience in the face of climate change (Byrne et al. 2020, Torda et al. 2017).

Host-associated microbes scored among the most vulnerable to climate change stressors, particularly for ocean warming (Table 5). 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 4) (Hansen et al. 1992, Falkowski et al. 2008, Glasl et al. 2017, 2018a). 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). Zooplankton were considered more vulnerable to climate change stressors than phytoplankton (Table 5), but impacts will be highly variable across the diversity of these two groups. Anthropogenic stressors and their interactions will impact phyto- and zooplankton growth, development, physiology, abundance and distribution, altering blooms, benthic-pelagic coupling and functioning (Huntley & Lopez 1992, Edwards & Richardson 2004, Richardson & Schoeman 2004, Kirby et al. 2007, Gao et al. 2012, Häder & Gao 2015, Carrillo-Baltodano & Morales-Ramirez 2016, Dupuy et al. 2016). 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

Table 5 Potential impact (PI) of six pertinent stressors on 70 functional groups on the GBR

Taxa	Functional group	Warming	Acidification	Cyclones	Fisheries	Disease	Outbreaks
Microbes	Phototrophic	9.0	1.0				
	Host-associated	16.0	4.0			1.0	
	Chemoautotrophic	4.0	1.0				
	Heterotrophic	9.0	1.0				
Algae	Phytoplankton						
	Algal turfs	1.0					
	Leathery	1.0		2.3			
	Foliose			0.3			
	Calcareous	4.0	4.0	2.3			
	CCA	9.0	9.0				
Sponges	Heterotrophic	1.0	7.1	16.0	1.0	1.0	
	Phototrophic	1.0	1.0	16.0	1.0	1.0	
	Boring	0.4		0.3		1.0	
	Cryptic	1.0	1.0	1.0		1.0	
Coral	Tabular	16.0	9.0	16.0	0.1	2.8	16.0
	Staghorn	16.0	9.0	16.0	0.4	2.8	16.0
	Branching (other)	16.0	9.0	16.0	0.1	1.8	16.0
	Massive	16.0	6.3	1.8	0.1	1.8	1.8
	Encrusting	16.0	6.3	1.8	0.1	1.8	2.8
	Free-living	12.3	6.3	4.0		1.8	1.8
	Soft corals	12.3	4.0	11.1	0.1	1.0	
	Foraminifera	4.0	6.3	7.1		0.4	
Worms	Nematodes						
	Nemertea			0.3			
	Polychaetes			0.3			
	Spirobranchus	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	16.0	16.0	9.0			0.3
	Barnacles	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	9.0	16.0	0.3			
	Parasitic	4.0	9.0	0.3			
Molluscs	Gastropods (H)	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	16.0	16.0	16.0	1.0		
	Bivalves	16.0	16.0	4.0	1.0	1.0	
	Chitons	9.0	9.0	1.0			
	Cephalopods	1.0	4.0	0.3	2.3		
Echinoderms	Seastars (H)	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)	9.0	1.0	1.0	1.0		

(*Continued*)

Table 5 (*Continued*) Potential impact (PI) of six pertinent stressors on 70 functional groups on the GBR

Taxa	Functional group	Warming	Acidification	Cyclones	Fisheries	Disease	Outbreaks
	Sea urchins (regular)	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	11.1	4.0	11.1			1.8
	Farmers		1.8	7.1			
	Scrapers (scarids)		1.8	0.1	0.1		
	Browsers (nasos)		1.8	0.4	0.1		
	Browsers (siganids)		1.8	0.4	0.4		
	Browsers (other)		1.8	0.4	0.4		
	Bolbometopon	1.8	4.0	1.8	0.4		
	Excavators (other)		1.8	1.8	0.1		
	Detritivores	0.4	1.8	7.1			
	Planktivores	11.1	4.0	11.1			2.8
	Corallivores	16.0	11.1	2.8			4.0
	Invertivores (labrids)	4.0	4.0	1.8	0.1		
	Invertivores (other)	4.0	4.0	1.8	1.8		
	Invertivores (lutjanids)	4.0	4.0	1.0	0.4		
	Eels	7.1	4.0	1.0			
	Piscivores (residents)	11.1	4.0	2.8	16.0		
	Piscivores (transients)	7.1	4.0	1.8	16.0		
	Cleaner wrasse	7.1	1.8	11.1			

Note: Exposure was considered in context of offshore reefs. Shading denotes highest scores; maximum PI = 16 (dark); high PI ≥ 10 (mid); medium PI ≥ 7 (light); blank cells denote PI = 0.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

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,b), and corallivorous, planktivorous and cryptobenthic fishes (Munday 2004, Pratchett et al. 2004, 2008b, Wilson et al., 2006 2014, Cole et al. 2010, Bellwood et al. 2012a, Hempson et al. 2018c, Rice et al. 2019) (Table 5). 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 & Pratchett 2006, Cole et al. 2008, 2010, Graham et al. 2009, Thompson et al. 2019), while their feeding adds further pressure on coral condition (Cole et al. 2009). Butterflyfish (Chaetodontidae) 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 & Arthur 2018). The close contact relationships

Table 6 Potential impact (PI) of three water quality stressors on 70 functional groups on the GBR

			Inshore			Offshore	
Taxa	Functional group	Nutrients	Sediments	Pollutants	Nutrients	Sediments	Pollutants
Microbes	Phototrophic		4.0	16.0		1.0	
	Host-associated	16.0	9.0	16.0	4.0	2.3	
	Chemoautotrophic			9.0			
	Heterotrophic			9.0			
Algae	Phytoplankton		1.0	9.0		0.3	
	Algal turfs		1.0	9.0		0.3	
	Leathery		1.0	4.0		0.3	
	Foliose		9.0	4.0		2.3	
	Calcareous		9.0	4.0		2.3	
	CCA	4.0	16.0	9.0	1.0	4.0	
Sponges	Heterotrophic		7.1	11.1		1.8	
	Phototrophic		16.0	11.1		4.0	
	Boring		7.1	9.0		1.8	
	Cryptic		9.0	16.0		2.3	
Coral	Tabular	12.3	9.0	1.6	3.1	2.3	
	Staghorn	12.3	9.0	1.6	3.1	2.3	
	Branching (other)	12.3	7.1	1.6	3.1	1.8	
	Massive	6.3	6.3	1.6	1.6	1.6	
	Encrusting	6.3	9.0	1.6	1.6	2.3	
	Free-living	4.0	6.3	1.6	1.0	1.6	
	Soft corals	4.0	9.0	1.6	1.0	2.3	
	Foraminifera		6.3	2.3		1.6	
Worms	Nematodes						
	Nemertea						
	Polychaetes						
	Spirobranchus		4.0	9.0		1.0	
Crustaceans	Decapods (H)			4.0			
	Decapods (P)			4.0			
	Coral-associated		4.0	9.0		1.0	
	Barnacles		4.0	4.0		1.0	
	Stomatopods			4.0			
	Cleaner shrimp			4.0			
	Infauna			1.0			
	Zooplankton		1.0	4.0		0.3	
	Parasitic			1.0			
Molluscs	Gastropods (H)		1.0	4.0		0.3	
	Gastropods (P)			4.0			
	Triton snails			4.0			
	Drupella			4.0			
	Tridacnidae		9.0	4.0		2.3	
	Bivalves		1.0	4.0		0.3	
	Chitons						
	Cephalopods	1.0		4.0	0.3		
Echinoderms	Seastars (H)		1.0	4.0		0.3	
	Seastars (P)			4.0			
	CoTS			1.0			
	Sea cucumbers (DF)			4.0			

(*Continued*)

Table 6 (*Continued*) Potential impact (PI) of three water quality stressors on 70 functional groups on the GBR

		Inshore			Offshore		
Taxa	Functional group	Nutrients	Sediments	Pollutants	Nutrients	Sediments	Pollutants
	Sea cucumbers (SF)		1.0	4.0		0.3	
	Sea urchins (regular)		1.0	4.0		0.3	
	Sea urchins (irregular)			1.0			
	Brittle stars			1.0			
	Feather stars			4.0			
Fishes	Cryptobenthic	0.4	4.0	7.1	0.1	1.0	
	Farmers		11.1	7.1		2.8	
	Scrapers (scarids)		16.0	4.0		4.0	
	Browsers (nasos)		7.1	4.0		1.8	
	Browsers (siganids)		7.1	4.0		1.8	
	Browsers (other)		7.1	4.0		1.8	
	Bolbometopon	0.4	11.1	4.0	0.1	2.8	
	Excavators (other)		16.0	4.0		4.0	
	Detritivores	1.8	7.1	4.0	0.4	1.8	
	Planktivores	0.4	4.0	7.1	0.1	1.0	
	Corallivores	7.1	11.1	4.0	1.8	2.8	
	Invertivores (labrids)		7.1	7.1		1.8	
	Invertivores (other)		7.1	7.1		1.8	
	Invertivores (lutjanids)		4.0	4.0		1.0	
	Eels	1.8	7.1	4.0	0.4	1.8	
	Piscivores (residents)	4.0	7.1	7.1	1.0	1.8	
	Piscivores (transients)	1.8	7.1	7.1	0.4	1.8	
	Cleaner wrasse	0.4	1.8	4.0	0.1	0.4	

Note: Exposure was considered in context of inshore and offshore reefs. Shading denotes highest scores; maximum PI = 16 (dark); high PI ≥ 10 (mid); medium PI ≥ 7 (light); blank cells denote PI = 0.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

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, 2015, Clark et al. 2017, Messmer et al. 2017, Pratchett et al. 2017b). In the 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 functioning (Kerry & Bellwood 2012, 2015a,b). Conversely, cephalopod populations are proliferating globally (Doubleday et al. 2016), as recognised in the increasing trends in cephalopod fisheries catches (Caddy & Rodhouse 1998, Rodhouse et al. 2014). Cephalopods did not score as vulnerable here (Table 5), in line with global trends and suggestions that they may fare better in a future ocean compared to other marine taxa due to their 'live fast, die young' life cycles (Doubleday et al. 2016, Rosa et al. 2019).

Herbivorous fish groups were considered generally resilient, with densities of some grazing species (e.g. parrotfishes) even documented to increase postdisturbance, perhaps due to the increased algal production that typically follows coral mortality (Diaz-Pulido & McCook 2002, Cheal et al. 2008, 2010, Wilson et al. 2009, 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). Habitat degradation reduces postsettlement success of corals, and shifts towards algal-dominated systems may limit reef recovery (Roth et al. 2018). Coral-algal phase shifts have documented impacts on fisheries productivity (Ainsworth & 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 dynamic process (van de Leemput et al. 2016), in general, resilience and recovery of coral reefs will depend on the reversibility of seaweed blooms postdisturbance, with grazing herbivores deemed particularly critical (Arthur et al. 2006, Bellwood et al. 2006a, Hughes et al. 2007b, Diaz-Pulido et al. 2009, Adam et al. 2011, 2015b, Doropoulos et al. 2013, Bonaldo et al. 2014, Mumby et al. 2014, 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 & 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, 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, *Culcita*) through coral predation may reduce the resilience and recovery of corals to climate change stressors (Bruckner et al. 2017, Shaver et al. 2018, Bruckner & Coward 2019, 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 & Yang 1995, Ben-Tzvi et al. 2006, Rowley 2008), though increased water circulation close to the coral surface as caused by *Spirobranchus* may decrease host susceptibility to bleaching (Strathmann et al. 1984), as posited for other coral-associated groups (Chase et al. 2018).

Ocean warming

Marine organisms are more vulnerable to warming than terrestrial taxa, making increasing ocean temperatures one of the most broadly confronting contemporary stressors (Richardson & 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 & 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.

Recent temperature-induced bleaching events have had catastrophic impacts on coral reefs globally. On the GBR, back-to-back warming anomalies over 2016 and 2017 resulted in mass bleaching and mortality of corals, particularly in the northern sections of the reef, where coral cover decreased by >80% (Hughes et al. 2017b, 2018b). This has contributed to significant alterations to whole-reef community structure and patterns of reproduction and recruitment (Hughes et al. 2018b, 2019a, Stuart-Smith et al. 2018).

Host-associated phototrophic microbes and most coral groups rated among the most vulnerable to ocean warming (Table 5). 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, 2016, Baird et al. 2009). 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 & Gassman 1990, Glynn 1996, LeTissier & 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, 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 & Marshall 1998, 2002, Marshall & Baird 2000, Obura 2001, McClanahan et al. 2004, Adjeroud et al. 2005, Thompson & Dolman 2010, Kennedy et al. 2018). Yet these faster-growing corals are critical to postbleaching recovery (Adjeroud et al. 2009, Linares et al. 2011, Ortiz et al. 2014, 2018), and there may be some resilience to the coral bleaching phenomenon through thermally tolerant zooxanthellae and microbiomes (Berkelmans & van Oppen 2006, Epstein et al. 2019b), 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 & 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 (Poloczanska et al. 2013, Matz et al. 2018).

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 & 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, while other algae may benefit from waters higher in temperature (warming) and CO_2 (acidification), with a competitive advantage over corals (Diaz-Pulido & McCook 2002, Diaz-Pulido et al. 2007, 2009, 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 & 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, 2016, Prazeres et al. 2015). 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, 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 & 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, 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 & Diaz-Pulido 2013, Webster et al. 2013a,b, 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 & 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, 2014, Albright et al. 2013, 2018, Kennedy et al. 2013, Cyronak et al. 2018, Eyre et al. 2018, McMahon et al. 2019), sediment dynamics (Eyre et al. 2014, Cyronak & 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 functioning, 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 also 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 5), 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). Unsurprisingly, calcifiers were considered the most vulnerable to ocean acidification here (Table 5). 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, 2012, 2014, Briffa et al. 2012, Devine et al. 2012, Domenici et al. 2012, Allan et al. 2013, Watson et al. 2014, 2017, Ferrari et al. 2017, Jarrold 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 & Diaz-Pulido 2013, Espinel-Velasco et al. 2018).

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 mediate or buffer the impacts of ocean acidification through their bioturbation activity and contributions to reef biogeochemistry (Schneider et al. 2011, 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).

Cyclones

While tropical cyclones and storms are not expected to increase in occurrence in a changing climate, they are predicted to increase in severity (Lough 2007). 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 5). Zooplankton scored low, yet cyclone and storm events can drive homogenisation of zooplankton communities with potential knock-on effects to higher trophic levels (McKinnon et al. 2003). 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 & Connell 1999, Adjeroud et al. 2005, Madin 2005, Madin & 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 5). 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 respective 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 postdisturbance (Brandl et al. 2016). Grazing fishes (e.g. detritivores, parrotfishes) may help to maintain fish diversity postdisturbance on some reefs (Wilson et al. 2009, Ceccarelli et al. 2016).

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 functioning 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 & Moreno 2003, Bellwood et al. 2004, Newton et al. 2007, Cinner et al. 2016, 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 5). 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.

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 & Rizzari 2019), including in the context of recreational spearfishing (Case Study 3). 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 & 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 & Zahnow 2018, Frisch & Rizzari 2019). The Queensland shark control programme 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 programme, 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).

Deposit-feeding sea cucumbers are particularly prone to overfishing due to their ease of collection and 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 & 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

CASE STUDY 3: FUNCTIONAL IMPACTS OF RECREATIONAL SPEARFISHING ON THE GREAT BARRIER REEF

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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 practise (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 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, 2012, Godoy et al. 2010). 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 & Kapuscinski 2017), as for recreational fishing in general.

A survey of over 140 spearfishers active on the GBR was conducted to determine which functional groups of coral reef fishes were preferred by spearfishers. From a list of 22 common GBR fishes (Table CS3.1), spanning nominal herbivores ($n = 8$), invertivores ($n = 3$) and piscivores ($n = 11$), coral trout (*Plectropomus* spp.) were outlined as the preferred targets (Figure CS3.1), as in recreational line-based and commercial fisheries on the GBR (Leigh et al. 2014, DEE 2017). The coral trout fishery on the GBR is considered well managed (DEE 2017), which is reflected in the recent re-evaluation of this group from Near Threatened to Least Concern (Choat & Samoilys 2018). Nominally piscivorous species (including Lutjanidae, Lethrinidae and *Plectropomus*) represented ~75% of the preferred catch of spearfishers, while nominal herbivores were lesser preferred (Figure CS3.1). This may be associated with the campaign aimed at spearfishers to limit herbivore catches on the GBR to protect species that reduce algal growth and support reef health and functioning (GBRMPA 2016, 2018a). Tuskfishes (*Choerodon* spp.) were the preferred invertivores (Figure CS3.1), which are broadly distributed across the GBR (Platten et al. 2002, Fairclough et al. 2008). As a Near Threatened and monandric protogynous hermaphroditic species where males only occur in the largest size bracket (Fairclough & 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 & Nakazono 2004).

While spearfishing has the potential to impact viable fish stocks (Hughes et al. 2007a, Meyer 2007, Frisch et al. 2008, 2012, Godoy et al. 2010), the Queensland (and Australian) spearfishing community has been highly responsive to previous management campaigns and exhibits self-regulatory and monitoring approaches that are vital to fisheries conservation and advocacy

Table CS3.1 List of species included in surveys of spearfishers operating on the GBR

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. (2002)
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	LC	32–17	120	38	7	Choat & Samoilys (2018)
Rachycentridae	*Rachycentron canadum*	Cobia	P	LC	75	200	70	2	Babatunde et al. (2018)

Notes: Data obtained from the online FishBase resource, unless otherwise stated. Legal limit data are taken from the Department of Agriculture and Fisheries, Queensland Government.
Abbreviations: H, herbivore; I, invertivore; P, piscivore; LC, least concern; V, vulnerable; NT, near threatened; N/A, data not available.

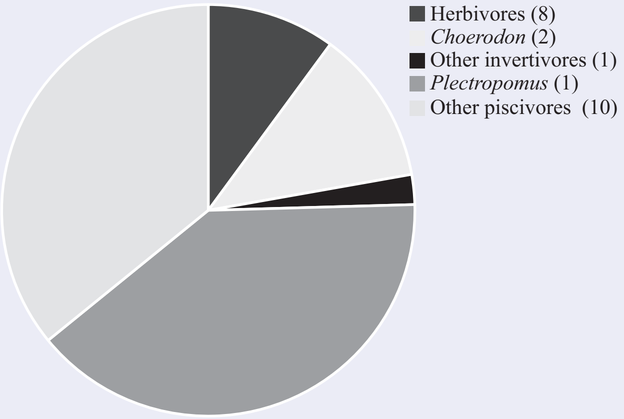

Figure CS3.1 Contribution of select coral reef fishes to the estimated catch of spearfishers active on the GBR. Number of species in each group in parentheses.

(Young et al. 2014, 2016, GBRMPA 2016). We highlight the importance of 1) educating groups on spearfishing-selectivity for species with vulnerable reproduction (e.g. coral trout, tuskfishes) and 2) monitoring catch trends for key species within the spearfishing community to inform self-regulation. Quantitative data on catch sizes, target species and catch per unit effort are needed, particularly for target species and those with vulnerable reproductive biology.

et al. 2014, Richards & Day 2018) and three species of teatfish are proposed to be listed in CITES Appendix II (Di Simone et al. 2019). 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 & 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. 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 & Wassenberg 2000) and illegal practises in no-take zones (Davis et al. 2004, Arias & Sutton 2013, Williamson et al. 2014a, Bergseth et al. 2015, Weekers & Zahnow 2018). The impact of recreational spearfishing is assessed in detail in Case Study 3. We acknowledge that assessment beyond the broad taxonomic and functional groups examined here is necessary to determine specific impacts from fisheries on the GBR. It will also be important to assess fisheries operating outside of coral habitat, including soft-bottom, interreefal, coastal and intertidal habitats where many commercially important invertebrates on the GBR are targeted, including prawns and scallops (Gribble 2003, Courtney et al. 2008, 2015, GBRMPA 2014b). Future work should also consider social, cultural and economic values of fisheries targets on the reef.

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 the Echinodermata is well documented (Uthicke et al. 2009). On the GBR, outbreaks of *Acanthaster* cf. *solaris* (CoTS) are the most extensive, destructive and researched outbreak candidate, gaining considerable traction in reef management (Westcott et al. 2016, Sweatman &

Cappo 2018). As scored here, population outbreaks (namely in consideration of CoTS) were outlined to have the greatest potential impact on tabular, staghorn and other branching corals (Table 5). *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 less-preferred coral species are consumed during extreme outbreaks or when food is scarce (Chesher 1969, Pearson & 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, 2018b,c).

Outbreaks of other marine invertebrates have received considerably less attention on the GBR and in general. High densities of *Drupella* sp. (Muricidae) 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), similar to other corallivorous gastropods, including *Coralliophila* (Muricidae) (Shaver et al. 2018) and *Dendropoma* (Vermetidae) (Smalley 1984, Shima et al. 2010). While these gastropods 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* have direct impacts on the persistence of 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 invertebrates, including sea cucumbers and sea stars, can have repercussions on coral recruitment, recovery and functioning (Zhang et al. 2018, Bruckner & Coward 2019). 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).

Diseases 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 & Caldwell 2019). Disease proliferation in other marine environments is a portent of the devastating impacts and rapid rate of spread that can occur, including the *Diadema* die-off in the Caribbean (Hughes 1994, Mumby et al. 2006b, Feehan & Scheibling 2014) and sea star wasting disease on the US west coast (Bates et al. 2009, Hewson et al. 2014, Eisenlord et al. 2016, Montecino-Latorre et al. 2016). While expert 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 5). White Syndrome primarily impacts tabular acroporids compared to other coral species and functional forms (Hobbs & 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).

In the marine environment, disease proliferation is largely induced by temperature anomalies (Bruno et al. 2007, Harvell et al. 2007, Sato et al. 2009, 2011, 2016, Maynard et al. 2011, Ruiz-Morenol et al. 2012, 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 & 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, 2016). While the transmission of coral disease between individuals and among populations remains understudied (Shore & 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 inform local response plans (Maynard et al. 2011, Beeden et al. 2012). To date, it seems that Australia's biosecurity strategies regarding terrestrial, agricultural and human-based diseases typically receive greater attention in contingency planning (Craik et al. 2017).

Water quality Water quality stressors (nutrients, sediments, pollutants) were not considered severe threats in the context of offshore reefs (Table 6), assumedly driven by low exposure at distance from the coastline. This is most likely because the three water quality stressors assessed here are closely related to aeolian processes. Water quality scores did not consider impacts from other sources of pollution, including shipping, noise pollution, plastics and oil and gas. Broader consideration of these pollution types should be considered in future work. When assessed in context of nearshore reefs, nutrients, sediments and pollutants were considered to have greater impacts across our functional groups (Table 6).

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 & 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 typically exhibit slower rates of growth and recovery (MacNeil et al. 2019, Mellin et al. 2019). Microbial groups scored among the most vulnerable to water quality stressors, particularly host-associated groups (Table 6). Microbes can be the first biological responders to environmental perturbation (Bourne et al. 2016, Glasl et al. 2017, 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 4).

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 & 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 6), in line with the literature (Bainbridge et al. 2009, 2014, Brodie et al. 2013, Tsatsaros et al. 2013, Waterhouse et al. 2013). 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 & 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 & Davies 1991, Fabricius 2005, 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

CASE STUDY 4: MICROBIAL COMMUNITIES AS INDICATORS OF WATER QUALITY ON THE GREAT BARRIER REEF

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Microorganisms are fundamental drivers of biogeochemical cycling in coral reef ecosystems (Gast et al. 1998, Bourne & 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 available information on pelagic microbial communities across GBR regions (Table CS4.1; Figure CS4.1). Relative microbial abundances were used to identify patterns in communities along inshore to offshore gradients in the context of riverine floodwaters and water quality plumes (Angly et al. 2016).

Pelagic microbial communities across the GBR respond in a deterministic way to environmental fluctuations and drivers. This means that microbial community dynamics can be modelled to better understand how ecosystem functioning can 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 CS4.2) (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 CS4.2) (Dinsdale et al. 2008). These two photoautotrophic bacterial families have different capacities to use organic nitrogen (Scanlan & West 2002, Zubkov et al. 2003), and so the Prochlorococcaceae:Synechococcaceae relative abundance ratio can be used as an indicator for nutrient enrichment at a range of spatial and temporal scales (Figure CS4.2).

Table CS4.1 Summary of published and unpublished microbial 16S rRNA data sets for the GBR; BPA = BioPlatforms Australia (https://data.bioplatforms.com/).

Region	No. samples	No. locations	Rarefaction depth	Sequencing platform	Taxonomic assignment	Primer pair and refs	Reference
Tully	78	7	250	454	SILVA and Greengenes	pyroLSSU926F/ pyroLSSU1392R	Angly et al. (2016)
Burdekin	48	3	25,000	Illumina Miseq 2 × 300	SILVA	27F/519R	Glasl et al. (2019)
Coral Sea	9	6	100,000	Illumina Miseq 2 × 300	SILVA	27F/519R	BPA
Yongala (Burdekin)	97	1	30,000	Illumina Miseq 2 × 300	SILVA	27F/519R	BPA
Heron Island	16	4	50,000	Illumina Miseq 2 × 300	SILVA	515F/806Rb	Epstein et al. (2019a)
Mackay	8	4	1,350	454	GreenGenes	63F/533R	Alongi et al. (2015)

Another example of a microbial-based indicator exists in the ratio between Pelagibacteraceae and SAR86, 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. 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. 2019). 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 functioning and health.

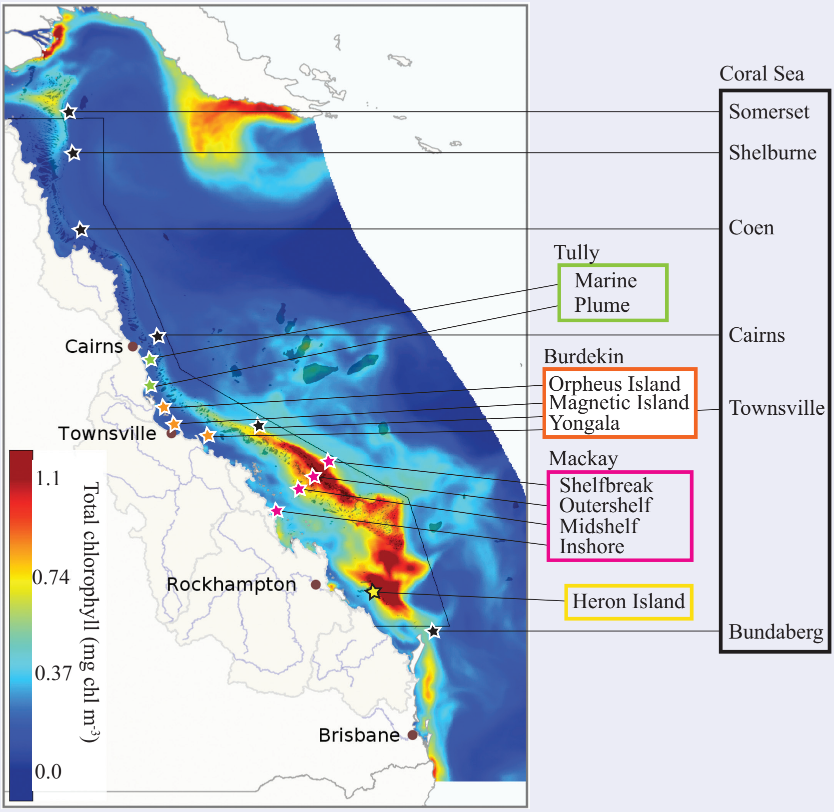

Figure CS4.1 Regions and locations on the GBR covered in the literature for pelagic microbial data sets (see Table CS4.1). Chlorophyll data obtained from eReefs (June 2016) (CSIRO GBR4 Hydrodynamic Model v2.0), with online map generation by AIMS.

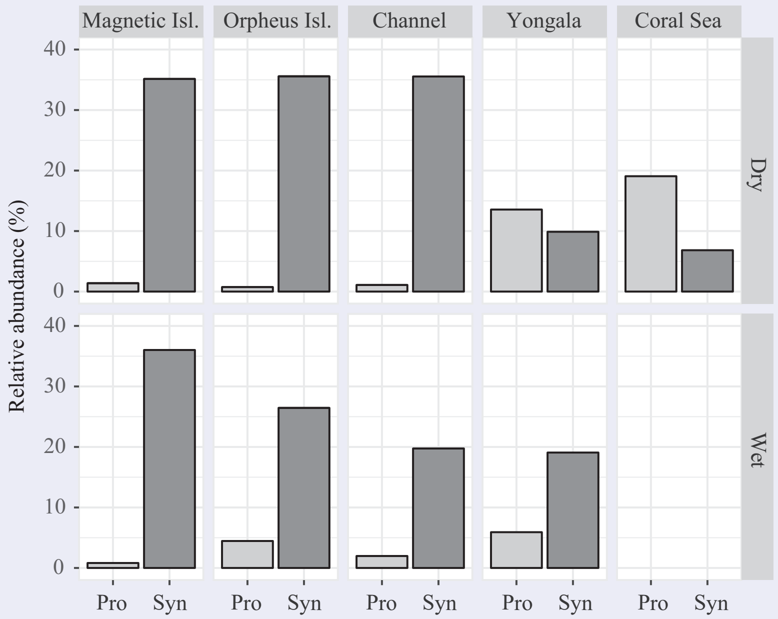

Figure CS4.2 Relative abundance of the cyanobacteria Prochlorococcaceae (Pro) and Synechococcaceae (Syn) during wet and dry seasons in the Burdekin region (see Figure CS4.1). Data provide comparison between inshore (Magnetic Island, Orpheus Island and Channel), mid-shore (Yongala) and open ocean (Coral Sea) regions. Coral Sea only sampled in dry season.

coral cover (Browne et al. 2010 2013, Browne 2012, Perry et al. 2012b) but with trade-offs in feeding regimes (Anthony 2000, Anthony & Fabricius 2000, Anthony & 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 6), yet both sponges and their microbiomes seem relatively resilient to high sediment loads on the GBR (Pineda et al. 2017b,c, 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, 2013, 2014). Foraging success of visual predators like planktivorous damselfishes can be significantly impaired in turbid environments (Wenger et al. 2012, Johansen & Jones 2013). Herbivorous fishes rated among the most vulnerable to sediments (Table 6), with some species shown to decrease grazing activity when sediments loads are too high in the EAM (Bellwood & Fulton 2008, Goatley & 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 & Williams 1993, Birrell et al. 2005, Bellwood & Fulton 2008, Arnold et al. 2010, Goatley & 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 & Bellwood 2010, Marshell & 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). 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).

Pesticides, herbicides, trace metals and agricultural nutrients (e.g. nitrogen, phosphorus) that influence eutrophication are commonly measured on nearshore reefs of the GBR at concentrations above Australian water quality guidelines (Lewis et al. 2009, 2012, Brodie & Waterhouse 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, functioning and services (Fichez et al. 2005, van Dam et al. 2011, de Valck & Rolfe 2018). In the context of nearshore systems on the GBR, 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 abundance, with negative 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, 2012, Shaw et al. 2009,). 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 & Brodie 2015, Babcock et al. 2016a, Wolfe et al. 2017, Uthicke et al. 2018, Wolff et al. 2018), although the links are tenuous and unresolved (Pratchett et al. 2014, 2017a, Wolfe et al. 2017).

Rainfall is highly variable in northeast Australia, and there is no real consensus on projections for precipitation events in the coming decades (Whetton et al. 2005). However, the intensity of drought and rainfall events is expected to increase, elevating risks associated with flood events and water quality (Lough 2007, Lovelock & Ellison 2007, Adame et al. 2019). Overall, water quality stressors are likely to combine with other environmental factors with significant additive impacts, particularly in the context of thermal stress (Wooldridge & Done 2009, Negri et al. 2011, van Dam et al. 2011, Lewis et al. 2012, van Dam et al. 2012, 2015, Banc-Prandi & 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 & 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 & Rolfe 2018). A better understanding of the direct impacts of pollutants (e.g. pesticides, metals, nutrients) on coral reef organisms, and the functioning and services they provide, is essential to ensure management goals are biologically relevant and postdisturbance recovery is supported (Fichez et al. 2005, van Dam et al. 2011).

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 7). 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 7). Host-associated phototrophic microbes were the most vulnerable microbial group, considered especially vulnerable inshore, as for CCA (Table 7). The most vulnerable invertebrates were coral-associated decapods, several mollusc groups (particularly giant clams; Tridacnidae) and deposit-feeding sea cucumbers (Table 7). Piscivores (resident, transient) were considered the most vulnerable of the reef fishes with the lowest recovery potential (Table 7), strongly influenced by their potential to be impacted by fisheries (Table 5). 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 7). Once considered abundant, densities of triton snails on the GBR have remained extremely low since their extensive overharvest in the 1930s (Endean 1969, Endean & Stablum 1973, Hall et al. 2017). Deposit-feeding sea cucumbers were also suggested to have particularly low recovery potential (Table 7), 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 & Byrne 2015, Purcell et al. 2016b).

Combined assessment of functionally important and vulnerable groups

In order to identify key species for targeted management on the GBR, we compared scores for functional importance against scores for vulnerability (Figure 4). Using the median values for both axes, four quadrants were established to represent priority targets (Figure 4);

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.

Not surprisingly, most coral groups scored highly for both measures and are considered top priority (Figure 4). 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 4). The remaining microbial groups were considered lower priority owing to their low scores for vulnerability (Figure 4), despite free-living microbes (i.e. those in seawater or sediment) and bacteria emerging as important bioindicator tools for monitoring reef health (Case Study 4) (Glasl et al. 2017, 2018a), as for phytoplankton (Revelante & 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,b). 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 4). However, the opportunistic nature of

Table 7 Total potential impact (PI) and vulnerability (V) of 70 functional groups on the GBR, including their predicted recoverability and certainty of scores

		Inner GBR		Outer GBR			
Taxa	Functional group	PI	V	PI	V	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	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

(Continued)

Table 7 (*Continued*) Total potential impact (PI) and vulnerability (V) of 70 functional groups on the GBR, including their predicted recoverability and certainty of scores

		Inner GBR		Outer GBR			
Taxa	Functional group	PI	V	PI	V	Recoverability	Certainty
	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

Note: Values are shown for inner and outer reefs. Dark cells = top 10th percentile of scores (bottom 10th for recoverability); light cells = top 25th percentile.

Abbreviations: H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders

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 4).

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 4). 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 4). This highlights the importance of using a multi-level approach in assessing species' functionality.

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

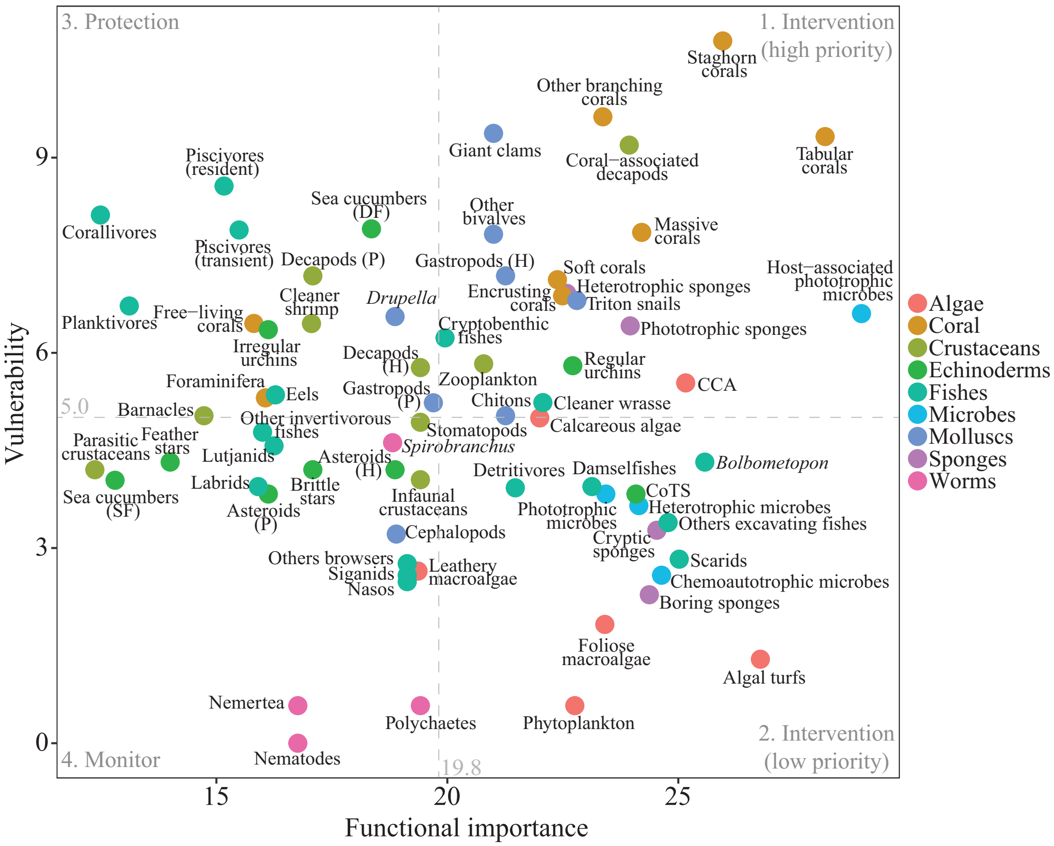

Figure 4 Assessment of the functional importance and vulnerability of 70 species groups. Dotted grey lines represent the median values for each axis creating four management quadrats; 1) Intervention (high priority), 2) Intervention (low priority), 3) Protection, and 4) Monitor. Colours represent taxonomic groups. H = herbivores, P = predators, DF = deposit feeders, SF = suspension feeders.

of taxonomy and ecosystem processes (see methods). This analysis presents weighted impacts of stressors for species at their highest levels of functioning and vulnerability. These data may be particularly useful in guiding where attention could be focussed 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 5A,B). As previously, global change stressors (ocean warming, ocean acidification, cyclones) were considered to have the greatest potential impact overall, especially offshore (Figure 5B). 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 5B), as would be expected (Brodie & Waterhouse 2012, Lam et al. 2018, MacNeil et al. 2019). This will likely be exacerbated as the intensity of rainfall events increases over the coming decades (Lough 2007). 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 5A), 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 the context of CoTS on the GBR. Echinoderms and fishes

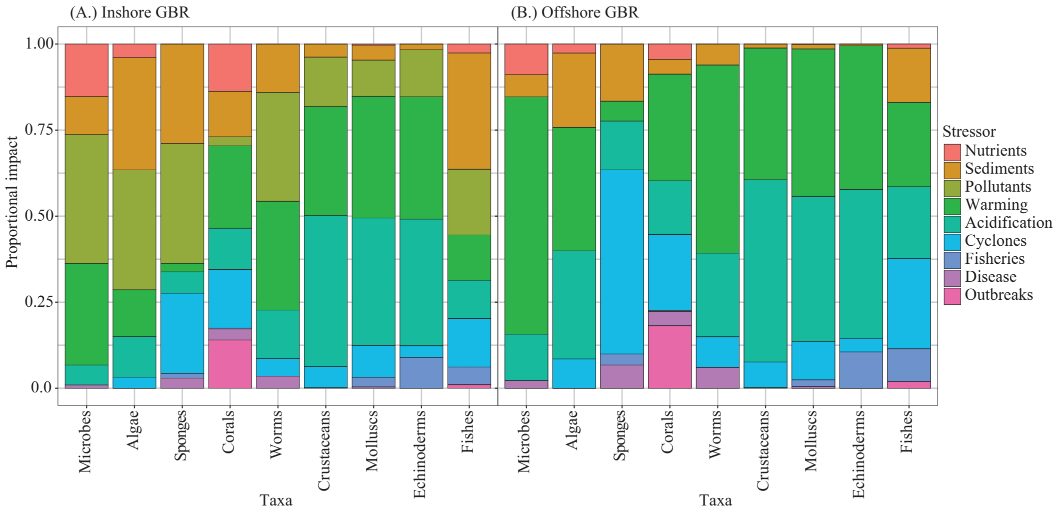

Figure 5 The proportional impact of each stressor on taxonomic groupings (A) inshore and (B) offshore. Each column represents the relative proportion of the functional importance and vulnerability of all species groups within the taxa-stressor combination.

were the major groups impacted by fisheries (Figure 5A,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 5B).

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 6), as reviewed for adult and larval life stages across this great diversity of species (Przeslawski et al. 2008, 2015, Byrne 2011). 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 6), including offshore (Figure 7). This is in line with the literature that suggests grazing activity can be significantly impaired when sediment loads are too high in their algal food source (Bellwood & Fulton 2008, Goatley & 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 6 and 7). 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 6 and 7) – 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 a broader context of reef functioning and threat sensitivity. Fisheries were suggested to have a disproportionate impact on deposit-feeding sea cucumbers and were the major stressor impacting functioning of piscivorous fishes (resident and transient) (Figures 6 and 7). It would be important to partition these broad 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 7).

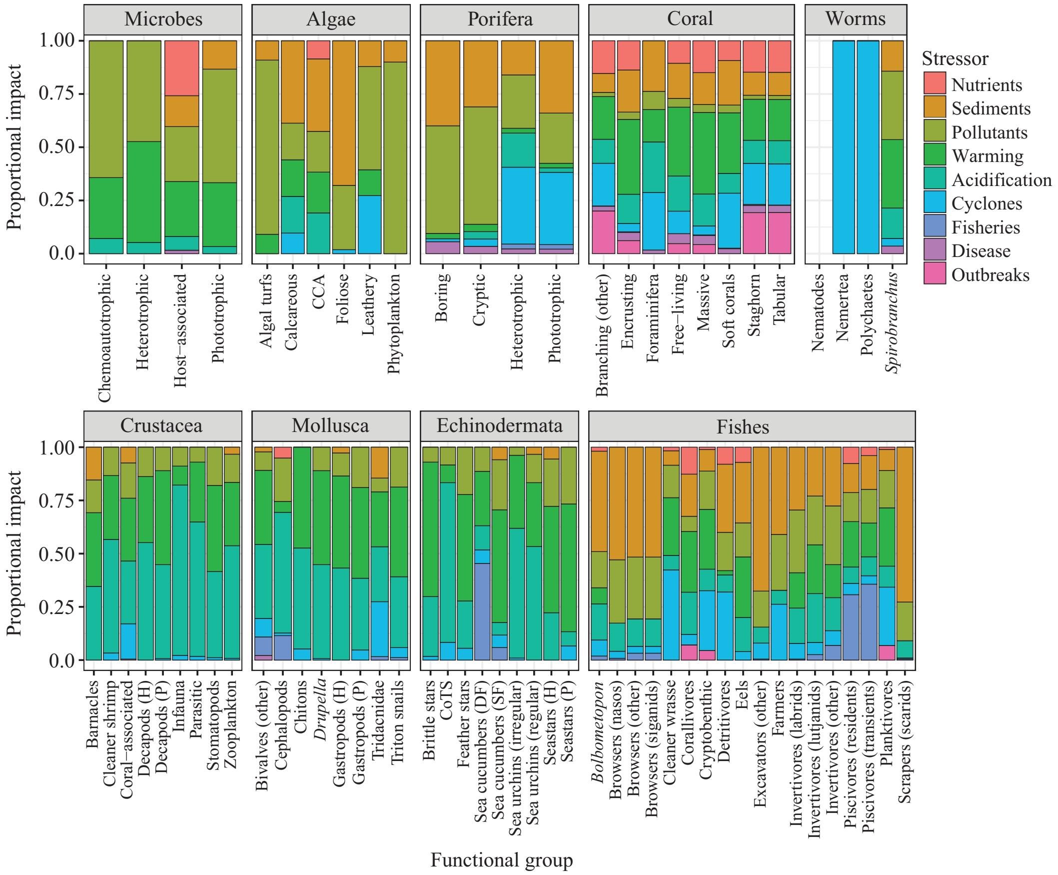

Figure 6 The proportional impact of each stressor on our 70 groups of species as a factor of their functional importance inshore.

Process-level vulnerability

To examine the impact of our nine stressors on ecosystem processes, the additive functional importance and vulnerability of each taxa were 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 previously), analyses at the level of ecosystem processes showed little variation in potential impact (Figure 8A, B). Global change stressors were calculated to have the greatest proportional impact on ecosystem processes, especially offshore (Figure 8B). As previously, impact from water quality stressors on ecosystem processes were proportionately greater inshore (Figure 8A). 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 8–10). 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).

This analysis became more informative when examined as a proportion of each stressor separately. The impact of fisheries was evidently greatest for the predation process (Figures 9 and 10), 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

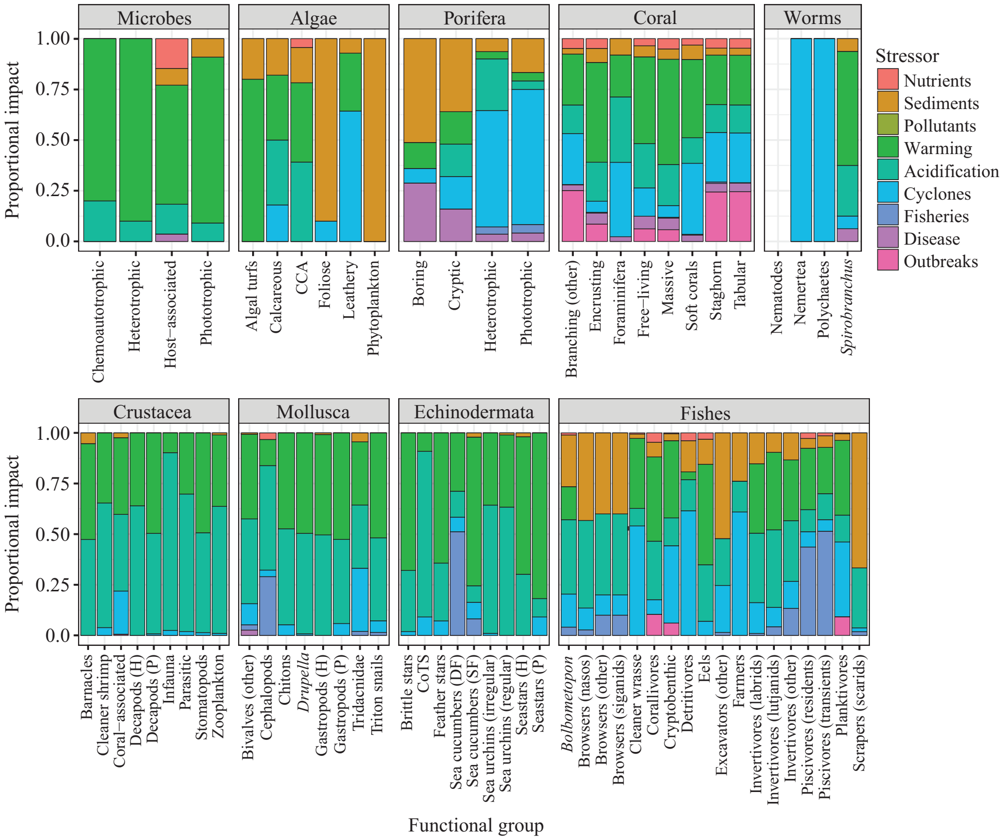

Figure 7 The proportional impact of each stressor on our 70 groups of species as a factor of their functional importance offshore.

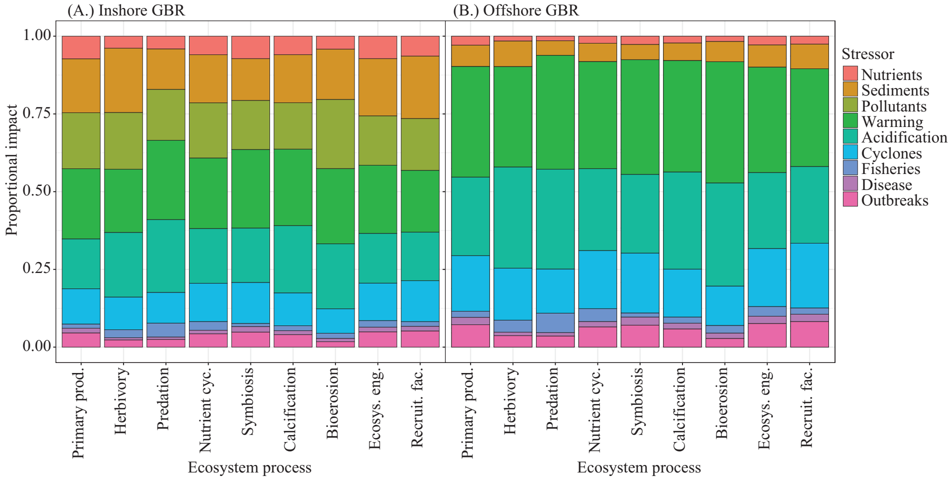

Figure 8 The proportional impact of each stressor on ecosystem processes (A) inshore and (B) offshore. Each column is a relative proportion of the functional importance and vulnerability of all species groups within each process-stressor combination.

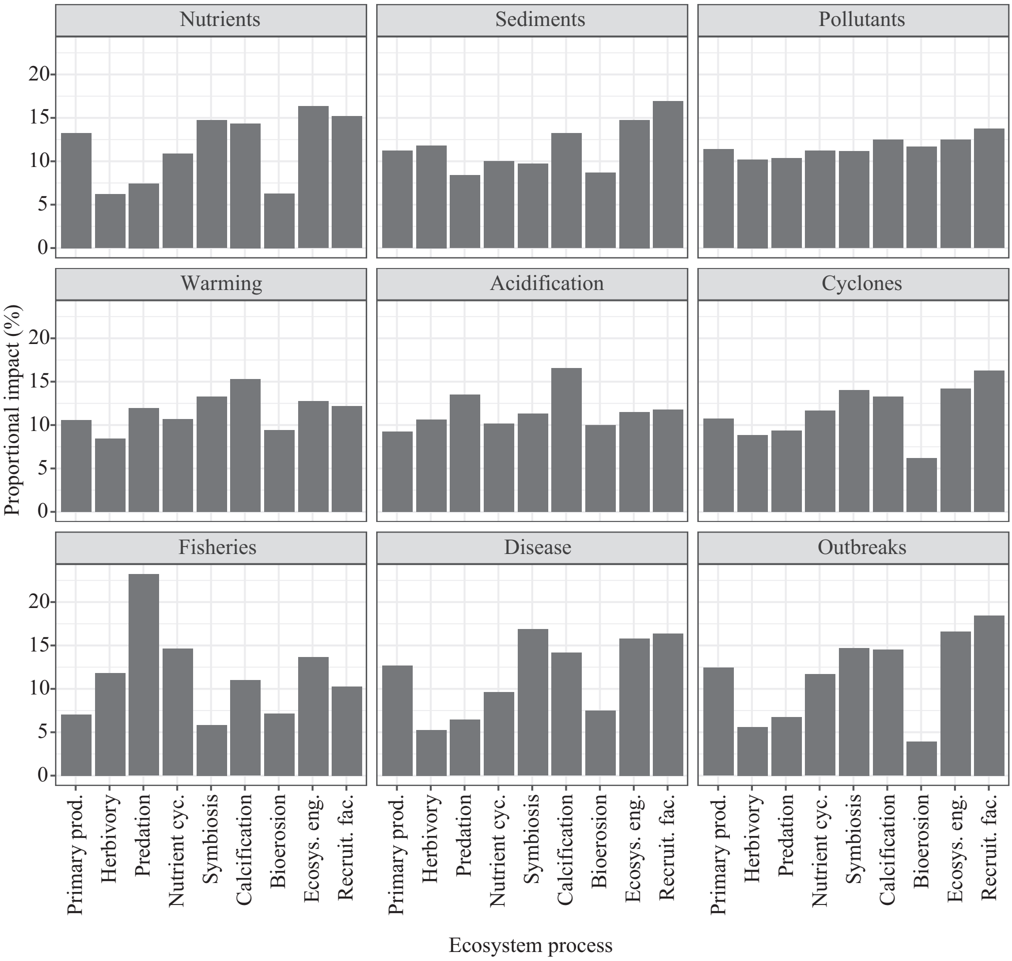

Figure 9 The proportional impact of each stressor on ecosystem processes in context of inshore regions of the GBR. Each column represents the relative proportion of the functional importance and vulnerability within each stressor.

triton snails, which rated highest for predation in context of CoTS, but these gastropods were not considered vulnerable to fisheries here, as records of exploitation are only 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 9 and 10), 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 9 and 10), 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 9 and 10). 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 9 and 10) attributed to the broad sweeping effects stressors can have in complex systems like coral reefs.

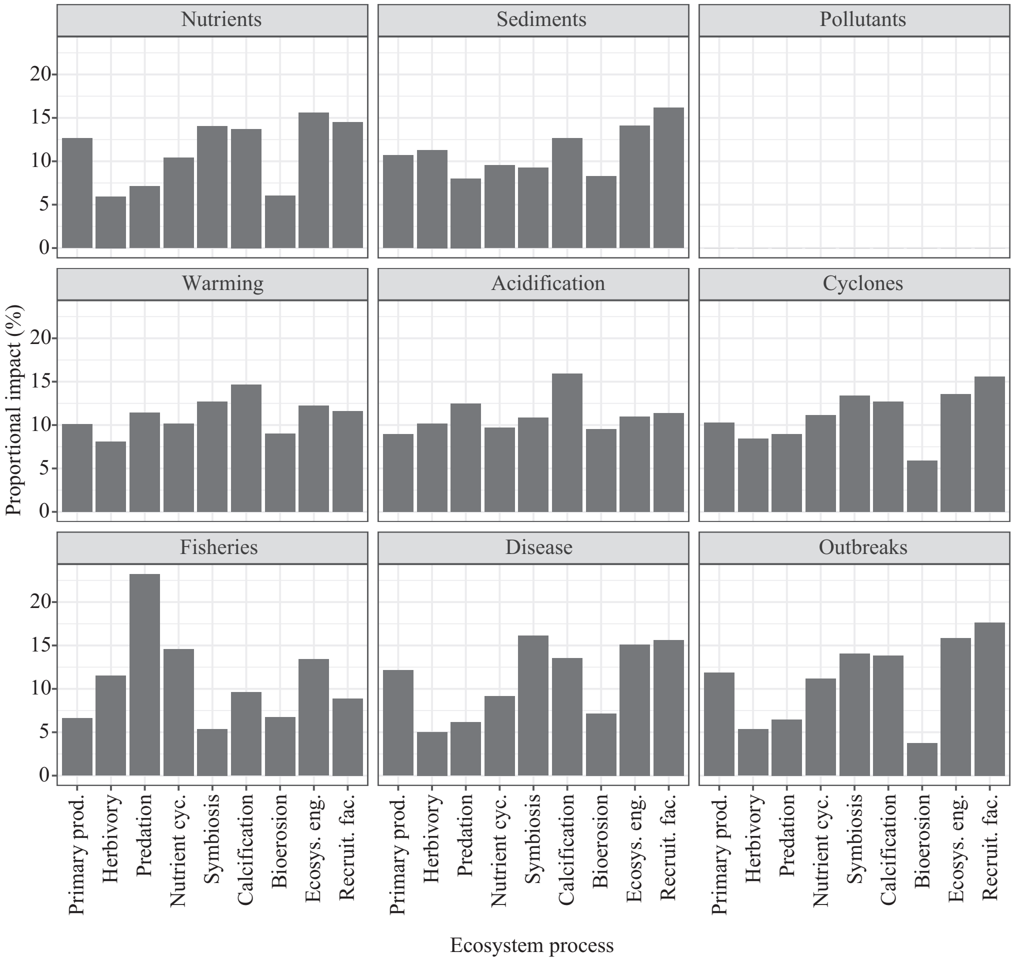

Figure 10 The proportional impact of each stressor on ecosystem processes in context of offshore regions of the GBR. Each column represents the relative proportion of the functional importance and vulnerability within each stressor. Data absent for pollutants offshore due to null score for exposure (see methods).

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) (see methods). Groups that scored in the top 66th percentile were categorised as a higher priority for management that would likely benefit from direct measures of protection or even represent cases where management has already proved effective. Those in the bottom 33th percentile were deemed lower management priorities 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).

Interestingly, species that scored lowest for their functional importance and vulnerability on the GBR were also regarded as the least manageable (Figure 11). This may reflect expert bias and the

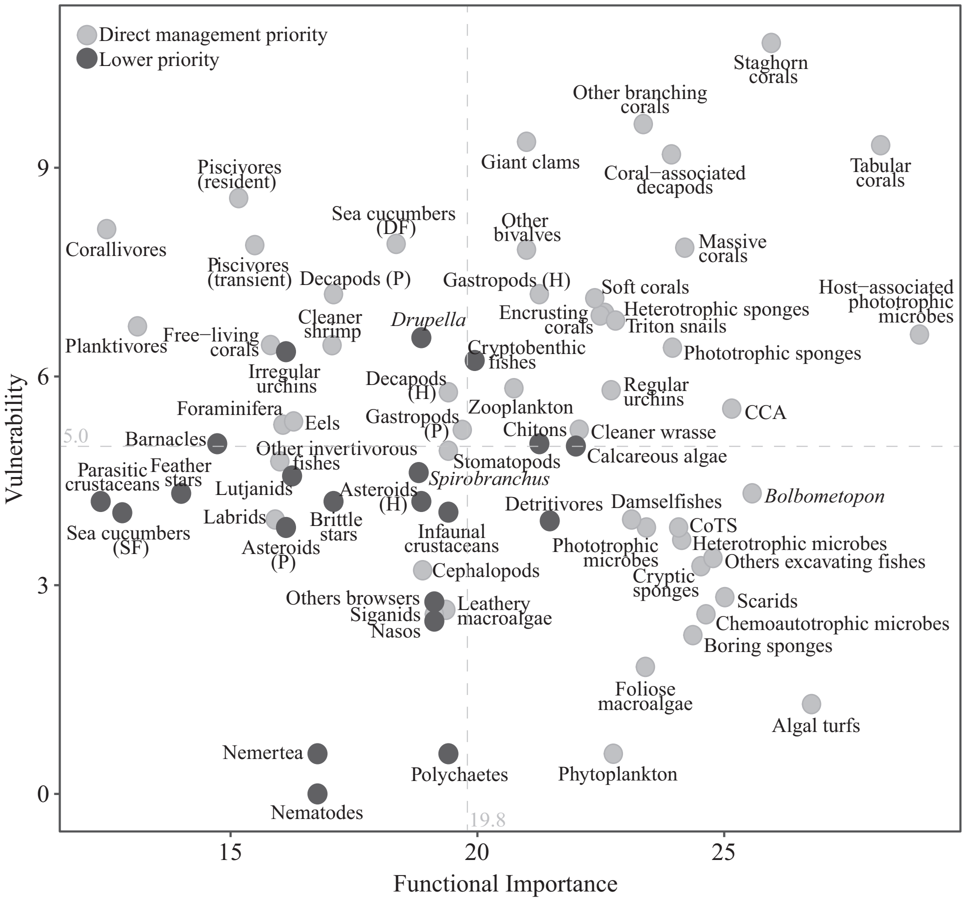

Figure 11 Perceived manageability of each species group relative to their rated functional importance and vulnerabilities on the GBR. Dotted grey lines represent the median values for each axis. H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

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 11), 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 of marine worms (Figure 11). Five groups of reef fishes (cryptobenthics, *Naso* sp., other browsers, detritivores, lutjanids) rated as low priority (Figure 11), 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 & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 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, 2001, 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 4) (Glasl et al. 2017, 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 11).

Addressing scientific certainty

Scientific certainty, as expressed by our expert panel, varied among the 70 functional groups (Figure 12). 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 12). 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 12). 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

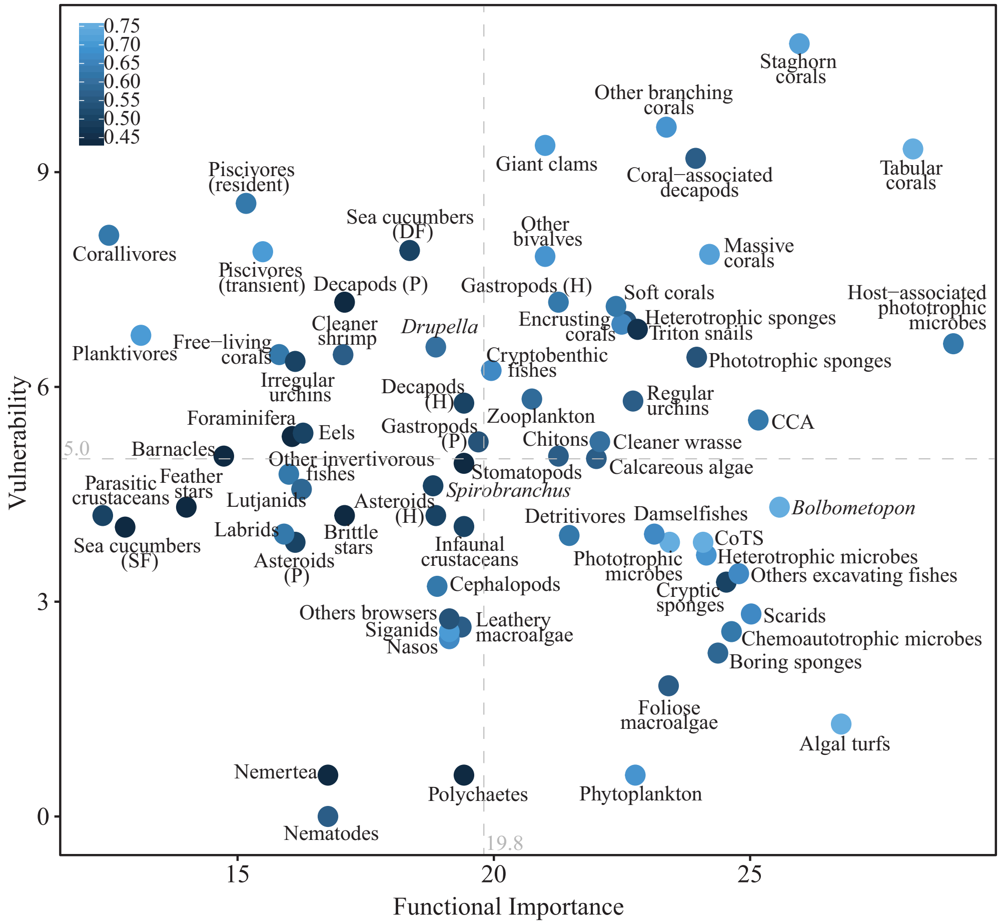

Figure 12 Scientific (expert) certainty in scores for functional importance and vulnerability of the 70 functional groups. Shading reflects scores of high (light) to low (dark) certainty. Dotted grey lines represent the median values for each axis. H, herbivores; P, predators; DF, deposit feeders; SF, suspension feeders.

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 7), 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).

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; that is, we are sure that they are functionally important, vulnerable and manageable on the GBR. Groups with comparatively low levels of certainty are briefly reviewed subsequently 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.

Cryptic predators: Eels and octopuses

Due to the difficulties surveying the cryptic habitats they typically occupy, little data exist for muraenids (eels) 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 & 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 & Strasburg 1960, Hixon & Beets 1993, Fishelson 1997, Young & 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 that exist in a similar trophic space. Benthic predators like octopuses and muraenids 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 & Doherty 1995) and their contributions to fisheries productivity as both predators and prey (Connell 1998, Beukers-Stewart & Jones 2004, Taylor & Bennett 2008). Surprisingly little information exists regarding their functional ecology on the GBR and in general (Ponder et al. 2002). Interestingly, cephalopod populations are proliferating globally, and they may fare better in a future ocean compared to other marine taxa due to their 'live fast, die young' life cycles (Doubleday et al. 2016, Rosa et al. 2019).

Deposit-feeding sea cucumbers

Although they have important roles in bioturbation, carbonate chemistry, nutrient cycling, benthic productivity and infaunal community structure (Uthicke & Klumpp 1998, Uthicke 1999, 2001, Wolkenhauer et al. 2010, Schneider et al. 2011, 2013, Lee et al. 2017, Wolfe & Byrne 2017a, Wolfe et al. 2018), sea cucumbers may be more influential in lagoon systems – outside of the focal habitat here. Large deposit-feeding holothuroids are likely to have a greater influence on ecosystem-scale carbonate chemistry in closer association to reef structure (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, 2016b, Eriksson & Byrne 2015), as globally recognised (IUCN Red List for Threatened Species) (Conand et al. 2014, Purcell et al. 2014, Richards & Day 2018). Empirical data on their recruitment and reproduction (e.g. Wolfe & 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*), in light of the recent discussions to reopen its fishery (DAF 2018) without any fisheries-independent data since its closure (owing to overfishing) in 1999.

Marine worms

This broad group boasts an incredible diversity across a range of functioning 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 & Kupriyanova 2015). Bioerosion is perhaps the most well-documented functional role of marine worms on the GBR (Hutchings & Kiene 1986, Hutchings 2008), but the lack of spatially explicit information on their population densities across the GBR hinders the ability to upscale their contributions into carbonate budget calculations (see Case Study 2). 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 & 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), but explicit trophic contributions are notoriously difficult to quantify for soft-bodied cryptic fauna, and attention to these gaps in knowledge is required.

Cryptic sponges

In general, the functional ecology of sponges is better documented on Caribbean reefs than for the Indo-Pacific, including the GBR (Wilkinson 1983, 1987, Maldonado et al. 2015, Mumby & Steneck 2018). Although conspicuous sponges ranked in the top-priority space, largely owing to their higher-ranked vulnerability (Figure 4), cryptic (and boring) sponges scored higher in their functional importance and are highlighted here under precautionary principles, owing to the uncertainty in their scores (Figure 12). Cryptic sponges can be the most significant invertebrate bioeroders on coral reefs (Neumann 1966, Glynn & 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 is well appreciated (Wulff & Buss 1979, Wilkinson 1983, Hutchings 2011), facilitating recruitment processes and reef recovery (Fox et al. 2003, Fox & 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 changes in the 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 & Bell 2018), but possibly shifting from heterotrophic towards phototrophic communities (Bennett et al. 2017, 2018, Bell et al. 2018). For *Cliona*, the most abundant bioeroding sponge genus on the GBR, tolerance to ocean warming may be low (Ramsby et al. 2018a). Yet 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).

Crustaceans

As for the marine worms, the functional and taxonomic diversity of crustaceans on the GBR is poorly characterised. Crustaceans are the most diverse marine arthropods and are often termed 'insects of the sea', spanning 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, 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 & Thorrold 1993, McKinnon et al. 2005, 2007). Among the most broadly recognisable 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 interreefal 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*) have received considerable attention in the literature (see: Stella et al. 2011b), as reflected by a higher relative certainty in expert scores here (Figure 12). 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 (see Case Study 1). 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.

Conclusions

Management of the Great Barrier Reef

Composed 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 & 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 focussed 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 for ecosystem-based management on the reef, particularly involving land-based riparian and coastal activities (e.g. water quality, riverine discharge, port development) (Brodie & 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 taxa to support ecosystem functioning and stability in a future ocean (Richards & Day 2018).

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 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 functioning, 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.

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 (Richards & 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. It appears that functional groups that met expectations may already benefit from specific incorporation in management initiatives and broad-scale habitat protection as offered by the GBRMP zoning system, as discussed in the following sections. Novel cases are outlined as those that may benefit most from this process-based assessment, as they are not specifically considered in current management strategies. In any case, a default management strategy should exist in education, which can enhance pro-environmentalism, self-efficacy, 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, Curnock et al. 2019).

Who were the winners?

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 & Dolman 2010). As addressed in Case Study 2, 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 & Marshall 1998, Marshall & 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 postdisturbance recovery (Pearson 1981, Connolly & Muko 2003, Ortiz et al. 2014, 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). Thus, current management strategies on the GBR are aligned with maintaining a key species identified in this process-based assessment.

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. 2019b), owing to the local adaptation required in brooding reproductive modes where gene flow is retained (Ayre & Miller 2004, Miller & Ayre 2004, Baums 2008, Torda et al. 2013a,b). It is increasingly important to determine how coral larval density and supply may scale up to support reef recovery (Doropoulos et al. 2017a, 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, 2008, 2011, Hobbs & Frisch 2010, Maynard 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 and cyclones, vessel groundings and anchor damage are often more significant for branching and tabular corals compared to other coral morphologies (Riegl & Velimirov 1991, Riegl & Riegl 1996, Connell et al. 1997, Hughes & Connell 1999, Dinsdale & Harriott 2004, Madin 2005). But 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, 2018, GBRMPA 2017), 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 programmes and plans to operationalise resilience-based management (GBRMPA 2018b). Tabular corals are easily recognisable and render themselves important features for monitoring by citizen science groups and in education in support of increased awareness, compliance and protection at their greatest level of functioning.

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 & 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 & 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 & 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, 2017, Barton 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 & Edwards 1995) and the Caribbean (Bruckner & Bruckner 2001, 2010, Ladd et al. 2018, 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, 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 were to develop further, then functionally important species like *A. hyacinthus* are suggested.

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 is also well recognised (Webster et al. 2004, 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, 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).

Microbes can be the first biological responders to environmental perturbation (Bourne et al. 2016, Glasl et al. 2017, 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 4). Free-living microbes and bacteria in reef seawater and sediments may be more sensitive indicators of environmental change than coral-microbes (Glasl et al. 2019). Specifically, the Prochlorococcaceae:Synechococcaceae relative abundance ratio provides an indicator of the contribution of nutrient enrichment in GBR waters, which seems to be sensitive both at spatial and temporal scales (Case Study 4). Yet, despite this potential, we have a poor understanding of how microbes 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.

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 communities, as the current lack of data hinders our potential to use microbes in reef-monitoring programmes. 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. This functional group is not part of a specific management initiative on the GBR at present, but programmes such as the Australian Marine Microbial Biodiversity Initiative (AMMBI) conducted by IMOS and Bioplatforms Australia (IMOS 2018) provide an opportunity to expand the sampling and biobanking of marine microbes. Currently, AMMBI includes just one site on the GBR, the Yongala, an iconic mid-shelf shipwreck (Brown et al. 2018). 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 and health. This would require a combination of analytical techniques (omic approaches: genomic and transcriptomic sequencing, metabolomics, epigenetics) to characterise communities, including *in situ* visualisation to link localisation with broader reef functioning.

Crustose coralline algae CCA 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*) (Matsuda 1989, Diaz-Pulido & McCook 2008), shaping cryptobenthic communities within the reef matrix (e.g. *Mesophyllum*, *Lithothamnion*) (Enochs & Manzello 2012), and in coral recruitment facilitation (e.g. *Titanoderma*) (Heyward & Negri 1999, Harrington et al. 2004, Arnold et al. 2010, Diaz-Pulido et al. 2010, Doropoulos et al. 2012a, 2018). CCA are calculated to be the primary non-coral contributors to net carbonate production on the GBR (Case Study 2) 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 & 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 communities 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 & 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.

At present, CCA may benefit from the GBRMPA zoning scheme through the protection of particular sections of reef from direct impacts, including anchor damage and fisheries activity, but this is regionally specific. 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 programmes. On the GBR, CCA taxa abundant on offshore reefs include *Neogoniolithon*, *Lithophyllum* and *Porolithon* species (Diaz-Pulido & 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). Attention to these knowledge gaps requires urgent action to ensure CCA can be directly incorporated in management schemes for consideration by local (e.g. GBRMPA) and global (e.g. IUCN Red List) protection agencies, especially for priority species with key roles, such as *Titanoderma* and *Porolithon*, which work to uphold the OUV of the GBR and coral reefs in general.

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 & 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. Ocean acidification may have direct impacts on coral reef settlement success through impacts on CCA (Doropoulos et al. 2012a, Doropoulos & 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. 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, 2012, Anthony et al. 2008).

Algal turfs and the epilithic algal matrix Algal turfs were rated the most functionally important group regarding production functioning, and third overall, 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, 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 & Goertemiller 1987, Klumpp & McKinnon 1989), harbour detritus and 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 & 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 & 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 & McKinnon 1992). They lay the foundations for benthic production functioning, 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 & Steele 2016), and, conversely, herbivores directly regulate turf canopy height (Carpenter & 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 & Larkum 1983, Klumpp & 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 & Williams 1993, Vermeij et al. 2010, Clausing et al. 2014, Bejarano et al. 2017, 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 & Williams 1993, Birrell et al. 2005, Bellwood & Fulton 2008, Arnold et al. 2010, Goatley & Bellwood 2012, Clausing et al. 2014, Doropoulos et al. 2017a,b, 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 and on coral reefs in general. 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. 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).

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, 2011a). On turf- and macroalgal-rich reefs, the relative abundance and diversity of microbial communities 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 & 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 impact micro-scale circulation and can alter turf metabolism and chemistry across diffusive boundary layers (Carpenter & 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 is difficult to quantify, and knowledge gaps remain (Case Study 2) (Hutchings 1986, Glynn & Manzello 2015). Concerns over shifting carbonate budgets should address all forms of bioerosion, including rates within the EAM and endolithic algae, especially given the propensity for turf algae to rapidly colonise dead coral substrate following perturbation (Diaz-Pulido & 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).

At present, the primary management objective regarding algal turfs on the GBR exists in the maintenance of herbivore assemblages, particularly those that regulate the EAM, to reduce algal growth and facilitate the competitive dominance of reef-building corals. While herbivores are not a common fisheries target on the GBR (e.g. Case Study 3), herbivore-centric management campaigns are already underway to minimise herbivore landings in support of reef resilience in a changing ocean (GBRMPA 2016, 2017). Additionally, *in situ* cultivation of some macroalgal 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).

Crown-of-thorns starfish outbreaks (and triton snails) The pervasive impacts of coral predation by CoTS have been extensively documented (e.g. Pratchett et al. 2014, 2017a, Babcock et al. 2016a, Cowan et al. 2017, 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, 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 & 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 to the contrary, precautionary measures should continue to focus on improving water quality across catchment areas to mitigate the potential for runoff-induced eutrophication to enhance larval success.

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 & 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 programmes is encouraged, including involvement with citizen science groups and in education. 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 & Cappo 2018). Information is particularly limited for CoTS juveniles (Case Study 5), although recent work demonstrates high densities of juvenile CoTS can be detected (Wilmes et al. 2016, 2018, 2020), and that juveniles can survive for years before the ontogenetic shift to coral (Deaker et al. 2020a,b). Characterising this life stage may provide an important opportunity to improve the early detection of outbreaks and their management (Sweatman & Cappo 2018).

CASE STUDY 5: JUVENILE CROWN-OF-THORNS STARFISH ‘IN WAITING’: THE MISSING LINK IN POPULATION AND CONNECTIVITY MODELS

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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, 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.

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

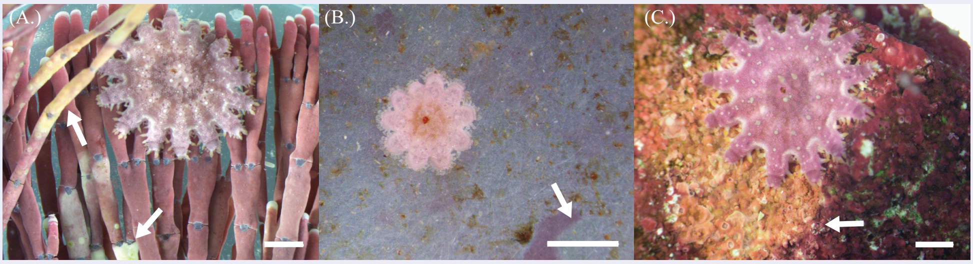

Figure CS5.1 Juvenile CoTS leave feeding scars (white arrows) on algal food sources; (A) *Amphiroa* sp., (B) biofilm and (C) CCA (scale bars = 2 mm).

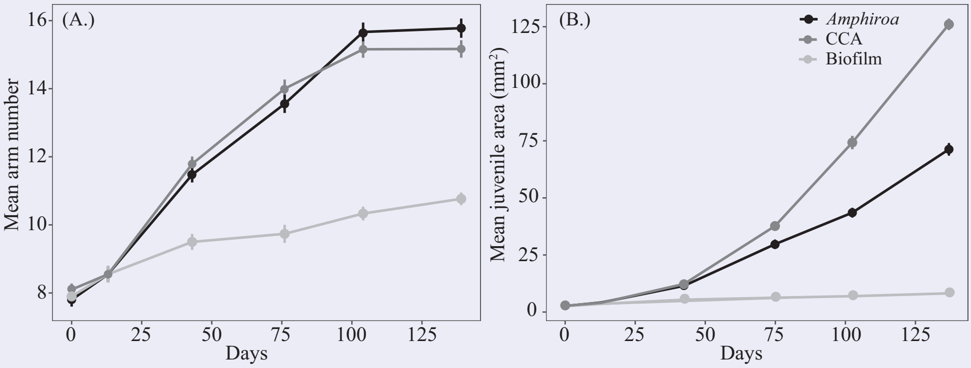

Figure CS5.2 Mean (±SE) (A) number of arms and (B) area of CoTS juveniles raised on one of three algal diets.

(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.

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, 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.

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. 2006a, Burkepile & 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 functioning (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). 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 & 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 & 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 & 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 & Hamilton 2004, Donaldson & Dulvy 2004, Chan et al. 2012, Bejarano et al. 2013, 2014); though it is generally not fished on the GBR (Case Study 3). 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.

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, 2016, Ainsworth & Mumby 2015, Graham et al. 2015, Roff et al. 2015), 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 & 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, 2010, Wilson et al. 2009, 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 functioning requires sufficient parrotfish stocks (Mumby 2016). Protection through Herbivore Management Areas 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, which act as ‘natural lawnmowers and keep seaweed levels under control by grazing’ (GBRMPA 2016, 2017). Maintaining herbivore assemblages, particularly those that regulate the EAM, would facilitate the competitive dominance of reef-building corals. 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 & 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 & Williams 1993, Vermeij et al. 2010, Clausing et al. 2014, Bejarano et al. 2017, 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. 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.

Who were the surprises?

Chemoautotrophic microbes There is a growing awareness of the importance of chemoautotrophic microbes (e.g. Archaea) in many marine habitats. 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 & Taylor 2012, Bourne & Webster 2013a) and altered community dynamics following bleaching stress (e.g. *Crenarchaeota*) (Lopez-Legentil et al. 2008, 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 & Loya 2002). Motile archaeal communities are prevalent within the coral mucus and are likely involved in complex nutrient cycling (Kellogg 2004, Frade et al. 2016), while anaerobic methanotrophic Archaea (ANME) can be tightly coupled with nitrogen cycling and sulphate reduction in complex communities within coral polyps (Figure 13) (Wegley et al. 2007, Kimes et al. 2010, Bourne & Webster 2013a). There has also been an increased interest in microaerophilic and anaerobic processes within benthic substrates. Microbial communities vary between oxic (e.g. *Planctomycetaceae*, *Proteobacteria*) and anoxic (e.g. ANME) sediments, where they play functionally important roles in organic matter degradation and nutrient cycling (Figure 13) (Rusch et al. 2009, Rusch & Gaidos 2013).

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. Archaeal communities 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 4) (Angly et al. 2016), but improved detection and monitoring of microbial groups is required, including for spatially explicit Archaea.

Microbial communities can likely be used to provide early warning signals for ecosystem change (Bourne et al. 2016, Glasl et al. 2017, 2018a), but this emerging bioindicator tool requires further development. As in the microbes section above, chemoautotrophic microbes are not specifically included in a management strategy on the GBR, but AMMBI (Brown et al. 2018, IMOS 2018), and similar monitoring platforms provide the opportunity to expand sampling and biobanking of important marine microbe groups. If such monitoring requires a refined or targeted methodology, we recommend that this functionally important chemoautotrophic group be a prime candidate. In

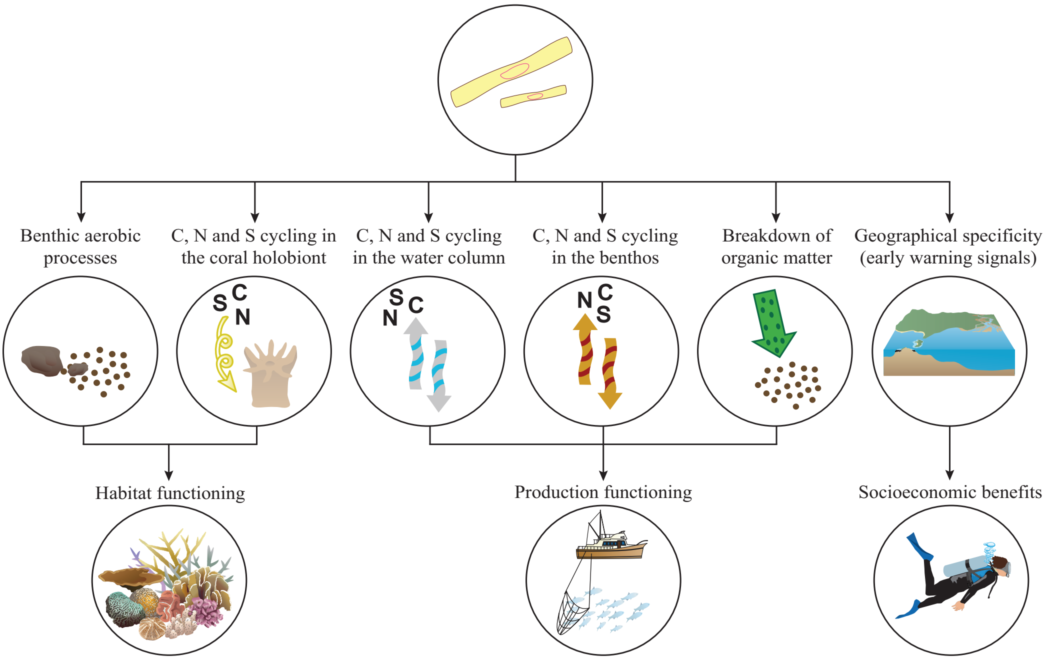

Figure 13 Schematic of the influences of chemoautotrophic microbes (e.g. Archaea) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

the meantime, precautionary measures should maintain focus on water quality while links between runoff (nutrients, sediments, etc.) and microbial assemblages are characterised.

Cleaner wrasse Cleaner wrasses were the only fish group that scored in the top priority quadrant for important and vulnerable species (Figure 4) that were also considered a higher-priority candidate for management (Figure 11). 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 4) but were deemed a lower priority for management compared to the other fishes examined (Figure 11), likely owing to their incredible display of population productivity for a vertebrate (Depczynski & Bellwood 2003, Goatley et al. 2017, Brandl et al. 2018, 2019).

The ecological importance of cleaning organisms and their cleaning stations in marine community dynamics 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 very low densities, cleaner wrasse can shape reef fish assemblages through the active removal of deleterious ectoparasites, dead skin and mucus from client fishes (Figure 14). 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

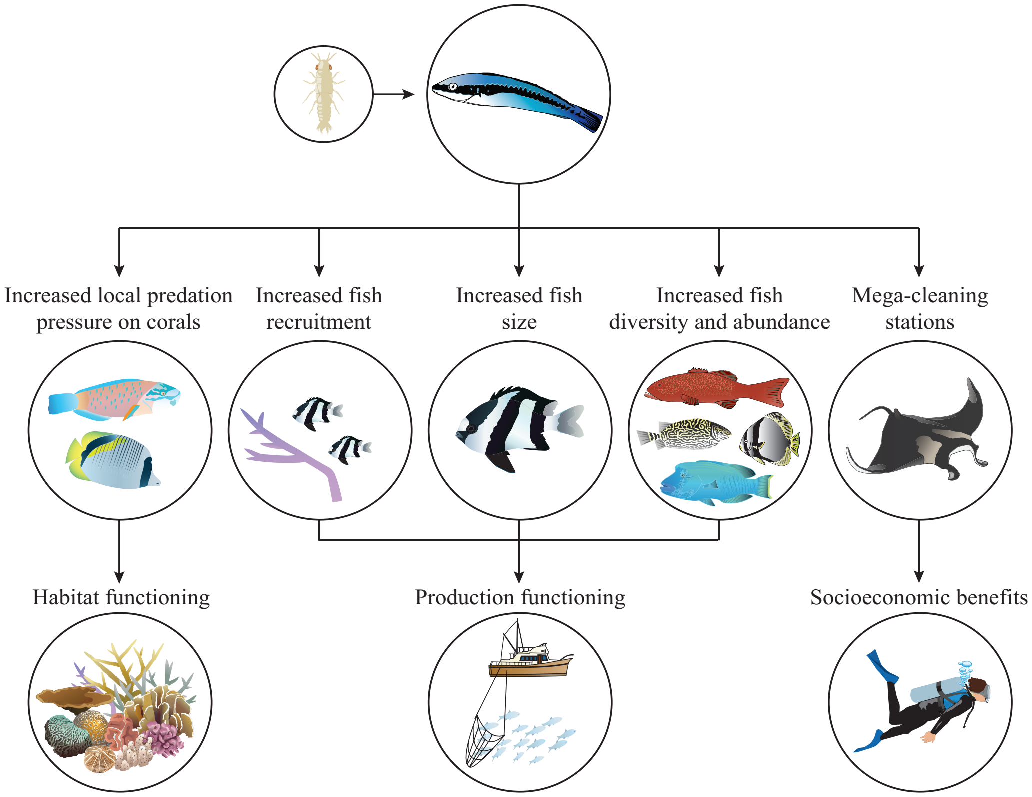

Figure 14 Schematic of the influences of cleaner wrasse (*Labroides dimidiatus*) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/) and (Hutson et al. 2018).

to parasitic micropredation (Grutter et al. 2008, 2011, Penfold et al. 2008, 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 14). 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 the context of ecosystem functioning, the symbiotic relationship established between cleaners and a diversity of marine fauna is likely to improve production functioning on coral reefs (Figure 14) – although direct links to fisheries productivity are yet to be quantified. Cleaners also have the potential to influence habitat functioning 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.

In the context of ecosystem services, cleaners attract a diversity of marine megafauna, including manta rays, turtles, mola mola, sharks and large predatory fishes, to specific reef locations (Oliver et al. 2011, Jaine et al. 2012, Couturier et al. 2014, 2018, Murie & Marshall 2016). 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 14). Manta rays can spend ~8 hr per day engaging in cleaning activity, which inspire tourist hotspots (Marshall & 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 & 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,b). The influence of cleaners on regional- and global-scale socioeconomics seems so poorly appreciated, and their broader integration into ecosystem monitoring, citizen science and tourism initiatives seems important.

Little information exists regarding the vulnerabilities of cleaner wrasses. Globally, they are primary targets for the aquarium industry but 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 & 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, 2018, Triki 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 and 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), particularly since gnathiid isopod densities show fast recovery post bleaching (Sikkel et al. 2019). 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.

The biological, functional and socioeconomic benefits of cleaning stations provide a strong case for the need to protect these localised habitats to maintain ecosystem functioning and the services cleaners support (Figure 14). At present, cleaner wrasse are not specifically protected on the GBR or elsewhere. We suggest that protecting cleaning stations as hubs of ecosystem functioning may be a more appropriate and successful management initiative than protecting the cleaners themselves. 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, as outlined in the GBRMPA Blueprint for Resilience regarding herbivores and tabular corals (GBRMPA 2017, 2018a).

Bivalves Giant clams (Tridacnidae) and other bivalves (e.g. oysters) scored surprisingly high for habitat functioning, driven by processes of calcification and recruitment facilitation. Shell and 'bed' construction by bivalves can contribute significant structural complexity to the reef, 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 & 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. Shallow-water benthic bivalves are natural controllers of eutrophication and water quality through their filter-feeding processes (Figure 15), perhaps most importantly on nearshore reefs (Klumpp et al. 1992, Klumpp & 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*, which can dominate reef and intertidal areas on nearshore (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

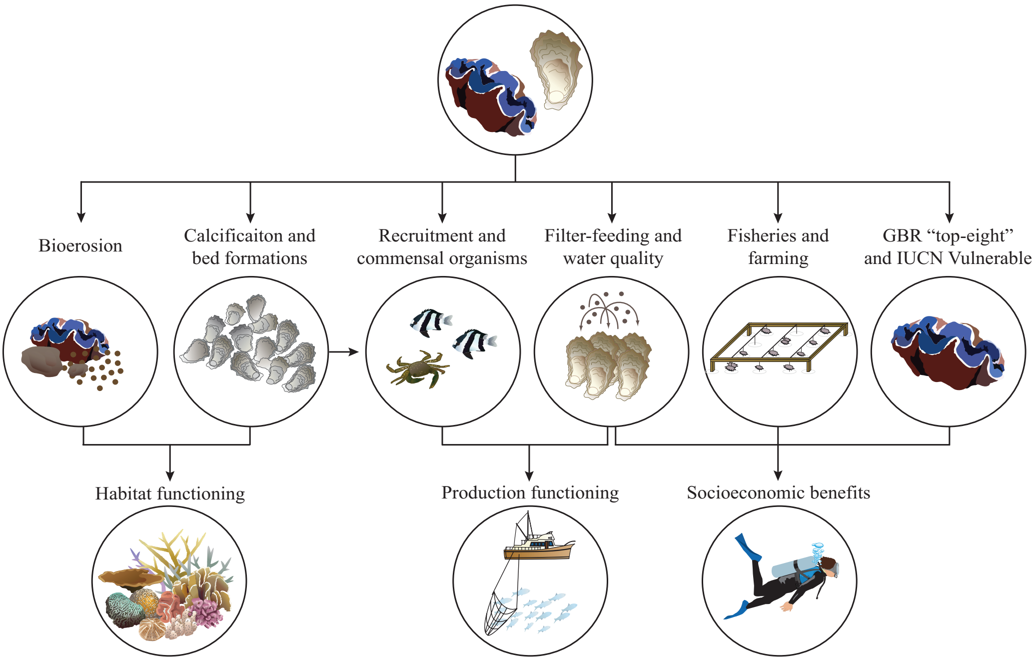

Figure 15 Schematic of the influences of bivalves (e.g. Tridacnidae, oysters) on ecosystem processes, functioning and services. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

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.

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 nearshore populations.

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, 2015), but this occurs beyond the focal reef-centric 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, nearshore 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 1996a,b, Richards & 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. 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 to optimise benefits from the natural infrastructures of reef-forming molluscs, including fisheries production, shoreline protection, water filtration and tourism (Figure 15). Precautionary measures should maintain focus on water quality to enhance the resilience and survival of bivalves on the GBR and elsewhere.

Coral-associated decapods Coral-associated decapods are strongly bound to their coral host, where they take refuge from a range of reef and cryptic predators, including squirrel fishes, wrasses and eels (Hiatt & Strasburg 1960). From a bottom-up perspective, coral-associated crabs can form up to 70% of a reef fish's 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 & Lewis 2008, Stella et al. 2010, 2011b). Obligate-dwellers are considered highly beneficial to their coral hosts, as they actively defend the host from predators, including CoTS, *Drupella* and *Dendropoma*, and contribute to the removal of excess sediment that would otherwise smother the corals (Figure 16) (Glynn 1980, 1983, Pratchett 2001, Stewart et al. 2006, Stier et al. 2010, Stella et al. 2011b). Further, some obligates (e.g. *Cymo*) have been shown to slow the progression of disease in their coral host (Figure 16) (Pollock et al. 2013).

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. 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. In light of intensifying degradation of coral reefs, any direct benefits to corals through management, as offered through the GBRMPA zoning scheme, would surely support broader resilience of coral-associated organisms to environmental change. There is no specific protection or management initiative outlined for coral-associated decapods at present, which would prove difficult to implement and monitor given their small and cryptic nature. Broader protection of their coral habitat and education on the importance of coral-associated organisms to reef functioning are likely to be the most reasonable and effective management strategies for this group.

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,b). 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

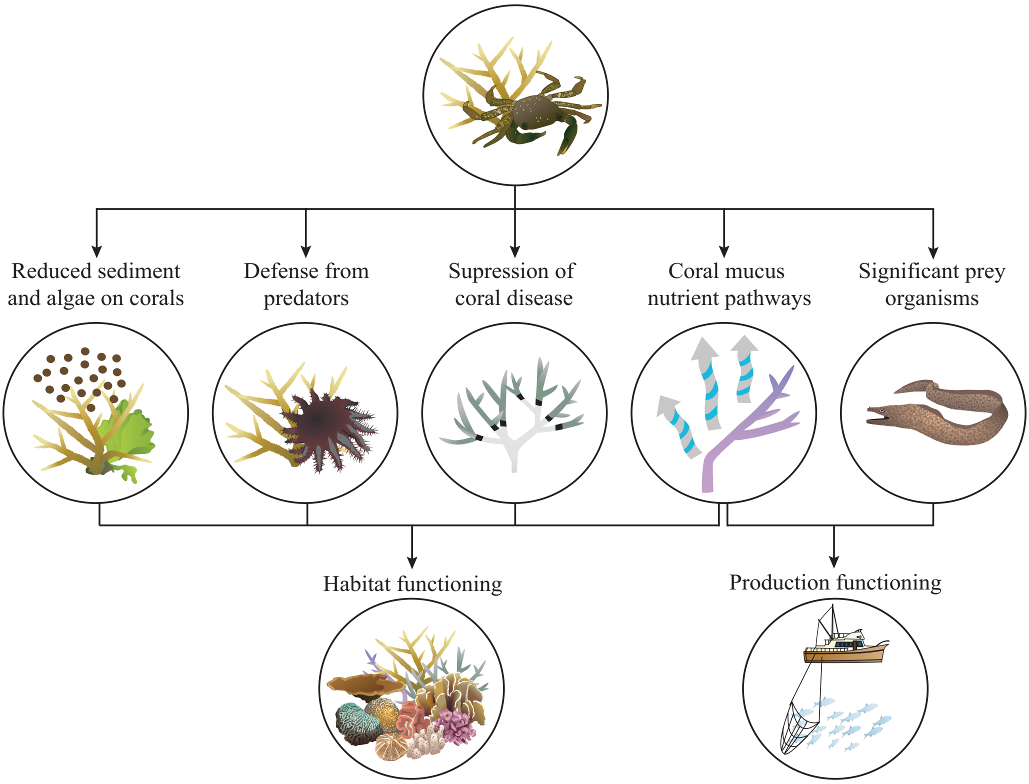

Figure 16 Schematic of the influences of coral-associated decapods on ecosystem processes and functioning. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

and reproduction, which intensifies inter- and intraspecies competition (Glynn et al. 1985, Stella et al. 2011a, 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, particularly when coral mortality occurs at large spatial scales.

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. This is likely due to the broad distributions and/or high densities of predominant groups, including blennies (Wilson 2000, 2001, 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 17) (Crossman et al. 2001, 2005, Wilson et al. 2003, Bellwood et al. 2014). The rapid population turnover of blennies in particular

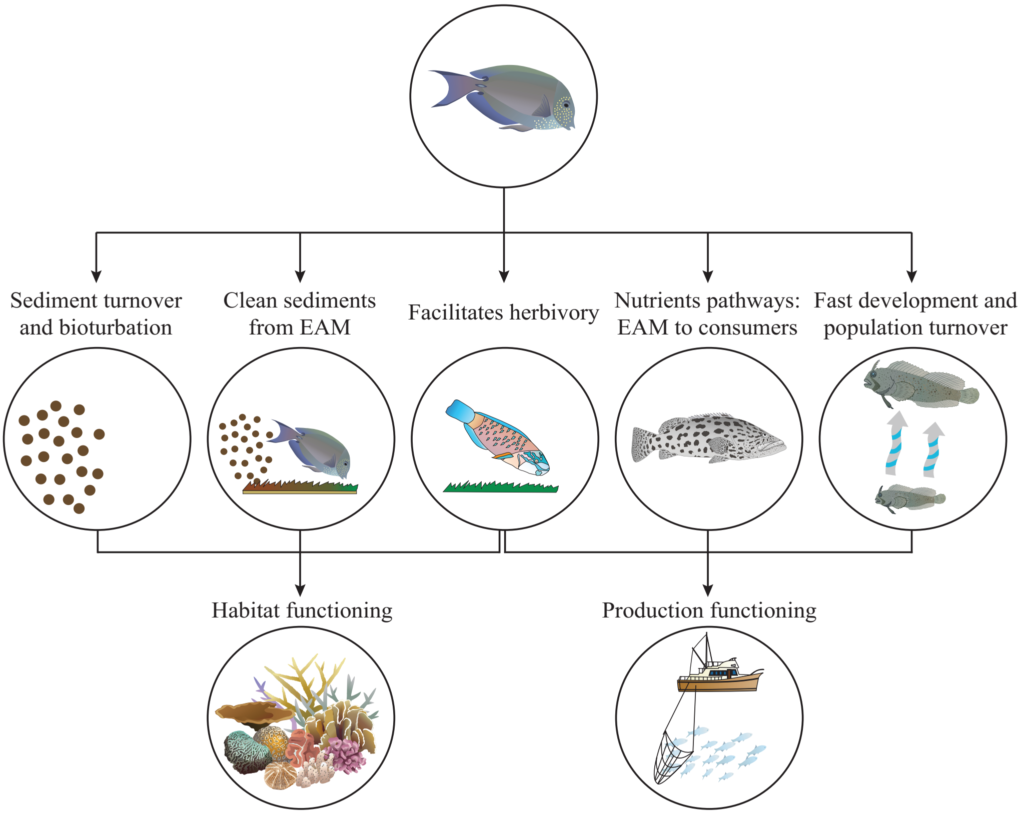

Figure 17 Schematic of the influences of detritivorous fishes (e.g. blennies, *Ctenochaetus striatus*) on ecosystem processes and functioning. Symbols courtesy of the Integration and Application Network (ian.umces.edu/symbols/).

(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 17). Further, post disturbance and associated losses in coral cover and 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, 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.

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 & Bellwood 1993, Goatley & Bellwood 2010, Krone et al. 2011, Cheal et al. 2013, Tebbett et al. 2017b,d, 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, 2018), which has been shown to facilitate herbivory by other species (Goatley & Bellwood 2010, Marshell & 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. 2017c,d, 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, are management strategies that would likely benefit this group.

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 five individuals and a minimum size limit of 25 cm on the GBR, but they are not heavily targeted and exhibit particularly fast growth rates to a distinct size (Trip et al. 2008, Choat et al. 2012). The biology of *C. striatus* may render them particularly resilient across their expansive range, given fishing intensity remains low (Trip et al. 2008). Specific consideration of key detritivores, such as *C. striatus*, in reef monitoring programmes is recommended to ensure that groups with important contributions to ecosystem functioning are well documented and safeguarded in a future ocean. Management and education initiatives may also be implemented for detritivores, as already exist for herbivores and tabular corals (GBRMPA 2017, 2018a).

Overview and synthesis

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 functioning 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 and in providing targeted information to safeguard species, biodiversity and functioning into the future (Halpern et al. 2007, McClanahan et al. 2014, Rogers et al. 2015, Shaver & Silliman 2017, Richards & Day 2018). We present a broad review of the literature for priority coral reef species on the GBR and for typical reef crest and reef slope habitats more generally. 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 functioning, are of OUV and contribute greatly to the integrity and cultural values of the GBR and its World Heritage property (GBRMPA 2014c). The information here provides a first step to inform holistic management aiming to preserve important reef species, values and processes and the opportunity to build out from the current framework in context of biological functioning to other important coral reef biomes (e.g. mangroves, seagrass meadows, interreefal areas) and values (e.g. social, cultural, economic).

The preservation of biodiversity is critical to maintain coral reef functioning (Clements & Hay 2019), but we must augment the precautionary principle of conserving biodiversity with predictive science that informs practical and specific solutions (Naeem et al. 2012). Conservation success depends on the recognition and inclusion of specific taxa that support positive interactions, with disproportionate benefits to ecosystem functioning (Halpern et al. 2007, Shaver & Silliman 2017, Renzi et al. 2019). We present a range of desired outcomes for priority groups (tabular corals, branching corals, microorganisms, crustose coralline algae, algal turfs, crown-of-thorns starfish and herbivorous parrotfishes) to empower research and holistic management. In the context of the GBR, past and present management schemes (e.g. GBRMPA zoning [Day 2002, Fernandes et al. 2005, 2009], Blueprint for Resilience [GBRMPA 2017, 2018a]) are commended for their efforts, and momentum should be maintained. Novel taxa (chemoautotrophic microbes, cleaner wrasse, bivalves, coral-associated crabs and detritivorous fishes) may benefit from consideration in these (or similar) initiatives, including expanding current research and monitoring programmes 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. For novel candidates and groups where scientific certainty was particularly low (cryptic predators, deposit-feeding sea cucumbers, marine worms, cryptic sponges and crustaceans), 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.

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Supplementary Tables are provided online at https://www.routledge.com/9780367367947