Quantifying the role of parrotfish in the production and cycling of carbonate in coral reef ecosystems

Robert Thomas Yarlett

Submitted by R. T. Yarlett, to the University of Exeter as a thesis for the degree of Doctor of Philosophy in Physical Geography, July 2018.

I certify that all material in this thesis which is not my own work has been identified and that no material has previously been submitted and approved for the award of a degree by this or any other University.

Signature………………………………………………………………………………

Abstract

Parrotfish are a diverse and ubiquitous group found on coral reefs worldwide. They are categorised into three main feeding modes; the browsers, scrapers and excavators, which together perform a number of important functional roles on coral reefs. Scraper and excavator parrotfish are common on most Indo-Pacific coral reefs where their roles in bioerosion, sediment production, grazing pressure and sediment reworking have been shown to influence benthic community composition, reef growth potential and sediment supply to reef habitats and reef associated sedimentary landforms. However, despite the widely known importance of parrotfish on coral reefs, our understanding of how their roles in carbonate cycling vary among species and among whole parrotfish communities in different reef habitats remains limited. This thesis produces original contributions to knowledge in the areas of species specific bioerosion estimates for the central Indian Ocean, bottom-up controls of habitat type on parrotfish assemblages and how variations in parrotfish assemblages translate to contributions to carbonate cycling processes among different reef habitats. The study was carried out across eight habitats on an atoll-edge reef platform in the central Maldives, where it was found that parrotfish community composition was driven by reef structural complexity and substrate type. Parrotfish occurred in six of the eight habitats, comprising ~44% of the platform area. Among these habitats, overall grazing pressure, bioerosion rates, sediment reworking and sediment production varied markedly. These processes were also found to have different spatial patterns over the reef platform, showing that they are not necessarily tightly coupled. In addition, reef habitats can vary in their importance for both sediment supply, and the relative importance of reworked sediment. Parrotfish produced a wide range of sediment size fractions, from <32 to 2000 µm and produced predominantly coral sands (>80%) between 125 and 1000 µm in diameter. This is comparable to the grain types found on local reef islands, and it is likely that the most significant supply of this material is from habitats on the atoll-edge side of the platform (which make up ~20% of the total platform area). Quantifying parrotfish functional roles and understanding the drivers behind these processes is important for informing future empirical

and modelling studies, particularly as coral reefs undergo a time of dramatic environmental change.

Contents

Acknowledgements

I'd like to start by thanking Professor Chris Perry for giving me the opportunity to undertake this extremely cool project. Your supervision and guidance has been invaluable and is hugely appreciated. In return, I promise never to accidentally eat your lunch again! I'd also like to extend my thanks to Prof Rod Wilson who was jointly responsible for giving me this opportunity (Chris shouldn't take full responsibility) and for all the support and guidance in the field and many helpful discussions. Many thanks go to Dr Al Harborne for helpful meetings in opposite sides of the globe, and the many discussions about fish surveying which helped strengthen chapter 5. Thanks also to Professors Steve Simpson and Simon Jennings for the useful meetings about fish, maths and stats.

A huge amount of thanks goes to Dr Mike Salter for effectively being an additional supervisor, for the opportunities to get involved in the Australia field work, and for generally being a great source of advice and an excellent field companion. Many thanks also go out to my friends and colleagues from the reef team, past and present, for the many helpful discussions; Jamie, Holly, Gary, Emi, Ines, Kyle and Fraser.

I'd like to thank the staff of the former KorallionLab Marine Research Station for facilitating my fieldwork, and particularly Ibrahim Sikder and Billal Hossan for their hospitality, company and keeping me well fed. The support of staff at Lizard Island Research Station, Australia, and Small Island Research Station, Maldives was also greatly appreciated. KorallionLab intern, Kate Philpot, also deserves a big thank you for helping with some of the field data collection for chapter 4. The technical lab support provided by Richard Hartley (Geography, Plymouth University) and Dr Christian Hacker (Biosciences, Univeristy of Exeter) was invaluable for much of the data collected for chapter 6. The handy work of Neville England is also hugely appreciated, thanks very much for constructing the camera frames. Many thanks also go to Stirling Tebbet and Rob Strite of James Cook University for their excellent barrier netting skills.

My family, particularly my parents, sister and Nan of course deserve a huge amount of thanks for the encouragement and keeping me motivated when I

most needed it. You guys can stop reading at this point, just pretend you found the rest of the thesis interesting.

My PhD experience wouldn't have been anywhere near as fun without my friends in Exeter (from work, the post-grad society, tennis and salsa) and from the GW4+ DTP. Special mention goes to Alex Whittle for helping with some of the data analysis and GIS work.

The research carried out in this thesis was funded by a Natural Environment Research Council studentship (NE/L002434/1). Special thanks goes to the GW4+ DTP managers, past and present, for organising the many training opportunities, for supporting myself, Tom, Becky and Rose throughout the Environment YES competition and for facilitating my workplace secondment at the Marine Biological Association. Additional funding to support the cost of the Scanning Electron Microscope work was provided by the International Association of Sedimentologists through the post-graduate grant scheme. The DigitalGlobe Foudation provided the satellite imagery used to produce the habitat map in chapter 3 and its associated figures that appear throughout the thesis.

Many thanks to Professor Nick Graham (Lancaster University) and Dr Jamie Stevens (University of Exeter) for their helpful suggestions and time and input as examiners of this thesis.

Publications

Publications from this thesis:

Yarlett RT, Perry CT, Wilson RW, Philpot KE (2018) Constraining species-size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates. Mar Ecol Prog Ser 590:155-169

Publications closely associated with this thesis:

Perry CT, Morgan KM, **Yarlett RT** (2017) Reef habitat type and spatial extent as interacting controls on platform-scale carbonate budgets. Front Mar Sci 4:185

Conference presentations

Yarlett RT, Perry CT, Wilson RW, Simson S., Harborne A, Jennings S. Influence of Habitat Type on Reef-Scale Rates of Parrotfish Bioerosion and Sediment Production. Oral presentation presented at: European Coral Reef Symposium Dec 2017, Oxford, UK

Yarlett RT, Perry CT, Wilson RW, Simson S., Harborne A, Jennings S. Quantifying Reef-Scale Rates of Parrotfish Bioerosion and Sediment Production. Oral presentation presented at: Indo-Pacific Fish Conference Oct 2017, Pape’ete, Tahiti, French Polynesia

Yarlett RT, Perry CT, Wilson RW, Simson S., Harborne A, Jennings S. Quantifying Parrotfish Bioerosion and Sediment Production in Coral Reef Ecosystems. Oral presentation presented at: CLEScon June 2017, Exeter, UK

Yarlett RT, Perry CT, Wilson RW, Simson S., Harborne A, Jennings S. Quantifying the Physical Functional Roles of Parrotfish in Coral Reef Ecosystems. Oral presentation presented at: Reef Conservation UK Nov 2016, London, UK

Yarlett RT, Perry CT, Wilson RW, Simson S., Harborne A, Jennings S. Quantifying the Contribution of Parrotfish to Carbonate Cycling in Coral Reef Ecosystems. Poster session presented at: Wessex Congress April 2016, Oxford, UK

List of figures

List of tables

List of abbreviations

Abbreviation	Definition
ANOVA	Analysis of Variance
ABR	Annual Bioerosion Rate
AGP	Annual Grazing Pressure
ARR	Annual Reworking Rate
BPM	Bites Per Minute
CCA	Crustose Coralline Algae
EAM	Epilithic Algal Matrix
ENSO	El Niño Southern Oscillation
GBR	Great Barrier Reef
GSSA	Grazing Scar Surface Area
LOESS	Locally Weighted Regression
MaxN	Minimum Count
NE reef	North-East Reef (Vavvaru habitat - Z6)
NMDS	Non-Metric Multidimensional Scaling
PBS	Proportion of Bites producing Scars
PCA	Principal Components Analysis
PVC	Polymerizing Vinyl Chloride
RUV	Remote Underwater Video
SAsubstrate	Surface Area of substrate grazed per year
SCP	Secondary Carbonate Producers
SE	Standard Error
SEM	Scanning Electron Microscope
SE patches	South-East Patch Reefs (Vavvaru habitat – Z7)
SST	Sea Surface Temperature
TAAG	Total Annual Area Grazed
TAHB	Total Annual Habitat Bioerosion
TAHR	Total Annual Habitat Reworking
UVC	Underwater Visual Census
VBSS	Video Bioerosion for each size class of each species
VGSS	Video Grazing for each size class of each species
VRSS	Video Reworking for each size class of each species

Chapter 1 General introduction

Chlorurus sordidus (terminal phase). The most abundant parrotfish species at Vavvrau, the primary study site for this thesis. Photo credit: Kate E. Philpot

1.1 Brief overview

With increasing concern and uncertainty over the future of coral reefs, understanding the functional roles of keystone reef organisms and their contributions to ecosystem processes is essential for effective reef conservation and management (Green & Bellwood 2009, Cheal et al. 2016, D'Agata et al. 2016, Hughes et al. 2017b). The functional roles of one such keystone group, the parrotfish (Scarinae tribe of the family Labridae), are well documented, and have been shown to have a major influence on both ecological and physical reef processes (Bellwood 1995a, Bruggemann et al. 1996, Westneat & Alfaro 2005, Mumby et al. 2006, Lokrantz et al. 2008, Cowman et al. 2009, Perry et al. 2014b). Through their foraging behaviour, parrotfish act as dominant algal grazers on coral reefs, thereby promoting coral growth and recruitment (Mumby et al. 2006, Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Bejarano et al. 2013, Afeworki et al. 2013, Steneck et al. 2014). In addition, parrotfish actively erode the reef framework and ingest, rework and transport sediment (Bellwood 1995, 1996, Bruggemann et al. 1996, Bellwood et al. 2003, Hoey & Bellwood 2008, Alwany et al. 2009, Ong & Holland 2010, Morgan & Kench 2016). In doing so, parrotfish influence the growth potential of coral reefs and generate sediment that can be incorporated into the reef framework or transported to reef habitats, islands and beaches (Perry et al. 2014b, Perry et al. 2015a, Morgan & Kench 2016a).

While a number of the abovementioned studies have examined the processes of grazing and bioerosion by parrotfish, there are a number of data and knowledge gaps regarding their functional roles on coral reefs and their contributions to carbonate cycling; 1) There are a lack of detailed inter-species and size class specific data to inform estimates of substrate bioerosion in many regions, 2) few studies examine "bottom-up" controls of reef habitats on parrotfish communities and the influence of this on overall parrotfish functional roles and 3) the role of parrotfish in sediment generation, and the relative importance of new and reworked sediment among different habitats, is poorly understood.

Fully understanding parrotfish functional roles and their influence on reef ecological and physical structure is important given that parrotfish populations are threatened in many regions by habitat degradation and overfishing (Bellwood et al. 2004, 2012, Clua & Legendre 2008, Tzadik & Appeldoorn 2013, Taylor et al. 2014, 2015, Heenan et al. 2016). In this thesis, I integrate studies of substrate grazing, bioerosion, sediment production and sediment reworking by whole parrotfish assemblages across different habitats over a reef platform scale. These roles were examined on reefs in the central Maldives, an ideal location for the study because 1) parrotfish are not a target fishery, 2) there are a diverse array of habitat types on the atoll edge reef platforms, and 3) because coral reefs in the region were in relatively good "health" at the time of study (McClanahan 2011, Perry et al. 2017). This environment therefore represents a near-natural model for examining the roles of parrotfish on coral reefs, and from which the impacts of environmental disturbances can then be examined.

1.2 Thesis aim

This thesis aims to quantify the contribution of parrotfish to bioerosion, grazing, sediment production, and sediment reworking over different reef habitat types on an atoll edge reef platform, from which potential impacts to the reef system as a result of environmental disturbances can be inferred.

1.3 Research questions

1. How do rates of substrate bioerosion differ between parrotfish species and size classes in the Maldives?
2. How do overall bioerosion rates and grazing pressures vary among reef habitats on a reef platform as a function of species assemblage and size structure?
3. How do overall sediment production rates vary among reef habitats on a reef platform as a function of species assemblage and size structure, and what is the relative importance of new to reworked sediment?

4. What are the characteristics (grain size and type) of sediment produced by different species and sizes of parrotfish, how does this influence the quantity of different sediment size fractions produced in different habitats and how does this material compare to that found on local reef islands?
5. What are the potential impacts of fishing pressure and habitat degradation on the contributions of parrotfish communities to bioerosion, grazing, sediment production and sediment reworking, do impacts differ among reef habitats and what are the implications of this for the reef system?

1.4 Objectives

Objective 1: How do parrotfish species assemblages and size classes vary across all ecologically and structurally distinct habitats over a reef platform?

Objective 2: How do bite rates, grazing scar production rates, grazing scar volumes and resultant bioerosion rates vary among a range of representative species, life phases, and size classes of Maldivian parrotfish?

Objective 3: What are the links between habitat type (rugosity, substrate type and structural complexity) and parrotfish species assemblages?

Objective 4: What are the contributions of parrotfish species and size classes to grazing and bioerosion in different reef habitats over a reef platform and how do overall bioerosion rates and grazing pressure vary among these habitat types?

Objective 5: What are the contributions of parrotfish species and size classes to sediment re-working in different reef habitats over a reef platform and how do overall sediment reworking rates vary among these habitat types?

Objective 6: What sediment size fractions are produced by a range of representative parrotfish species and size classes?

Objective 7: What is the total amount of sediment produced by parrotfish in different reef habitats, factoring for direct export from the system by parrotfish?

Objective 8: What is the importance of endogenous calcium carbonate production in the context of overall parrotfish sediment production?

Objective 9: What are the impacts of current major threats to coral reefs (habitat degradation in the form of loss of structural complexity and fishing pressure) on important parrotfish functional roles (bioerosion, grazing, sediment reworking and sediment production)?

Chapter 2 Current understanding of the role of parrotfish in carbonate production and cycling in coral reef ecosystems

Scarus rubroviolaceus (terminal phase) in the rocky rubble habitat on the Vavvaru reef platform. Parrotfish grazing scars are clearly visible on the substrate behind the fish. Photo credit: Kate E. Philpot.

2.1 Background

Coral reefs are focal points of marine carbonate production, and are built through a balance of constructional and erosional processes by the organisms that inhabit them (Stearn et al. 1977, Scoffin et al. 1980, Glynn 1997). The structure (herein termed "reef framework") built by these organisms protects adjacent shorelines (Lugo-Fernández et al. 1998, Ferrario et al. 2014), and supports a diverse ecosystem on which ~15% of the world's population directly depend (Carté 1996, Hoegh-Guldberg 1998, Moberg & Folke 1999, Bell et al. 2006, Donner & Potere 2007, Ruckelshaus et al. 2013). The production of carbonate in the form of carbonate skeletons (predominantly by scleractinian corals and crustose coralline algae) and carbonate sediments provides the material to build the reef framework, and a range of reef associated sedimentary landforms including beaches and islands (Kench et al. 2005, Perry et al. 2011b, 2015a).

Another dominant control on carbonate accumulation on coral reefs is the process of bioerosion, sensu Neumann (1966). A bioeroder is defined as "any organism that, through its assorted activities, erodes and weakens the calcareous skeletons of reef building species" (Glynn 1997). The process of bioerosion can be differentiated into an "internal" process within carbonate substrates (e.g. that attributed to polychaetes, sponges and bivalves) or "external" processes on carbonate substrates (e.g. by fish and urchins). The resultant net rate of carbonate accumulation from these constructional and erosional processes can range from negative (net erosional) rates, up to ~10 kg $CaCO_3$ m^{-2} yr^{-1}; between -0.98 and 9.52 kg $CaCO_3$ m^{-2} yr^{-1} on the reefs of Bonaire, for example (Perry et al. 2012). Despite being an erosional process, bioerosion can benefit coral reefs by 1) creating sedimentary substrata for a range of reef associated species (particularly burrowing benthic organisms including fish, annelids, and crustaceans), 2) contributing to topographic complexity by creating cavities in the reef framework, and 3) facilitating coral recruitment by creating space where larvae can settle, thereby promoting carbonate production (Hutchings 1986, Glynn 1997). However bioerosion also weakens the reef framework, making it more susceptible to chemical and physical erosion (Hutchings 1986).

A number of fish groups (e.g. Acanthuridae, Scaridae, Balistidae, Monacanthidae, Tetradodontidae and the Canthigasteridae) are defined as bioeroders, actively eroding reef framework through the act of grazing or by fragmenting coral colonies whilst feeding or foraging (Glynn 1997). Of these, the parrotfish are widely considered to be the dominant bioeroders. Parrotfish also contribute significantly to a number of other reef processes that either directly or indirectly influence reef carbonate budgets such as grazing, sediment reworking and sediment production (reviewed by Bonaldo et al. 2014).

Previous studies of parrotfish sediment production have focussed on the material produced through the process of bioerosion (Bellwood 1996, Bruggemann et al. 1996, Hoey & Bellwood 2008), but recent research has revealed that, to our knowledge, all marine teleosts also precipitate new calcium carbonate within their intestine as a result of continuously drinking seawater. This carbonate is egested into the environment typically as silt grade (<60 µm) sediment (Walsh et al. 1991, Salter et al. 2012). A study by Perry et al. (2011a) suggested that calcium carbonate produced by marine teleosts could contribute up to 14% of fine carbonate sediments produced across the Bahamian archipelago. If this process is also significant in the parrotfish, this would add a previously unrecognised component to their role in sediment generation on coral reefs, making their influence on carbonate production and cycling even more important than previously recognised.

Due to the potentially wide ranging role of parrotfish in carbonate production and cycling on coral reefs, there is a need to better understand and quantify the roles that parrotfish perform in bioerosion, grazing, sediment production and sediment reworking, and how these processes vary between species, size classes, and in different habitat types. In addition, it is important to predict how these processes could be affected as a result of environmental change on coral reefs, which are threatened worldwide by anthropogenic and natural disturbances. These stressors, including rising sea surface temperatures (SST), overfishing, tropical storms, disease and increased nutrient and sedimentation inputs from land can cause both localised and regional scale degradation. Parrotfish are a popular commercial fishery in some regions (McManus et al. 2000), and their populations are also affected by changes in the condition of their habitat such as declining coral cover and structural complexity (Wilson et al. 2006, Tzadik & Appeldoorn 2013). While some existing studies have demonstrated the ecological impacts of changing parrotfish population dynamics on coral reefs (Mumby 2006), the impacts on roles associated with carbonate cycling have been comparatively understudied (Perry et al. 2008). Quantifying processes such as these can help to inform conservation management decisions (Bellwood et al. 2004, Hughes et al. 2005), as the "health" and "resilience" of coral reefs, and ultimately the ecosystem services they provide are dependent on the functional roles (sensu, Done et al. 1996) of the organisms that inhabit them (Worm et al. 2006, Mora et al. 2011).

Previous work on the functional roles (mainly grazing and bioerosion) of parrotfish have covered the Caribbean (Bruggemann et al. 1994a, b, c, Bruggemann et al. 1996), Arabian Seas (Hoey et al. 2016a), Red Sea (Alwany et al. 2009, Hoey et al. 2016a), Western Indian Ocean (Lokrantz et al. 2008), the Great Barrier Reef (Bellwood 1995a, b, Bellwood et al. 2003, Hoey & Bellwood 2008) and the Pacific (Jayewardene 2009, Ong & Holland 2010). However, the central Indian Ocean represents a geographic area which has received little attention, see Morgan & Kench (2016) for a good exception. Fisheries activities in the Maldives primarily focus on large pelagic fish. Skipjack Tuna are the major commercial fishery, comprising ~70% of the total catch (Adam 2006, McClanahan 2011). Fishing of reef species such as grouper, snapper and bait fish does occur, but because of the methods used (primarily hook and line, hand line and baited drop line) parrotfish are rarely a targeted or accidental catch (Adam 2006). Coral reefs in the Maldives were also in relatively good "health" during the field seasons of this project (prior to the 2016 El Niño induced bleaching event in the Indian Ocean - Perry et al. 2017). The Maldives therefore represents a model study region to investigate the contributions to carbonate production and cycling by near-natural parrotfish populations, from which the impacts of environmental disturbances can then be predicted.

2.2 Substrate grazing and bioerosion by parrotfish

Parrotfish are clearly distinguished from other Labrids by their unique feeding apparatus. The teeth of parrotfish are fused together in a beak-like structure (Bellwood & Choat 1990, Bellwood 1994). Within the parrotfish, three distinct feeding modes exist; the “browsers”, “scrapers” and the “excavators”, which are defined by their osteology, myology, functional interpretations of the jaws and feeding behaviour (Bellwood & Choat 1990). Browsers predominantly feed on macroalgae and so do not ingest carbonate. This thesis therefore focusses on the scrapers and excavators. Scrapers have weaker, lighter and more complex jaw (<1.2% body weight) and muscle (<2.0% body weight) structures compared to excavators, and generally produce fewer scars on reef substrates (Bellwood & Choat 1990). Excavators have more robust dentition (>1.5% body weight) and muscle (>2.5% body weight) structure (Figure 2-1), enabling them to remove chunks of substrate, now thought to be targeting endo- and epilithic cyanobacteria (Clements et al. 2016) but also ingesting algae, and occasionally live coral, coralline algae, macroalgae and anything else that may be living on or in the reef substrate (Smith & Paulson 1974, Bellwood & Choat 1990, Bellwood 1994, Bruggemann et al. 1994b, c, McAfee & Morgan 1996, Rotjan & Lewis 2005, Bonaldo et al. 2006). Feeding on live coral by parrotfish (Rotjan & Lewis 2005, 2008) has created debate as to whether parrotfish are good or bad for the ecological health of coral reefs (Mumby 2009). However, corallivory is thought to be restricted to a few excavating species, with only one (*Bolbometopon muricatum*) selecting live coral as its preferred food type (Bellwood et al. 2003).

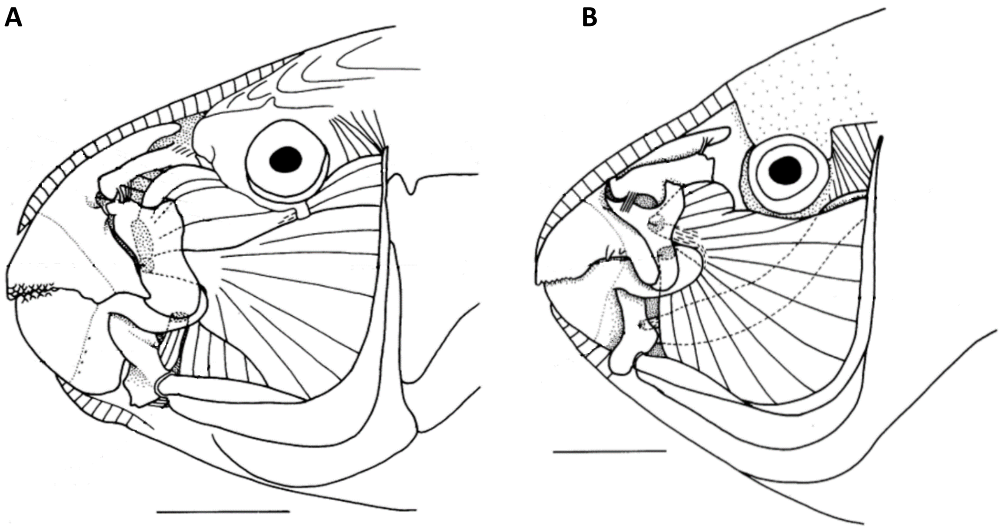


Figure 2-1 Jaw and muscle structure of an excavator (A. Chlorurus sordidus) compared to a scraper (B. Scarus frenatus). Scale: 10mm. Adapted from Bellwood (1994).

As well as their feeding mode, parrotfish foraging behaviour, which has direct influence for their roles in grazing and bioerosion, can be influenced by their life phase. Many parrotfish species are protogynous hermaphrodites and undergo dramatic colour changes as they mature between their juvenile (usually female), initial (usually female) and terminal (male) life phases, although primary males (born as males) do exist and a few species are monochromic (Robertson & Choat 1974, Robertson & Warner 1978). The transition between life phases in parrotfish is controlled by hormones which influence behaviour (Cardwell & Liley 1991) and may therefore affect bite rates. During post-settlement juvenile phases, parrotfish are omnivorous and feed almost entirely on crustaceans (Bellwood 1988, Chen 2002). Once they reach ~32 mm in length (with some variation depending on species) their jaws begin to develop and their diet shifts focus to the ingestion of algae and sand (Bellwood 1988, Chen 2002). From this point, the size of an individual parrotfish is important in determining its contribution to different functional roles on coral reefs (Bruggemann et al. 1996, Bonaldo & Bellwood 2008, Lokrantz et al. 2008). Feeding by juveniles has been observed to be sporadic and infrequent but in general, bite rates have been observed to decrease with increasing body size (although this is based on few observations, e.g. Bruggemann et al. 1994b). This is accompanied by an increase in the volume of material ingested per bite (Bruggemann et al. 1996).

Only excavators over ~20 cm (fork length) produce a high proportion of grazing scars (>50%) while feeding, often making them significant contributors to bioerosion (Bruggemann et al. 1996).

Bite rate may also be influenced by social behaviour. In some species for example, territorial terminal phase males spend less time on foraging activities (70% of daily active period) compared to non-territorial individuals (90%) and take fewer bites per day (Bruggemann et al. 1994a). Total food intake by territorial individuals has however been observed to equal that of non-territorial individuals by taking higher yields per bite (Bruggemann et al. 1994a). Social behaviour with other species can also influence substrate choice, with the aggressive behaviour of damselfish preventing some parrotfish species from grazing their algal gardens (Bellwood 1995b). Grazing scar size has also been observed to increase with water depth, perhaps compensating for the lower nutritional quality of photosynthetic food resources as light attenuates (Bruggemann et al. 1994b).

Parrotfish feed on photosynthetic organisms (including cyanobacteria and algae), so feeding only occurs during daylight hours and feeding patterns are thought to be controlled by light intensity (Bruggemann et al. 1994b, Clements et al. 2016). Bite rates have also been shown to differ throughout the day, increasing throughout the morning before reaching a peak in the afternoon, then decreasing and halting before sunset (Bruggemann et al. 1994b). At night, some parrotfish species sleep in holes in the reef wrapped in mucus cocoons, and are therefore in a non-feeding state. These cocoons act as a predator deterrent and may also have other benefits such as antibiotic properties (Shephard 1994, Videler et al. 1999). In addition to light inensity, environmental factors such as wave energy (Fulton et al. 2001) and sediment load in the Epilithic Algal Matrix (EAM) can influence bite rate, as well as the distribution of parrotfish and the roles they perform in different reef habitats (Bellwood & Fulton 2008, Hoey & Bellwood 2008).

While scrapers produce smaller grazing scars than excavators, they often have higher bite rates, although this is species and size dependant, as summarised for reefs worldwide in Bonaldo et al. (2014). Some scrapers can remove algae at a faster rate than excavators because of this high bite rate, helping to prevent algal encroachment on juvenile corals (Box & Mumby 2007). However, because the scars of excavators are larger and deeper, it takes longer for algae to fully recolonize the scar area (several days) compared to those produced by scrapers (Bonaldo & Bellwood 2009). While scrapers do erode framework material, an excavator of the same size as a scraper is likely to erode substantially more material (Bellwood & Choat 1990, Bruggemann et al. 1996). For example, excavator *Chlorurus gibbus* erodes considerably more material than *Scarus rubroviolaceus* due to their difference in feeding modes, despite their similar size (Table 2-1). The material eroded from the reef framework is processed along with organic material, ingested, broken down, and egested into the reef environment as sediment (Bellwood 1995a, 1996).

Table 2-1 All known published bioerosion rates for Indo-Pacific parrotfish (excluding Yarlett et al. 2018 which is presented in this thesis as Chapter 4).

Species	**Feeding Mode**	**Max. Size (TL, cm)**	**Bioerosion (kg individual^{-1} yr^{-1})**	**Original Source**
Bolbometopon muricatum	Excavator	130	5690	Bellwood et al. 2003
Chlorurus microrhinos	Excavator	70	1017.7	Bellwood 1995a
Chlorurus gibbus	Excavator	70	294	Alwany et al. 2009
Chlorurus strongylocephalus	Excavator	70	405	Morgan & Kench 2016
Chlorurus perspicillatus	Excavator	60	301	Ong & Holland 2010
Chlorurus spilurus	Excavator	40	24	Bellwood 1995a
Chlorurus sordidus	Excavator	40	55	Morgan & Kench 2016
Chlorurus sordidus	Excavator	40	42.3	Alwany et al. 2009
Cetoscarus bicolor	Excavator	70	250	Alwany et al. 2009
Scarus frenatus	Scraper	50	44	Alwany et al. 2009
Scarus niger	Scraper	45	15	Alwany et al. 2009
Scarus ferrugineus	Scraper	41	43	Alwany et al. 2009
Scarus ghobban	Scraper	90	253	Alwany et al. 2009
Scarus rubroviolaceus	Scraper	70	14-380	Ong & Holland 2010

2.3 Sediment generation by parrotfish

2.3.1 Sediment production, reworking and transport

In addition to the sediment produced by erosion of the reef framework, parrotfish ingest and process loose sediment retained within the EAM on the substrates they feed on. This is termed “sediment reworking” (Scoffin et al. 1980, Bellwood 1996, Bruggemann et al. 1996). The transit time of food and ingested sediment in the parrotfish gut has been estimated at between 4-6 hours, corresponding to filling the gut approximately twice per day (Smith & Paulson 1974). Parrotfish are very mobile so during this time they will be swimming and foraging in different parts of the reef. Some species have been observed to move between reef zones whilst foraging and also move off-slope or to designated “defecation sites” away from feeding areas (Bellwood 1995b). This actively transports sediments around the reef system. The loose sediment and framework material ingested by parrotfish are triturated by modified gill arch elements known as the pharyngeal mill, resulting in a reduction in grain size and increasing the chance of hydrological transport and potential loss of carbonate from the reef system post-egestion (Bellwood 1996).

It was previously assumed that sediment was predominantly removed from reef substrates by physical (abiotic) processes (Hubbard et al. 1990). However, sediment reworking and transport examined in surgeonfish has been observed to “clean” hard substrates of sediment, and thereby promote coral larvae settlement (Goatley & Bellwood 2010, Krone et al. 2010). How far these reworked sediments are transported can influence whether these carbonates are reincorporated, or exported from the reef system. There have been some suggestions that high sediment loads can deter grazing by herbivorous fish (Bellwood & Fulton 2008), but Bonaldo & Bellwood (2011) found that in low quantities, sediments were insufficient to deter parrotfish from grazing and that reworking by parrotfish and surgeonfish is likely to assist sediment removal by abiotic factors. Despite the potential importance of sediment reworking, few studies have estimated the quantities of sediment reworked by different species and sizes of parrotfish, or how the rates of this process vary between reef habitats as a function of substrate sediment load.

The proportion of newly eroded framework to existing loose sediment ingested and reworked by parrotfish has been reported to vary with body size and feeding mode, although this has not been widely studied (Bellwood 1996, Bruggemann et al. 1996). Scrapers have been shown to ingest a higher proportion of loose sediment compared to eroded framework, while the opposite is true for excavators. For example, sediments in the gut of excavator *Chlorurus gibbus* consisted of only 2.4% reworked sediment, compared with 27% for smaller excavator *Chlorurus sordidus* (Bellwood 1996). While excavators ingest a lower proportion of loose sediment compared to newly eroded reef framework, they may still ingest a larger volume of loose sediment compared to scrapers. The proportion of eroded to reworked sediment is also likely to vary within species as a function of fish body size, and also between habitats as a function of sediment load on reef substrates, but this has not yet been examined.

The size fractions of sediment produced by parrotfish have been reported to be influenced by feeding mode, although very few studies have presented data on this. Hoey & Bellwood (2008) measured the proportions of different size fractions of sediments produced by 4 parrotfish species on the Great Barrier Reef (GBR), ranging from small to large, scraping to excavating species. All species studied were observed to produce sediment ranging from <63 µm to >1000 µm. Smaller scraping *Scarus spp.* and excavating *C. sordidus* were shown to produce mainly finer size classes of sediment, primarily <63 µm (~27%), and very little sediment (<10%) in size fractions over 500 µm. Large excavating species, *Chlorurus microrhinos* appeared to produce more sediments (~30%) in the 250-500 µm size fraction, while in *Bolbometopon muricatum,* a more uniform distribution of sediment size fractions (~10-20%) over size classes between <63 µm to >2000 µm was observed. The size fractions, shape and density of this sediment is important when considering the fate of these sediments on coral reefs (Braithwaite 1973, Kench & McLean 1996, Kench 1997). Finer size fractions (depending on their shape and density) may be more susceptible to hydrodynamic transport and export from the reef. In contrast, coarser size fractions are likely to have a higher settling velocity and stay within the reef platform, and may form a more significant component of benthic sediments and reef associated sedimentary landforms (Braithwaite 1973, Kench & McLean 1996, Kench 1997). Parrotfish foraging behaviour and the associated roles in reef carbonate production and cycling is therefore complex. In addition to “secondary” carbonate sediment production through bioerosion and sediment reworking, it is possible that parrotfish, as with all marine teleost fish, also contribute new “primary” sediment to coral reefs that are produced endogenously within the intestine.

2.3.2 Endogenous carbonate production by marine teleost fish

So far, sediment production by parrotfish has been discussed in the context of the erosion of reef framework and loose sediment. However, other unrelated research has shown that, based on current knowledge, all marine teleosts precipitate calcium carbonate within their intestines as a by-product of osmoregulation. This is driven by the ingestion of Ca^{2+} ions in seawater which fish must drink continuously to remain hydrated (Walsh et al. 1991, Cooper et al. 2010). Once seawater is ingested, Ca^{2+} and Mg^{2+} ions enter the intestine where they combine with HCO_3^- secreted by epithelial cells within the intestinal lumen. This causes calcium carbonate to precipitate in the fish intestine (Walsh et al. 1991, Wilson et al. 1996, 2002, 2009, Perry et al. 2011a; Figure 2-2). These carbonates are then egested into the environment in mucus coated pellets along with other waste products.

On a physiological level, carbonate precipitation is thought to facilitate water absorption within the intestine by increasing the osmotic gradient for water to diffuse across (Grosell et al. 2004, Whittamore et al. 2010). It also plays a role in calcium homeostasis, preventing excessive calcium absorption and the formation of renal stones in the kidneys (Wilson & Grosell 2003). Once the carbonates enter the environment, the mucus membrane breaks down and the carbonates disperse. The timescales over which this occurs are not well documented. As an indication of the potential importance of this process, Wilson et al. (2009) estimated that marine teleosts may (conservatively) contribute 3-15% of total oceanic carbonate production.

The chemistry and morphology of carbonates produced differs between species, and varies from low to high Mg-calcite (range 0.5 - 40 mol%), aragonite, and amorphous carbonates (Salter et al. 2012). This has important consequences for the fate of the carbonates upon entering the environment. In terms of $MgCO_3$ content of carbonates produced by reef fish, those below a threshold of ~15 mol% are likely to be stable in shallow tropical waters and those above are more likely to dissolve. The morphologies range from amorphous carbonates to spheres, needles, ellipsoids and dumb-bells, which all have different susceptibilities to disaggregation upon entering the environment (Salter et al. 2012). High-Mg calcites for example, are known to be highly soluble in comparison to calcite and aragonite (Morse et al. 2003). Calcium carbonate becomes more likely to dissolve with depth due to the increasing pressure and lower temperatures (Millero 2007) generally below a lysocline, resulting in higher concentrations of HCO_3^- and CO_3^{2-} , and thereby increasing the titratable alkalinity of seawater. There is uncertainty amongst oceanographers as to the reason behind carbonate dissolution at depths shallower than the lysocline (Milliman et al. 1999), but it is thought it could be attributed to the dissolution of high-Mg calcites produced by marine teleost fish (Wilson et al. 2009). This process could potentially raise the pH of surface waters of the ocean and reduce rates of ocean acidification.

Research into endogenous carbonate production by teleost fish also has relevance to the production of sediments in shallow, tropical marine waters. The origins of a significant proportion of the fine-grained carbonate sediments that accumulate in these settings, including Mg-calcites (particularly <63 µm) is unknown (Gischler & Zingeler 2002). Perry et al. (2011a) first hypothesised that marine fish could make up a significant proportion of this unknown source, and estimated that fish may contribute up to 14% of total carbonate mud production across the Bahamian archipelago. However, further investigations of their production and preservation potential are needed to understand whether they are a previously unrecognised source of shallow marine sediments, or whether they dissolve over time in the environment (Salter et al. 2012).

Fish are more likely to produce higher volumes of endogenous carbonates in shallow tropical locations than fish found in cold, deep-sea, temperate or polar environments. This is because the environmental conditions in shallow tropical seas are favourable for carbonate production and preservation. Warmer temperatures can increase carbonate production rate because metabolic rate in ectothermic fish increases exponentially with temperature, and with an increase in metabolic rate comes an increase in the quantity of carbonate produced (Wilson et al. 2009). Carbonates are also more likely to be preserved in the tropics due to the warmer temperatures and higher carbonate saturation state (Morse et al. 2003, Millero 2007, Perry et al. 2011a). In addition, increases in dissolved CO_2 in seawater causes an increase in partial pressure of CO_2 in fish blood, which stimulates HCO_3^- secretion in the intestine and thereby also increases carbonate production rate (Grosell et al. 2004, Pörtner et al. 2004, Wilson et al. 2009). So carbonate production by teleost fish is likely to increase with increasing carbon emissions and CO_2 uptake at the oceans surface.

While the range of fish species with reported endogenous carbonate production rates is increasing, there has currently been only one report of production by parrotfish, in *Sparisoma chrysopterum* (Salter et al. 2012). This species was observed to produce a range of crystal morphologies but with a predominantly low Mg content (1-5 mol% $MgCO_3$). However, this species is a browser, and there have been no studies of endogenous carbonate production in scraping or excavating parrotfish species. The significance of this processes in the context of total sediment production by scraping and excavator parrotfish is therefore unknown.

Despite the ideal environmental conditions for fish endogenous carbonate production on coral reefs, scraping and excavating parrotfish present an interesting study group because of their unusual gut chemistry. Intestinal fluids in most teleost fish are more alkaline than seawater (in the region of pH 8.4-9.0) facilitating the precipitation of calcium carbonate (Walsh et al. 1991). However, Smith & Paulson (1974) observed values ranging from pH 6.4-8.2 in the intestinal fluids of two species of parrotfish, with the more acidic end of the spectrum being found in feeding individuals. It was proposed that this may be an adaption to dissolve ingested calcium carbonate in order to access additional nutritional resources within the reef framework (Smith & Paulson 1974, 1975). One potential hypothesis that arises from this is that scraping and excavating parrotfish do not produce endogenous carbonates within their intestines because gut conditions prevent their formation. If this is the case, it poses an interesting question around how parrotfish process excess calcium. Further investigations of parrotfish carbonate production rate and gut chemistry are therefore needed to understand the significance of this process in the parrotfish.

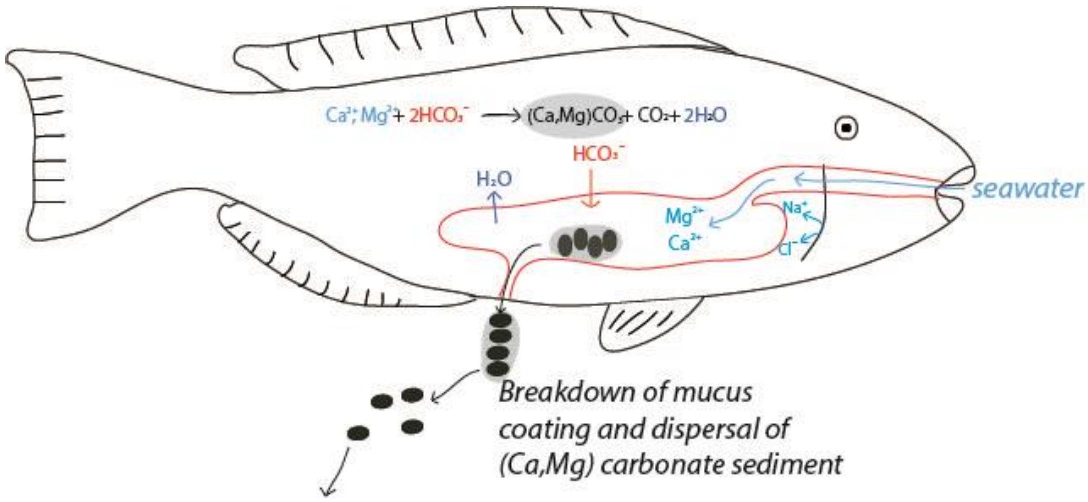


Figure 2-2 Calcium and Magnesium ions enter the fish gut in seawater where they bind to bicarbonate ions secreted by intestinal epithelial cells, resulting in the precipitation of Mg-rich calcium carbonate, which is excreted along with waste products, and water, which is absorb in the intestine via osmosis, facilitated by the precipitated carbonates. Adapted from Salter (2012).

2.4 Parrotfish contributions to coral reef carbonate budgets

The physical structure of coral reefs underpins a number of important ecosystem services, such habitat provision for reef associated species (many of which are commercially important) and coastal protection from wave energy (Graham & Nash 2013, Nash et al. 2013, Graham 2014, Ferrario et al. 2014). For this reason, it is important to understand the processes controlling reef structural maintenance and growth potential to help inform reef and coastal management policies. Reef carbonate budget assessments are often used as an indicator of reef growth and are estimated from the contributions of reef organisms to biological construction and erosion (Stearn et al. 1977, Scoffin et al. 1980, Glynn 1997, Perry et al. 2012). Parrotfish contribute to coral reef carbonate budgets through the processes of bioerosion and sediment production (Glynn 1997, Perry et al. 2012, Bonaldo, Hoey, & Bellwood 2014), but endogenous carbonate production may also add new carbonate in the form of silt-grade sediments to the system (Walsh et al. 1991, Perry et al. 2011a, Salter et al. 2012).

Early estimates of bioerosion on coral reefs involved measures of the amount of material removed from experimental blocks (e.g. Kiene 1985). However, it is difficult to determine the contributions to bioerosion by specific groups of organisms using these methods. A few studies have since made direct estimates of parrotfish bioerosion rates based on observations and measurements of foraging activities (Bellwood 1995a, Bruggemann et al. 1996, Bellwood et al. 2003, Alwany et al. 2009, Ong & Holland 2010, Morgan & Kench 2016a). Although even fewer studies provide data for both excavating and scraping species, which is important to include in carbonate budget assessments because of the differences in their contributions to substrate erosion, scar sizes and feeding rates (Bruggemann et al. 1994c, Bruggemann et al. 1996). Bioerosion rate data forms an important component of carbonate budget calculations and makes it possible to determine the proportion of total reef bioerosion caused by parrotfish, compared to production and erosion rates by other organisms (Scoffin et al. 1980, Perry et al. 2012). At some sites in Bonaire for example, parrotfish bioerosion was considerably lower than that of coral production (2.75 ± 1.39 compared to 12.07 ± 4.89 kg m^{-2} year $^{-1}$) so the net carbonate budget was positive, but at other sites, parrotfish bioerosion exceeded that of coral production (0.95 ± 0.62 compared to 0.20 ± 0.13 kg m^{-2} year $^{-1}$) which over long timescales may influence the capacity of the reef to grow (Perry et al. 2012).

On ecologically “healthy” reefs, parrotfish can directly help to maintain a positive budgetary state by producing sediment, either through bioerosion, sediment reworking or endogenous production. The sediment generated by parrotfish can be reincorporated into the reef framework, cementing the structure together (Hutchings 1986, Glynn 1997). These processes performed by parrotfish are summarised in Figure 2-3. Parrotfish also indirectly influence carbonate budgets by promoting the recruitment of reef building organisms by creating space on reef substrates through algal grazing.

Loss of grazers (primarily parrotfish and urchins) in combination with other stressors has, in some locations, caused “phase shifts” from coral dominated to macroalgae dominated reefs (Done 1992, Hoegh-Guldberg 1998, Hughes et al. 2003, McManus & Polsenberg 2004, Worm et al. 2006, Pratchett et al. 2014). In the short term (years to decades), this has detrimental consequences to the ecological “health” of the reef. In the long term (decades-centuries), unless there is recovery of carbonate producing organisms, the maintenance of the reef framework may deteriorate, depending on the response of bioeroders to future environmental change (Perry et al. 2008, 2013, Perry et al. 2014b).

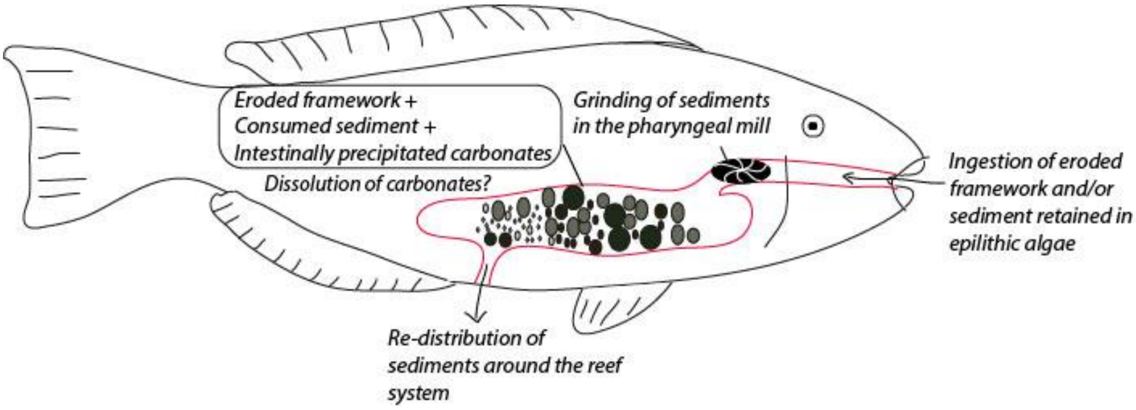


Figure 2-3 Eroded substrate material and sediments are ingested by parrotfish during grazing. These are broken down and ground to smaller size fractions by the pharyngeal mill before entering the intestine, where there is the potential for intestinal carbonate production. All of these carbonates are released into environment.

2.5 Environmental change and parrotfish carbonate cycling

The importance of biodiversity for maintaining ocean ecosystem services is becoming increasingly apparent (Micheli et al. 2014). Certain functional groups on coral reefs are now thought to be irreplaceable (Bellwood et al. 2003, Johansson et al. 2013), contradicting previous views of functional redundancy in diverse ecosystems, whereby the loss of one group can be compensated by the actions of another (Bellwood et al. 2004). Parrotfish perform a range of important functional roles on coral reefs, influencing a number of ecosystem processes (reviewd by Bonaldo et al. 2014). However, coral reefs worldwide are directly and indirectly threatened by natural and anthropogenic environmental changes (Hoegh-Guldberg 1998). These changes may have knock on effects on parrotfish populations and the functional roles they perform. The direct impact of fishing pressure, and the indirect impact of reef habitat degradation are topical threats known to influence parrotfish assemblages, but how this translates to their contributions to carbonate production and cycling has received little attention.

2.5.1 Habitat degradation

Habitat degradation, through the loss of living coral cover and structural complexity, is known to alter reef fish assemblages (Wilson et al. 2008, Coker et al. 2012, Pratchett et al. 2014). Coral mortality can occur after disturbances such as abnormally high Sea Surface Temperature (SST), El Niño Southern Oscillation (ENSO), nutrient stress and increased sedimentation, and may occur rapidly following a bleaching event (Eakin 1996, 2001, Hoegh-Guldberg 1998, D'Angelo & Wiedenmann 2014). Wilson et al. (2006) predicted that a disturbance resulting in 10% decline in coral cover would cause a decline in abundance of 62% of reef fish species. However, in the case of three species of parrotfish studied (*Chlorurus sordidus, Scarus niger,* and *S. frenatus*) an increase in abundance (>0.5 proportional change in abundance) with declining coral cover was predicted, presumably because of an associated increase in substrate availability for feeding. However, this may also resemble the migration of fish to an area of greater food supply (Wilson et al. 2006).

In contrast, Tzadik & Appeldoorn (2013) found that three out of four parrotfish species studied preferred areas of high coral cover, despite a strong negative correlation between coral and algal abundance at the sites studied. This may have been because the high coral cover habitats in this study were also the most structurally complex (rugose), and parrotfish abundance has been shown to increase with topographic complexity (Graham & Nash 2013, Darling et al. 2017, Richardson et al. 2017a). Parrotfish use holes and crevices in the reef to sleep, so some degree of structural complexity is likely to be an essential habitat requirement for parrotfish. The loss of structural complexity on a reef can also occur rapidly, for example as a result of physical damage by storms. Alternatively, loss of reef structure can be the result of years to decades of erosion after coral mass mortality. The synergistic impacts of multiple stressors can cause loss of both living coral cover and structural complexity and has been observed in the Caribbean over the past 50 years (Hughes 1994).

Understanding the changing dynamics of parrotfish populations in response to habitat degradation may have consequences for reef carbonate budgets. During events that cause large scale coral mortality (such as the recent El Niño induced bleaching event) carbonate production was significantly reduced (Eakin

1996, 2001, Perry & Morgan 2017a, b). Some of these events have also been associated with an increase in algal abundance (Done 1992). If bioerosion rate exceeds that of carbonate production, reefs can enter a net erosional state (Perry et al. 2014b, Perry & Morgan 2017a, b). If this condition is prolonged, reefs may lose their structural complexity and may also have a reduced capacity to keep pace with projected future sea level rise (Perry et al. 2018). In some cases in the Caribbean, the decline in dominant framework builders has been matched by the loss of bioeroding parrotfish and urchins as a result of overfishing and pathogens (Perry et al. 2013). This has caused some reefs to enter a state of stasis, where there is little to no net reef accretion or erosion, which again, if prolonged, could prevent reefs matching projected sea level rise.

2.5.2 Exploitation of parrotfish

Of major concern in oceans worldwide is the impact of overfishing. This is both in terms of ensuring sustainable yield and the impact that altering fish biomass and size structure can have on ecosystem processes (Jackson et al. 2001, Worm et al. 2006). It is thought that approximately 55% of coral reef fisheries on island nations worldwide are unsustainable (Newton et al. 2007). Fishing activities often preferentially select larger individuals, which are more economically viable. Apex predators are often the first to be removed on a reef system, after which large herbivorous fish, such as the parrotfish, are targeted (McManus et al. 2000). Targeted removal of large parrotfish may significantly affect the overall contribution of a parrotfish community to their roles in grazing, bioerosion and sediment production.

Based on the available data, altering the size classes of parrotfish present on a reef may influence the size fractions of sediment produced by the parrotfish community (Hoey & Bellwood 2008). For example, a shift in population size structure towards smaller individuals (<20 cm, under which little bioerosion occurs) may not only reduce the total quantity of sediment produced by a parrotfish community, but also increase the relative proportion of finer grain sizes (particularly <500 µm) to coarser grain size being produced (Bellwood 1995b, Bruggemann et al. 1996, Hoey & Bellwood 2008). This would increase the likelihood of hydrodynamic transport and export from the reef. However, this is currently speculative and in need of investigation.

As the contribution of different parrotfish to their functional roles is size dependent, overfishing of this group is likely to significantly alter community level rates of grazing pressure and bioerosion (Bruggemann et al. 1996, Lokrantz et al. 2008, Bellwood et al. 2012, Yarlett et al. 2018). For example, Lokrantz et al. (2008) estimated that 75 individuals of *C. sordidus* at 15 cm in size would be needed to compensate for the loss of one 35 cm individual in terms of the surface area of reef framework grazed. However, whether any increases in abundance of smaller individuals could compensate for the loss of larger individuals is uncertain.

The process of grazing is also thought to be pivotal in preventing phase shifts on coral reefs (Mumby 2006, Hughes et al. 2007, Mumby et al. 2007, Bejarano et al. 2013). However, many parrotfish species avoid browsing on macroalgae, raising concerns over the potential for parrotfish to reverse phase shifts (Hoey & Bellwood 2011). Bellwood et al. (2006) unexpectedly observed batfish, rather than parrotfish removing macroalgae and facilitating recovery of an experimental macroalgae covered patch reef. However, this has only been observed under small scale experimental conditions, and given that batfish are comparatively uncommon, it is far from certain whether the group would be able to achieve this removal over reef scales (Bellwood et al. 2006). Fishing pressure on parrotfish may therefore increase the susceptibility reef habitats to shifts from coral dominated to alternative states following disturbances, from which point recovery is not guaranteed. More data are required to determine safe rates of parrotfish extraction from coral reefs without compromising ecosystem health.

2.6 Knowledge Gaps

From this review, a number of knowledge and data gaps have been identified, and form the basis for this thesis.

While parrotfish are known to be important bioeroders, the available data on bioerosion rates are restricted to few species in just a few studies (summarised in Table 2-1). There are even fewer studies that examine how bioerosion rates vary within species as a function of fish size (Bruggemann et al. 1996, Ong & Holland 2010). This is important to understand in order to make community level assessments of parrotfish functional roles, as these will be made up of fish of a range of sizes. These data will also help to determine the number of smaller individuals needed to compensate for the extraction of larger individuals. In addition, the available data show very high variability, even for conspecifics in different locations (see Table 2-1), demonstrating that considerably more data are needed on these processes.

Through their functional roles, parrotfish are known to have a top-down influence on reef habitat ecological and physical structure, influencing coral demographics, algal cover and rates of framework erosion (Bellwood 1995a, Mumby et al. 2006, Bonaldo et al. 2014). However, there are very few studies by comparison that investigate the importance of the bottom-up influence of habitat type on parrotfish assemblages. To extend this, there has been little work on the extent to which habitat type and condition influence parrotfish assemblages, and how this translates to their roles in bioerosion, grazing, sediment production and sediment reworking (see Hoey & Bellwood 2008 for some work on this topic).

Regarding the role of parrotfish in sediment production, very few studies examine the grain size and type of the material produced, and the available data extend to just a few species (Bellwood 1996, Hoey & Bellwood 2008, Morgan & Kench 2016a). More specifically, there are currently no studies examining the effect of fish size (within species) on the characteristics of the sediment produced. These characteristics are likely to have a strong influence on the fate and transport potential of the material upon entering the environment (Kench & McLean 1996, Kench 1998). In addition, no studies to date have considered the potential for endogenous carbonate production by parrotfish to contribute a new primary source of sediment to reef environments.

A deeper understanding of the above knowledge gaps will help to predict the impacts of environmental disturbances on parrotfish functional roles, and what consequences this will have for coral reefs. Addressing these knowledge gaps will also help in understanding how responses to different disturbances will vary between reef habitat types. This will help to identify the habitats, processes and ecosystem services that are most at risk.

These knowledge gaps are addressed through a series of chapters, structured as outlined below.

2.7 Chapter Outline

The following chapters in this thesis build on this summary of existing knowledge and are outlined below.

Chapter 3: Vavvaru site description and study species

Description and justification for the primary study site. A habitat map is presented for reference throughout the thesis and the key representative study species are introduced. Details on research permits, ethical approval, and assumptions used throughout the thesis are also presented here.

Chapter 4: Constraining species-size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates

This chapter presents new feeding metrics (bite rate, proportion of bites producing scars and bite scar volume) for six common Maldivian parrotfish species. These metrics are used to make bioerosion rate estimates of different size classes of these species. These data are then compared to existing metrics on parrotfish bioerosion for regional comparisons.

Chapter 5: Inter-habitat variability in parrotfish bioerosion rates and grazing pressure: influence of habitat type on key parrotfish functional roles

Overall bioerosion rates and grazing pressures are estimated and compared for different parrotfish communities in different habitat types. The key contributors to these roles are examined and multivariate analyses are used explain the environmental drivers behind the spatial patterns of the parrotfish communities.

Chapter 6: Parrotfish sediment production on a Maldivian reef platform: sedimentary products and the relative importance of new and reworked sediments

The sedimentary characteristics (grain size and type) of the material produced by six common Maldivian parrotfish species are examined. Estimates of sediment reworking rate and total sediment production are made and compared across different reef habitat types, and the relative importance of sediment produced from bioerosion, reworked sediment, and endogenously produced sediment is discussed.

Chapter 7: Discussion on anticipated impacts of habitat degradation and fishing pressure on parrotfish functional roles, thesis key findings and directions for future research

This chapter demonstrates the use of the data presented throughout this thesis, and discusses how fishing pressure and habitat degradation can alter parrotfish assemblages and influence their overall roles in bioerosion, grazing pressure, sediment reworking and sediment production. The key findings of thesis are then summarised and directions for future work are suggested.

Chapter 3 Vavvaru site description and study species

Vavvaru Island, Lhaviyani Atoll, Maldives was the primary study site for the work carried out in this thesis. Work was carried out through the Korallionlab Marine Research Station, which was situated on Vavvaru Island before being permanently closed in 2017. Photo credit: Robert T. Yarlett.

3.1 Primary study site: Vavvaru, Lhaviyani Atoll, Maldives

The Maldives was chosen as the primary study region for this project for a number of reasons. Firstly, the parrotfish populations in the Maldives are considered to be relatively "healthy" compared to other coral reefs in the Indian Ocean and even globally (McClanahan 2011). This is likely to be because the commercial fishing industry in the Maldives focusses on tuna, leaving reef fish populations comparatively unexploited, aside from former shark and grouper fisheries and the collection of reef fish for the aquarium trade, which largely excludes parrotfish (Newton et al. 2007; Risk & Sluka 2000). The primary fishing methods used in the Maldives are based around hook and line and longline approaches, which are not prone to catching parrotfish (parrotfish are more susceptible to net and trap fisheries). In addition, spearfishing, which is often used to catch parrotfish (particularly in recreational fisheries) is illegal in the Maldives. Secondly, at the time of study (prior to the 2016 El Niño induced bleaching event), coral reefs were considered to be in good condition in the Maldives (Perry et al. 2017). Because of these two factors, parrotfish assemblages were considered to resemble that of a reasonably natural, unmodified reef system. This makes the region ideal for determining the influence of different habitat types on parrotfish density, body size and species composition, independent of human modification.

The Maldives experiences two monsoon periods, with winds from the west-northwest during April-November (mean wind speed; 5.1 m s^{-1}), and winds from the east-northeast during December-March (mean wind speed; 4.9 m s^{-1}) (Kench & Brander 2006). Daylight hours in the Maldives are fairly consistent throughout the year (~12 hours per day), with <30 minutes variation over the year in Malé, Central Maldives, and sea surface temperatures varying by <2 °C annually. Seasonal influences on parrotfish feeding and bioerosion rates are therefore assumed to be minimal. The reef platforms at these sites are typically very shallow (on average <2 m) with coral cover extending down only to ~8 m on outer platform slopes (Perry et al. 2017). While depth may influence parrotfish feeding (Bruggemann et al. 1996) it is thought to have limited influence at the sites in the present study because of the largely consistent depth of the platform.

Data were collected during field seasons in early 2015 and 2016, primarily from an atoll edge reef platform site (Vavvaru, Lhaviyani Atoll) in the northern-central Maldives (N 5°25’5.0”; E 073°21’14.0”; Figure 3-1) through the Korallionlab Marine Research Station. Other than the field station, Vavvaru Island is uninhabited. Two other field sites were also used during the study. Some of the data on parrotfish feeding metrics were collected in the Southern Maldives (Kan’dahalagalaa and Maahutigalaa, Gaafu Dhaalu Atoll) because of a temporary closure of Korallionlab in 2016, but most data were collected at Vavvaru Island. Work on endogenous carbonate production by parrotfish was conducted on conspecifics at Lizard Island, Australia through the Lizard Island Research Station. This work was conducted at Lizard Island because of the excellent lab and aquarium facilities available. These facilities were required to carry out this work and were unfortunately not available at sites in the Maldives.

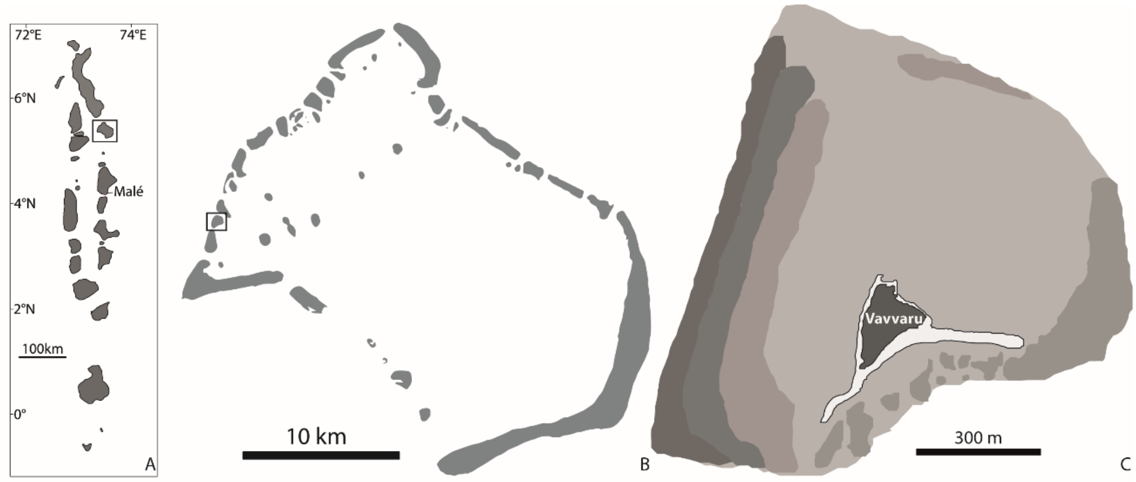


Figure 3-1 A) The location of Lhaviyani Atoll in the Maldives, B) The location of Vavvaru Island Island on Lhaviyani Atoll, and C) A schematic of the Vavvaru reef platform showing the position of Vavvaru island. Darker shaded areas represent the position of major reef zones where the majority of data were collected.

3.2 Vavvaru Habitat Map

The reef platform at Vavvaru comprised of eight distinct marine habitats which varied in topographic complexity, substrate type and benthic community composition, making the site ideal for examining how habitat type influences parrotfish assemblages and the resultant impact of these assemblages on parrotfish functional roles. These habitat types were delineated in-situ based on field observations and measures of the rugosity, substrate characteristics and benthic communities (as presented in Perry et al. 2017). The cover and spatial extent of each of these habitats was estimated by producing a habitat map of the Vavvaru reef platform (Figure 3-2, as published in Perry et al. 2017). The map was produced in ERDAS IMAGINE 2015 using Quickbird imagery of western Lhaviyani Atoll taken on 09/07/2008 (provided by DigitalGlobe Foundation; http://www.digitalglobefoundation.org/). The image was chosen due to the calm sea state at the time of collection, and because it is relatively free of cloud cover and sun glint, allowing a clearer view of the reef platform compared to more recent data. While Vavvaru Island itself has changed position slightly since 2008 (see Perry et al. 2017), the area and characteristics of the habitats are unlikely to have changed considerably since reefs in the Maldives were not significantly affected by the 2010 bleaching event (Pisapia et al. 2016). Atmospheric and water column correction were not considered necessary to produce the habitat map because the classification was performed using only a single date image (Song et al. 2001) of a reef platform with a reasonably consistent shallow depth (typically <4 m) (Perry et al. 2017). A subset of the image around Vavvaru Island was orthorectified and pan-sharpened prior to conducting a supervised maximum likelihood classification. A signature file was created to train the software to recognise areas of known habitat type, based on field observations. Pixels that were known to have been incorrectly classified, likely due to natural habitat heterogeneity, were recoded to the correct class. This matches the aims of the habitat map; to measure the area of geomorphic zones identified in the field, rather than examine within habitat substrate variability. A dataset of 146 ground validated points was used to conduct an accuracy assessment of the classification, which revealed an accuracy of 77.24%. The classified image was imported into ArcMap, and the number of pixels assigned to each class extracted. The number of pixels was then multiplied by the x and y sensor resolution (0.6 m resolution in both x and y axes) to derive the area of each habitat (Table 3-1).

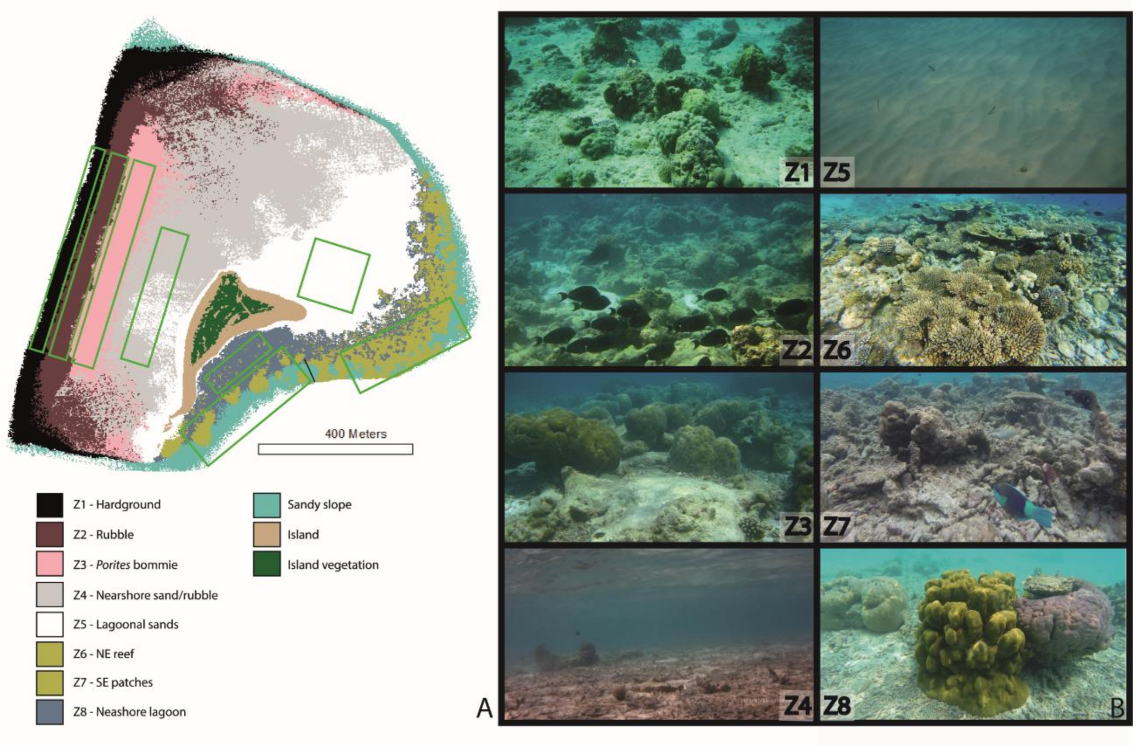


Figure 3-2 A) Habitat map produced from Quickbird imagery of western Lhaviyani Atoll taken on 09/07/2008 (provided by DigitalGlobe Foundation; http://www.digitalglobefoundation.org/) and ground validated points. Produced by Robert Yarlett. For map publication and position of ground points see Perry et al. (2017). The black line marks the division of NE reef and the SE patches (the classification methods could not differentiate between the two habitats so the area of each habitat was calculated separately using sub-sets of the satellite imagery). The green boxes represent the main surveying areas. B) Representative images from each of the eight identified habitats and Vavvaru Island. Photo credit for Z1, 2, 3 and 5: Chris Perry, for Z4, 6, 7 and 8: Robert Yarlett.

The far western edge of the Vavvaru reef platform consists of a limestone hardground habitat (Figure 3-2B, Z1) with reasonably high coral cover (18.81%) at 4-6 m depth. A characteristic feature at the far west of this habitat is a very steep wall, which marks the edge of Lhaviyani atoll and drops off into deep water. Moving east, the hardgrounds transition into a gently sloping rubble and *Pocillopora spp.* dominated habitat (from ~5 m at the hardground/rubble transition, sloping gently up to a shallow rubble ridge at ~1 m depth; Figure 3-2B, Z2) and then into a shallow (<2 m) habitat dominated by *Porites spp.* bommies (Figure 3-2B, Z3). The central area of the platform is made up of the two largest and relatively featureless marine habitats; a sand and rubble habitat (Figure 3-2B, Z4), and an extensive sandy lagoon (Figure 3-2B, Z5) situated to the north of Vavvaru Island. The island itself is situated off-centre, towards the south-east of the platform. To the north east of the platform (east of the sandy lagoon) is an *Acropora spp.* dominated reef habitat (Figure 3-2B, Z6). Moving south, this reef habitat becomes more fragmented and transition from the north-east reef (NE reef) into the south-east patch reefs (SE patches; Figure 3-2B, Z7). Both of these reef habitats are shallow on their nearshore sides (<2 m) but form part of the reef slope at the eastern edge of the platform, where coral cover extends down to ~8 m (and deeper in some parts of the NE reef). Between Vavvaru Island and these eastern reef habitats is a nearshore lagoon (Figure 3-2B, Z8), which is comprised predominantly of sand, but also has small (< 10 m^2) scattered patch reefs, which increase in frequency towards the reef habitats. Sand channels separating the SE patches lead from the nearshore lagoon to the sand talus on eastern slope, which extends into the atoll lagoon. The area of the delineated habitats is shown in Table 3-1.

Table 3-1 Area (m^2) of the eight delineated habitats on the Vavvaru reef platform and Vavvaru Island. Areas are also expressed as a % of the total platform area, and % of the total marine area (platform area excluding Vavvaru Island).

Habitat	Area (m^2)	% of Platform Area	% of Marine Habitats
Z1 – Hardground	68769	8.25	8.68
Z2 – Rubble	96380	11.56	12.17
Z3 – *Porites* bommie	80756	9.68	10.19
Z4 – Nearshore sand/rubble	241250	28.93	30.45
Z5 – Lagoonal sands	184375	22.11	23.27
Z6 – NE reef	51633	6.19	6.52
Z7 – SE patches	14551	1.74	1.84
Z8 – Nearshore lagoon	54465	6.53	6.88
Island (bare sand)	27717	3.32	
Island vegetation	14052	1.68	
Island (total)	41769	5.01	
Reef total (NE reef + SE patches)	66185	7.94	8.35

3.3 Primary Study Species

At the primary study site (Vavvaru Island), 15 species of parrotfish across five genera (*Chlorurus spp., Scarus spp., Cetoscarus spp., Hipposcarus spp.,* and *Calatomus spp.*) were identified from the eight reef habitats. Based on preliminary measures of numerical dominance (Perry et al. 2017) and to ensure representation of the full range of sizes (including both initial and terminal life phases) and feeding modes (both scrapers and excavators) the following species (as shown in Figure 3-3) were chosen for focussed study (species and total length, excluding caudal fin filaments); excavators: *Chlorurus sordidus* (up to ~40 cm) and *C. strongylocephalus* (up to 70 cm but few over ~60 cm), and scrapers: *Scarus frenatus* (up to ~50 cm), *S. niger* (up to ~ 45 cm), *S. psittacus* (up to ~30 cm), and *S. rubroviolaceus* (up to ~70 cm, but few over ~60 cm). These species are widespread throughout the Indian Ocean, and closely related species are found on reefs across the Indo-Pacific (Choat et al. 2012). Throughout this project, process data for the remaining species on the platform, for which data are absent, were assumed to match that of the most closely related species (based on Choat et al. 2012) or species with closest morphological resemblance (Table 3-2).

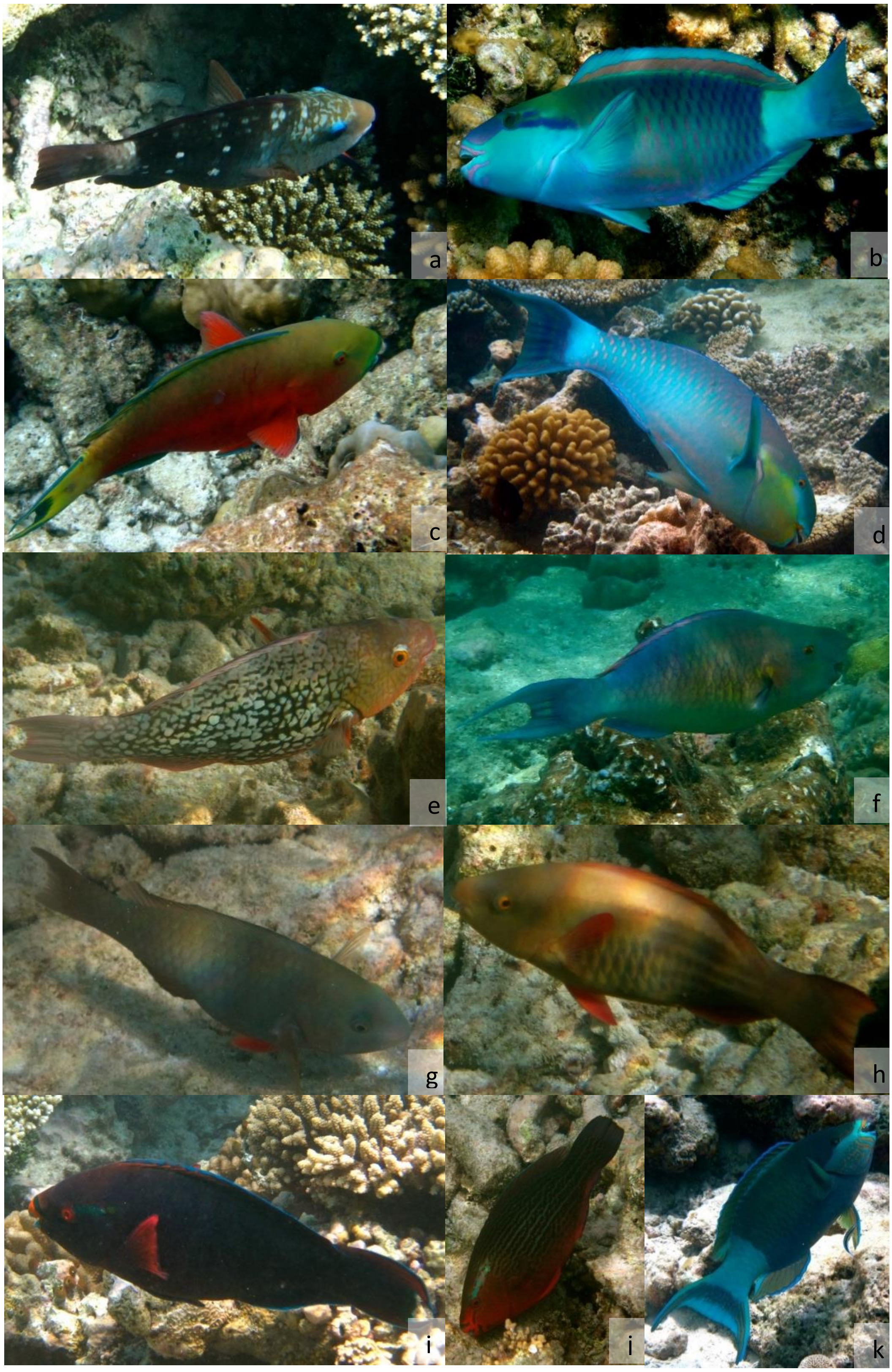


Figure 3-3 Six representative parrotfish species were chosen for the study. (a-d) Excavators; (a-b) *Chlorurus sordidus*, (a) Initial Phase, (b) Terminal Phase, and (c-d) *Chlorurus strongylocephalus,* (c) Initial Phase, (d) Terminal Phase. (e-k) Scrapers; (e-f) *Scarus rubroviolaceous,* (e) Initial Phase, (f) Terminal Phase, (g) *Scarus psittacus*-Initial Phase, (h and k) *Scarus frenatus* (h) Initial Phase, (k) Terminal Phase, and (i-j) *Scarus niger*, (i) Terminal Phase and (j) Initial Phase. Photos provided by Kate Philpot.

Table 3-2 Comparable species assumptions for species where process data are absent.

Species	Data assumption
Chlorurus enneacanthus	*Chlorurus sordidus*
Scarus tricolor	*Scarus niger*
Scarus scaber	*Scarus frenatus*
Scarus prasiognathos	*Scarus frenatus*
Scarus viridifucatus	*Scarus frenatus*
Scarus russelii	*Scarus frenatus*
Hipposcarus harid	*Scarus frenatus*
Cetoscarus bicolor	*Chlorurus strongylocephalus*
Juveniles	Lowest measured bioerosion rate at < 15 cm

3.4 Research permits and ethical approval

3.4.1 Research permits

All work undertaken in the Maldives was carried out under the permits 30-D/INDIV/2014/2363 and (OTHR)30-D/INDIV/2015/451 issued by the Ministry of Fisheries and Aquaculture, Malé, Maldives.

All work undertaken around Lizard Island Australia was carried out with Queensland Animal Ethics Approval (ref: CA 2013/11/733), under a General Fisheries Permit (Permit No.: 168991) and a Marine Parks Permit (ref: G14/36689.1).

3.4.2 Ethics statement

Ethical considerations for all aspects of the project involving field observations, collection and handling of fish were reviewed and approved by the Geography Ethics Committee and Animal Welfare and Ethical Review Board (AWERB), University of Exeter, UK, and follows the recommendations of the Home Office following the Animals (Scientific Procedures) Act 1986 (ASPA), Fish Modules 1-3. Project code: 2015/711.

Chapter 4 Constraining species – size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates

Chlorurus strongylocephalus (terminal phase) feeding on dead coral substrate. Photo credit: Kate E Philpot.

As published in the journal Marine Ecology Progress Series:

Yarlett RT, Perry CT, Wilson RW, Philpot KE (2018) Constraining species-size class variability in rates of parrotfish bioerosion on Maldivan coral reefs: implications for regional scale bioerosion estimates. Mar Ecol Prog Ser 590: 155-169

4.1 Context

Parrotfish are important bioeroders on coral reefs and exert a strong influence on reef carbonate budgets. They also generate large volumes of carbonate sand that contribute to local beach and reef island maintenance. However, as discussed in Chapter 2, sections 2.2 and 2.6, there is a paucity of data with which variations in bioerosion rates as a function of species, feeding modes, and body size of parrotfish can be constrained. In addition, there is limited knowledge regarding how resultant rates may vary within and between reef building regions. In this chapter, I address research question 1 which asks how bioerosion rates vary across different parrotfish species and size classes, by making direct bioerosion rate estimates for six common parrotfish species in the Maldives, a geographic gap in these data. To do this, I address objective 2 which asks how bite rates, the proportion of bites that produce scars and grazing scar volumes vary between these species and size classes. I then use these metrics to estimate annual bioerosion rates for individual fish. These species are representative of the full range of parrotfish sizes and feeding modes found in the central Indian Ocean region, so these data underpin the rates applied to species assemblages in later chapters.

4.2 Introduction

The structural complexity and growth potential of coral reefs underpin many reef ecosystem services, such as shoreline protection, and habitat provision for a diverse array of marine organisms, including many commercially important species (Lugo-Fernández et al. 1998, Moberg & Folke 1999, Ruckelshaus et al. 2013, Ferrario et al. 2014). These systems are shaped by a combination of biological, physical and chemical constructional and erosional processes (Scoffin 1992, Perry & Hepburn 2008). Framework construction is primarily the result of the production of carbonate skeletons by corals, while the most pervasive form of erosion is that by bioeroding organisms. This leads to weakening or erosion of the reef substrate (Stearn et al. 1977, Scoffin et al. 1980, Glynn 1997). Assessments of rates of carbonate accumulation (e.g. by corals and coralline algae, and by sediment producers such as *Halimeda spp.* and foraminifera), less that lost through bioerosion (e.g. by fish, urchins, sponges and microborers) can thus be used to measure reef carbonate budgets (sensu Perry et al. 2008), which can provide an indication of net reef framework accumulation or loss. As a result, carbonate budget assessments are becoming increasingly relevant in the light of recent global coral bleaching events, which have caused large scale coral mortality in a number of regions (Hughes et al. 2017a, b), and with potential negative impacts on reef growth capacity (Perry & Morgan 2017a, b).

On the erosional side of the carbonate budget question, parrotfish (family Labridae) are often identified as especially important bioeroders (Bellwood et al. 2003, Perry et al. 2015b). Whilst feeding primarily on dead coral and rubble substrates (Bruggemann et al. 1994a, Bellwood 1995a, Afeworki et al. 2011), many parrotfish take bites out of the reef framework, likely targeting cyanobacteria (Clements et al. 2016). This framework material is ingested along with organic matter, broken down by modified gill arch elements known as the pharyngeal mill (Bellwood & Choat 1990, Carr et al. 2006), processed in the gut, and egested as sediment (Bellwood 1995b, 1996, Morgan & Kench 2016a). These parrotfish can be categoried into “scraping” or “excavating” feeding modes, which are defined based on their musculo-skeletal systems around the jaw, and feeding behaviour (Bellwood & Choat 1990).These bioerosion and sediment generation processes are increasingly recognised not only as an important component in coral reef carbonate budgets (Perry et al. 2014b), but also as an important source of sediment to both reef and lagoonal sediments (Scoffin et al. 1980), and to reef associated landforms such as reef islands and beaches (Perr et al. 2015a, Morgan & Kench 2016a, Perry et al. 2017).

Much of the recent work on parrotfish functional roles is summarised in Bonaldo et al. (2014), but early work by Gygi (1975), Ogden (1977) Frydl & Stearn (1978) and (Scoffin et al. 1980) in the Caribbean highlighted the importance of parrotfish bioerosion. These early studies used estimates of daily gut throughput and sediment content in the gut to estimate bioerosion and sediment reworking rates (the ingestion, processing and egestion of loose sediment on the reef). More direct estimates of parrotfish bioerosion, involving observations of daily bite rates and measures of grazing scar dimensions, were then introduced by Bellwood (1995a) on the Great Barrier Reef, and (Bruggemann et al. 1996) in the Caribbean. While more recent studies have quantified these processes for more species in different regions (e.g. Great Barrier Reef: Bellwood et al. 2003; Red Sea: Alwany et al. 2009; Hawaii: Ong & Holland 2010), our understanding of the variability in these processes between species, sizes and geographic locations remains very limited. There are ~99 recognised species of parrotfish worldwide, and over 70 species are categorised into scraping or excavating feeding modes, many of which are geographically widespread (Choat et al. 2012). Yet direct estimates of parrotfish bioerosion rates are restricted to data from just 15 species from specific locations (Bellwood 1995a, Bruggemann et al. 1996, Bellwood et al. 2003, Alwany et al. 2009, Ong & Holland 2010, Morgan & Kench 2016a). There is therefore little understanding of how bioerosion rates vary both among species, and among closely related species in different regions, with much of the current data restricted to the largest terminal phase males (see Bruggemann et al. 1996, Ong & Holland 2010 for exceptions). In addition, studies examining how bioerosion rates differ between scraping and excavating species are sometimes contradictory (Bruggemann et al. 1996, Alwany et al. 2009, Ong & Holland 2010). Some further studies contribute useful data on parrotfish bite rates and grazing scar dynamics in the context of algal grazing (such as Fox & Bellwood 2007, Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Bejarano et al. 2013), however, even with this additional data, accessible datasets on parrotfish bioerosion rates are limited given their diversity and geographic distribution.

The present study aimed to address a key geographic gap with respect to parrotfish bioerosion data, by presenting rates, as well as associated feeding metrics, for six of the most common species present on Maldivian coral reefs. The central Indian Ocean remains an area where parrotfish populations are reported to be relatively healthy compared to other regions due to the lack of reef-based fishing pressure (McClanahan 2011), and are the most important bioeroding organisms in the region as a result (Perry et al. 2015a, Perry et al. 2017), yet region specific rates are limited (but see Morgan & Kench 2016a for data on two species). The species studied are representative of the range of sizes (including both initial and terminal life phases) and feeding modes of parrotfish found in the region. In addition, I consider how the bioerosion rate estimates from the present study compare with published data on the same, or closely related species in different regions, work that highlights the importance of collecting local rate data to inform bioerosion estimates.

4.3 Methods

4.3.1 Bite rates and length of feeding day

Previous work suggests that parrotfish feed for ~ 80-90% of daylight hours (Bellwood 1995a). Observations of parrotfish bite rates were therefore carried out with coverage throughout the day between sunrise (~06:20) and sunset (~18:20) to ensure capture of the start and end of feeding, and to constrain for variation in bite rates throughout the day. Only initial phase *S. psittacus* were observed as terminal phase males were rarely sighted. Individuals of a target study species, size and life phase were chosen for observation on a first seen basis to ensure random selection. Following standard protocols (Bellwood & Choat 1990, Bellwood 1995a, Bruggemann et al. 1996, Ong & Holland 2010, Morgan & Kench 2016a), fish were given ~2 minutes to become accustomed to the observer, during which time the species, life phase, size class (designated into one of the following size categories: < 15 cm, 16 to 30 cm, 31 to 45 cm and > 46 cm), and start time of the observation was recorded. A pilot study conducted prior to fieldwork (using PVC pipes underwater), revealed that the observer could consistently bin objects into 15 cm categories at a range of distances and angles relative to the object, and thus this was chosen over 10 cm bins which had a higher frequency of errors. Only initial and terminal phase parrotfish were studied as juveniles are thought to contribute extremely little to bioerosion (Bruggemann et al. 1996). Fish were then observed for 3-5 minutes, counting the total number of substrate bites by each species per unit of time, which was later converted to bites per minute (bpm). A LOESS regression with standard error was fitted to the data to help determine daily patterns. The length of the feeding day was determined from the time of day that the first bites by each species were observed, until the point at which no further feeding was observed. Mean daily bite rates (bpm) were converted into total daily bites by multiplying by the length of the feeding day (in minutes). Observations taken before and after, and within the first and last 5 % of the feeding day (if the observation appeared to be outside the feeding hours of the fish) were excluded.

4.3.2 Proportion of bites producing grazing scars and grazing scar volumes

Observations of the proportion of bites that produce grazing scars (PBS), and measurements of grazing scar volume were conducted for *C. sordidus, C. strongylocephalus, S. frenatus, S. niger* and *S. rubroviolaceus*. Very small initial phase (<15 cm) *C. strongylocephalus* were rarely sighted, and grazing scar volumes were thus assumed to be comparable to that of <15 cm *C. sordidus* as the closest excavator relative (Choat et al. 2012). For *Scarus psittacus,* grazing scar volume metrics were assumed to be comparable to *S. niger* for similar size categories due to similarities in fish morphology, feeding mode and bite rate. Individuals of a target study species were again chosen on first seen basis. To measure PBS, each fish was observed until a foray (a series of bites in quick succession), or a number of successive bites could be clearly observed. Both the total number of bites observed, and the number of observed new scars produced were recorded in order to determine PBS.

To measure the volume of parrotfish grazing scars, feeding was observed until the first observable grazing scar (such as those seen in Figure 4-1) was produced. Where the location of the scar was both identified and accessible, the scar was measured. The length, width, and where possible, depth of scars was measured using Vernier callipers, following conventional methods (Bellwood 1995a, Bruggemann et al. 1996, Bonaldo & Bellwood 2008, 2009, Ong & Holland 2010). The depths of the scars for large *Chlorurus strongylocephalus* could be measured fairly consistently. However, for most scrapers and smaller excavators, scar depth was extremely shallow (~0.1 mm), and therefore often within the natural heterogeneity of the substrate. Depths of these scars therefore could not always be reliably measured, and thus, in these instances, a 0.1 mm depth assumption was used for excavators and large (>30 cm) *S. rubroviolaceus* (following assumptions made by Bellwood & Choat 1990 and

Bellwood 1995a regarding scar size of excavators and large scrapers). For all other scrapers, as a function of the structural differences in jaw structure and resultant shallower “scrapes” compared to excavators (Bellwood & Choat 1990, Nanami 2016), a 0.05 mm depth was assumed. Grazing scars can occur as one mark, in which case the total length, width and where possible, depth was measured. Where grazing scars occurred as two marks made by the upper and lower jaws, the length, width and depth of both marks were measured. The volume of the grazing scar was assumed to be that of a rectangular prism and thus calculated as: *Bite volume* $(cm^{-3}) = (L_1 \times W_1 \times D_1) + (L_2 \times W_2 \times D_2)$, where L= length, W=width, D= depth, 1= first mark, 2= second mark (if present). This method may slightly overestimate grazing scar volume, but has been shown to be not significantly different to validated grazing scar measurements in the lab (Bellwood 1995a, Ong & Holland 2010).

Figure 4-1 Parrotfish grazing scars; a, scars on dead coral substrates, b, many of the larger scars, such as that indicated, are likely to be that of excavators such as *Chlorurus strongylocephalus* or *Cetoscarus bicolor*, c, parrotfish grazing scars are observed on some live corals, such as *Porites spp.*

4.3.3 Bioerosion and new sediment generation rates

The bioerosion rate for an individual (ind) of each size class of each species of parrotfish was calculated as follows (adapted from Bruggemann et al. 1996 and Ong & Holland 2010):

Volume removed per day $(cm^3\ ind^{-1}\ day^{-1})$ = *mean bites* $ind^{-1}\ day^{-1}$ x *mean proportion of bites leaving scars x mean bite scar volume* (cm^3)

The overall error terms for this equation were calculated using an expanded 3-term version of Goodman’s estimator (following Bellwood 1995a, Bruggemann et al. 1996, Ong & Holland 2010):

$$\begin{aligned}SE_{(\bar{x}\cdot\bar{y}\cdot\bar{z})}^2 &= (\bar{x}\cdot\bar{y})^2\cdot SE_z^2 + (\bar{x}\cdot\bar{z})^2\cdot SE_y^2 + (\bar{y}\cdot\bar{z})^2\cdot SE_x^2\\ &\quad + (\bar{x})^2\cdot SE_y^2\cdot SE_z^2 + (\bar{y})^2\cdot SE_x^2\cdot SE_z^2 + (\bar{z})^2\cdot SE_x^2\cdot SE_y^2\\ &\quad + SE_x^2\cdot SE_y^2\cdot SE_z^2\end{aligned}$$

Where SE = standard error, $\bar{x}$ = mean bites per day, $\bar{y}$ = mean proportion of bites leaving scars, and $\bar{z}$ = mean bite volume.

Resultant annual bioerosion rates per individual fish were then calculated by multiplying the volume removed per day by the substrate density (taken as 1.5 g cm^{-3} as the average of locally measured rates; Morgan & Kench 2012), and by the number of days in a year:

Bioerosion rate (kg ind^{-1} yr^{-1}) = volume removed per day (cm^{3} ind.$^{-1}$ d^{-1}) × 0.0015 kg cm^{-3} × 365 d yr^{-1}

4.3.4 Statistical Analysis

Statistical analyses were conducted in R version 3.3.2. One-way ANOVA, Welch one-way test or Kruskal-wallis tests (depending on what assumptions the data met) were used to test for differences in bite rate, PBS and scar volume among species and size classes. Data for initial and terminal phase parrotfish within each species were pooled, and presented here as a function of size class (Table 4-1). This was due to the smaller two size classes (<15 cm and 16 to 30 cm) being made up primarily by initial phase parrotfish, while the larger two size classes (31 to 45 cm and >46 cm) were made up primarily of terminal phase males. A LOESS curve was fitted to the bite rate data to help determine daily patterns.

4.4 Results

4.4.1 Bite Rates and Length of Feeding Day

The length of the feeding day was consistent across all six species studied. Feeding typically commenced between 06:30 and 07:00, about 10-40 minutes after sunrise, and had ceased by 18:00, about 20 minutes before sunset (11 – 11.5 hour feeding day, 11 hours was used in calculations). All species appeared to exhibit a bimodal pattern (i.e. two peaks) in their feeding activity, albeit subtle in some species, with a first peak typically occurring around 11:00, and a second, often larger peak between 15:00 and 16:00 (Figure 4-2). Bite rate differed significantly among species ($F_{5,259} = 33.184$, $p < 0.001$, Table 4-1), with pairwise t-test comparisons revealing significant differences ($p < 0.05$) between all pairs of species, with the exceptions of *C. strongylocephalus* and *S. rubroviolaceus*, and *S. niger* and *S. psittacus*. These differences in bite rate appeared to occur primarily among smaller individuals (Table 4-2). Mean bite rate varied from 7.88 ± 0.63 bpm for *Chlorurus strongylocephalus* to 23.65 ± 1.42 bpm for *Scarus niger*. No consistent relationship was apparent between fish size and bite rate (Table 4-1). *S. frenatus* and *S. niger*, both showed a significant increase in bite rate with fish size ($F_{2,84} = 5$, $p < 0.01$ and $F_{2,110} = 9.6$, $p < 0.01$ respectively).

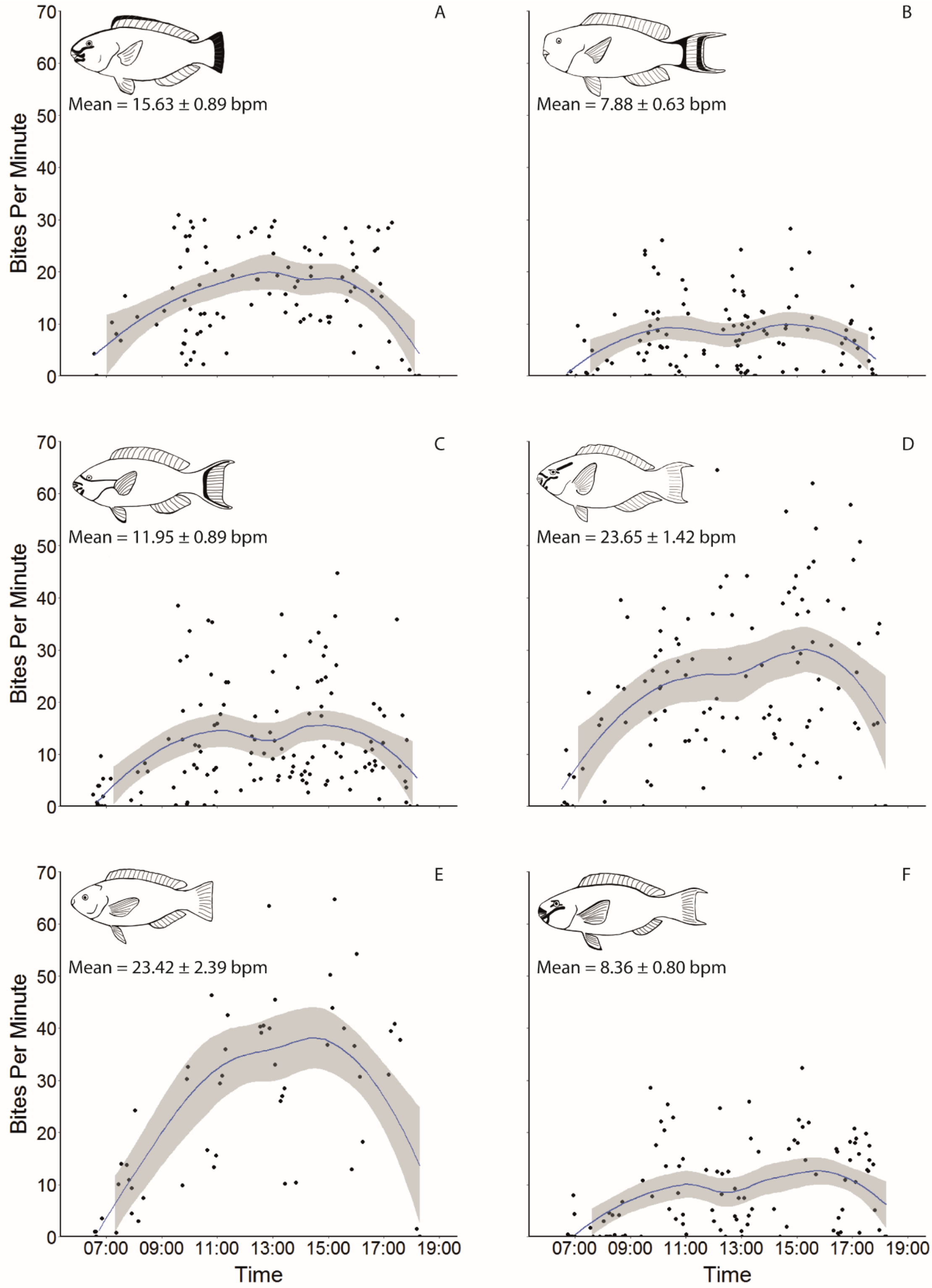


Figure 4-2 Daily bite rate patterns (bites per minute), including the full range of sizes and initial and terminal life phases for excavators: A) *Chlorurus sordidus* B) *Chlorurus strongylocephalus* and scrapers: C) *Scarus frenatus* D) *Scarus niger* E) *Scarus psittacus* and F) *Scarus rubroviolaceus*. A LOESS curve is fitted to show the general trend in bite rate over the course of the day. The grey shaded area represents standard error.

Table 4-1 Mean bites per minute (bpm) for each size class of the six study species. Within species = pairwise statistical comparison between size classes within species; size classes assigned the same letter are not significantly different (P = >0.05). Pairwaise comp. = pairwise statistical comparisons between individuals of the same size class across species. Values are not significantly different to the other species listed: *C.s = Chlorurus, sordidus, C.st = C. strongylocephalus, S.f = Scarus frenatus, S.n = S. niger, S.p = S.psittacus, S.r = S. rubroviolaceus*. N/A = Not applicable because species does not reach the size class at the study.

Species	**Size (cm)**	**N**	**Mean**	**SE**	**Within Sp.**	**Pairwise comp.**
C. sordidus	<15	26	18.25231	2.046745	A	S.n, S.p
	16 to 30	34	17.14000	1.307449	A	S.f, S.n
	31 to 45	32	16.90656	1.155723	A	S.f
	>46	N/A	N/A	N/A		
C. strongylocephalus	<15	4	6.965000	0.9860063	A	S.f, S.r
	16 to 30	21	10.296667	1.3327757	A	S.f, S.r
	31 to 45	37	7.262162	1.0909511	A	
	>46	39	9.072308	1.2161017	A	S.r
S. frenatus	<15	19	8.978421	1.453600	A	C.st, S.r
	16 to 30	43	13.984419	1.471914	B	C.s, C.st
	31 to 45	49	15.493061	1.672830	B	C.s, S.r
	>46	N/A	N/A	N/A		
S. niger	<15	20	23.17300	3.502616	A	C.s, S.p
	16 to 30	36	21.81278	2.131744	A	C.s
	31 to 45	41	31.53268	2.007945	B	
	>46	N/A	N/A	N/A		
S. psittacus	<15	34	29.18500	2.758080	A	C.s, S.n
	16 to 30	11	32.42636	4.822018	A	
	31 to 45	N/A	N/A	N/A		
	>46	N/A	N/A	N/A		
S. rubroviolaceus	<15	6	5.425000	2.468292	ABC	C.st, S.f
	16 to 30	23	6.756522	1.699362	A	C.st
	31 to 45	32	13.936875	1.456668	B	S.f
	>46	25	7.492800	1.553906	AC	C.st

Table 4-2 Total daily bites for each size class of the six study species. See Table 4.1 for more information.

Species	Size (cm)	N	Mean	SE
C. sordidus	<15	26	12045.00	1350.85
	16 to 30	34	11312.40	862.92
	31 to 45	32	11160.60	762.78
	>46	N/A	N/A	N/A
C. strongylocephalus	<15	4	4596.90	650.76
	16 to 30	21	6798.00	879.63
	31 to 45	37	4791.60	720.03
	>46	39	5986.20	802.63
S. frenatus	<15	19	5925.76	959.38
	16 to 30	43	9226.80	971.46
	31 to 45	49	10223.40	1104.07
	>46	N/A	N/A	N/A
S. niger	>15	20	15292.20	2311.73
	16 to 30	36	14394.60	1406.95
	31 to 45	41	20811.57	1325.24
	>46	N/A	N/A	N/A
S. psittacus	<15	34	19262.10	1820.33
	16 to 30	11	21401.40	3182.53
	31 to 45	N/A	N/A	N/A
	>46	N/A	N/A	N/A
S. rubroviolaceus	<15	6	3583.80	1629.07
	16 to 30	23	4461.60	1121.58
	31 to 45	32	9193.80	961.40
	>46	25	4943.40	1025.58

4.4.2 Proportion of bites producing scars and mass removed per grazing scar

With the exception of large (>46 cm) *C. strongylocephalus*, not every bite produced an observable grazing scar (Figure 4-3). PBS increased significantly ($p < 0.05$), although not always consistently, with fish size in all species except *S. niger* ($p > 0.05$). Only around a quarter of bites by fish in the smaller size classes of most species (< 15 cm) produced scars, and at this size there were no significant differences between species ($H_4 = 7$, $p = 0.13$). However, higher PBS (ranging between 0.5, and almost 1.0, depending on species) were observed in the larger size classes, and statistically significant differences were observed between species (Table 4-3). The mass of framework substrate removed per grazing scar increased consistently with fish size in all species studied, and was significant ($p < 0.05$) in all species (Figure 4-4). Excavators eroded markedly more material per grazing scar compared to scrapers, and consistently eroded more material compared to scrapers for the same size class (Table 4-4). For example, *C. strongylocephalus* eroded up to 0.26 ± 0.08 g of substrate per bite for individuals over 45 cm, compared to 0.002 ± 9.13e-04 g per bite by comparably sized *S. rubroviolaceus* (a scraper). No significant differences were found between scraping species at any size class (Table 4-4). A summary of all statistical tests for bite rates and grazing scars is displayed in Table 4-5.

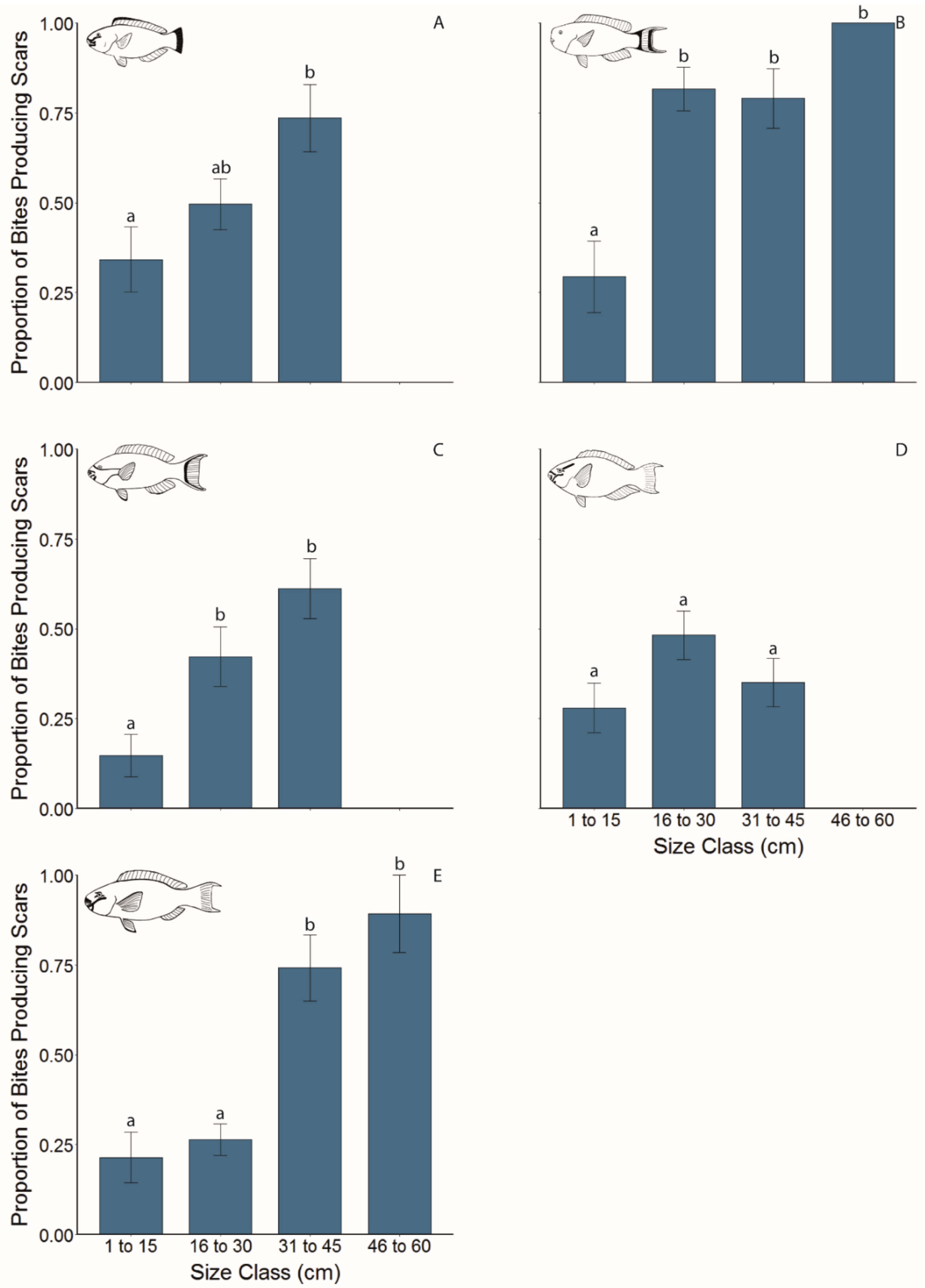


Figure 4-3 Average proportion of bites that produce grazing scars for size classes for excavators: A) *Chlorurus sordidus* B) *Chlorurus strongylocephalus* and scrapers: C) *Scarus frenatus* D) *Scarus niger* and E) *Scarus rubroviolaceus*. Error bars represent 1 standard error of the mean. Letters represent pairwise statistical differences between size classes, bars with the same letter are not statistically significantly different, bars with different letters are statistically significantly different.

Table 4-3 Average proportion of bites that produce grazing scars by species and size class. See Table 4-1 for more information.

Species	Size (cm)	N	Mean	SE	Pairwise comp.
C. sordidus	<15	16	0.341875	0.09032450	C.st, S.f, S.n, S.r
	16 to 30	24	0.496250	0.07077678	S.f, S.n
	31 to 45	10	0.736000	0.09373959	C.st, S.f, S.r
	>46	N/A	N/A	N/A	
C. strongylocephalus	<15	5	0.2940000	0.09907573	C.s, S.f, S.n, S.r
	16 to 30	22	0.8172727	0.06042484	
	31 to 45	16	0.7906250	0.08269154	C.s, S.f, S.r
	>46	10	1.0000000	0.00000000	S.r
S. frenatus	<15	19	0.1473684	0.05954428	C.s, C.st, S.n, S.r
	16 to 30	24	0.4229167	0.08284235	C.s, S.n, S.r
	31 to 45	11	0.6118182	0.08350088	C.s, C.st, S.r
	>46	N/A	N/A	N/A	
S. niger	<15	14	0.2800000	0.06917091	C.s, C.st, S.f, S.r
	16 to 30	26	0.4823077	0.06720647	C.s, S.f, S.r
	31 to 45	15	0.3513333	0.06673235	
	>46	N/A	N/A	N/A	
S. rubroviolaceus	<15	14	0.2142857	0.07052172	C.s, C.st, S.f, s.n
	16 to 30	9	0.2644444	0.04359253	S.f, S.n
	31 to 45	10	0.7420000	0.09163696	C.s, C.st, S.f
	>46	7	0.8928571	0.10714286	C.st

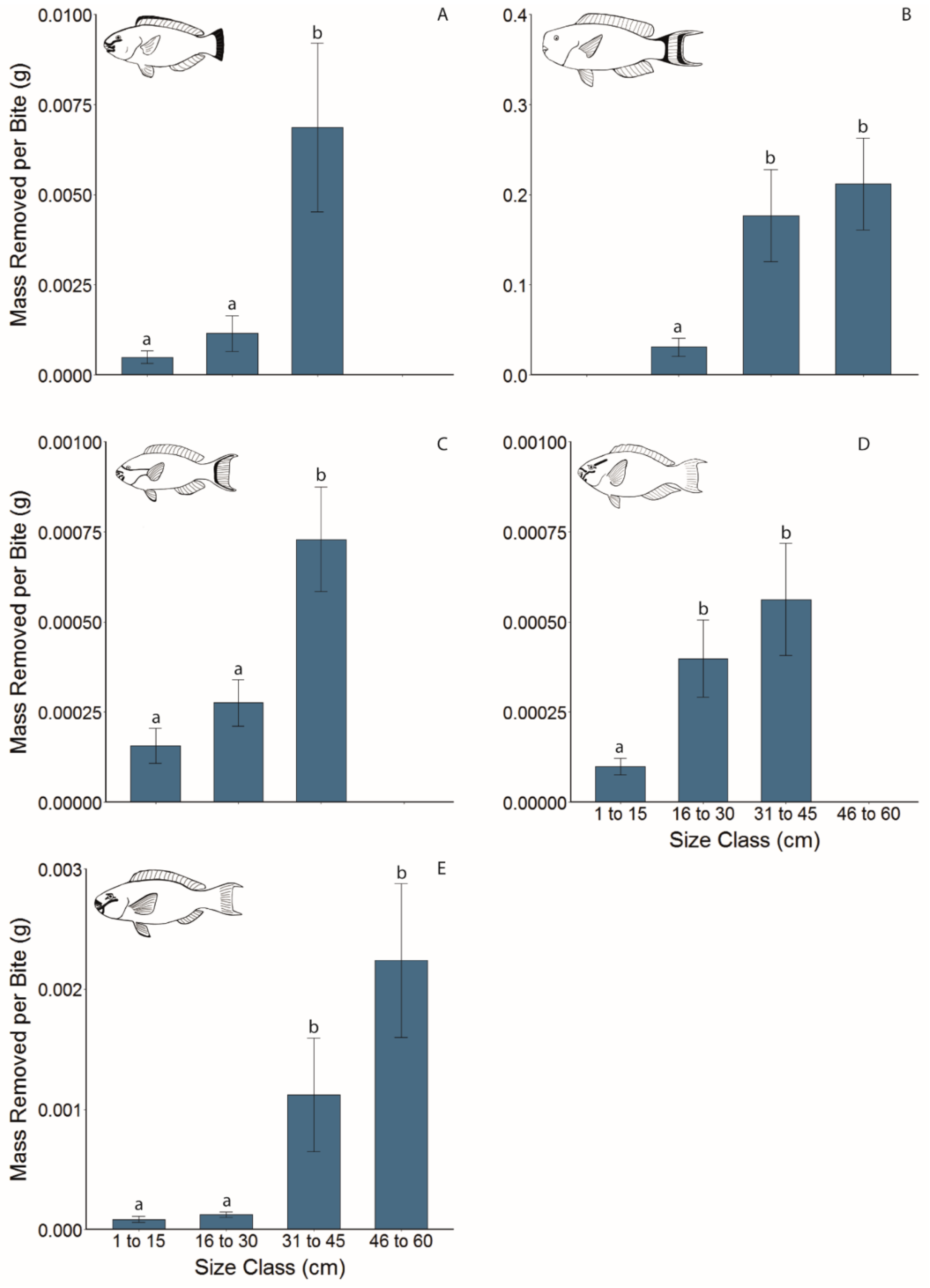


Figure 4-4 Average mass of substrate removed per grazing scar for size classes of excavators: A) *Chlorurus sordidus* B) *Chlorurus strongylocephalus* and scrapers: C) *Scarus frenatus* D) *Scarus niger* and E) *Scarus rubroviolaceus*. Error bars represent 1 standard error of the mean. Letters represent pairwise statistical differences between size classes, bars with the same letter are not statistically significantly different, bars with different letters are statistically significantly different.

Table 4-4 Average mass removed by grazing scars (g) by species and size class. See Table 4-1 for more information.

Species	**Size (cm)**	**N**	**Mean (g)**	**SE**	**Pairwise comp.**
C. sordidus	<15	13	0.0004932692	0.0001698334	S.n
	16 to 30	22	0.0011488636	0.0004988169	
	31 to 45	7	0.0068678571	0.0023380313	
	>46	N/A	N/A	N/A	
C. strongylocephalus	<15	N/A	N/A	N/A	
	16 to 30	19	0.03079934	0.01012978	
	31 to 45	12	0.17688750	0.05117699	
	>46	12	0.21175625	0.05100581	
S. frenatus	<15	6	0.0001562500	4.881406e-05	S.n, S.r
	16 to 30	11	0.0002761364	6.436324e-05	S.n, S.r
	31 to 45	10	0.0007293750	1.450337e-04	S.n, S.r
	>46				
S. niger	<15	14	9.910714e-05	0.0000226189	C.s, S.f, S.r
	16 to 30	12	3.984375e-04	0.0001070937	S.f, S.r
	31 to 45	9	5.625000e-04	0.0001559998	Sf, S.r
	>46				
S. rubroviolaceus	<15	4	0.0000843750	2.359323e-05	S.f, S.n
	16 to 30	7	0.0001232143	2.120418e-05	S.f, S.n
	31 to 45	12	0.0011218750	4.731376e-04	S.f, S.n
	>46	7	0.0022392857	6.387967e-04	

4.4.3 Bioerosion Rates

Estimates of annual bioerosion rates (kg ind^{-1} yr^{-1}) revealed considerable variation among species and between feeding modes (Figure 4-5, Table 4-5). Excavating parrotfish erode considerably more framework material compared to scrapers in all size classes. *C. strongylocephalus* had the highest bioerosion rate among the excavators, with the largest individuals (>46 cm) eroding 462 ± 128 kg ind^{-1} yr^{-1}. By comparison, *S. rubroviolaceus* had the highest bioerosion rate among the scrapers, with the largest individuals (>46 cm) calculated to erode ~3.6 ± 1.4 kg ind^{-1} yr^{-1}. In all species, rates of bioerosion increased with body size. Comparisons to published rates for conspecifics are displayed in Table 4-7.

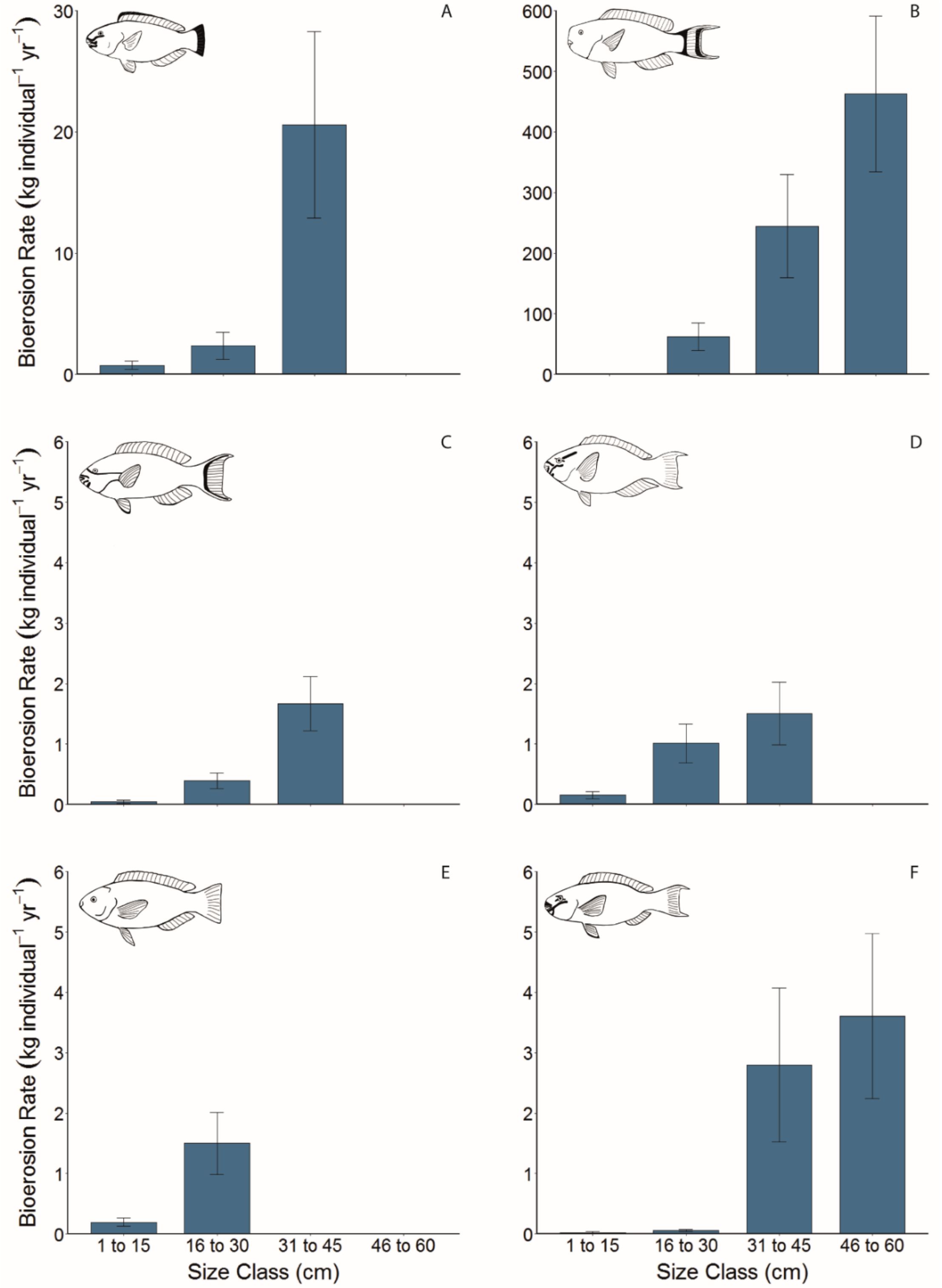


Figure 4-5 Annual bioerosion rates by size class for excavators: A) *Chlorurus sordidus* B) *Chlorurus strongylocephalus* and scrapers: C) *Scarus frenatus* D) *Scarus niger* E) *Scarus psittacus* F) *Scarus rubroviolaceus*. Data are mean ± cumulative SE. Note the different y-axis scales.

Table 4-5 Summary of statistical tests for bite metrics (bite rate, PBS and mass removed per grazing scar).

Test	**Bite rate**	**F**	**Df**	**p**
Welch one-way test	Between species (all data)	33.2	5, 258	< 0.01
	Between species (<15 cm)	9.1	5, 33	< 0.01
	Between species (16-30 cm)	10.9	5, 61	< 0.01
	Between species (31-45 cm)	31.8	4, 102	< 0.01
	C. sordidus (between sizes)	0.7	2, 64	>0.05
	S. frenatus (between sizes)	5.1	2, 84	<0.01
One-way anova	*C. strongylocephalus* (between sizes)	0.7	3, 111	>0.05
	S. niger (between sizes)	9.6	2, 110	<0.01
	S. rubroviolaceus (between sizes)	6.6	3, 105	<0.01
		T	**Df**	**p**
t-test	Species (>46cm)	1.7	70	>0.05
	S. psittacus (between sizes)	-2.0	17	>0.05
	Proportion bites producing scars	**H**	**Df**	**p**
Kruskal Wallis	*C. sordidus* (between sizes)	10.3	3	<0.05
	C. strongylocephalus (between sizes)	16.4	3	<0.001
	S. frenatus (between sizes)	16.6	3	<0.001
	S. niger (between sizes)	6.8	3	>0.05
	S. rubroviolaceus (between sizes)	23.2	3	<0.001
	Between species (<15 cm)	7.1	4	>0.05
	Between species (16 to 30 cm)	21.2	4	<0.001
	Between species (31 to 45 cm)	16.3	4	<0.01
		W		**p**
Wilcoxon	Between species (>45 cm)	40		>0.05
	Grazing scar volumes	**H**	**Df**	**p**
Kruskal Wallis	*C. sordidus* (between sizes)	19.8	3	<0.001
	C. strongylocephalus (between sizes)	13.9	3	<0.01
	S. frenatus (between sizes	12.2	3	<0.01
	S. niger (between sizes)	17.9	3	<0.001
	S. rubroviolaceus (between sizes)	21.2	3	<0.001
	Between species (<15 cm)	15.1	4	<0.01
	Between species (16 to 30 cm)	38.4	4	<0.001
	Between species (31 to 45 cm)	31.4	4	<0.001
		W		**p**
Wilcoxon	Between species (>45 cm)	79		<0.01

Table 4-6 Annual bioerosion rates (kg ind.$^{-1}$ yr^{-1}) by size class ± cumulative error.

Species	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**45 to 60 cm**
Chlorurus sordidus	0.741397 ± 0.341101	2.354055 ± 1.103516	20.5911 ± 7.684972	N/A
Chlorurus strongylocephalus	0.243326 ± 0.12656	62.45718 ± 22.76786	244.5914 ± 84.83448	462.6796 ± 128.4209
Scarus rubroviolaceus	0.023651 ± 0.015725	0.053061 ± 0.018697	2.79342 ± 1.275277	3.607531 ± 1.368947
Scraus frenatus	0.049804 ± 0.027727	0.393299 ± 0.128589	1.665181 ± 0.44452	N/A
Scarus niger	0.154891 ± 0.058374	1.009664 ± 0.324977	1.501203 ± 0.520661	N/A
Scarus psittacus	0.195101 ± 0.069385	1.501134 ± 0.514264	N/A	N/A

Table 4-7 Standardised bioerosion rates for "large" Indo-Pacific parrotfish. Where size class of fish was specified, the largest size class was used for comparison. Data on bites per minute and volume of grazing scars were averaged where there were seasonal or site differences. GBR = Great Barrier Reef

Species	**Alwany et al. (2009)** **(Red Sea)**	**Bellwood (1995)** **(GBR)**	**Bellwood et al. (2003)** **(GBR)**	**Morgan & Kench (2016)** **(Maldives)**	**Ong & Holland (2010)** **(Hawaii)**	**This study** **(Maldives)**
	kg ind^{-1} yr^{-1}	kg ind^{-1} yr^{-1}	kg ind^{-1} yr^{-1}	kg ind^{-1} yr^{-1}	kg ind^{-1} yr^{-1}	kg ind^{-1} yr^{-1}
Excavators						
Bolbometopon muricatum			3482.6			
Cetoscarus bicolor	222.8					
Chlorurus gibbus	250.5					
Chlorurus microrhinos		582.1				
Chlorurus strongylocephalus				344.1		441.1
Chlorurus sordidus	31.2			35.5		19.4
Chlorurus spilurus		9.8				
Chlorurus perspicillatus					233.1	
Scrapers						
Scarus ferrugineus	22.1					
Scarus frenatus	24.4					1.6
Scarus ghobban	142.2					
Scarus niger	4.8					1.4
Scarus psittacus						1.5
Scarus rubroviolaceus					296.7	3.4

4.5 Discussion

Accurately measuring and understanding the factors that control parrotfish bioerosion rates are essential given the importance of this process to reef carbonate budgets and to sand supply rates that influence the maintenance of both reefs and reef islands (Perry et al. 2014b, 2015b, Morgan & Kench 2016a). This study contributes to this important area of research by significantly extending the available dataset for parrotfish bioerosion rates in the central Indian Ocean. New size specific estimates for previously studied “excavator” species are presented, along with data for four previously unstudied “scraping” species in this region. The results of the present study show similarly high functional variability between species, sizes and feeding modes of parrotfish, as demonstrated in studies from other geographic locations (Bruggemann et al. 1996, Alwany et al. 2009). However, despite broad similarities to the findings in these earlier studies (Bellwood 1995a, Bruggemann et al. 1996, Bellwood et al. 2003, Alwany et al. 2009, Ong & Holland 2010, Morgan & Kench 2016a), my data suggest surprisingly high variability in bioerosion rates when comparing rates for the same species (or species within the same clade) between regions. These differences could suggest: 1) that local environmental conditions are a major control on parrotfish bioerosion rates; and/or 2) that challenges associated with directly measuring some key variables, especially those linked to the grazing scars themselves, may be responsible for exaggerating some observed variability.

4.5.1 Maldivian parrotfish bioerosion rates

Three key measures are required to calculate parrotfish bioerosion rate; bite rate, the proportion of bites that produce scars (referred to in this chapter as PBS), and grazing scar volume. Each of these measures showed high variability among species, and with size and feeding modes of parrotfish, resulting in markedly different bioerosion rates. However, the feeding patterns I observed were comparable across all species studied. Bite rate in all species gradually increased throughout the morning, peaking in late morning and mid-afternoon, and halting abruptly ~20 minutes before sunset. Parrotfish feeding patterns were once thought to correlate with rates of algal photosynthesis, and resultant nutritional quality of the algae on which parrotfish were assumed to feed (Afeworki et al. 2013). This nutritional quality hypothesis may still stand despite recent evidence that parrotfish are likely to be microphages, targeting protein rich cyanobacteria living on and within the reef framework (Clements et al. 2016), as cyanobacteria are also photosynthetic. However, the results from the present study differ to those previously published (e.g. Bruggemann et al. 1994b, Bellwood 1995a, Bonaldo et al. 2006, Ong & Holland 2010) by having a subtle, yet consistent, bi-modal pattern. An initial peak occurs in all species at ~11:00, followed by a second which occurs between 15:00-16:00 (Figure 4-2). We hypothesise that this may be due to the process of photoinhibition in cyanobacteria following high light intensity, which may cause a dip, or halted increase in nutritional quality (Long & Humphries 1994, Zemke-White et al. 2002, Takahashi & Murata 2008), and which may be especially pronounced in extremely shallow environments such as the reef platforms studied here (mostly <2 m). This phenomenon warrants further investigation to confirm the observed pattern and to examine its significance and causes.

While the feeding patterns observed in the present study are in broad agreement with much of the literature (Bruggemann et al. 1996, Ong & Holland 2010, Morgan & Kench 2016a), the major difference observed here is that I observed no significant decrease in bite rate with fish size. While this is not the first study to show that this trend is not always present (Bonaldo & Bellwood 2008), it is the first, to the author's knowledge, that shows an increase in bite rate with fish size in two species (*S. frenatus* and *S. niger*). This was unexpected given that feeding rates typically decline with body mass as a result of lower energetic requirements per unit mass in larger fish. It is unclear whether bite rate and feeding rate are tightly coupled, and whether this higher bite rate equates to a higher intake of food. Regardless, these higher bite rates did not correspond to higher bioerosion rates (Figures 4-2 & 4-5). In fact, the species with the lowest bite rates had the highest bioerosion rates for their respective feeding modes (*C. strongylocephalus* for the excavators and *S. rubroviolaceus* for the scrapers). This is explained by the relatively larger scar volumes produced in these species compared to those that have faster bite rates. The volume of grazing scars appears to be the key variable in determining observed patterns of bioerosion, and the only variable to increase consistently with fish size (Figure 4-4). The proportion of bites producing observable scars is also a contributing factor, with larger individuals, especially larger excavators, typically having a higher proportion of bites producing scars (Figure 4-3).

Large (>45 cm) excavators (particularly *C. strongylocephalus*) had especially high bioerosion rates, and can erode up to 462 ± 128 kg $CaCO_3$ ind^{-1} yr^{-1}. This rate is over 130 times higher than that for comparably sized scraping species (e.g. *S. rubroviolaceus*). Bioerosion rate also increased significantly with fish size, a trend that is especially pronounced in excavators. While it is no surprise that larger individuals of a species erode more substrate compared to smaller individuals, an ability to quantify how much more "large" parrotfish erode is critically important to consider from a reef management perspective (Birkeland & Dayton 2005). In some regions, parrotfish are a target fishery and a source of protein for local communities (McClanahan 1994, Aswani & Sabetian 2010, Bellwood et al. 2012, Taylor et al. 2015) and in these cases, larger individuals are commonly targeted (Bellwood et al. 2012), thereby reducing the local mean size of parrotfish (Taylor et al. 2015). Based on my results, the implications of targeted fishing efforts for reef bioerosion in a system such as this (that supports an abundance of large parrotfish and especially >45 cm excavators) is likely to be profound. Specifically, the loss of larger individuals may result in a considerable reduction of total bioerosion by the wider parrotfish population, with implications for coral recruitment success (Bellwood et al. 2004, Mumby 2006), shifts in carbonate budget states (Perry et al. 2014b), and modified rates and grain sizes of sediment supply to reefs and reef islands (Perry et al. 2015a). Past studies would suggest that fishing pressure on large excavators results in an increase in biomass of smaller excavators (Bellwood et al. 2012). The question remains whether this increase in smaller parrotfish would be sufficient to compensate for the loss of larger individuals.

4.5.2 Regional comparisons

Data on parrotfish bioerosion rates now spans the Red Sea, Great Barrier Reef, Caribbean, north-central Pacific and the central Indian Ocean. In the Indo-Pacific, some species of parrotfish are widespread, or closely related species (within the same clade) exist in adjacent regions (Choat et al. 2012). The available evidence suggests that very high variability exists between regions for the same species, or clade (Bonaldo et al. 2014). For example, bioerosion rates for adults in the *C. gibbus/strongylocephalus/microrhinos* (CH2) clade of parrotfish, which one would expect to be comparable, vary between 290 and 1018 kg ind^{-1} yr^{-1} (Bonaldo et al. 2014). This would suggest strong regional variability, and a strong influence of local environmental conditions on parrotfish feeding. Two potential causes of this variability can be suggested, firstly the different values applied for feeding day length, which is used to account for seasonal variation in daylight hours (Bellwood 1995a); and secondly, substrate density, which varies between 1.4 g cm^{-3} (Alwany et al. 2009) to 2.4 g cm^{-3} (Bellwood 1995a, Bellwood et al. 2003), based on locally reported measurements. As a consequence, some variation in bioerosion rates between regions due to these local environmental factors should be expected. However, another potential cause for variability in bioerosion rate calculations is whether to factor for the proportion of bites that produce observable grazing scars, which some studies include (Bruggemann et al. 1996, Ong & Holland 2010), but others do not (Bellwood 1995a, Bellwood et al. 2003, Alwany et al. 2009, Morgan & Kench 2016a). Thus, comparisons of parrotfish bioerosion between regions is not straight forward.

To account for these environmental and methodological differences, and in order to aid bioerosion rate comparisons between regions, I have sought to factor for these issues by producing a table of “standardised” bioerosion rate calculations (Table 4-7). To do this, bite rate and grazing scar data have been extracted from the literature, and consistent values applied for length of the feeding day (11 hours), substrate density (regional average of 1.43 g cm^{-3}), derived from published data summarised in ReefBudget supporting data for the Indo-Pacific (http://geography.exeter.ac.uk/reefbudget/) and the proportions of bites producing scars where they had not been previously included (based on data from the present study; see Table 4-3). The impact of these conversions is a marked reduction in within-species/clade variability. For example, the observed variability for the CH2 clade is reduced by ~55%, and for *S. niger* by ~75%. However, relatively high variability between regions clearly remains.

Three primary reasons are considered likely causes of this remaining variability. Firstly, environmental variables such as depth, wave exposure and habitat type, and interactions with other species (e.g. predation risk) are known to affect parrotfish biorosion rates but are more difficult to control for (Bellwood 1995a, Bruggemann et al. 1996, Bejarano et al. 2017, Davis et al. 2017). In addition, local conditions such as water temperature, currents, and the extent of internal substrate erosion may also affect parrotfish bioerosion rates but are rarely (if ever) reported. Differences in substrate "softness", or the extent of internal (endolithic) bioerosion may be especially important in the case of "exceptionally large" individuals of some scraping species. *S. rubroviolaceus* for example, has been observed to produce shallow scars, comparable to that of excavators, in "soft" or internally bioeroded substrate (Bellwood & Choat 1990). This may partly explain the difference observed for *S. rubroviolaceus* between the present study (average scar volume for >45 cm individuals is 2.4 ± 0.9 mm^3) and Ong & Holland (2010) (average scar volume for >45 cm individuals is 93.2 ± 15.3 mm^3), a 293 kg ind^{-1} yr^{-1} difference after standardisation, although it is uncertain whether this could result in such substantial variation between regions.

Secondly, as previously mentioned, not all studies provide an estimate of fish size, other than indicating adult size ranges (e.g. Bellwood 1995a, Bellwood et al. 2003, Alwany et al. 2009). As shown in the present study, different sizes of fish erode significantly different quantities of material. I assume in the present study that the largest size classes of parrotfish from studies which provide fish size estimates are most comparable. However, impacts from fishing for example, may reduce mean fish size on a reef (Taylor et al. 2015), so this assumption may not be true. If terminal phase males are smaller or larger compared to my assumptions, this may explain some of the observed variability in bioerosion rates. The results of the present study demonstrate the importance of indicating fish size when presenting bioerosion rate data.

Finally, it might be reasonable to assume that some of this variability is due to the challenges involved with measuring parrotfish feeding characteristics in the field, particular grazing scars. Observations need to be carried out in very close proximity to a grazing parrotfish to observe scar production accurately. Where scar production is observed, scar depth for most species is extremely shallow (<0.5 mm) and is therefore often within a substrates natural topographic heterogeneity, and impractical to measure using conventional tools such as callipers. Scar depth assumptions are therefore often applied to most species (e.g. 0.1mm for *C. sordidus* in Bellwood 1995a and the present study), but it is unclear how these assumptions match up to natural variability in scar depth.

Measuring grazing scar production and volume precisely is key to accurately estimating parrotfish bioerosion rates, yet methods to measure these variables differ among studies. For example, there are different approaches with regards to grazing scars that are not visible to the naked eye, which is particularly relevant in parrotfish <15 cm (Bellwood 1995a). Indeed, many of the measurements in the <15 cm size category in the present study are likely to have been estimated for fish at the larger end of this size range. Some studies have attempted to measure these very small grazing scars under a dissecting microscope, rather than exclude them (Bellwood 1995a, Bonaldo & Bellwood 2008). However, such scars are difficult to locate after production, making it challenging to attribute a mark on the substrate to a particular feeding event. These scars also contribute extremely little to bioerosion, and so factoring for the proportion of bites producing observable grazing scars was thus considered a more appropriate and conservative approach here. In addition, while a rectangular prism shape is assumed in this study, which has been shown to be comparable to laboratory validated bite scar volumes (Bellwood 1995a, Ong & Holland 2010), an ellipsoidal shape is assumed in Alwany et al. (2009). Different approaches such as these may result in markedly different outcomes when calculating bioerosion rates. I therefore suggest future research into methods that more accurately estimate grazing scar volumes, or that new methods to validate parrotfish bioerosion rates are required to improve the accuracy of these calculations. This is especially important given the potential for parrotfish bioerosion to influence reef and reef island growth potential in some regions, such as the central Indian Ocean (Perry et al. 2014b, 2015b, Perry et al. 2015a).

Future research should also consider regional differences in community level parrotfish bioerosion, in addition to species comparisons. The high bioerosion, and resultant sand generation rates reported in the Maldives (Perry et al. 2015b) may not be replicated where parrotfish biomass, or abundance of large excavators is lower, such as in the western Indian Ocean where parrotfish are a target fishery (McClanahan 2011). While the importance of algal grazing by parrotfish is now beginning to be considered in reef management (Jackson et al. 2014), physical functional roles such as bioerosion and sediment production are not yet taken into account. Recent studies have shown that parrotfish may not influence macroalgae and coral cover in all locations (Carassou et al. 2013, Russ et al. 2015), however, bioerosion was not examined in these studies and may not be tightly coupled with grazing pressure. It is therefore unclear whether parrotfish play an important role in the context of reef carbonate budgets in these locations, and is something to consider before dismissing the benefits of reduced fishing pressure on parrotfish for reef resilience. Further research into parrotfish bioerosion rates across a broader range of species is also needed, along with investigations into environmental controls on these rates. Expanded data on rates of bioerosion to capture some of this currently missing species diversity would significantly improve the accuracy of reef-scale estimates of parrotfish bioerosion, which is essential to making community scale estimates of bioerosion, and assessing the growth potential of reefs and reef islands (Perry et al. 2014b, Perry et al. 2015a).

Chapter 5 Inter-habitat variability in parrotfish bioerosion rates and grazing pressure: influence of habitat type on key parrotfish functional roles

Photo taken in the north-east reef habitat at Vavvaru. Photo credit: Robert T Yarlett.

5.1 Context

Fish perform a variety of functional roles on coral reefs, but it is unclear how variations in species assemblages influence the overall contributions of fish to these roles in different reef habitat types. Parrotfish are dominant bioeroders and algal grazers on coral reefs, making them important for structuring reefs both physically and ecologically. This chapter builds on chapter 4 by applying the species and size specific bioerosion rates and bite surface areas to parrotfish assemblages in the eight delineated reef habitats over the Vavvaru reef platform. To do this, I first address objective 1 which asks how parrotfish species and size classes vary across the main reef habitats on the Vavvaru platform. These data are then used to answer research question 2, on how these variations in parrotfish assemblages translate to overall bioerosion rates and grazing pressure in each of the habitats. In addition, I use multivariate statistics to address objective 3, which asks how habitat type influences parrotfish assemblages. Objective 4 is then addressed, which asks how different parrotfish species and size classes contribute to bioerosion and grazing in different reef habitats. Key species and inter-habitat variability in these important ecosystem processes are also compared.

5.2 Introduction

Coral reefs are built and shaped, both structurally and ecologically, by the organisms that inhabit them. The processes of carbonate production (e.g. by scleractinian corals and coralline algae), and bioerosion (e.g. by fish and urchins) are especially important for controlling reef growth and structural complexity. Ultimately, these processes can influence nearshore wave energy regimes, and habitat provision for many commercially important species (Lugo-Fernández et al. 1998, Moberg & Folke 1999, Ruckelshaus et al. 2013, Ferrario et al. 2014). Grazing is important for limiting algal cover, which benefits coral demographics, and so also has an indirect influence on carbonate production rates (Mumby 2006, 2009, Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Mumby & Harborne 2010, Kennedy et al. 2013, Bejarano et al. 2013, Afeworki et al. 2013, Steneck et al. 2014). On coral reefs, parrotfish graze algal turfs and some species are also important substrate bioeroders (Bellwood 1995b, Lokrantz et al. 2008, Perry et al. 2014b). Although now thought to be targeting cyanobacteria living on and within the reef framework, at least on Indo-Pacific reefs (Clements et al. 2016), parrotfish remove algal turfs as a result of feeding primarily on dead coral and rubble substrates (Bruggemann et al. 1994a, Bellwood 1995a, Afeworki et al. 2011). To access endolithic resources, many parrotfish species erode and ingest carbonate substrate, which is broken down by modified gill arch elements known as the pharyngeal mill (Bellwood & Choat 1990, Carr et al. 2006). This material is then processed in the gut along with organic matter, and excreted back into the environment as sediment (Bellwood 1995a, 1996, Hoey & Bellwood 2008). In some regions, parrotfish bioerosion and the resultant sand generation can dominate reef sediment production (Perry et al. 2015a, Morgan & Kench 2016a, Perry et al. 2017). These bioerosion and grazing processes form an important component of overall reef carbonate production cycling and act as a “top-down” influence on reef ecological and physical structure (Hutchings 1986, Bellwood et al. 2004, Mumby 2006, Box & Mumby 2007, Perry et al. 2014b).

Grazing pressure and bioerosion rates can vary significantly between different species and size classes and also between “scraper” and “excavator” species (Bruggemann et al. 1996, Lokrantz et al. 2008, Ong & Holland 2010, Yarlett et al. 2018). This becomes important for understanding community level processes because fish density and community composition can vary among habitat types, or along gradients of structural complexity (McClanahan 1994, McClanahan & Arthur 2001, Komyakova et al. 2013, Darling et al. 2017, Richardson et al. 2017a). Comparisons between the Red Sea, Arabian Sea and Arabian Gulf revealed marked regional differences in parrotfish bioerosion rate and grazing pressure because of variations in species assemblage and functional composition (Hoey et al. 2016a). Identifying the environmental drivers (or “bottom-up” controls) of habitat type on community composition, and identifying habitat preferences for key bioeroding and grazing species, may help to understand how these processes might be affected by changes to habitat condition as a result of ongoing environmental change (Hoey & Bellwood 2008, Green & Bellwood 2009, Perry et al. 2017).

However, despite extensive research into the roles of bioerosion and grazing by parrotfish, our knowledge of bottom up controls on parrotfish communities, and how this influences their functional roles, is poorly understood. This is particularly the case in the central Indian Ocean. Hoey & Bellwood (2008) demonstrated how the functional roles of parrotfish vary between inner, mid, and outer reef environments on the Great Barrier Reef. However, many reef systems can have a very different habitat structure compared to barrier reefs, for example; atoll reef platforms, fringing reefs, or systems with large lagoons, reef flats, seagrass meadows or mangrove forests. These systems differ in terms of the spatial extent of their main habitats, the species that they support, their benthic community composition, geomorphology and the extent to which they are influenced by external factors such as terrestrial nutrient and sediment inputs. While a number of studies identify important bioeroding species and size classes of parrotfish, it is also important to understand how changes in species composition and size classes between habitats influences overall community functional roles. In many regions, it is difficult to tease apart the influences of fishing pressure and habitat type on parrotfish communities (Cordeiro et al. 2015). However, the Maldives represents an example environment where there is no legal parrotfish exploitation, so the influence of fishing is minimised, making it an ideal natural laboratory for examining the influence of habitat type specifically. Here, I examine the contributions of parrotfish species to grazing and bioerosion across an atoll-edge reef platform in the central Maldives (Vavvaru Island, Lhaviyani Atoll). Specifically, I investigate; 1) the influence of habitat type on the density and species composition of parrotfish assemblages over a reef platform, and 2) how total grazing pressures and bioerosion rates, and the main contributors to these processes, vary among habitat types as a function of parrotfish assemblage.

5.3 Methods

5.3.1 Remote Underwater Video (RUV) Fish Surveys and Analysis

Parrotfish density was measured using un-baited Remote Underwater Video (RUV). This approach was chosen to extend survey time and detect all species present, while minimising observer influence on fish behaviour (Watson et al. 2005). This is particularly crucial in very shallow water habitats such as those over much of the Vavvaru platform. RUV has the benefits of providing a permanent record of the survey, which allows the observer to re-check counts, measurements and species identification. In addition, RUV can be used to survey multiple areas simultaneously over multiple hours (Harborne et al. 2015, 2016).

A range of Go-Pro Hero 4, 3+ and Intova Sport HDII cameras were mounted onto PVC frames and deployed for a minimum of 1 hour, which is considered long enough to capture both common and rare species (Watson et al. 2010). In each of the 8 delineated habitats, 15 RUVs were randomly deployed, but ensuring they were at least 20 m apart. The deployments spanned the length of the parrotfish feeding day (~0630-1830) with three replicate videos for the following time intervals; sunrise-0900, 0900-1130, 1130-1400, 1400-1630, 1630-sunset (i.e. three replicate RUVs in each of the five time intervals in each of the eight habitats - the camera was randomly re-deployed in a new location in each time bin, so all 15 replicates were deployed in new locations). Four 50 cm scale bars with 5 cm increments were initially placed at 1 m intervals up to 4 m in front of the camera. These were removed ~30 s into each recording to avoid unnecessary disturbance to fish behaviour. A screen overlay was then used to mark the position of the scales during data collection using Windows Media Player and allow approximate sizing of fish.

Over 200 hours of video footage was analysed, totalling nearly 12 000 individual parrotfish observations. Analysis of each video began once the scale bars were removed, and after allowing 2 minutes for observers to leave the area and avoid human disturbance. All parrotfish entering the field of view within 4 m (the furthest scale bar) of the camera were recorded at their entry time, identified to species level and life phase, and assigned to one of the following size classes; <15 cm, 16 to 30 cm, 31 to 45 cm, >46 cm. A pilot study conducted prior to fieldwork revealed that classifying objects (PVC pipes) into 15 cm size categories using this method was correct 98% of the time, compared to 82% for the more commonly used 10 cm size bins, so 15 cm size categories were used for greater accuracy. The 4 m distance from the camera limit was chosen to ensure that water visibility and distance of fish from the camera did not interfere with species ID. Juvenile parrotfish were recorded without species information because of challenges associated with accurate identification and because juveniles are likely to be functionally similar regardless of their feeding mode (Bruggemann et al. 1996). Having a fixed field of view also reduces the potential for observer bias when estimating the survey area compared to UVC (Harvey et al. 2004). A dataset of ~3500 recordings of parrotfish video entry and exit times was used to estimate a mean parrotfish residence time in the survey area of each video (e.g. parrotfish spent on average 26 seconds in Intova camera video frames).

The videos provide an estimate of parrotfish density per unit area (estimated from the area directly in front to 4 m in front of the camera and constrained on both sides by the field of view) per unit time (calculated from the length of video analysed). This approach is then used to estimate the amount of parrotfish bioerosion and grazing that occurs in given area of reef, over given period of time, regardless of whether the same or different individuals are entering the survey area.

5.3.2 Inter-Habitat Variability in Parrotfish Species Assemblages- Statistical Analyses

Environmental variables (substrate type, rugosity and benthic community, including cover of different coral growth forms) for Vavvaru habitats was extracted from the Perry et al. (2017) *ReefBudget* dataset (Table 5-2). To simplify the model, the following data were pooled; branching and table corals, data for all massive coral species, data for encrusting coral growth forms and “other corals”. Transect cover data for sediment producers, soft corals, macroalgae and “other” showed collinearity and were also pooled together. The variable ‘water depth’ was removed as it showed collinearity with variable ‘limestone pavement’ (hardground), likely because this substrate type and deeper water were largely associated with the hardground habitat. Water depth can influence grazing pressure (Fox & Bellwood 2007) but is reasonably consistent over much of the Vavvaru platform, other than the hardground habitat and the platform edge (see bathymetry map in Perry et al. 2017). Tidal range in the area is small (typically 0.2-0.4 m, max range at strong spring tides ~ 1.0 m), and was considered unlikely to cut off fish from leaving or entering any part of the reef at any time. For similar reasons, exposure was not factored into the model. This is partly because exposure is a difficult measure to quantify, but more importantly because any assumptions of exposure applied correlate closely with the massive coral abundance and limestone pavement variables, as these are the defining features of the more exposed western habitats.

Principal Component Analysis (PCA) was carried out on standardised transect level habitat data (substrate type, rugosity and benthic community composition) to explore differences between and within the delineated habitats. A further PCA was carried out to explore variation in parrotfish species assemblages among habitats (on data averaged by time category; n = 5 per habitat) and a one-way Analysis of Variance (ANOVA) carried out to investigate the influence of survey time on parrotfish density in each habitat. Groupings in the PCA were based on the previously delineated habitat types derived from field observations and supervised classification of remotely sensed imagery (Figure 3-2A). Links between habitat variables and parrotfish species assemblages were then explored using non-metric multidimensional scaling (NMDS) analysis based on Bray-Curtis dissimilarities. In this analysis, habitat data (transects averaged by habitat) and parrotfish survey (data averaged by time category in each habitat) were used. A Welch one-way test was also used to compare fish density between habitats. Statistical analyses were conducted in R version 3.3.2, using the ‘vegan’ package (Oksanen et al. 2017) for multivariate analyses.

5.3.3 Parrotfish Bioerosion Rates

To estimate overall parrotfish bioerosion rates in each habitat, local species and size class specific bioerosion rates were first extracted from Yarlett et al. (2018) (Chapter 4) for six of the most abundant species at Vavvaru, representing the full range of sizes and feeding modes present; *Chlorurus sordidus, C. strongyloephalus, Scarus rubroviolaceus, S. frenatus, S. niger* and *S. psittacus*. Rates for other species were matched to the most closely related species (based on Choat et al. 2012), or species with the most comparable morphology (see Table 3-2). Bioerosion rates for each size class of each species observed during the video was then estimated using the following equation:

$VBSS\ (kg\ survey\ area^{-1}\ video\ duration^{-1}) = No.\ individuals\ observed \times residence\ time\ (s) \times bioerosion\ rate\ (kg\ ind^{-1}\ s^{-1})$

Where VBSS = Video bioerosion for each size class of each species.

These values were then converted to bioerosion rates per m^2 using the estimated survey area of the video, and then to annual bioerosion rates (ABR) per m^2 by scaling to the length of the feeding day (11 hours; Yarlett et al. 2018) and multiplying by 365. This was repeated for all 15 replicate videos in each habitat before finding an average annual erosion rate for each size class of each species.

Finally, total bioerosion rates for each habitat were estimated using the following equation:

$TAHB\ (kg\ habitat\ area^{-1}\ yr^{-1}) = \sum ABR\ (kg\ m^{-2}\ yr^{-1}) \times habitat\ area\ (m^2)$

Where TAHB = total annual habitat bioerosion. To compare total rates and spatial coverage of parrotfish bioerosion over the reef platform, a choropleth map was produced in ArcMap 10.3.1 using the habitat map (Figure 3-2A) and the values calculated for total parrotfish bioerosion.

5.3.4 Parrotfish Grazing Pressure

To estimate parrotfish grazing pressure, data were first collected on grazing scar surface area by observing an individual until it produced a clear and accessible grazing scar, the length and width of which was measured with Vernier callipers (Table 5-1; derived from data in Yarlett et al. 2018). These data were collected for the same representative species as described in section 5.3.3, and the same assumptions applied to other species observed. The surface area of substrate grazed per minute by different species and size classes was calculated as follows (note that it is assumed that all bites remove algae from the reef substrate):

$SAsubstrate\ (cm^2\,min^{-1}) = bite\ rate\ (bpm) \times GSSA\ (cm^2)$

Where SAsubstrate = surface area of substrate grazed per minute, bpm = bites per minute for the specific species size class and GSSA = grazing scar surface area for the specific species size class.

Grazing pressure for each size class of each species observed during the video was then estimated using the following equation:

$VGSS\ (cm^2\ survey\ area^{-1}\ video\ duration^{-1}) = No.\ individuals\ observed \times residence\ time\ (s) \times SA\ substrate\ (cm^2\ s^{-1})$

Where VGSS = Video grazing pressure for each size class of each species.

These values were then converted to grazing pressure per m^2 using the estimated survey area of the video, and then to annual grazing pressure (AGP) per m^2 by scaling to the length of the feeding day (11 hours; Yarlett et al. 2018) and multiplying by 365. This was repeated for all 15 replicate videos in each habitat before finding an average annual erosion rate for each size class of each species.

Finally, total grazing pressure for each habitat was estimated using the following equation:

$TAAG\ (cm^2\ habitat\ area^{-1}\ yr^{-1}) = \sum AGP\ (cm^2\ m^{-2}\,yr^{-1}) \times habitat\ area\ (m^2)$

Where TAAG = total annual area grazed. A choropleth map was again produced to compare total parrotfish grazing pressure over the reef platform.

Table 5-1 Mean grazing scar surface areas (cm^2) and standard errors (SE) for four size classes of five representative Maldivian parrotfish species.

Species	Size Class	N	Mean	SE
Chlorurus sordidus	<15 cm	13	0.03	0.01
	16 to 30 cm	22	0.05	0.01
	31 to 45 cm	7	0.19	0.05
	>46 cm	N/A	N/A	N/A
Chlorurus strongylocephalus	<15 cm	13	0.03	0.01
	16 to 30 cm	19	0.17	0.03
	31 to 45 cm	12	0.57	0.11
	>46 cm	12	0.88	0.17
Scarus frenatus	<15 cm	6	0.02	0.01
	16 to 30 cm	11	0.04	0.01
	31 to 45 cm	10	0.10	0.02
	>46 cm	N/A	N/A	N/A
Scarus niger	<15 cm	14	0.01	0.003
	16 to 30 cm	12	0.05	0.01
	31 to 45 cm	9	0.08	0.02
	>46 cm	N/A	N/A	N/A
Scarus rubroviolaceus	<15 cm	4	0.01	0.003
	16 to 30 cm	7	0.02	0.003
	31 to 45 cm	12	0.08	0.03
	>46 cm	7	0.15	0.04

5.3.5 Error Propagation

To calculate the cumulative errors associated with multiplying and adding variables with their own associated standard errors, the following rules for error propagation were used (where v = calculated value, x = variable 1 and y = variable 2, SE = standard error). For multiplication:

$$SEv = \sqrt{\left(\frac{SEx}{\bar{x}}\right)^2 + \left(\frac{SEy}{\bar{y}}\right)^2} \times \bar{v}$$

For addition:

$$SEv = \sqrt{(SEx1)^2 + (SEx2)^2 + \ldots + (SExn)^2}$$

Life phase has been shown to have no additive effect on bioerosion rate in six of the species studied in detail at this site (Yarlett et al. 2018), so initial and terminal phase data were pooled and presented as fish size. The density of initial and terminal phase parrotfish in each habitat are presented in Supplementary Tables 5-(1-6).

5.4 Results

5.4.1 Influence of habitat type on parrotfish density and community structure

Fifteen species of parrotfish belonging to five genera were identified over the Vavvaru reef platform, but these were restricted to six habitats. No parrotfish were observed in the central nearshore sand/rubble or lagoonal sand habitats. Of these 15 species, four were excavators (*Chlorurus sordidus*, *C. strongylocephalus, C. enneacanthus* and *Cetoscarus bicolor*) and ten were scrapers (*Scarus psittacus, S. frenatus, S. rubroviolaceus, S. niger, S. tricolor, S. russellii, S. prasiognathos, S. scaber, S. viridifucatus,* and *Hipposcarus harid*), as defined in (Bellwood & Choat 1990). One species of browser (*Calatomus carolinus*) was also observed and recorded, but was not factored into substrate bioerosion or grazing calculations. Principal Component Analysis (PCA) revealed that the six delineated habitats where parrotfish occurred, each differed in terms of structural complexity, substrate type and benthic community composition (Figure 5-1, environmental data summarised in Table 5-2). Principal component axis 1 (PC1; eigenvalue = 4.01, percentage explained = 36%), differentiated transects based on structural complexity; with rugosity and branching and table coral cover at strong positive PC1 scores, and sand with a strong negative PC1 score. PC2 (eigenvalue = 2.21, percent explained = 20%) differentiated habitats based on substrate type and also massive coral cover. Massive corals and limestone hardground had strong positive PC2 scores, while turf and rubble had strong negative PC2 scores. Parrotfish species assemblages differed markedly among these habitats (Figure 5-2; PC1; eigenvalue = 3.34, percentage explained 21%, PC2; eigenvalue = 2.47, percentage explained 15%). One-way ANOVA revealed that there was no significant influence of survey time category on parrotfish density in any habitat (p > 0.05), so data were pooled (fifteen replicate RUVs per habitat) for further analyses.

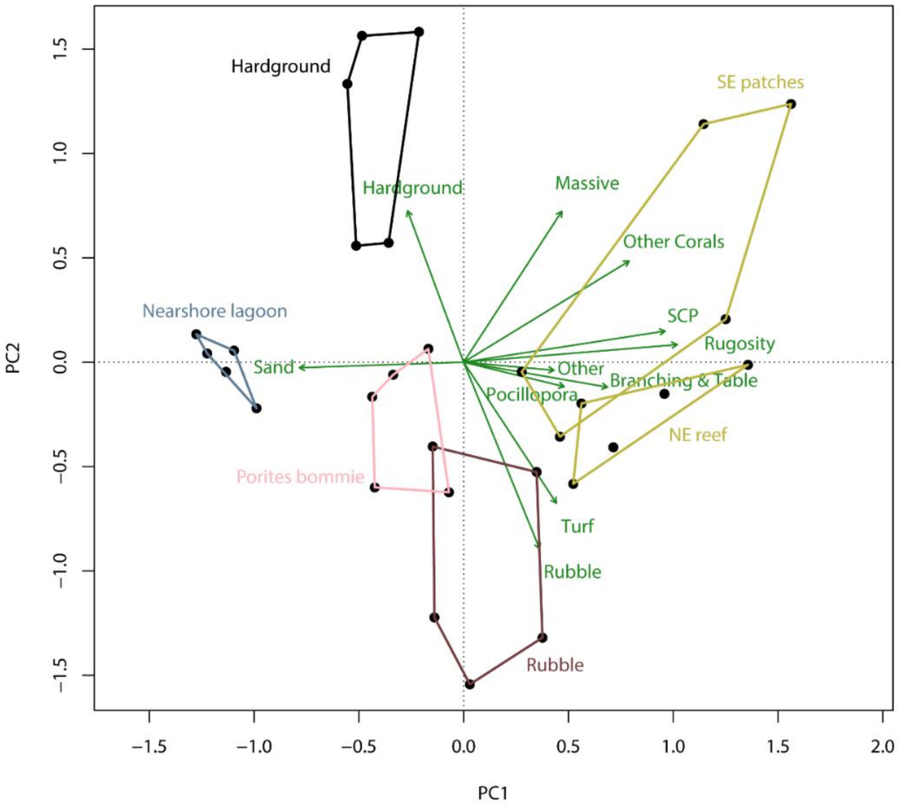


Figure 5-1 Principal Component Analyses (PCA) showing between and within habitat variability in substrate type, topographic complexity and benthic communities. Points represent transect level data, and are grouped according to previously delineated habitat types corresponding to the habitat map in Figure 3-2. The relative contribution of environmental variables to the observed variation is superimposed in green. SCP = Secondary Carbonate Producers.

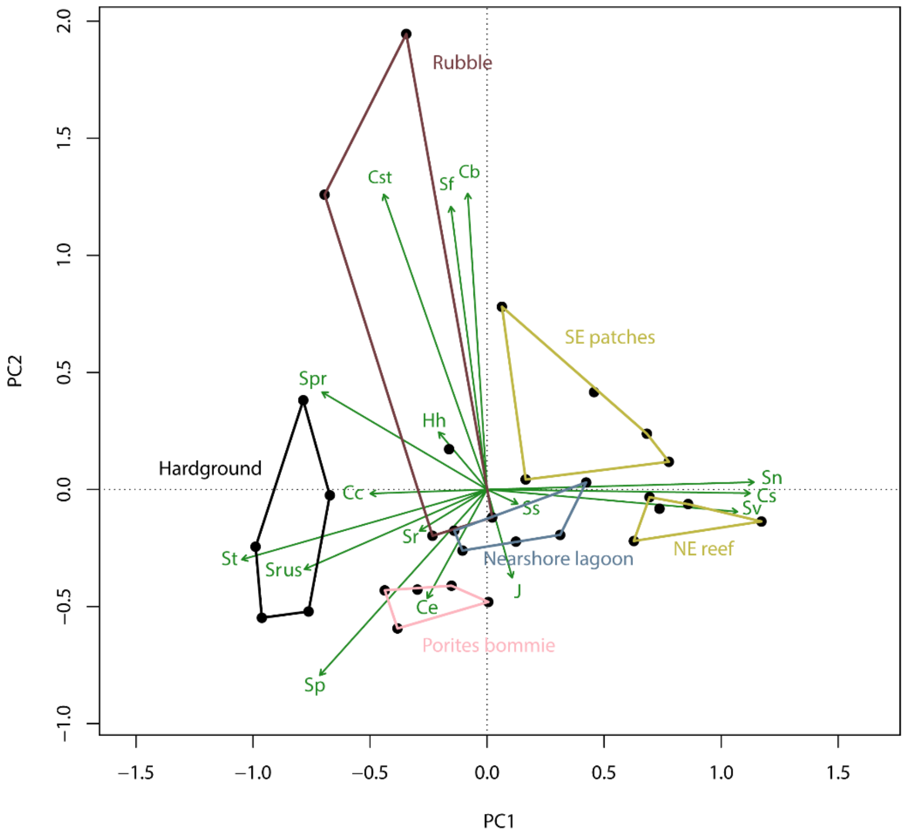


Figure 5-2 Principal Component Analyses (PCA) showing between and within habitat variability in parrotfish species assemblage. Points represent averaged timed categories (three videos per time category, five points per habitat), and are grouped as described for Figure 5-1. The relative contribution of different parrotfish species to the observed variation is superimposed in green. Species abbreviations: Cs - *Chlorurus sordidus,* Cst - *C. strongylocephalus*, Ce - *C. enneacanthus,* Cb - *Cetoscarus bicolor,* Sf - *Scarus frenatus,* Sr - *S. rubroviolaceus,* Sp - *S. psittacus,* Sn - *S. niger,* St - *S. tricolor,* Ss - *S. scaber,* Spr - *S. prasiognathos,* Sv - *S. viridifucatus,* Srus – *S. russelii,* Hh - *Hipposcarus harid,* Cc- *Calotomus carolinus*.

Table 5-2 Summary of environmental variables defining the six delineated habitats that supported parrotfish populations on the Vavvaru platform collected in February 2015 (Perry et al. 2017). Values are averages of 5 replicate transects per habitat. Rugosity is presented as a ratio index of straight line to topographic distance. All other variables are presented as average cm cover of transects. Complex corals = branching and table morphotypes, Massive corals = *Porites spp.* and other massive species, Other corals = encrusting species and other uncommon growth forms. SCP = secondary carbonate producers (e.g. *Halimeda spp.* and calcareous algae). Hardground = limestone pavement.

Habitat	**Rugosity Index**	**Complex Corals**	***Pocillopora***	**Massive Corals**	**Other Corals**
Z1 Hardground	1.34	5.0	23.4	150.4	65.6
Z2 Rubble	1.66	1.8	47.6	58.2	26.8
Z3 *Porites* bommie	1.34	11.8	23.0	113.4	18.0
Z6 NE reef	1.98	385.4	14.4	52.8	76.0
Z7 SE patches	2.23	127.2	42	202.4	150.4
Z8 Nearshore lagoon	1.09	6.2	1.6	6.4	1.2

	SCP	**Other**	**Turf**	**Rubble**	**Hardground**	**Sand**
Z1 Hardground	119	0.0	201.4	131.2	557.2	184.4
Z2 Rubble	257.8	5.4	1088.8	899.8	0.0	98.8
Z3 *Porites* bommie	196.4	14.0	594.6	513.0	0.0	291.4
Z6 NE reef	826.4	129.2	460.8	608.0	0.0	62.4
Z7 SE patches	764	7.0	727.0	367.4	0.0	166.4
Z8 Nearshore lagoon	6.8	0.0	121.0	129.8	0.0	904.0

Total parrotfish density was significantly different among habitat types (Figure 5-3; $F_{5,34} = 29.6$, $p < 0.001$). The nearshore lagoon had a significantly lower parrotfish density (0.013 ± 0.003 individuals m^{-2} min^{-1}) compared to other habitats, while the NE reef had a significantly higher parrotfish density (0.450 ± 0.050 individuals m^{-2} min^{-1}) compared to all other habitats (Figure 5-3, Table 5-3). The *Porites* bommie and SE patch reefs had comparable, reasonably high parrotfish densities (0.273 ± 0.057 and 0.244 ± 0.050 individuals m^{-2} min^{-1} respectively), which were significantly higher than that of the Hardground and Rubble habitats (0.090 ± 0.012 and 0.090 ± 0.024 individuals m^{-2} min^{-1} respectively; Figure 5-3, Table 5-3). The western hardground habitat had the highest species diversity (14 species), while the eastern nearshore lagoon had the lowest diversity (6 species).

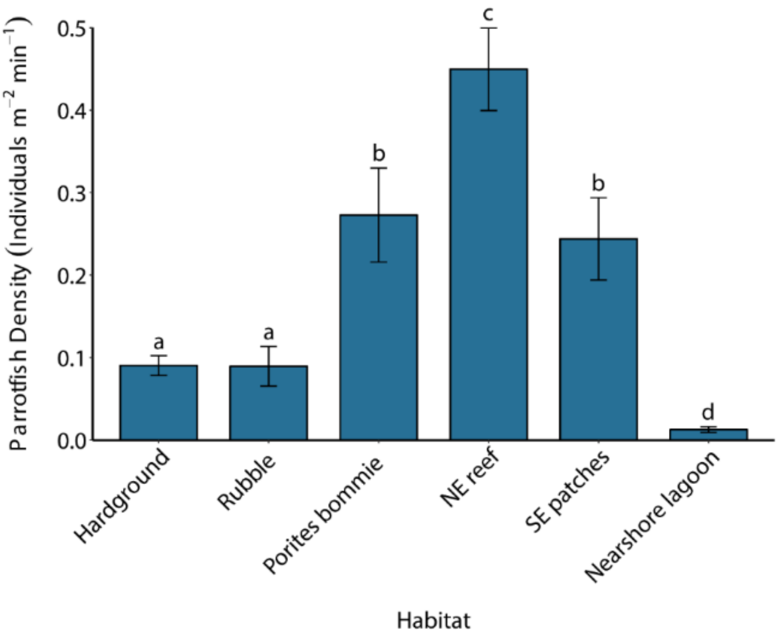


Figure 5-3 Overall parrotfish density in the six habitats where parrotfish were observed on the Vavvaru platform. Bars marked with different letters are statistically significantly different.

Table 5-3 Number of parrotfish species and total parrotfish density found in each habitat. Z1-8 refers to reef zones marked out in Figure 3-2.

	Z1	**Z2**	**Z3**	**Z4**	**Z5**	**Z6**	**Z7**	**Z8**
No. species	14	13	11	0	0	13	12	6
Total parrotfish density (No. indiv. m^{-2} min^{-1})	0.090 ± 0.012	0.090 ± 0.024	0.273 ± 0.057	0	0	0.450 ± 0.050	0.244 ± 0.050	0.013 ± 0.003

The number of species observed using RUV methodology from the present study was compared to the number observed using UVC approaches carried out in the same habitats for a carbonate budget study (Perry et al. 2017, Table 5-4). The RUV methodology detected roughly double the number of species in each of the habitats, and more than double in SE patch reefs and Nearshore lagoon habitats.

Table 5-4 Comparison of number of parrotfish species observed in each habitat detected from Remote Underwater Video (RUV) (present study) and Underwater Visual Census (UVC) methodology (Perry et al. 2017).

Habitat	# Species - Video	# Species - UVC
Hardground	14	7
Rubble	13	9
***Porites* bommie**	11	6
NE reef	13	7
SE patches	12	5
Nearshore lagoon	6	1

Non-metric multidimensional scaling (NMDS) analysis revealed species preferences to different environmental factors (Figure 5-4). Species grouped around the centre of the plot, such as *C. sordidus, S. scaber, S. psittacus, H. harid,* and juvenile parrotfish were generalists, and as shown in Figure 5-5, were present in all major reef habitats supporting parrotfish assemblages. Two species, *S. niger,* and *S. viridifucatus,* appeared to be strongly associated with high rugosity, high complex coral cover and diverse benthic communities. This is supported by Figure 5-5 which shows that these species are found in abundance in the NE reef and SE patch reef habitats, but are rare elsewhere on the platform. In contrast, *S. prasiognathos, S. tricolor, S. russelii* and *C. enneacanthus* appeared to show a preference for low rugosity and massive coral growth forms, which corresponds to the hardground, rubble and *Porites* bommie habitats. Some of these species showed a strong preference to specific habitats; Figure 5-5 shows that *S. russelii* was specific to the western hardgrounds, and *C. enneacanthus* was rarely observed outside of the *Porites* bommie zone. Specific preferences of *C. strongylocephalus, C. bicolor, C. carolinus* and *S. frenatus* were more difficult to determine, but did not appear to be as strongly associated with any particular habitat characteristics compared to the two previous distinct groups. Figure 5-5 shows that *S. rubroviolaceus* also occurs in all habitats supporting parrotfish assemblages, suggesting it is also a generalist, but its relative position on the NMDS (Figure 5-4) revealed that it can be also found in habitats with predominantly sandy substrates (the nearshore lagoon), which most other species strongly disassociate with.

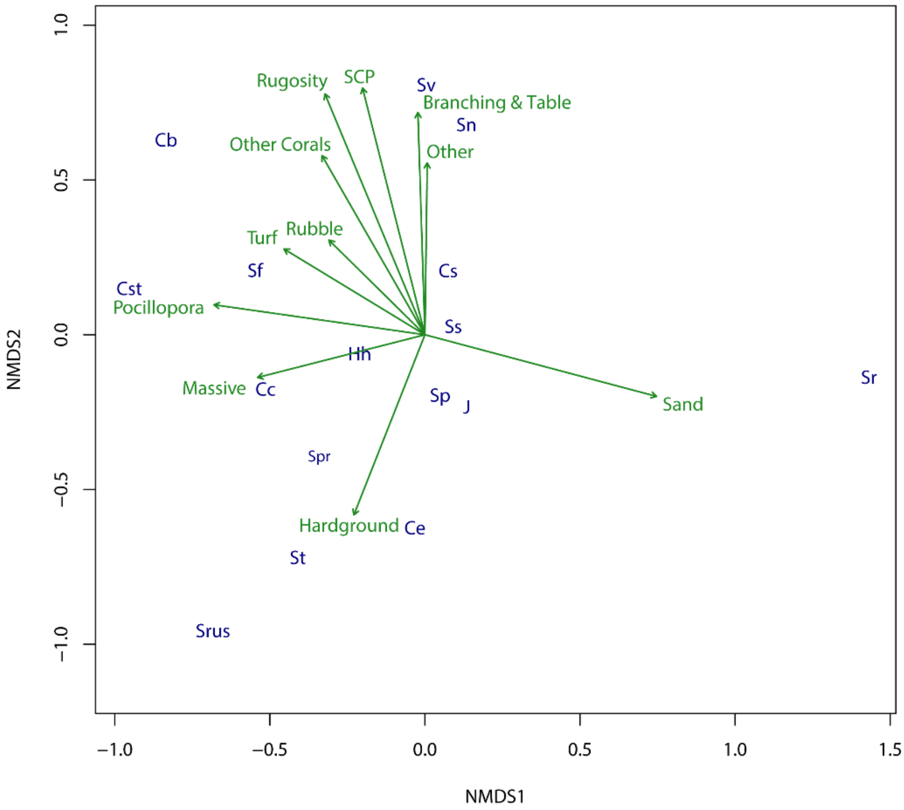


Figure 5-4 Non-metric multidimensional scaling analysis revealing environmental preferences of Vavvaru parrotfish species. The relative contribution of the environmental variables to the observed variability in species preferences is superimposed in green. Species abbreviations are as described in Figure 5-2.

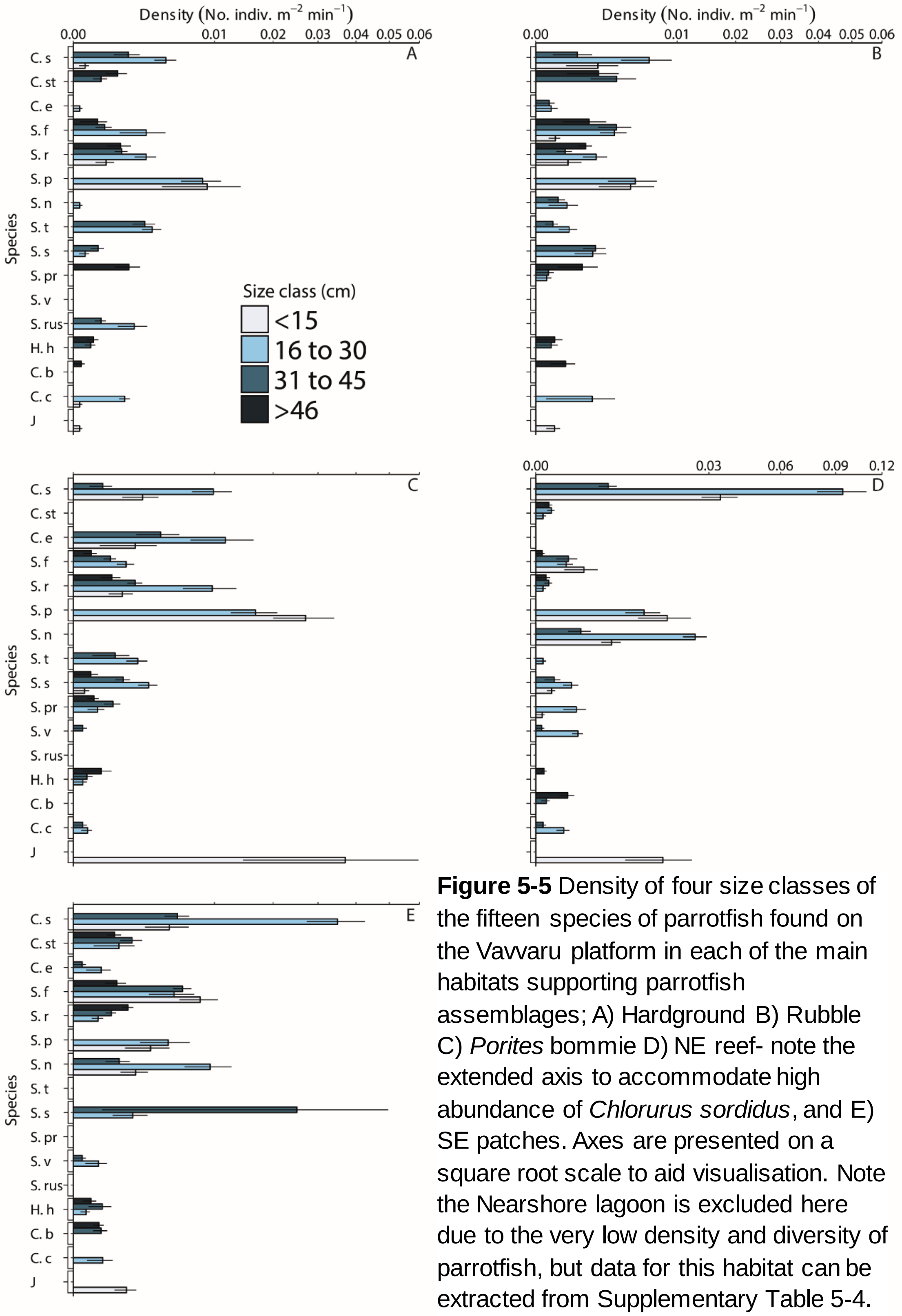


Figure 5-5 Density of four size classes of the fifteen species of parrotfish found on the Vavvaru platform in each of the main habitats supporting parrotfish assemblages; A) Hardground B) Rubble C) *Porites* bommie D) NE reef- note the extended axis to accommodate high abundance of *Chlorurus sordidus*, and E) SE patches. Axes are presented on a square root scale to aid visualisation. Note the Nearshore lagoon is excluded here due to the very low density and diversity of parrotfish, but data for this habitat can be extracted from Supplementary Table 5-4.

Species abbreviations: C. s- *Chlorurus sordidus*, C. st- *C. strongylocephalus*, C. e- *C. enneacanthus*, S.f- *Scarus frenatus,* S. r- *S. rubroviolaceus,* S. p- *S. psittacus*, S. n- *S. niger,* S. t- *S. tricolor*, S. s- *S. scaber*, S. pr- *S. prasiognathos*, S. v- *S. viridifucatus*, S. rus- *S. russelii,* H. h- *Hipposcarus harid,* C. b- *Cetoscarus bicolor*, C. c- *Calotomus carolinus*, J- Juveniles.

5.4.2 Species Contributions to Bioerosion and Inter-Habitat Variability in Bioerosion Rates

Despite the diversity of parrotfish on the Vavvaru platform, bioerosion was dominated in all habitats (except the nearshore lagoon) by excavating species (Figure 5-6; see Supplementary Tables in Appendix 1 for rates and standard errors). In the western hardground and rubble habitats, *C. strongylocephalus* were responsible for >80% of parrotfish bioerosion (0.39 ± 0.04 and 0.74 ± 0.11 kg m^{-2} yr^{-1} respectively) and were also dominant (albeit to a slightly lesser extent) in the SE patch reef habitat (>60%; 0.33 ± 0.03 kg m^{-2} yr^{-1}). These high rates were almost entirely the result of bioerosion by large (>30 cm) individuals. The *Porites* bommie habitat was an exception on the western side of the platform because no *C. strongylocephalus* were observed. Instead, *C. enneacanthus* were responsible for 55% of total parrotfish bioerosion (0.05 ± 0.01 kg m^{-2} yr^{-1}). In the NE reefs, *C. bicolor* and *C. sordidus* were the dominant bioeroders (0.22 ± 0.03 and 0.15 ± 0.02 kg m^{-2} yr^{-1} respectively). The nearshore lagoon was the only habitat where scrapers eroded more framework than excavators, but overall erosion rate in this habitat was very low (0.005 ± 0.0006 kg m^{-2} yr^{-1}).

Overall parrotfish bioerosion rates differed markedly among habitats over the Vavvaru reef platform, ranging from 0.00 to 0.86 ± 0.11 kg m^{-2} yr^{-1} (Figure 5-7, Table 5-5). Over half of overall platform-scale bioerosion occurred in the rubble habitat, despite this habitat making up only ~12% of the platform area. The NE reef and SE patches also had some of the highest total parrotfish bioerosion rates at 0.46 ± 0.03 and 0.55 ± 0.03 kg m^{-2} yr^{-1} respectively. Approximately ~20% of the platforms total parrotfish bioerosion occurred in these habitats combined. Parrotfish were not found in the central nearshore sand/rubble and lagoonal sands habitats, so were considered unlikely to make any meaningful contribution to substrate bioerosion over the area that these habitats occupy, which combined makes up over half of the platform area.

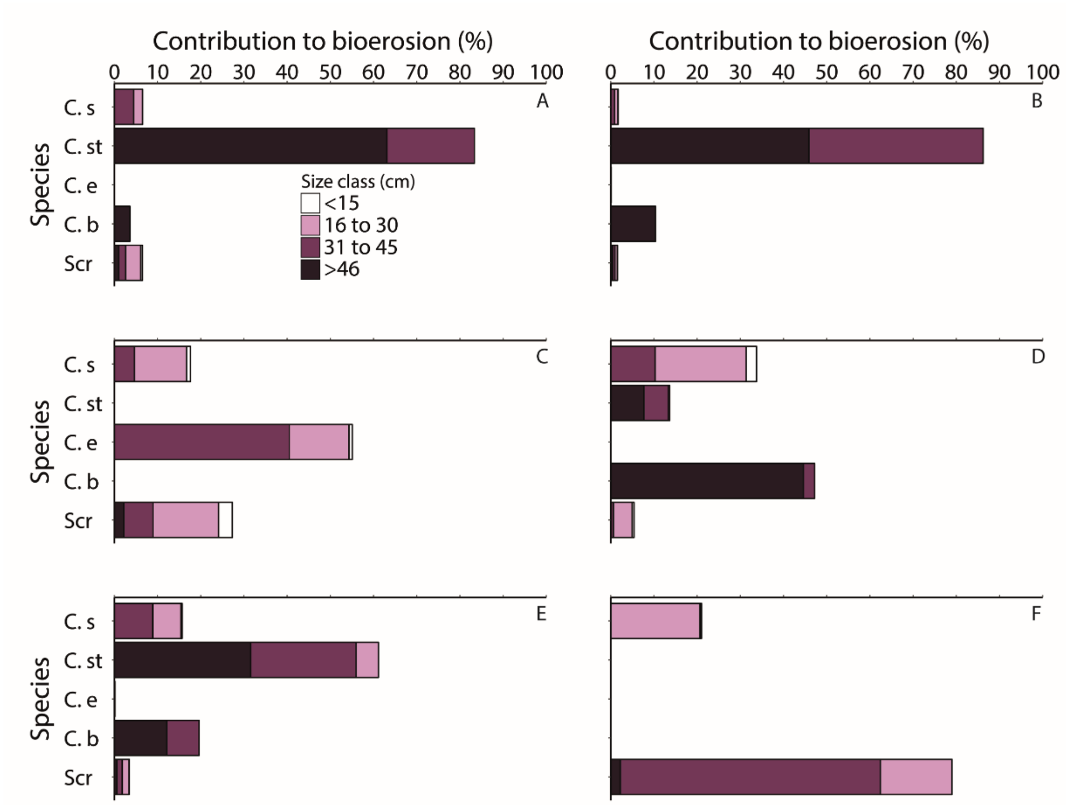


Figure 5-6 Percent contributions to total parrotfish bioerosion by four size classes of the fifteen species present in the six Vavvaru habitats supporting parrotfish: A-Hardground, B-Rubble, C-*Porites* bommie, D-NE reef, E- SE patches and F-Nearshore lagoon. Species abbreviations: C. s- *Chlorurus sordidus*, C. st- *C. strongylocephalus*, C. e- *C. enneacanthus*, C. b- *Cetoscarus bicolor*, Scr- Scrapers (pooled).

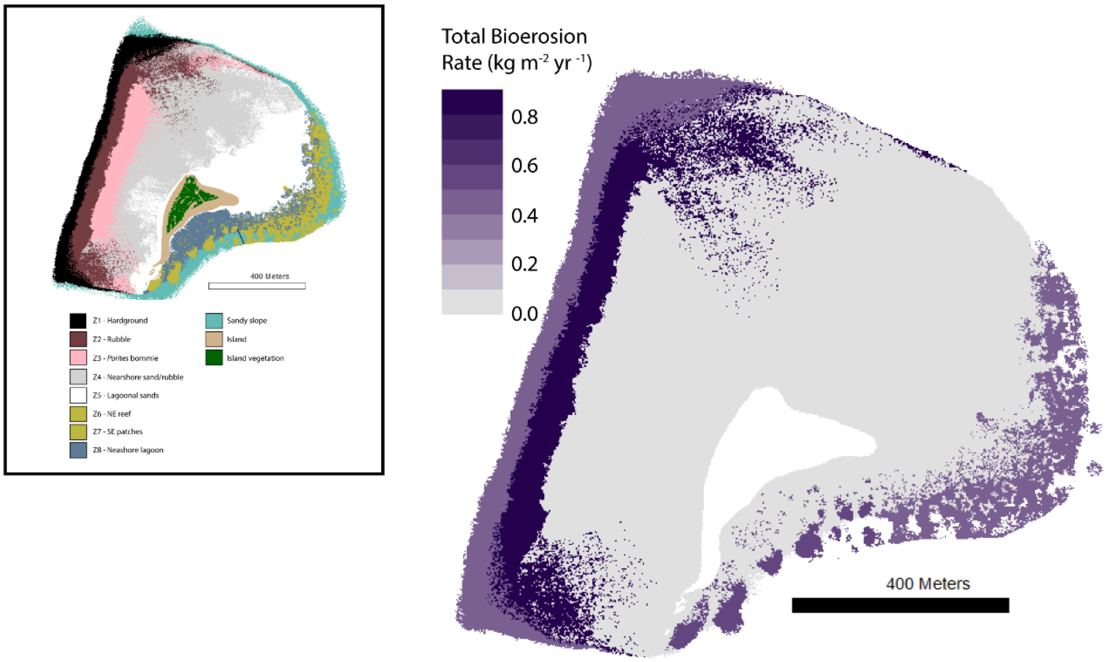


Figure 5-7 Choropleth map showing total rate of parrotfish bioerosion in each marine habitat on the Vavvaru platform. Inset of habitat map for reference.

Table 5-5 Total parrotfish bioerosion rate (± SE), total parrotfish bioerosion (± SE) and the relative % of total platform bioerosion that occurs in each of the eight habitats. The relative habitat sizes (in % of platform area) are shown for reference.

Habitat	Erosion rate (kg m^{-2} yr^{-1})	Total habitat erosion (kg yr^{-1})	% platform erosion	% platform area
Z1 – Hardground	0.46 ± 0.04	31762 ± 2607	20.76	8.25
Z2 – Rubble	0.86 ± 0.11	82697 ± 10779	54.05	11.56
Z3 – *Porites* bommie	0.08 ± 0.01	6796 ± 620	4.44	9.68
Z4 – Nearshore sand/rubble	0.00 ± 0.00	0 ± 0	0	28.93
Z5 – Lagoon sands	0.00 ± 0.00	0 ± 0	0	22.12
Z6 – NE reef	0.46 ± 0.03	23545 ± 1710	15.39	6.19
Z7 – SE patches	0.55 ± 0.03	7937 ± 479	5.19	1.74
Z8 – Nearshore lagoon	0.01 ± 0.00	276 ± 30	0.18	6.53

5.4.3 Species Contributions to Grazing and Inter-Habitat Variability Grazing Pressure

In comparison to bioerosion, a wider variety of parrotfish species and size classes had significant contributions to grazing (Figure 5-8; see Supplementary Tables 5-13 to 5-18 for calculated grazing pressures). Both scrapers and excavators contributed to substrate grazing but scrapers grazed a higher surface area compared to excavators in four of the six habitats occupied by parrotfish (Hardground, Porites bommie, and SE reef and nearshore lagoon; Tables 5-6 & 5-7). Some highly abundant species, such as *S. psittacus,* which contributed extremely little to bioerosion, proved to be very important in some habitats for grazing large surface areas of reef substrate (e.g. in the Hardground and *Porites* bommie habitat).

The surface area of substrate grazed by parrotfish also differed among reef habitats, but followed a different pattern to that of bioerosion (Figure 5-9). Parrotfish grazing pressure was highest in the NE reef habitat (110 134 ± 3848 m^{-2} yr^{-1}) - the equivalent of fully grazing the habitat every year. Relative to habitat surface area, grazing pressure on reef habitats was comparable in the *Porites* bommie and Hardground habitats (*Porites* bommie: 75%, Hardground: 84% of total habitat area) and slightly lower in the Rubble and SE patch reef habitats (Rubble: 46%, SE patches: 53%; Table 5-6).

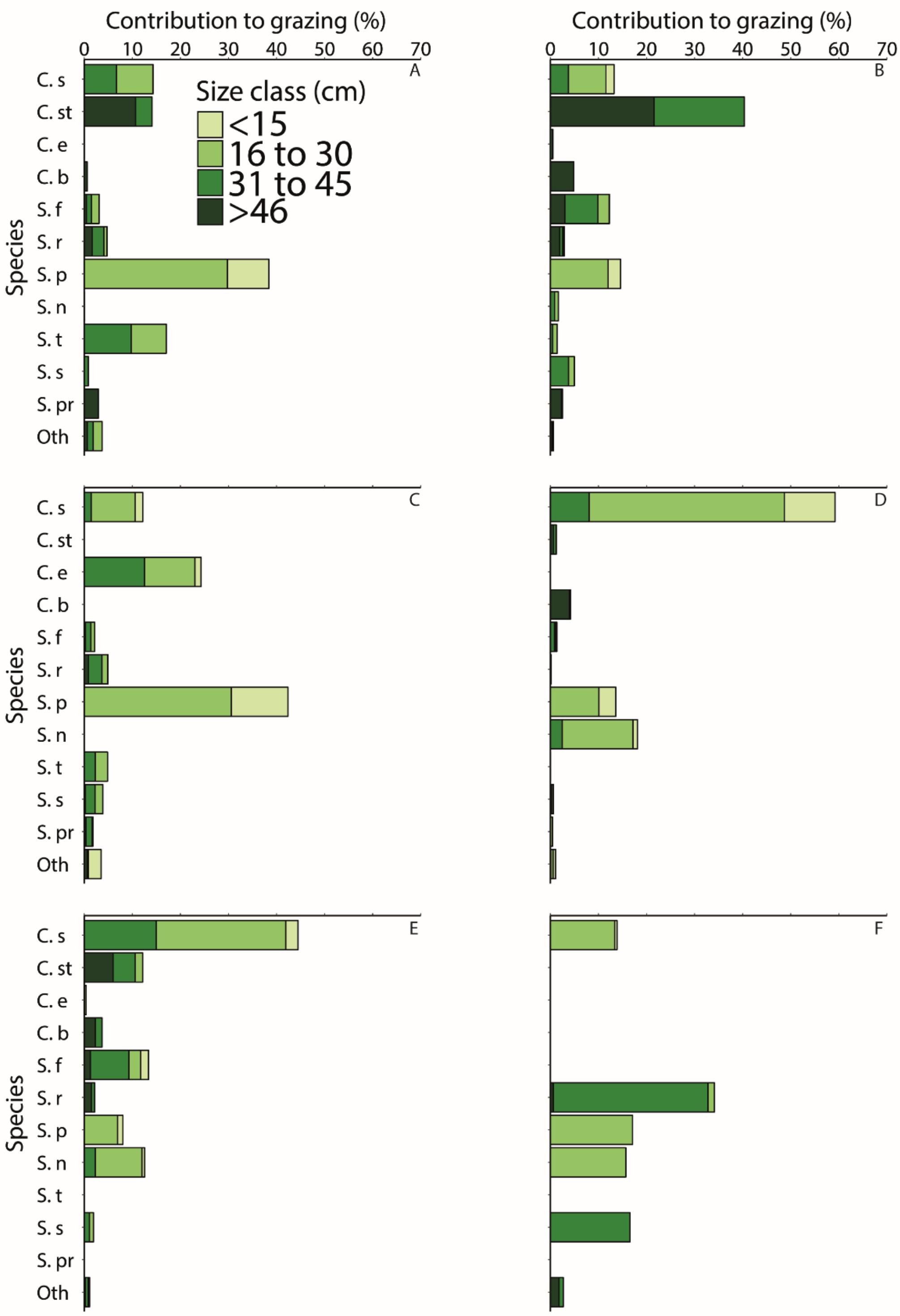


Figure 5-8 Percent contributions to total parrotfish grazing by each size class of fifteen species of parrotfish present in the six Vavvaru habitats supporting parrotfish: A-Hardground, B-Rubble, C-*Porites* bommie, D-NE reef, E- SE patches and F-Nearshore lagoon. Species abbreviations: C. s- *Chlorurus sordidus*, C. st- *C. strongylocephalus*, C. e- *C. enneacanthus*, S.f- *Scarus frenatus,* S. r- *S. rubroviolaceus,* S. p- *S. psittacus*, S. n- *S. niger,* S. t- *S. tricolor*, S. s- *S. scaber*, S. pr- *S. prasiognathos*, S. v- *S. viridifucatus*, S. rus- *S. russelii,* H. h- *Hipposcarus harid,* C. b- *Cetoscarus bicolor*, C. c- *Calotomus carolinus*, J- Juveniles.

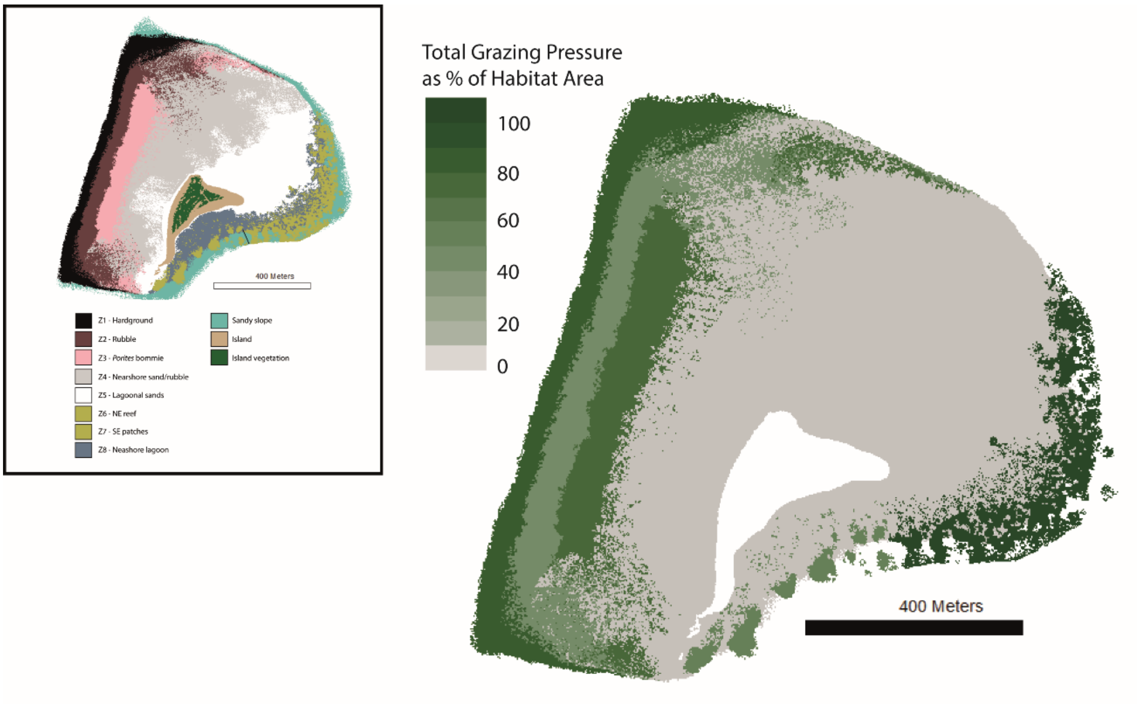


Figure 5-9 Choropleth map showing total rate of parrotfish grazing as a percentage of habitat area on the Vavvaru platform. Inset of habitat map for reference.

Table 5-6 Total area of substrate grazed by parrotfish per year in each reef habitat. Z1-8 refers to reef zones marked out in Figure 3-2.

	Z1	Z2	Z3	Z4	Z5	Z6	Z7	Z8
Habitat Area (m2)	68769	96380	80756	241250	184375	51633	14551	54465
Habitat Surface Area (m2) (Area × Rugosity)	92150	159990	107405	255725	191750	102233	32449	59367
Total area grazed by parrotfish (m2 yr-1)	77765 ± 3493	72921 ± 4079	80631 ± 36354	0	0	110134 ± 3848	17312 ± 542	3852 ± 288
% of habitat area grazed by parrotfish per year	84	46	75	0	0	107	53	6

Table 5-7 Percent contributions to bioerosion and surface area of substrate grazed by excavators and scrapers in Vavvaru reef habitats.

	Z1	Z2	Z3	Z4	Z5	Z6	Z7	Z8
Bioerosion								
Excavators	94%	98%	73%	0	0	95%	97%	21%
Scrapers	6%	2%	27%	0	0	5%	3%	79%
Grazing								
Excavators	29%	59%	36%	0	0	65%	61%	14%
Scrapers	71%	41%	64%	0	0	35%	39%	86%
Relative abundance								
Excavators	16%	34%	22%	0	0	60%	41%	17%
Scrapers	84%	66%	78%	0	0	40%	59%	83%

5.5 Discussion

Differences in benthic community, substrate type and degree of structural complexity among reef habitats can influence fish species assemblages (McClanahan 1994, McClanahan & Arthur 2001, Newman et al. 2006, Graham & Nash 2013, Komyakova et al. 2013, Darling et al. 2017, Richardson et al. 2017a). The size of holes and crevices in the reef framework can also contribute to determining the body size of fish in different habitats (Alvarez-Filip et al. 2011, Nash et al. 2013). In the case of the parrotfish, different species and size classes can vary significantly in the functional roles, such as bioerosion and grazing, that they perform on coral reefs (Bellwood 1995a, Bruggemann et al. 1996, Bellwood et al. 2003, Alwany et al. 2009, Ong & Holland 2010, Morgan & Kench 2016a, Yarlett et al. 2018). These functional roles are fundamental "top-down" processes that structure coral reefs both physically and ecologically, and so it is important to understand how they vary between reef habitats and to identify key species and size classes that contribute to them. It is also important to understand the "bottom-up" controls of habitat type on parrotfish assemblages, and how this translates to their functional roles, but this has not been as extensively studied to date.

5.5.1 Influence of reef habitat on parrotfish species assemblages and size classes

The analysis in the present study revealed that the eight delineated habitats on the Vavvaru platform were distinct in terms of their substrate type, rugosity and benthic community composition, and that each habitat supported a unique parrotfish species assemblage. Parrotfish have been shown to have relatively small home ranges (~150-300 m) and so may not venture far from these preferred habitat types (Howard et al. 2013, Welsh et al. 2013). Parrotfish density was significantly higher in rugose habitats, but only two species, *Scarus niger* and *S. viridifucatus,* appeared to be strongly dependant on high rugosity (rugosity index >1.9) habitats. These species were predominantly found in the eastern reef habitats, which were dominated by complex coral growth forms (branching and table corals). Despite being a generalist in terms of its habitat preferences, *Chlorurus sordidus* was found in particularly high densities (0.13 ind. m^{-2} min^{-1}) in the high-rugosity reef habitats (rugosity index of NE reef = 1.98 and SE patches = 2.23), particularly in the NE reef. Parrotfish have been found in previous studies to associate with areas of similarly high rugosity and structural complexity (Darling et al. 2017, Richardson et al. 2017a). One explanation for this could be that some parrotfish species use highly rugose and structural complex habitats as a refuge from predation (Hixon & Beets 1993, Bozec et al. 2013, Rogers et al. 2014). This may explain the particularly high density of <30 cm individuals in the eastern reef and *Porites* bommie habitats. Some parrotfish also sleep in crevices at night, wrapped up in mucus cocoons to avoid predator (and parasite) detection, so a certain degree of complexity would appear to be an essential habitat requirement for these species (Shephard 1994, Grutter et al. 2011).

While parrotfish densities increased with higher rugosity, the analysis in the present study revealed that a number of species (*S. prasiognathos, C. enneacanthus, S. tricolor* and *S. russelii*) actually showed an association with low rugosity (rugosity index 1.3-1.7) and massive, rather than complex coral growth forms. This disassociation with high rugosity habitats has also been observed for some *Sparisoma spp.* parrotfish in the Caribbean (Mumby & Wabnitz 2002). In the present study, these species were predominantly found in the western hardground, rubble and *Porites* bommie habitats, but the overall density in these habitats was low compared to that of the NE reef habitat (0.05 ± 0.006, 0.04 ± 0.006 and 0.14 ± 0.03 compared to 0.22 ± 0.02 ind. m^{-2} min^{-1}). Some of these species showed a strong preference for a specific habitat; *Scarus russelii* for example, was only found in the hardground habitat, perhaps showing a preference towards limestone pavement substrates, while *C. enneacanthus* was common in the *Porites* bommie habitat, but rarely observed elsewhere. No parrotfish species were found in the central lagoonal sands and nearshore sand/rubble habitats, which both had extremely low levels of rugosity (<1.06; Table 5-2). There were also low densities of parrotfish in the nearshore lagoon (rugosity = 1.09; Table 5-2). This is likely because these habitats are dominated by sand (Table 5-2; Perry et al. 2017), while parrotfish preferentially feed on dead coral and rubble substrates (Bruggemann et al. 1994a, Bellwood 1995a, Afeworki et al. 2011). One interpretation of these findings is that some topographic structure is an essential requirement for parrotfish, but the extent of suitable substrate for feeding is also a contributing factor. This suggestion is supported by observations made by Heenan et al. (2016), where it was suggested that controls on parrotfish density may be a trade-off between topographic complexity and food availability. This could explain why high coral cover habitats have been shown to support higher densities of parrotfish, yet a loss of live coral cover in these habitats and resultant increase in substrate availability for feeding could further increase parrotfish densities (as found in (Perry & Morgan 2017a, b).

The habitat preferences of *C. strongylocephalus, C. bicolor, S. frenatus and C. carolinus* were not as obvious and all these species appeared to be fairly generalist in nature. There may of course be other factors acting on the distribution of these species that were not revealed in the analyses. Firstly, species interactions may play a role in determining where certain species are found. This may explain why *C. enneacanthus* only occurred in the *Porites* bommie habitat – one of the few Vavvaru habitats where *C. strongylocephalus* were not observed. One reason for this could be competition for specific feeding resources if two species preferentially feed on the same specific microhabitat or on the same part for the substrate. For example, Adam et al. (2015) found that if two parrotfish species had matching feeding habits, they would typically be found in different areas of the reef. Secondly, physical or hydrodynamic factors may be a contributing factor to species distributions, but were not included in our analyses. However, the separation in species that appear to prefer the western or eastern habitats may, at least in part, be defined by exposure. The western atoll-edge habitats are more exposed, endure greater wave energy and stronger currents and also stronger monsoon winds compared to the more sheltered eastern habitats. Wave energy and currents are known to influence reef fish species assemblages and also affect fish swimming performance, so it is likely that these factors have a role to play in the observed species distributions (Fulton et al. 2001, Friedlander et al. 2003, Fulton & Bellwood 2004, Harborne 2013, Bejarano et al. 2017). Another factor that may contribute to species distributions is distance from the reef slope. Parrotfish have been observed to be more abundant and diverse near to the reef edge (Friedlander & Parrish 1998). However, in the present study, platform perimeter habitats did not necessarily have a higher parrotfish density (e.g. the *Porites* bommie habitat had a higher density than the hardground habitat), but they did have greater species diversity and accommodated larger parrotfish. This was especially pronounced on the western side of the platform (Figure 5-5).

5.5.2 Inter-habitat variability in overall parrotfish bioerosion rate and grazing pressure

Over 90% of total platform-scale parrotfish bioerosion occurred in the hardground, rubble, and NE reef habitats despite, combined, making up just 26% of the total platform area. Nearly 55% of this bioerosion occurred in the Rubble habitat alone, showing that over a reef scale, bioerosion and the resultant sand generation can be important over small spatial scales relative to the total reef area. The important contribution of the rubble habitat was partly because of the high overall parrotfish bioerosion rate in this habitat (0.86 ± 0.11 kg m^{-2} yr^{-1}), but also because it was the largest reef habitat in which parrotfish were found (96380 m^{-2}; ~12% of the platform area). Overall habitat bioerosion rates were driven by the density of excavators, rather than overall parrotfish density, even if scrapers heavily outnumbered excavators in terms of both density and biomass. For example, in the rubble habitat, the high bioerosion rate was because of a relatively high density of large excavator *Chlorurus strongylocephalus* (0.005 ± 0.002 ind. m^{-2} min^{-1}; species erosion rate for the rubble habitat = 0.74 ± 0.11 kg m^{-2} yr^{-1}) compared to other habitats. This species accounted for >80% of bioerosion in both the rubble and hardground habitats, despite making up only ~3% and ~12% of the relative abundance, respectively. The eastern NE reef and SE patch reef habitats also had reasonably high overall bioerosion rates (0.46 ± 0.03 and 0.55 ± 0.03 kg m^{-2} yr^{-1} respectively) but because of their relatively small spatial extent (51633 and 14551 m^{-2} respectively) the total quantity of framework eroded per year in these habitats was lower than that of the rubble habitat. There are of course other bioeroding organisms that contribute to total bioerosion rates (such as other fish groups, sponges, urchins, and boring molluscs) but previous work has shown that parrotfish are responsible for up to 80% of total bioerosion at Vavvaru, and on other Maldivian coral reefs (Perry et al. 2015a, Perry et al. 2017). These inter-habitat patterns of bioerosion are therefore likely representative of patterns of overall bioerosion rates, with the contributions of other organisms unlikely to significantly alter these patterns.

However, the habitat scale bioerosion rates presented in the present study are lower than that reported for the same site in Perry et al. 2017. This may partly be because of the lower local bioerosion rates for scrapers used in the present study (derived from Yarlett et al. 2018 – Chapter 4) compared to other reports for scrapers in the literature (e.g. Alwany et al. 2009, Ong & Holland 2010). In addition, the present study used a new approach to estimating rates of processes by examining how many parrotfish of different species and sizes are using a given area of reef over a given period of time. Typically, annual bioerosion rates are calculated from abundance or biomass estimates derived from UVC, which may yield different results and potentially over-estimate reef fish abundance (Lincoln Smith 1998, Ward-Paige et al. 2010). The RUV approached used in the present study is considered to appropriate for the aims of the study to estimate the rates of key parrotfish functional roles (Table 5-3).

Overall parrotfish substrate grazing pressure showed a different spatial pattern to that of bioerosion, showing that these functional roles are not necessarily tightly coupled. Unlike bioerosion rates, grazing pressure increased with overall parrotfish density, reaching a peak in the NE reef habitat at 110 134 ± 3848 m^{-2} of reef substrate yr^{-1} (more than the equivalent of fully grazing the habitat every year). This was driven by small excavator *C. sordidus* and scrapers *Scarus niger* and *S. psittacus,* which contributed 59, 18 and 14% to NE reef grazing pressure respectively. This inter-habitat variability may be because different habitat types can have different requirements for grazing pressure by parrotfish, and grazing pressure in general (Mumby 2016). As well as parrotfish foraging, there are other factors that influence grazing pressure on coral reefs, such as physical factors, and other reef organisms. Mumby (2016) suggested that different habitat types have different requirements for grazing pressure, with physical factors playing a more important role in some reef habitats. This may be the case for the western (hardground, rubble and *Porites* bommie) habitats at Vavvaru, which typically have a lower grazing pressure (up to 84% of the habitat area per year) compared to the more sheltered eastern reef habitats (up to 107% of the habitat area per year). In addition, parrotfish are not the only abundant grazers on the Vavvaru platform, and it is likely that other families such as surgeonfish and rabbitfish also have a significant influence on reef grazing pressure, and potentially their own unique inter-habitat patterns.

There are numerous studies investigating the influence of parrotfish fishing bans on reef resilience and coral recovery (McClanahan 1994, 1995, McClanahan & Arthur 2001, Mumby 2016, Mumby et al. 2006, 2012, Mumby 2006, Mumby & Harborne 2010, McClanahan 2011, Blackwood et al. 2012, Carassou et al. 2013, Kennedy et al. 2013, Bejarano et al. 2013, Steneck et al. 2014, O'Farrell et al. 2015, Bozec et al. 2016). Before making assumptions that protecting parrotfish will increase coral recovery, it is important to understand the capacity of the habitat in its current state to support a community of key grazing species. Environmental factors can influence the diversity, abundance and functional characteristics of local herbivorous fish communities (Cheal et al. 2013). A habitat that was once topographically complex with high coral cover may have been able to support a substantially higher parrotfish density than the post-degradation state with lower coral cover and topographic complexity. If this assumption is true, a parrotfish fishing ban may not work as effectively as anticipated.

The differences in the patterns of bioerosion and grazing are interpreted to be a function of the spatial distributions of key contributing species to these functional roles, controlled by habitat type. Contributions to the surface area of reef grazed were spread across a larger number of species and size classes compared to bioerosion. While contributions to bioerosion were dominated by excavating species, scrapers were found to have a considerably higher contribution to substrate grazing, and were dominant over excavators in four habitats (the hardground, *Porites* bommie, SE patch reefs and nearshore lagoon habitats). While the bites of scrapers may be smaller, the feeding rate for many scraping species in the Maldives is considerably higher (Yarlett et al. 2018). However, the fact that contributions to grazing are spread across a larger number of species compared to bioerosion, does not necessarily infer functional overlap. Previously, parrotfish have been categorised broadly into one of three functional groups, e.g. scrapers, excavators or browsers (Bellwood & Choat 1990, Green & Bellwood 2009, Cheal et al. 2012), but recent work has begun to show how different species can have different sub-roles within these broad categories. For example, Brandl & Bellwood (2014) found that different species, even those closely related such as *S. frenatus* and *S. oviceps* (Choat et al. 2012), utilise different microhabitats for feeding. This may explain the shifting dominance by different species in each habitat in terms of grazing and bioerosion rates. Different species may be better adapted to different substrate or habitat types, resulting in less functional overlap than one might initially assume. For example, *C. strongylocephalus*, especially at larger size classes may primarily utilise open, convex substrates for feeding and may not be able to feed under overhangs or between complex structures. This species is therefore unlikely to be able to perform the same role as the smaller excavator *C. sordidus,* which can utilise a much wider range of microhabitats due its size and mobility (Brandl & Bellwood 2014). Size is important to consider in the context of functional overlap between species and sizes of parrotfish and requires further investigation. A small (<20 cm) parrotfish may be able to utilise microhabitats that a larger individual of the same species cannot, and so may still be important despite a lower bioerosion or grazing pressure. Larger parrotfish may also be under lower predation pressure, and may be more likely to graze substrates with lower topographic complexity where smaller individuals may not venture.

5.5.3 Implications for coral reef ecosystems

The present study found that overall contributions of parrotfish to bioerosion and grazing varied markedly among eight reef habitats on an atoll-edge reef platform (Vavvaru), but these processes were not tightly coupled. It is suggested that both roles should be examined separately because they are influenced by different species and supported by different habitat characteristics. Previous studies focussing on the ecological roles of parrotfish (algal grazing), have suggested that parrotfish may not be ecologically important in rubble habitats because they can be poor habitats for corals (Adam et al. 2015). While the Vavvaru rubble habitat had a relatively low parrotfish grazing pressure and coral cover, this habitat had the highest overall parrotfish bioerosion rate. As a result, this habitat is likely the most important overall source of new biologically derived sediment for the reef platform at this site. Other studies have found that in some locations, fishing bans on “herbivorous” fish populations are having minimal effect on reef resilience (Carassou et al. 2013, Russ et al. 2015), but physical functional roles were not considered, and it may be that these habitats had other contributions to the reef system.

Sites in the southern Maldives suffered up to 75% coral mortality during the 2016 bleaching event in habitats comparable to eastern reefs at Vavvaru (Perry & Morgan 2017a). This resulted in a shift from a positive to net erosional budget state because of a loss of carbonate producers and increase in parrotfish bioerosion (Perry & Morgan 2017a, b), presumably caused by increased substrate availability for feeding, although there is currently little understanding of how availability and distribution of food resources (particularly cyanobacteria) influences parrotfish demographics. Questions remain over what influence the loss of topographic structure will have on the parrotfish assemblages (Perry & Morgan 2017a). If the reef structure were to collapse (due to persistent bioerosion or physical damage by waves or monsoon winds), available evidence suggests that the loss of structure may have a detrimental effect on parrotfish density (Graham 2014, Rogers et al. 2014). Results from the present study suggest that a loss of complexity may have particularly detrimental effects on species that rely on complex habitat types such as *S. niger* and *S. viridifucatus*. Reduced parrotfish density may reduce grazing pressure and bioerosion rate, which could result in an increase in algal abundance, reduced coral recruitment, and reduced sediment supply, although this would depend on the response of different species (see Chapter 7). Another bottom-up control on parrotfish assemblages that warrants further investigating is availability of food resources (particularly endo and epi-lithic cyanobacteria), particularly as there is evidence of within habitat spatial variability in bite intensity, which is thought to be caused by resource availability (Carlson et al. 2017).

In addition to the stressor of habitat degradation, parrotfish are unsustainably exploited in many island settings (Newton et al. 2007). Typically, the larger, more commercially viable individuals (often excavators) are extracted (Aswani & Sabetian 2010, Bellwood et al. 2012, Hamilton et al. 2016), thereby reducing mean fish size (Taylor et al. 2015). Large *Chlorurus spp.* for example, which are dominant bioeroders in the present study, have been shown to decline in abundance along a gradient of human fishing pressure (Bellwood et al. 2012). In contrast, small *Chlorurus spp.* have been shown to increase in abundance (Bellwood et al. 2012), presumably due to reduced competition for food resources, and the adaptability of the species to utilise a wide range of microhabitats (Brandl & Bellwood 2014). However, it is uncertain whether *C. sordidus* (or related species within the clade) are capable of compensating for the loss of large *C. strongylocephalus* (or related species within the clade) in terms of bioerosion. If bioerosion rates were to decline, this could reduce rates of sediment production, and may have a negative impact on reef island maintenance, and over long timescales (decades-centuries) may influence the capacity of reef islands to match rates of projected sea level rise (see Chapter 7 for further discussion). When considering measures to protect coral reefs, efforts to maintain a diversity of habitats is important to accommodate the wide range of fish species (Friedlander et al. 2003) and the important functional roles that they perform (Richardson et al. 2017a).

Further research into the bottom-up controls of habitat on parrotfish assemblages, and how this translates to their functional roles, will be essential as reefs undergo an unprecedented rate of environment change (Hoey et al. 2016a, Hughes et al. 2018). While previous work has examined the impact of fishing pressure on parrotfish assemblages, the impacts of this pressure on community level functional roles (Bellwood et al. 2012), and the impacts of habitat degradation on parrotfish functional roles are less well studied. In addition, there is little understanding of how these impacts vary among habitats (Nash et al. 2012). These issues are addressed in greater detail in Chapter 7.

Chapter 6 Parrotfish sediment production on a Maldivian reef platform: sedimentary products and the relative importance of new and reworked sediments

Photo taken from Vavvaru Island looking over the nearshore lagoon, south-east patch reefs and sand channels. Parrotfish are likely to be significant sediment suppliers to these environments. Photo credit: Robert T. Yarlett

6.1 Context

Sediment production on coral reefs is directly linked to reef framework construction and sediment supply to reef habitats and reef associated islands and beaches. One of the most persistent forms of sediment production is that by parrotfish, but we have little understanding of how production rates vary among reef habitat types with different parrotfish species assemblages, or the relative importance of sediment produced from eroded, reworked, and endogenous sources. In addition, available data on the grain size distribution and types of sediment produced, which may influence the fate of the material within the reef system, are sparse. In this chapter, I investigate research question 3, which asks how overall sediment production rates vary among reef habitats and the relative importance of reworked sediment, and research question 4, which asks what grain sizes and types of sediment are produced by parrotfish and how the quantity of different types of sediment produced varies among reef habitats. To achieve this, I address objective 5, which asks how contributions of different parrotfish species and size classes to sediment reworking varies among reef habitats on the Vavvaru reef platform, and combine these data with bioerosion rate estimates presented in chapter 4, to estimate total sediment production in each habitat, thereby addressing objective 7. Objective 6 is also addressed, which asks what grain size distribution and grain types are produced by parrotfish. These are compared to loose sediments in each habitat and that of local reef islands. The relative importance of endogenous carbonate production is also examined, addressing objective 8.

6.2 Introduction

Sediment production is a fundamental process contributing to the maintenance of both marine and coastal habitats in coral reef environments, including sandy lagoons, benthic sediments, seagrass meadows, reef islands and beaches (Hutchings 1986, Kench & Cowell 2000, Perry et al. 2015a). Reef sediment production can result from either physical (mechanical disturbance by waves and storms), chemical (marine cement precipitation) or biological (scraping, excavating, etching, boring and endogenous production by reef organisms) processes (Glynn 1997, Perry & Hepburn 2008, Perry et al. 2012). In some regions, biological sediment production, primarily as a result of bioerosion by reef animals (e.g. fish, urchins, sponges and molluscs), is a persistent and significant source of sediment on coral reefs (Scoffin et al. 1980, Bellwood 1995b, Glynn 1997, Perry et al. 2012). A number of factors can influence the fate of sediment within the reef system, such as grain size and type, density and shape (Braithwaite 1973, Kench & McLean 1996, Kench 1997), as well as physical and hydrodynamic processes operating within the system, such as wave energy and currents. Of these, the grain size distribution of sediments is one of the most important factors influencing where and how sediments get transported (Blott & Pye 2001).

In the central Indian Ocean, parrotfish are often the dominant biological sediment producers, and can account for over 85% of biological sediment production on some Maldivian coral reefs (Perry et al. 2015a, Perry et al. 2017). Using their unique beak-like feeding apparatus, parrotfish erode reef framework (in some cases reportedly up to several hundred kg individual^{-1} yr^{-1}; (Bellwood 1995a, Bruggemann et al. 1996, Bellwood et al. 2003, Alwany et al. 2009, Morgan & Kench 2016a, Yarlett et al. 2018) whilst feeding predominantly on dead coral and rubble substrates (Bruggemann et al. 1994a, Bellwood 1995a, Afeworki et al. 2011). In doing this, parrotfish are thought to be targeting protein rich epi and endolithic cyanobacteria (Clements et al. 2016). Parrotfish also consume loose sediments that have settled on these substrates or have been retained within the Epilithic Algal Matrix (EAM) (Scoffin et al. 1980, Bellwood 1996, Bruggemann et al. 1996). The eroded framework and loose sediment is ingested along with organic matter, broken down by modified gill arch elements known as the pharyngeal mill (Bellwood & Choat 1990, Carr et al. 2006), processed in the gut, and egested back into the environment as sediment (Bellwood 1995b, 1996, Morgan & Kench 2016a). Parrotfish have also been observed to transport carbonate sediments as a result of their movements between feeding and defecation areas and can potentially move sediments between reef habitats or off slope (Bellwood 1995b). In addition, to our knowledge, all marine teleost fish produce calcium carbonate endogenously as a by-product of osmoregulation. This process removes excess calcium ions from the body and prevents renal stone formation (Walsh et al. 1991, Wilson et al. 1996, 2009, Wilson & Grosell 2003, Perry et al. 2011b). This material is egested into the environment in mucus coated pellets and may contribute fine (silt grade) carbonates (low to high Mg –calcite, aragonite and amorphous carbonates) to sediments (Perry et al. 2011a, Salter et al. 2012). While endogenous carbonate production has been investigated in a number of fish families, including browsing parrotfish (Salter et al. 2012), it has not been investigated in carbonate ingesting scraping or excavating parrotfish (as defined by Bellwood & Choat (1990).

The total quantity of sediment produced by parrotfish, and the relative importance of new sediment generated by bioerosion, reworked existing sediment, and new endogenously produced sediment depends on what species and sizes are present within a habitat. Hoey & Bellwood (2008) examined variability in parrotfish functional roles on inner, mid and outer-shelf environments on the Great Barrier Reef, but there has been little further work examining how overall rates of parrotfish sediment production and reworking vary between habitat types in other coral reef ecosystems. In addition, we have very little understanding of the characteristics of parrotfish sediments, such as the grain sizes and types of sediment produced by different species, feeding modes (scrapers and excavators), and size classes (see Gygi 1975, Bellwood 1996, Hoey & Bellwood 2008 and Morgan & Kench 2016 for examples of a few species). The aims of this study are therefore to: 1) investigate rates of sediment production as a function of parrotfish species and size class, and examine the relative contributions of new (from bioerosion and endogenous production) to reworked existing sediment, 2) examine the sedimentary characteristics (grain size and type) of the material produced by a range of representative species and sizes of parrotfish, and 3) calculate how overall parrotfish sediment production and reworking rates vary among reef habitat types as a function of the species and sizes of parrotfish present.

6.3 Methods

Estimates of sediment reworking rates, total sediment production and sediment grain sizes produced in each habitat are made in the present study using the primary data collected as shown in Figure 6-1. Note, sediment production rate is derived from bioerosion rate estimates presented in Chapter 4 and the endogenous carbonate production work was carried out on conspecifics at Lizard Island Research Station, Australia.

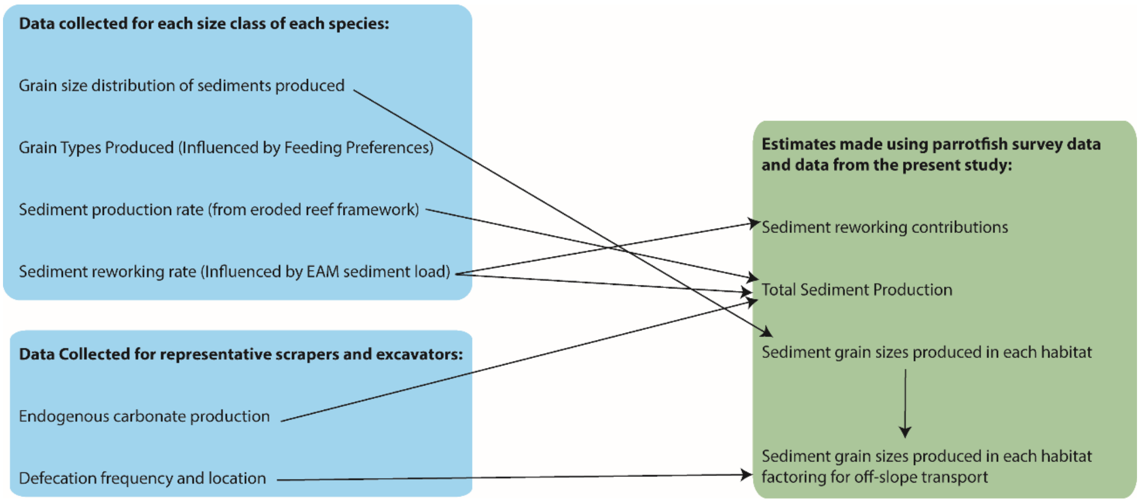


Figure 6-1 Methods diagram showing how primary data collection in the present study, along with parrotfish survey data are used to makes estimates of sediment reworking contributions, total sediment production and the grain sizes of sediment produced by parrotfish in Vavvaru reef habitats.

6.3.1 Faecal Sample Collection

Faecal samples were collected in the field from initial and terminal phase *Chlorurus sordidus, C. strongylocephalus, Scarus niger, S. frenatus, S. psittacus,* and *S. rubroviolaceus* in the following size classes: < 15 cm, 16 to 30 cm, 31 to 45 cm and > 46 cm (n = > 5 per size class per species). Individuals of target study species were observed until defecation was observed. Where possible, the excreted faecal pellet was collected using a large bulb pipette, and transferred to a 15 ml falcon tube. This required the fish to defecate near to the seafloor to prevent dispersal, and for the material to land on an accessible substrate with minimal potential for contamination by benthic sediments. This approach was used successfully in Morgan & Kench (2016a) and was chosen to avoid having to harvest >150 parrotfish for gut content analysis. Samples were transported to the laboratory, where they were left to settle out before decanting the seawater and rinsing in distilled water to remove salts. The samples were then bleached (5% sodium hypochlorite solution) for ~ 15 mins to neutralise organics (but avoiding excessive soaking time and potential risk of sample dissolution – Salter, personal communication) and transferred to a vacuum filter chamber with a 0.4 µm Whatman cellulose nitrate filter. Samples were then rinsed thoroughly in ~50 ml of distilled water. The filter with retained sediments was then removed from the chamber, dried and packaged for transport in preparation for grain size and composition analysis. Prior to further analysis, sediments were poured off the filter paper into a sample tube, and any sediments retained on the filter were gently scraped off using a blunt pair of tweasers to ensure retention of fines. Note that in the present study, samples collected from large (reaching marginally over 45 cm) *Scarus frenatus* were categorised into the largest size category (> 45 cm size category).

6.3.2 Sediment Grain Size and Type Analysis

The grain size distribution of the parrotfish faecal sediments collected was measured using laser diffraction. Five replicates of each size class of each target parrotfish species was analysed using a Malvern mastersizer 2000, which measured the equivalent spherical volume of each grain. Five “technical” replicates of each of these samples were collected to ensure data validity, and to account for any variation due to irregular grain shapes.

The proportion of different grain types in these sediment samples was examined using a Scanning Electron Microscope (SEM). Sub-samples of dried parrotfish faecal sediments were prepared by mounting onto aluminium SEM stubs using a double sided adhesive and coating with 20 nm of Gold/Palladium before being imaged under SEM. The SEM was prepared with a working distance of ~16 mm, an operating voltage of 10 kv and spotsize of 30. Magnification was adjusted until the surface structure of the grains in the field of view were clearly identifiable, often incorporating ~50 to 100 grains. A series of images with no overlap were taken systematically across the stub until at least 300 grains from the sample were imaged. During image analysis, each grain was identified into one of the following categories; Coral, Coralline Algae, *Halimeda spp.*, Mollusca, Foraminifera and where accurate ID was not possible, Unidentified. A minimum of 300 grains were identified per stub as considered representative of the composition (Cheetham et al. 2008). A thorough search for endogenous carbonate grain morphologies was also carried out at high magnification (X4000) allowing clear view of grains <2 µm in size in each sample.

6.3.3 Feeding Preferences and Defecation Rates

Feeding preferences of parrotfish were recorded to compare with grain type data. Bite rate observations were carried out as described in Chapter 4 (Yarlett et al. 2018). For each bite observed, the substrate type was recorded into one of the following categories: dead coral/rubble, live coral, coralline algae, *Halimeda spp.*, and sand. Defecation rate data were also collected during these observations to aid estimates of how often parrotfish were defecating in different areas. This was carried out by recording the number of defecations observed by the target individual within a five-minute observation.

6.3.4 Parrotfish Sediment Reworking Rates

To estimate the rate of sediment reworked by different size classes of parrotfish species, it was assumed that all bites ingested loose sediment retained within the Epilithic Algal Matrix (EAM). Grazing scars observed in all habitats in the present study typically “cleaned” the area of the bite down to the underlying substrate, so it was assumed that all sediment retained within the bite area was ingested. To estimate sediment reworking rates, the surface area of substrate grazed per bite by different size classes of each species was extracted from Chapter 5 (Table 5-1) and multiplied by the quantity of sediment found in that unit area of substrate for each habitat. Individual sediment reworking rates were then calculated as follows:

$Sediment\ Reworked\ (kg\ individual^{-1}\ min^{-1}) = Bites\ Per\ Minute\ (bpm) \times Sediment\ Ingested\ Per\ Bite\ (kg)$

Sediment reworking rates for each size class of each species observed during the video was then estimated using the following equation:

$VRSS\ (kg\ survey\ area^{-1}\ video\ duration^{-1}) = No.\ individuals\ observed \times residence\ time\ (s) \times reworking\ rate\ (kg\ ind^{-1}\ s^{-1})$

Where VRSS = Video reworking for each size class of each species.

These values were then converted to sediment reworking rates per m^2 using the estimated survey area of the video, and then to annual reworking rates (ARR) per m^2 by scaling to the length of the feeding day (11 hours; Yarlett et al. 2018) and multiplying by 365. This was repeated for all 15 replicate videos in each habitat before finding an average annual erosion rate for each size class of each species.

Finally, total sediment reworking rates for each habitat were estimated using the following equation:

$TAHR\ (kg\ habitat\ area^{-1}\ yr^{-1}) = \sum ARR\ (kg\ m^{-2}\ yr^{-1}) \times habitat\ area\ (m^2)$

Where TAHR = total annual habitat reworking. To compare total rates and spatial coverage of parrotfish sediment reworking over the reef platform, a choropleth map was produced in ArcMap 10.3.1 using the habitat map (Figure 3-2A) and the values calculated for total parrotfish sediment reworking.

6.3.5 Sediment Load within the Epilithic Algal Matrix (EAM)

Three loose substrate (rubble) samples (~ 50 cm^{-2}) were collected randomly from each habitat where parrotfish were found (Hardground, Rubble, *Porites* bommie, NE reef, SE patch reefs, and the eastern Nearshore Lagoon). No samples were collected from the western Nearshore Sand/Rubble or Lagoonal Sands habitats because no parrotfish were observed there (see Chapter 5). Each sample was retrieved from the reef and immediately (and carefully) placed in a zip lock bag to be transported to the lab. The height of epilithic algae was measured at 15 random points for each habitat on the collected rubble samples using Vernier callipers. The exposed surface of the rubble samples (i.e. the surface that parrotfish were able to feed on) was carefully rinsed and scrubbed using a wire brush to remove loose sediment and collected in a beaker, taking care not to dislodge sediment from other surfaces. The collected sediment was rinsed in distilled water to remove salts, soaked in 5% sodium hypochlorite solution (bleach) to neutralise organics, and rinsed a further two times in distilled water to remove the bleach before being dried and weighed. During each cleaning step, the sediment was left long enough to fully settle out before decanting the supernatant, ensuring that all sediment was retained, but reducing unnecessary soaking time which may increase the likelihood of dissolution. The surface area of each substrate sample was measured by wrapping foil around the exposed surface, which was then removed, laid flat, and photographed next to a ruler used for scale. The surface area of the foil, which corresponds to that of the rubble substrate, was then measured using the software image J. This method was chosen over collecting sediment in a quadrat or hoop area using underwater vacuums due to the topographic heterogeneity of the substrate, and so to avoid the risk of overestimating sediment load in the samples. A sub-sample of sediments collected from the EAM in each habitat were also analysed using laser diffraction as described in section 6.3.2.

6.3.6 Endogenous Carbonate Production

To investigate whether parrotfish produce endogenous carbonates, an addition set of experiments was carried out on fish collected on reefs around Lizard Island, Australia. This site was used because of the excellent lab and aquarium facilities on offer at Lizard Island Research Station, that weren’t available at sites in the Maldives. Parrotfish (3 x *Chlorurus spilurus* and 15 x *Scarus psittacus*) were collected using barrier nets, and transported to aquaria in aerated seawater transport containers. Individuals were then grouped by species and size and kept in aerated aquaria with running seawater pumped from local shallow waters. These aquaria were filtered to 1 µm to minimize external sediment or organic matter inputs and thereby prevent fish from ingesting sediment material during sampling. Temperature, pH and salinity in the aquaria was regularly monitored and ranged between 29-32 °C, a pH of 8.00-8.23, and a salinity of 34. False floors were used to allow faecal pellets to sink out of reach of the fish. Fish were left unfed for two days to allow egestion of any food ingested prior to capture and adjust to aquarium conditions. The aquaria were then thoroughly cleaned before the start of sample collection. Any carbonates produced from this point were assumed to be produced endogenously, and were collected within 24 h of egestion using Pasteur pipettes. These carbonates were then rinsed with distilled water to remove salts and soaked in 5% sodium hypochlorite (bleach) for ~20 mins to remove organic components. Two additional rinse steps were applied to ensure removal of salt and bleach residues. The cleaned sample was oven-dried at 40°C and packaged for transport. Once sample collection was completed, fish were transported in aerated containers by boat and released at the same site that they were caught.

6.3.7 Total Parrotfish Sediment Production

New sediment production rate for each size class of each species (i.e. sediment produced from eroded reef framework) was assumed to match bioerosion rate (as presented in Yarlett et al. 2018 and Chapter 4), as there is currently no concrete evidence for dissolution of carbonates within the gut, and there have been no attempts to quantify “messy feeding” whereby eroded material is not ingested. Total sediment production for each habitat was estimated as follows:

Total Sediment Production = Bioerosion + Reworked Sediment.

Endogenous carbonates were not factored into estimates of total sediment production because minimal production occurred, as detailed in the results.

6.3.8 Parrotfish Movement between Feeding and Egestion

The height of defecation from the seabed was estimated for 210 parrotfish representing scraping and excavating species (*C. sordidus, C.*

strongylocephalus and *S. niger*). Individuals of target study species were observed on a first seen basis, recording the species, size and life phase. For every defecation observed, the height from the seabed was estimated, and categorised into one of the following categories: 0-25 cm, 25-50 cm, 50-100 cm, >100 cm. Observations of parrotfish movements between feeding and defecating were carried out on 174 individuals from the following species; *C. strongylocephalus*, *C. sordidus*, *S. niger*, *S. frenatus*, *S. psittacus*, *S. rubroviolaceus*. Observations primarily took place on the eastern side of Vavvaru, because of the close proximity of different reef, lagoon and slope habitats, making it an ideal area to record movements between reef habitats. Individuals of a target study species were chosen at a first seen basis, and observed from feeding, until defecation was observed. Any movement between feeding and defecation areas was recorded into one of the following categories: 1) defecated whilst feeding, 2) defecated in feeding area/same habitat, 3) movement to apparent 'defecation zone', 4) movement to adjacent habitat to defecate or 5) defecating off slope.

6.3.9 Quantifying the production of different sediment size fractions in reef habitats

The annual production rate of different sediment size fractions (from <32 µm to 2000 µm along the Udden-Wentworth scale – Wentworth 1922) in each habitat was estimated from total annual sediment production by each size class of each species and the grain size distributions presented in the present study. Sediment transport by species known to egest sediments off slope (estimated from direct observations in the present study) was factored into calculations for perimeter habitats (Hardground, NE reef, SE patches).

6.3.10 Statistics and Error Propagation

Descriptive sedimentary statistics (D_{10}, D_{50}, D_{90} and sorting) were calculated using Gradistat (Blott & Pye 2001).

Many of the calculations in the present study involved summing or multiplying variables, each with their own associated standard errors. In these calculations, the following rules for error propagation were used. For multiplication:

$$SEv = \sqrt{\left(\frac{SEx}{\bar{x}}\right)^2 + \left(\frac{SEy}{\bar{y}}\right)^2} \times \bar{v}$$

Where $\bar{v}$ = calculated value, x = variable 1 and y = variable 2. And for addition and subtraction:

$$SEv = \sqrt{(SEx1)^2 + (SEx2)^2 + \ldots + (SExn)^2}$$

6.4 Results

6.4.1 Parrotfish Sediment Grain Size Distribution and Grain Type

All species and sizes of parrotfish investigated produced a wide range of sediment size fractions, from silt, to coarse sands (<32 - 2000 µm; Figure 6-2). These sediments were typically poorly sorted medium sands. The frequency of grains in all species gradually increased from fine size fractions (size fractions <63 µm) to peaks occurring between 125 and 1000 µm, but typically peaked in the 250-500 µm size fraction. There were few grains over 1000 µm, but grains up to 2000 µm were present in small numbers in some species. No consistent relationship was found between fish size class and average sediment grain size in 5 of the 6 species studied, with average (median - D_{50}) grain sizes typically between 300 – 500 µm (sedimentary statistics are presented in Table 6-1). However, in the species *Scarus frenatus,* average (D_{50}) grain size increased with fish body size, from 281.2 µm in <15 cm individuals to 515.5 µm in >45 cm individuals. Parrotfish faecal sediments originated almost entirely from coral (typically >80 %), with a small percentage (typically <20 %) of grains originating from *Halimeda spp.*, Crustose Coralline Algae (CCA), foraminifera, mollusc shell fragments and grains from unidentified origins (Figures 6-3 & 6-4). This was in agreement with parrotfish feeding preferences which show that >95% of bites were taken on dead coral and coral rubble substrates, while few bites (typically <2%) were taken on *Halimeda*, CCA or live coral (Table 6-2).

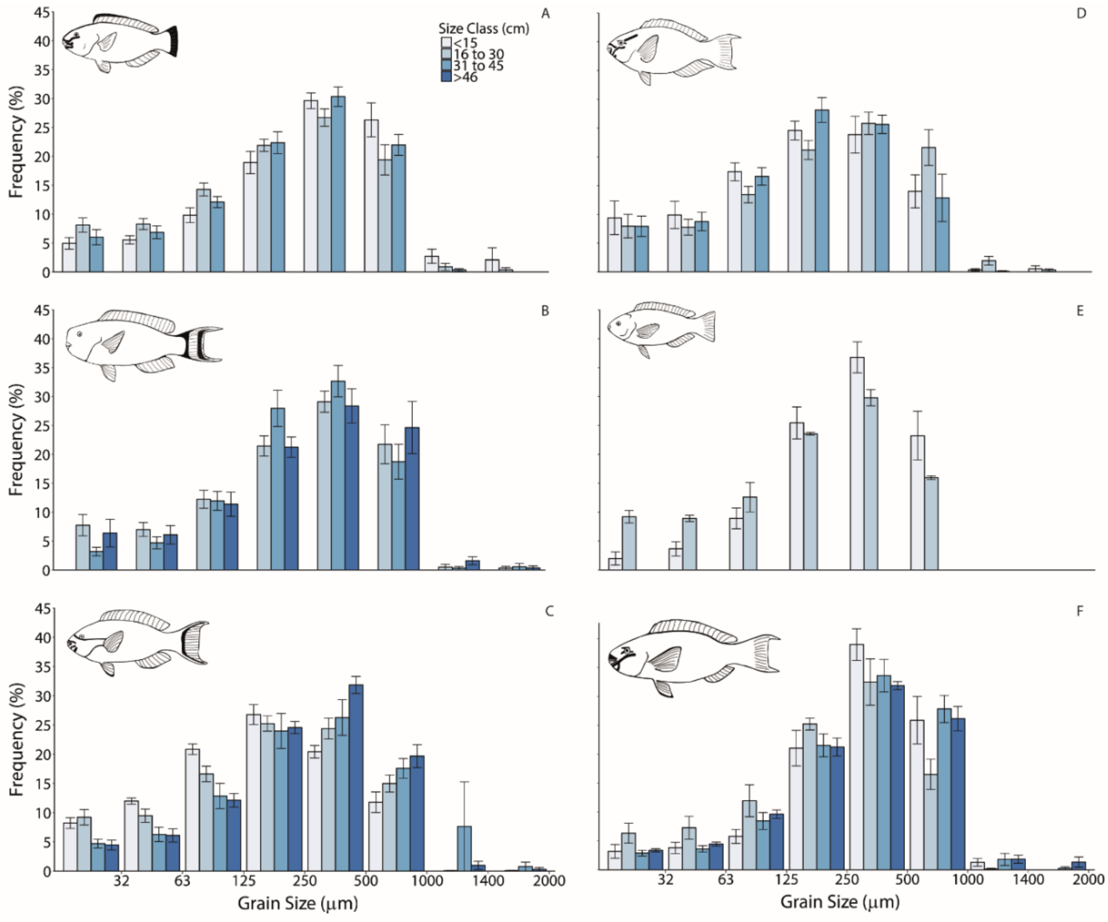


Figure 6-2 Grain size distributions of parrotfish derived sediments from excavators; A) *Chlorurus sordidus,* and B) *C. strongylocephalus*, and scrapers; C) *Scarus frenatus,* D) *S. niger*, E) *S. psittacus*, F) *S. rubroviolaceus*. For values and errors, see Supplementary Tables 6-20 to 6-25.

Table 6-1 Descriptive statistics of sediment grain sizes produced by different parrotfish size classes. *C. s – Chlorurus sordidus, C. st – Chlorurus strongylocephalus, S. f – Scarus frenatus, S. n – Scarus niger, S. p – Scarus psittacus, S. r – Scarus rubroviolaceus*.

Species	Size Class	D10 (μm)	D50 (μm)	D90 (μm)	Sorting (σ)
C. s	<15 cm	88.46	567.9	1310.4	2.614
	16 to 30 cm	78.28	340.4	1203.4	2.910
	31 to 45 cm	83.09	515.6	1207.9	2.609
	>46 cm	N/A	N/A	N/A	N/A
C. st	<15 cm	88.46	567.9	1310.4	2.614
	16 to 30 cm	80.27	509.8	1214.0	2.657
	31 to 45 cm	133.4	512.1	1188.1	2.455
	>46 cm	83.88	531.4	1254.1	2.637
S. f	<15 cm	75.18	281.2	1052.3	2.590
	16 to 30 cm	76.25	306.7	1121.4	2.624
	31 to 45 cm	87.21	515.1	1357.4	2.721
	>46 cm	88.30	515.5	1205.7	2.546
S. n	<15 cm	75.79	302.2	1124.4	2.634
	16 to 30 cm	79.04	353.1	1240.9	2.704
	31 to 45 cm	78.03	308.0	1080.7	2.570
	>46 cm	N/A	N/A	N/A	N/A
S. p	<15 cm	149.3	549.9	1211.1	2.179
	16 to 30 cm	76.69	333.1	1133.8	2.627
	31 to 45 cm	N/A	N/A	N/A	N/A
	>46 cm	N/A	N/A	N/A	N/A
S. r	<15 cm	150.7	578.1	1250.2	2.212
	16 to 30 cm	81.82	350.9	1146.0	2.562
	31 to 45 cm	145.4	575.7	1272.1	2.242
	>46 cm	135.5	565.9	1283.0	2.504

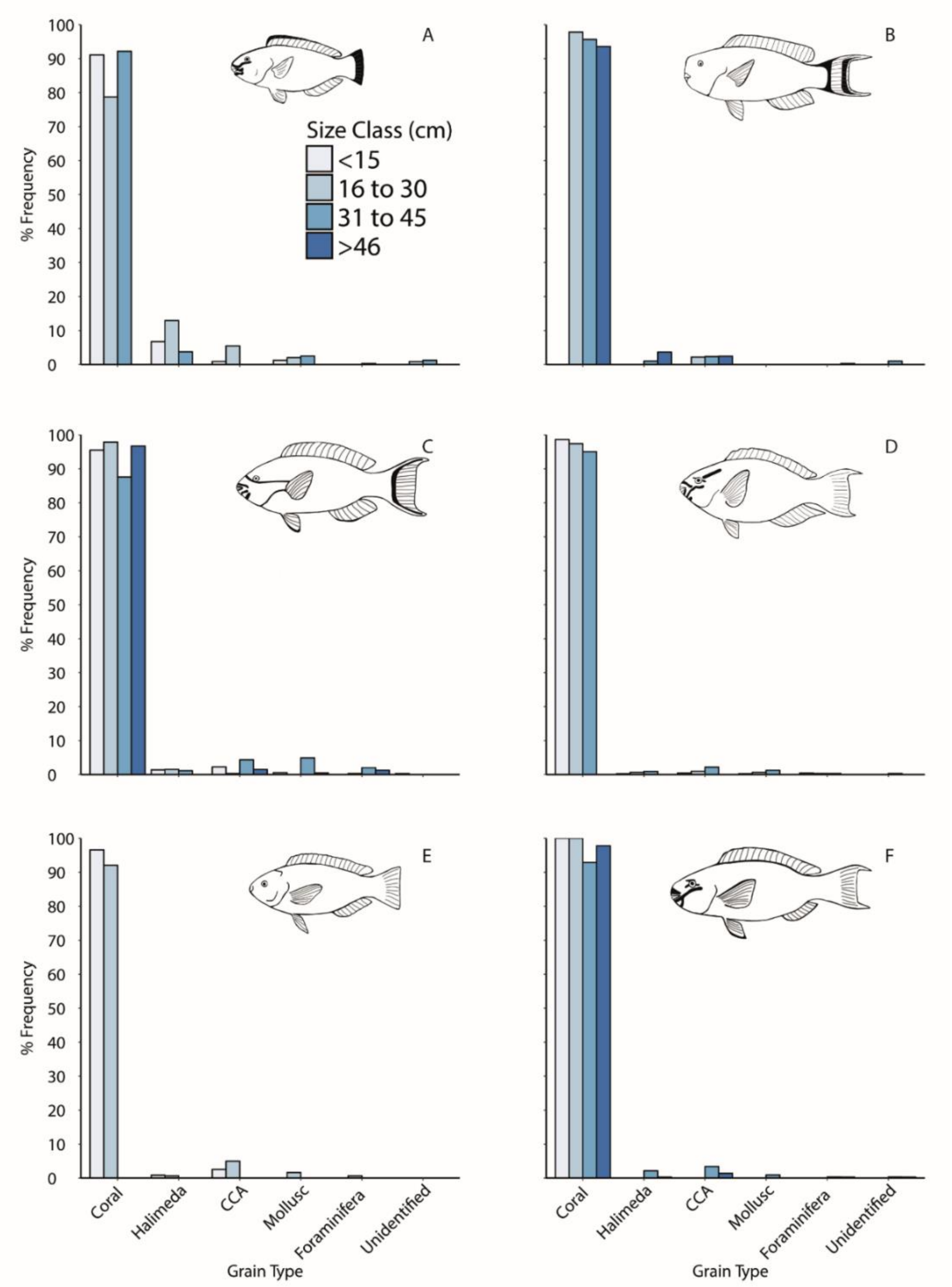


Figure 6-3 Composition of sediments produced by different size classes of six Maldivian parrotfish species; A) *Chlorurus sordidus,* B) *Chlorurus strongylocephalus,* C) *Scarus frenatus*, D) *Scarus niger*, E) *Scarus psittacus*, F) *Scarus rubroviolaceus*. For each size class of each species, 1 sub-sample of sediment was imaged and the origin of approximately 300 grains was identified. See Supplementary Tables 6-27 to 6-33 for percentages in each grain type.

Table 6-2 Percentage of bites on dead coral or rubble, live coral, *Halimeda*, sand, and Crustose Coralline Algae (CCA) by different size classes of six parrotfish species.

Species	**Size Class (cm)**	**Dead Coral/Rubble**	**Live Coral**	***Halimeda***	**Sand**	**CCA**
C. sordidus	<15	98.89	0.24	0.88	0.00	0.00
	16 to 30	98.31	0.44	1.26	0.00	0.00
	31 to 45	98.90	0.22	0.83	0.00	0.05
	>46	N/A	N/A	N/A	N/A	N/A
C. strongylocephalus	<15	95.61	0.00	4.39	0.00	0.00
	16 to 30	98.34	0.70	0.00	0.00	0.96
	31 to 45	99.75	0.11	0.00	0.07	0.07
	>46	99.56	0.44	0.00	0.00	0.00
S. frenatus	<15	94.93	0.15	1.88	0.00	3.04
	16 to 30	98.24	0.42	1.07	0.00	0.27
	31 to 45	97.69	1.07	0.72	0.03	0.49
	>46	100	0.00	0.00	0.00	0.00
S. niger	<15	98.35	0.33	0.87	0.00	0.46
	16 to 30	97.10	0.78	1.11	0.32	0.69
	31 to 45	98.87	0.33	0.66	0.10	0.03
	>46	N/A	N/A	N/A	N/A	N/A
S. psittacus	<15	97.67	0.25	1.12	0.56	0.40
	16 to 30	99.74	0.12	0.14	0.00	0.00
	31 to 45	N/A	N/A	N/A	N/A	N/A
	>46	N/A	N/A	N/A	N/A	N/A
S. rubroviolaceus	<15	98.55	1.45	0.00	0.00	0.00
	16 to 30	98.78	1.22	0.00	0.00	0.00
	31 to 45	99.30	0.13	0.00	0.57	0.00
	>46	99.89	0.11	0.00	0.00	0.00

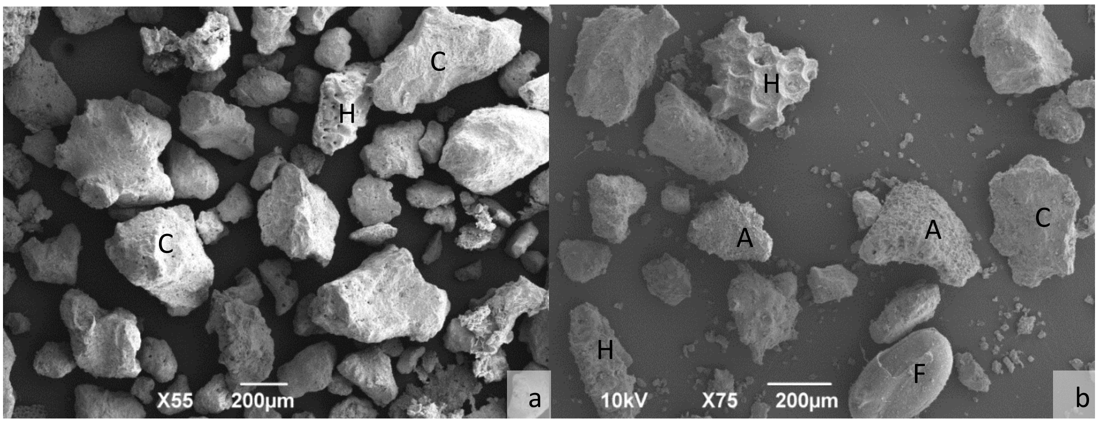


Figure 6-4 (a, b) SEM images of parrotfish faecal sediments, with examples of common grain types; C-Coral, H-*Halimeda* spp., A- Coralline Algae and F-Foraminifera.

6.4.2 Parrotfish Contributions to Sediment Reworking

Scrapers were the dominant contributors to sediment reworking in the Hardground, *Porites* bommie and Nearshore lagoon habitats (contributing to 71, 64 and 86% in these habitats respectively), while excavators were dominant in the Rubble, NE reef and SE patch reef habitats (59, 65 and 61% respectively; Table 6-3). The dominant species and size classes that contributed to sediment reworking differed between habitats (Figure 6-5). *Scarus psittacus* was the dominant sediment reworker in the Hardground (38%; 0.03 ± 0.004 kg m^{-2} yr^{-1}) and *Porites* bommie (42%; 0.04 ± 0.005 kg m^{-2} yr^{-1}) habitats, *Chlorurus strongylocephalus* in the Rubble habitat (40%; 0.03 ± 0.006 kg m^{-2} yr^{-1}), *C. sordidus* in the NE reef (59%; 0.24 ± 0.04 kg m^{-2} yr^{-1}) and SE patch reef habitats (44%; 0.13 ± 0.01 kg m^{-2} yr^{-1}), and *S. rubroviolaceus* in the Nearshore Lagoon (34%; 0.005 ± 0.001 kg m^{-2} yr^{-1}). Sediment reworking rates by different size classes of the six representative parrotfish species in different habitats are presented in Supplementary Table 6-1.

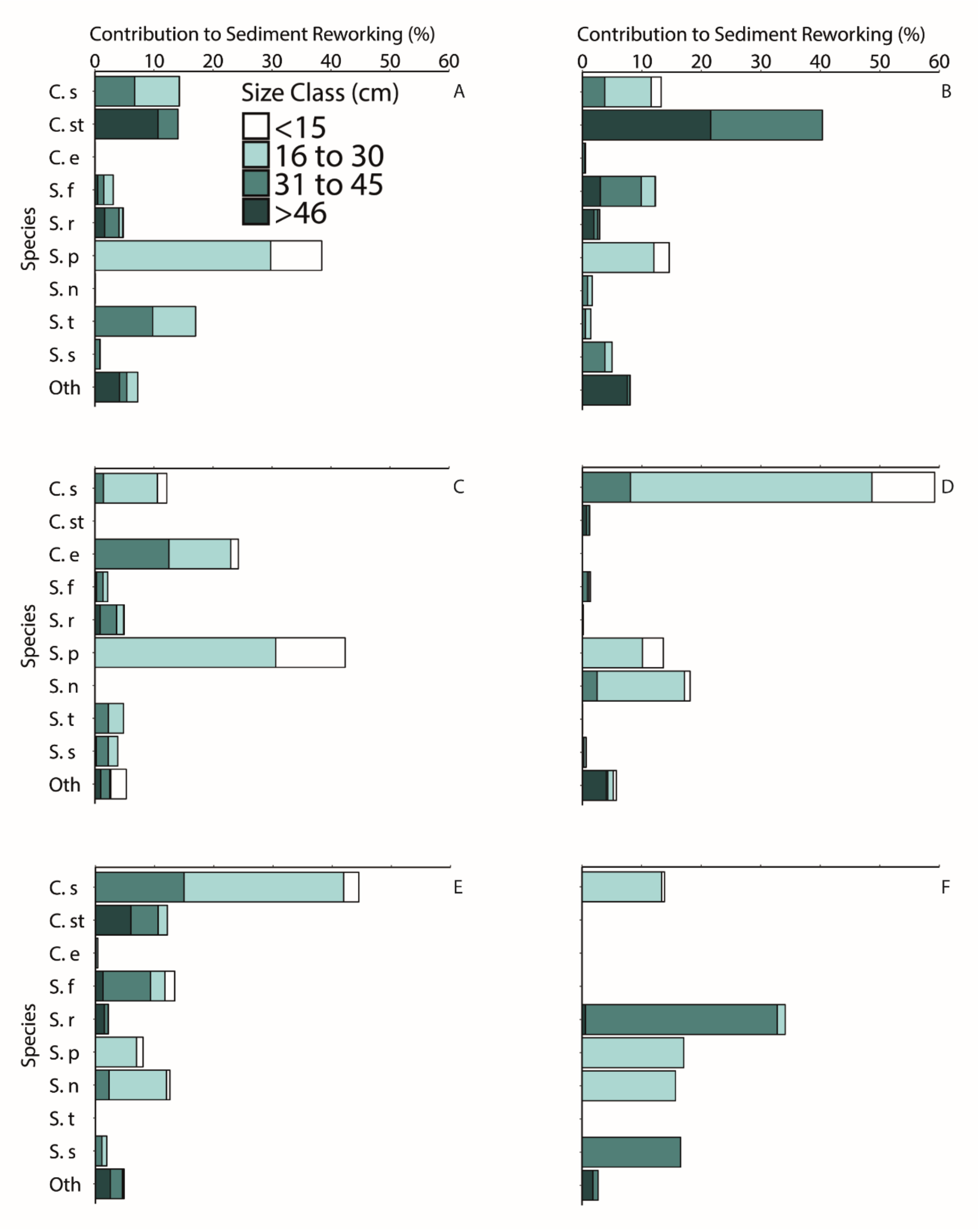


Figure 6-5 Percent contributions to total parrotfish sediment reworking by four size classes of fifteen species present in the six Vavvaru habitats supporting parrotfish: A) Hardground, B) Rubble, C) *Porites* bommie, D) NE reef, E) SE patches, and F) Nearshore Lagoon. Species abbreviations: C. s- *Chlorurus sordidus,* C. st- *C. strongylocephalus*, C. e- *C. enneacanthus,* S. f- *Scarus frenatus,* S. r- *S. rubroviolaceus,* S. p- *S. psittacus,* S. n- *S. niger,* S. t- *S. tricolor,* S. s- *S. scaber*, Oth- Other species pooled.

Table 6-3 Contributions of excavators and scrapers to sediment reworking in Vavvaru reef habitats Z1 - Hardground, Z2 – Rubble, Z3 – *Porites* bommie, Z6 – NE reef, Z7 – SE patch reef, Z8 – Nearshore lagoon.

Feeding Mode	Z1	Z2	Z3	Z6	Z7	Z8
Excavators	29%	59%	36%	65%	60%	14%
Scrapers	71%	41%	64%	35%	39%	86%

6.4.3 Epilithic Algal Matrix (EAM) Sediment Load, Grain Size Distribution and Composition

Sediment load within the EAM in eastern reef habitats (NE reef, SE patches, and the Nearshore lagoon) was approximately double that of the western reef habitats (~0.02 compared to 0.01 g cm^{-2}; Figure 6-6) but EAM canopy height showed no clear spatial patterns and was generally <2 mm in Vavvaru reef habitats (Table 6-4). These sediments were typically poorly sorted medium sands, ranging from <32 up to ~2800 µm. Average (D_{50}) grain sizes differed between habitats ranging from 251.7 µm in the NE reef, to 351.2 µm in the *Porites* bommie habitat (Table 6-5). Patterns of grain size distribution also varied among habitat types (Figure 6-7). Sediments shifted from fine (D_{50} = 296.4 µm) to coarser (D_{50} = 351.2 µm) grain sizes going inshore from the hardground to the *Porites* bommie habitat, and also from north to south between the NE reef and SE patches (D_{50} = 296.3 µm). The percentage of grains >1000 µm was consistently low across the platform. These sediments comprised mainly coral grains (>90%; Figure 6-8) in all habitats, although other grain types were observed, including *Halimeda spp.,* Crustose Coralline Algae (CCA), mollusc shell fragments and Foraminifera.

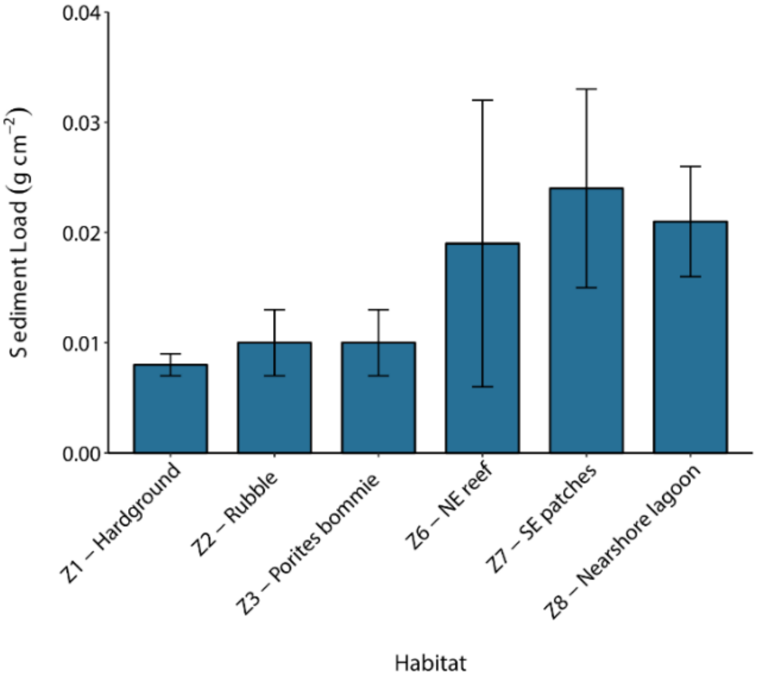


Figure 6-6 Sediment load retained within the Epilithic Algal Matrix (EAM) on coral rubble substrates in the six habitats supporting parrotfish assemblages. Error bars present one standard error of the mean.

Table 6-4 Average Epilithic Algal Matrix (EAM) algal turf canopy height on coral rubble substrates from the six Vavvaru habitats in which parrotfish were observed. Standard errors are shown in parentheses.

Habitat	**Algal Turf Canopy Height (mm) (SE)**
Z1 – Hardground	2.1 (± 0.3)
Z2 – Rubble	1.5 (± 0.4)
Z3 – *Porites* bommie	0.6 (± 0.3)
Z6 – NE reef	0.1 (± 0.0)
Z7 – SE patches	1.5 (± 0.0)
Z8 – Nearshore lagoon	0.9 (± 0.2)

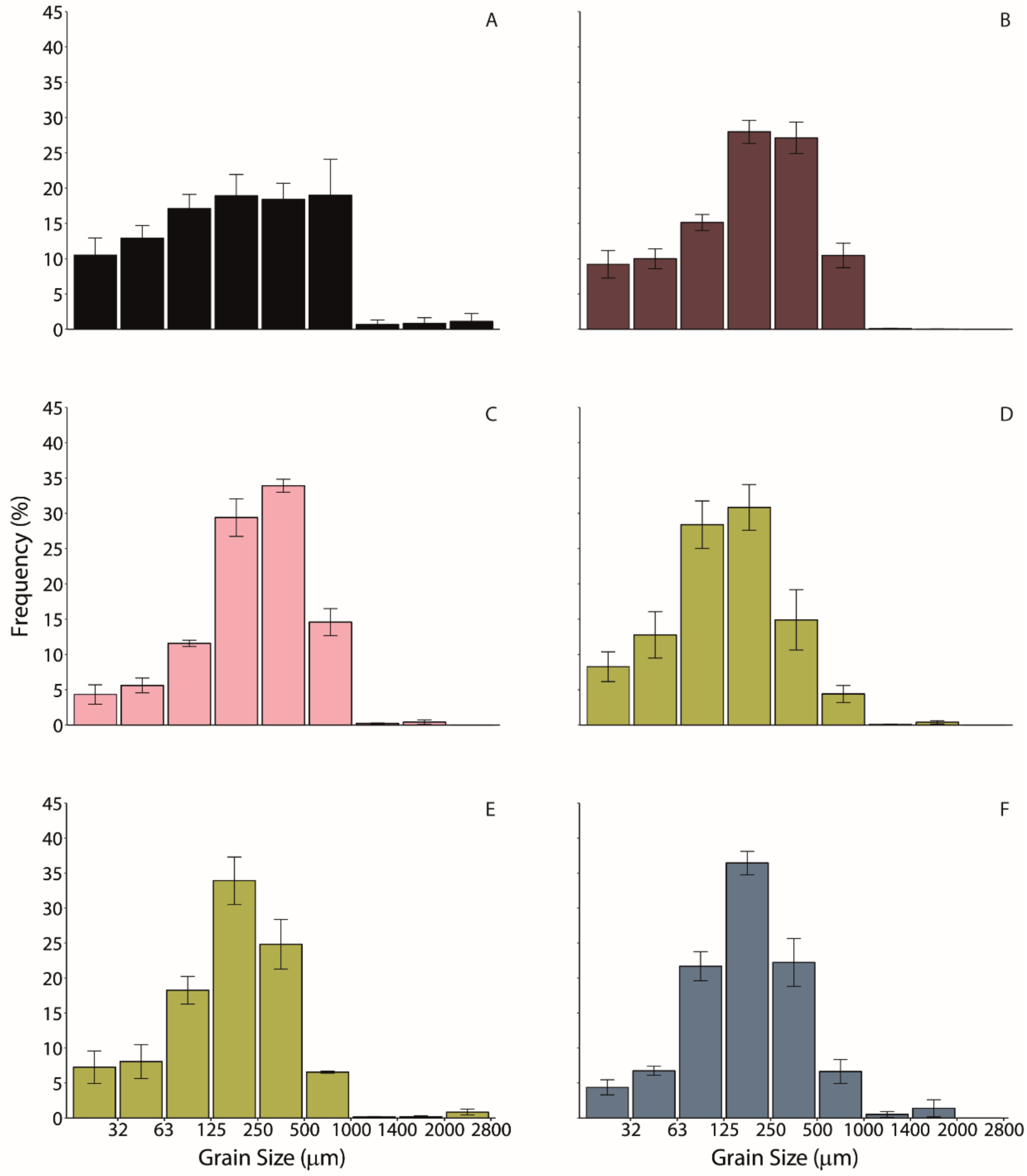


Figure 6-7 Grain size distribution of sediments retained within the Epilithic Algal Matrix (EAM). A) Hardground, B) Rubble, C) *Porites* bommie, D) NE reef, E) SE patch reefs, F) Nearshore lagoon. The colours designated to habitats correspond to those in the habitat map (Figure 3-2). See Supplementary Table 6-36 for data.

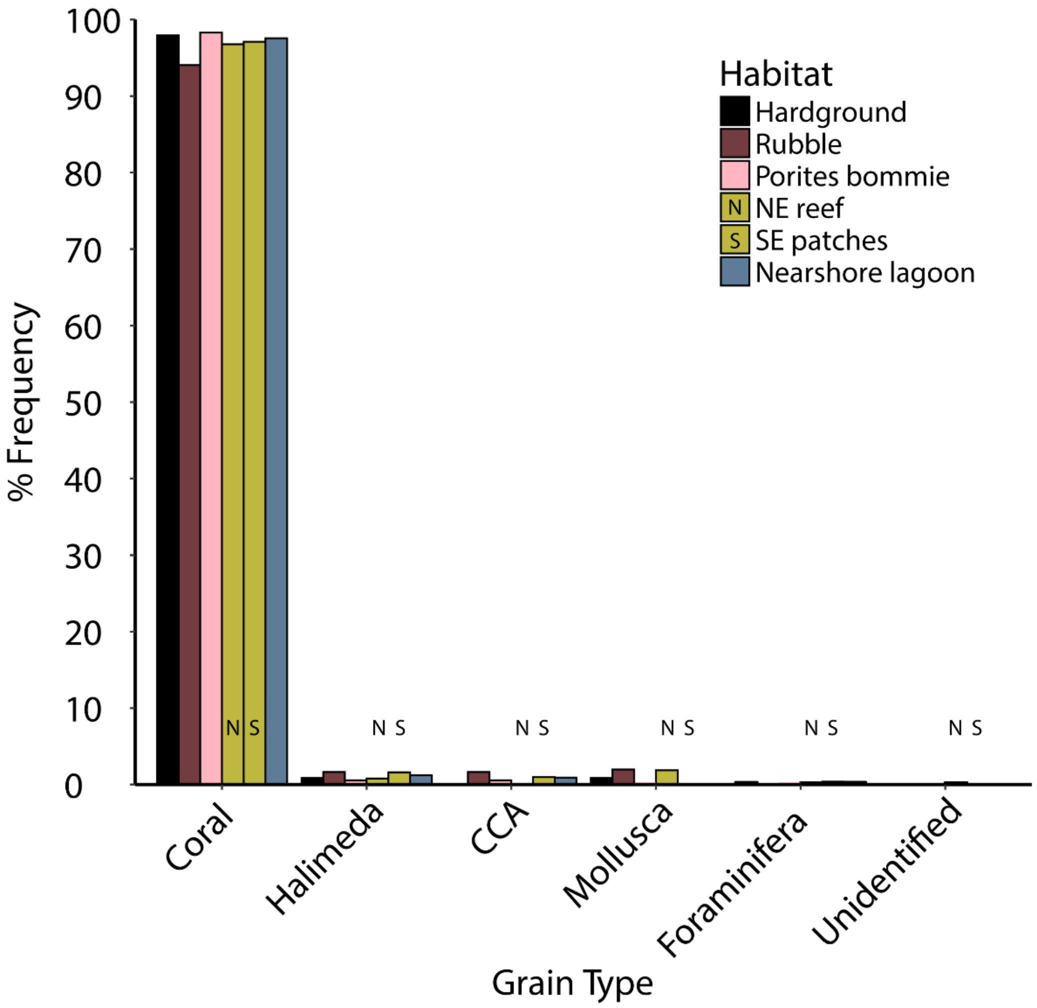


Figure 6-8 Percentage of grain types found in Epilithic Algal Matrix sediments in Vavvaru reef habitats. Based on 1 sub-sample of sediment from each habitat. At least 300 grains were identified in each sub-sample.

Table 6-5 Descriptive statistics of sediment grain sizes found in the Epilithic Algal Matrix of the six vavvaru reef habitats occupied by parrotfish.

Habitat	**D10 (μm)**	**D50 (μm)**	**D90 (μm)**	**Sorting (σ)**
Hardground	73.29	296.4	1228.9	3.027
Rubble	75.86	304.2	1018.5	2.574
Porites bommie	125.3	351.2	1127.6	2.252
NE reef	74.65	251.7	629.1	2.284
SE patches	79.51	296.3	687.2	2.279
Nearshore lagoon	86.83	295.0	693.8	2.239

6.4.4 Endogenous Carbonate Production

Endogenous carbonate samples examined under SEM revealed the presence of sheroids and rhombohedons (sensu Salter et al. 2012) in starved scraper and excavator parrotfish (Figure 6-9). However, despite thorough searching, these types of carbonates were not found under SEM in faecal samples of wild feeding fish. The contribution of endogenous carbonates to new sediment production was considered to be insignificant compared to that of eroded reef framework, and was excluded from estimates of total sediment production.

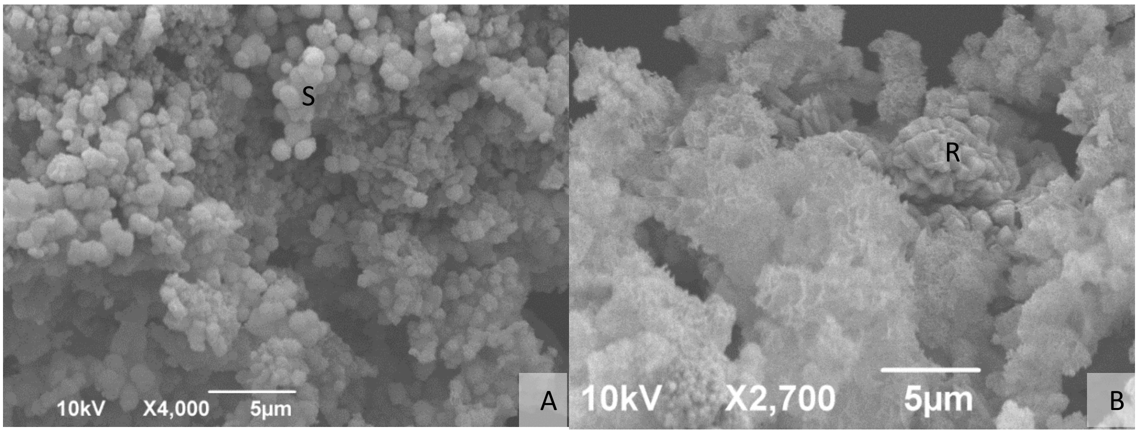


Figure 6-9 SEM images of endogenous carbonate grain morphologies; S - Spheroids (in A) and R – Rhomboids (in B) produced in non-feeding parrotfish.

6.4.5 Platform-Scale Rates of Parrotfish Sediment Production and Reworking

Overall parrotfish sediment production rates were highest in the rubble, NE reef and SE patch reef habitats, all of which produced over 0.8 kg sediment m^{-2} yr^{-1} (Figure 6-10A). However, a significant proportion (~35-50%) of sediment in the eastern reef habitats was reworked loose sediment, as oppose to new sediment produced from eroded framework material (Figure 6-10B, Table 6-6). In contrast, only ~8% of the sediment generated by parrotfish in the Rubble habitat was reworked loose sediment. Sediment reworking rates were considerably higher in the eastern reef habitats (NE reef: 0.41 ± 0.04 kg m^{-2} yr^{-1}; SE patch reef: 0.29 ± 0.02 kg m^{-2} yr^{-1}) compared to the western hardground, rubble, and *Porites* bommie habitats (0.09 ± 0.004, 0.08 ± 0.007 and 0.10 ± 0.006 kg m^{-2} yr^{-}

^{1}). These rates were typically lower than bioerosion rates, except in the Nearshore Lagoon (0.01 ± 0.001 kg m^{-2} yr^{-1}) and the *Porites* bommie habitats. When habitat scale was taken into account, it was estimated that 45% of parrotfish derived sediment was produced in the rubble habitat (89988 ± 10798 kg yr^{-1}), while the NE reef and SE patch reefs contributed 22% (44470 ± 2798 kg yr^{-1}) and 6% (12092 ± 535 kg yr^{-1}) respectively. The hardground habitat was in fact the third highest sediment producer, contributing 19% (37984 ± 2625 kg yr^{-1}) of total parrotfish derived sediment to the platform.

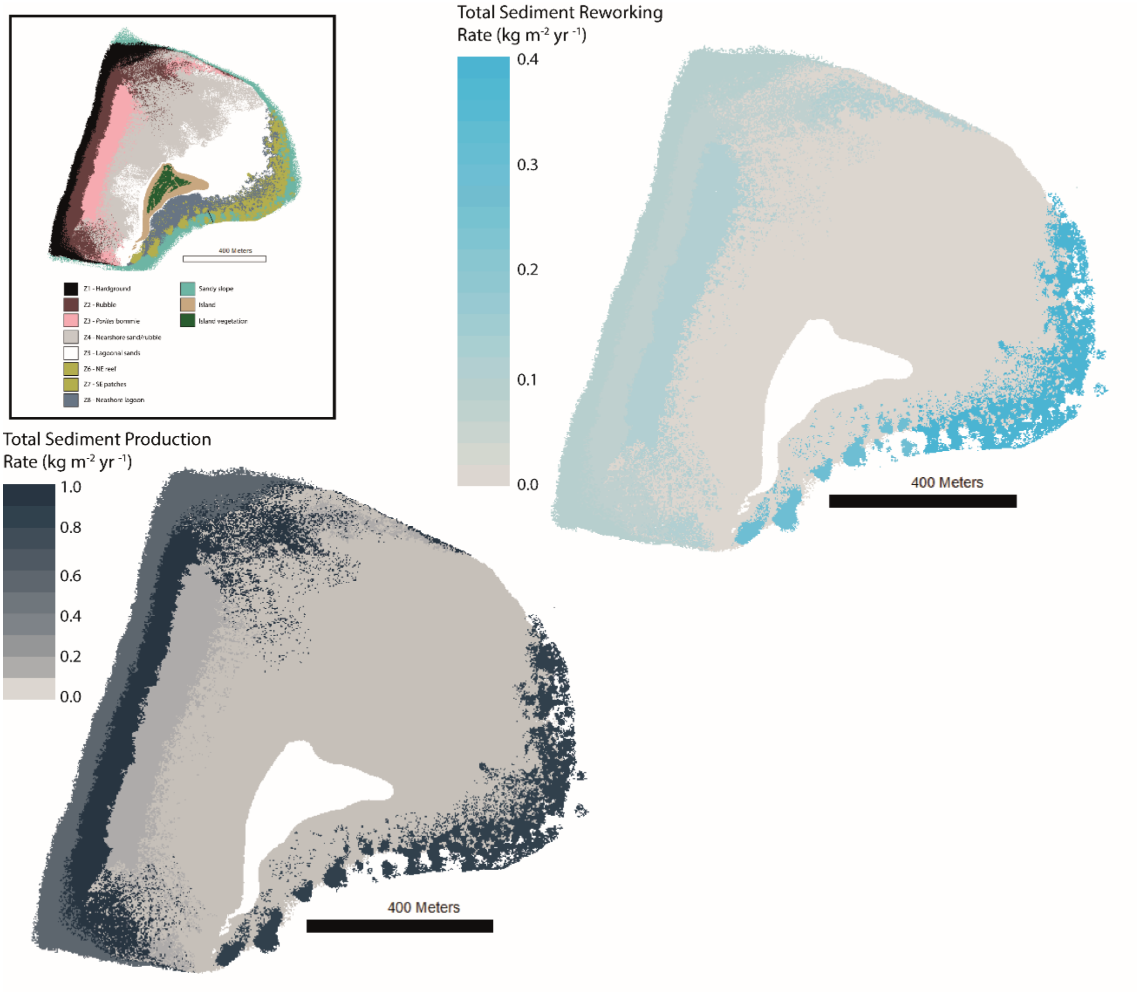


Figure 6-10 Choropleth maps showing A) Inter-habitat variability in total sediment production by parrotfish over the Vavvaru platform and B) Inter-habitat variability in sediment reworking rates over the Vavvaru platform. Inset of habitat map for reference.

Table 6-6 Rates and annual total quantities of parrotfish sediment production in Vavvaru reef habitats, and the contribution of reworked sediment.

	Z1	Z2	Z3	Z4	Z5	Z6	Z7	Z8
Total Sediment Production (kg yr^{-1})	37984 ± 2625	89988 ± 10798	14857 ± 797	0	0	44470 ± 2798	12092 ± 535	1085 ± 118
% Contribution to Total Platform Parrotfish Sediment Production	19%	45%	7%	0	0	22%	6%	1%
Reworked Sediment (kg yr^{-1})	6221 ± 306	7292 ± 640	8063 ± 500	0	0	20925 ± 2214	4155 ± 239	809 ± 74
Total Sediment Production Rate (kg m^{-2} yr^{-1})	0.55 ± 0.04	0.93 ± 0.11	0.18 ± 0.01	0	0	0.86 ± 0.05	0.83 ± 0.04	0.020 ± 0.001
Sediment Reworking Rate (kg m^{-2} yr^{-1})	0.090 ± 0.004	0.076 ± 0.006	0.100 ± 0.006	0	0	0.405 ± 0.043	0.286 ± 0.016	0.015 ± 0.001
% of Total Sediment Reworked	16.4%	8.1%	54.3%	0	0	47.0%	34.4%	74.6%

6.4.6 Sediment Transport by Parrotfish

In total, over 1000 observations of parrotfish feeding and egestion were carried out over the study, but there was no clear evidence that any species used specific defecation sites. Egestion rate decreased with increasing fish size in four of the six species observed (Table 6-7). Parrotfish typically egested sediment within the same habitat, including during feeding, and within an estimated 50 cm of the seabed, with relatively few, typically < 20%, of parrotfish observed moving to adjacent habitats between feeding and egesting (Tables 6-8 & 6-9). Only two species, *Chlorurus strongylocephalus* and *Scarus rubroviolaceus* displayed evidence of specific movement off slope before defecating (Table 6-8). Frequency of off-slope defecations for *Cetoscarus* *bicolor* was assumed to match that to *Chlorurus strongylocephalus* as the closest (large excavator) representative species examined in detail during the present study.

Table 6-7 Defecation rates (No. defecations min^{-1}) for different size classes of six species of Maldivian parrotfish.

Species	Size Class (cm)	n	Mean	SE
C. sordidus	<15	33	0.34	0.07
	16 to 30	39	0.26	0.06
	31 to 45	32	0.23	0.06
	>46	N/A	N/A	N/A
C. strongylocephalus	<15	4	0.33	0.16
	16 to 30	24	0.33	0.07
	31 to 45	42	0.40	0.06
	>46	45	0.34	0.05
S. frenatus	<15	28	0.30	0.07
	16 to 30	49	0.19	0.04
	31 to 45	53	0.14	0.04
	>46	5	0.06	0.06
S. niger	<15	26	0.13	0.04
	16 to 30	44	0.05	0.02
	31 to 45	43	0.04	0.02
	>46	N/A	N/A	N/A
S. psittacus	<15	49	0.27	0.04
	16 to 30	11	0.44	0.13
	31 to 45	N/A	N/A	N/A
	>46	N/A	N/A	N/A
S. rubroviolaceus	<15	7	0.35	0.12
	16 to 30	28	0.27	0.07
	31 to 45	41	0.17	0.04
	>46	33	0.16	0.04

Table 6-8 Percentage of defecations observed; 1) whilst a parrotfish was feeding in a reef habitat, 2) within the same habitat that the parrotfish had been feeding, 3) after a parrotfish had moved to an adjacent habitat after feeding, and 4) when a parrotfish moved off slope at the edge of the reef platform.

Species	**During Feeding**	**Within Same Habitat**	**Adjacent Habitat**	**Off Slope**	**No. Observations**
C. sordidus	48.65	48.65	2.70	0.00	37
C. strongylocephalus	13.64	65.91	2.27	18.18	44
S. frenatus	10.53	73.68	15.79	0.00	19
S. niger	42.11	36.84	21.05	0.00	19
S. psittacus	19.23	76.92	3.85	0.00	26
S. rubroviolaceus	34.48	48.28	10.34	6.90	29

Table 6-9 Percentage of defecations at different heights above the seabed for three species of Maldivian parrotfish

Species	**0-25 cm**	**25-50 cm**	**50-100 cm**	**>100 cm**	**No. observations**
C. sordidus	64.55	30.00	5.45	0.00	110
S. niger	51.61	41.94	6.45	0.00	31
C. strongylocephalus	5.80	8.70	18.84	66.67	69

6.4.7 Variation in the Production of Different Sediment Size Fractions among Reef Habitats

The grain size distribution of the sediment produced by parrotfish communities was comparable across all Vavvaru reef habitats (D10 = 81 – 88 µm, D50 = 504 – 527 µm, D90 = 1203 – 1252 µm), but the quantities of each size fraction produced varied as a function of total sediment production rates (Tables 6-10 & 6-11). The dominant size fractions produced were 125 – 250, 250 – 500 and 500 – 1000 µm. The dominance of the Rubble habitat in terms of the quantity of different size fractions produced was especially pronounced after factoring for off-slope sediment transport by *C. strongylocephalus, Cetoscarus bicolor* and *S. rubroviolaceus* in the Hardground, NE reef and SE patch reef habitats (Figure 6-11).

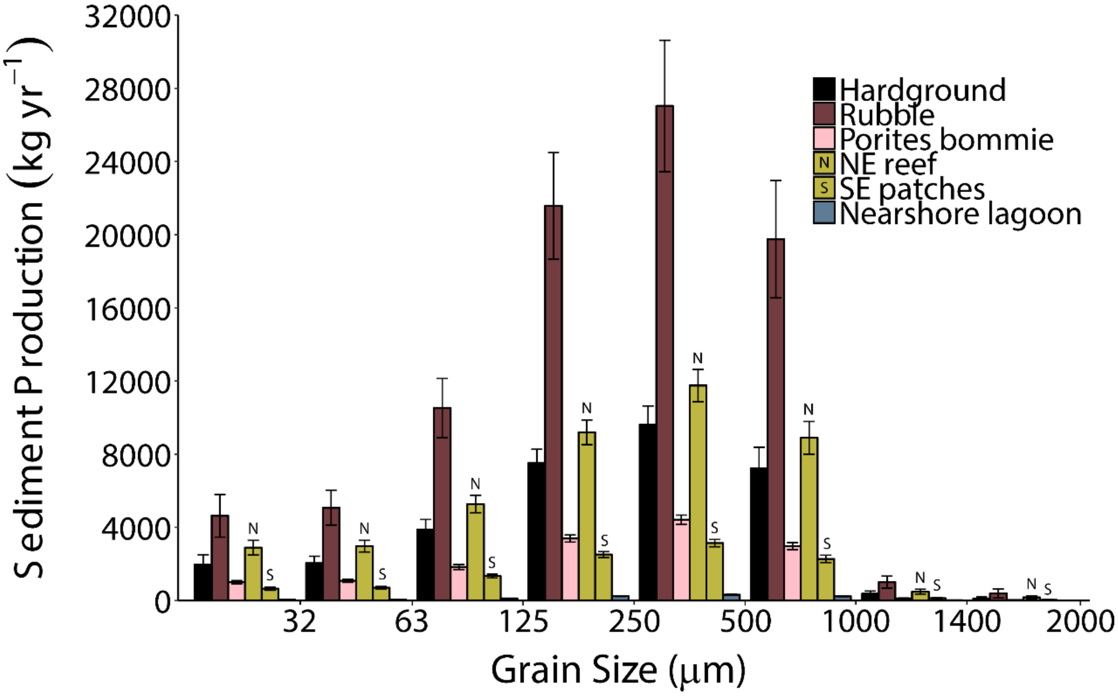


Figure 6-11 Quantity of sediment produced in different size fractions in six Vavvaru reef habitats. Parrotfish sediment transport off slope is factored into perimeter habitats (Hardground, NE reef, SE patches).

Table 6-10 Quantity of sediment (kg, ± standard error) in different size fractions produced by the parrotfish assemblage in each Vavvaru habitat (excluding sediment transport off platform).

	<32	**<63**	**<125**	**<250**	**<500**	**<1000**	**<1400**	**<2000**
Hardground	1973 ± 532	2048 ± 376	3881 ± 551	7530 ± 743	9617 ± 1015	7222 ± 1152	371 ± 153	108 ± 96
Rubble	4636 ± 1159	5070 ± 953	10521 ± 1617	21575 ± 2910	27037 ± 3593	19753 ± 3212	1006 ± 331	390 ± 246
***Porites* bommie**	1005 ± 90	1080 ± 81	1836 ± 140	3394 ± 199	4419 ± 257	2976 ± 195	117 ± 30	29 ± 11
NE reef	2893 ± 400	2977 ± 318	5276 ± 476	9198 ± 674	11755 ± 886	8898 ± 893	486 ± 129	173 ± 90
SE patches	653 ± 86	703 ± 67	1339 ± 102	2513 ± 162	3142 ± 199	2276 ± 198	131 ± 40	41 ± 18
Nearshore lagoon	62 ± 6	67 ± 6	124 ± 12	242 ± 20	322 ± 28	239 ± 23	25 ± 13	4 ± 2

Table 6-11 Descriptive statistics for the sediment grain sizes produced by parrotfish assemblages in the six Vavvaru habitats occupied by parrotfish.

Habitat	D10 (µm)	D50 (µm)	D90 (µm)	Sorting (σ)
Hardground	84.24	517.5	1229.0	2.611
Rubble	87.69	521.1	1229.9	2.572
Porites bommie	81.23	504.5	1203.3	2.630
NE reef	81.15	507.3	1226.1	2.654
SE patches	83.69	510.8	1224.2	2.615
Nearshore lagoon	85.04	526.5	1251.8	2.617

6.5 Discussion

A consistent sediment supply is crucial for the maintenance of many coral reef habitats and associated sedimentary landforms (Hutchings 1986, Kench & Cowell 2000, Perry et al. 2011b, 2015a, Perry et al. 2017). On atolls and remote reefs isolated from terrigenous inputs, this sediment is entirely derived from sources on the reef (Morgan & Kench 2016b). The grain size distribution of these sediments is a fundamental property affecting their transport and deposition post-egestion (Blott & Pye 2001). All parrotfish investigated in the present study produced a wide range of sediment size fractions, from silt grade (<63 µm) to coarse sand (>1000 µm), with fine (125 – 250 µm) to coarse sands (500 – 1000 µm) being the dominant size fractions produced (mean grain sizes typically between 300 – 580 µm). These sediments predominantly consisted of coral grains, reflecting the preferred feeding substrate of parrotfish in the present study (over 95% of bites on dead coral and coral rubble substrates). The types of sediment produced by parrotfish are thus comparable to that observed on local reef islands and it is likely that parrotfish are very important suppliers to these deposits (Perry et al. 2015a). This is because parrotfish are the dominant biological sediment producers on many Maldivian reefs by a considerable margin, being responsible for >80% of production through bioerosion (Perry et al. 2015a, Perry et al. 2017).

Parrotfish also produce the right size fractions of sediment for reef island maintenance, while other organisms, such as sea urchins, produce finer size fractions with few grains >500 µm (Chazottes et al. 2004). Physical erosion by wave energy (tropical storms and cyclones are rare in the Maldives) is more likely to result in the production of coral rubble and gravel grain sizes of sediment compared to bioerosion by parrotfish (Done et al. 1996). Persistent abrasion and dissolution may also eventually reduce this material to finer grain sizes but coral skeletons have been shown to be very durable and highly resistant to abrasion (Ford & Kench 2012). Much of the breakdown of this material is likely to be accelerated by parrotfish bioerosion and reworking. However, it should be noted that even where parrotfish egested intact pellets near the seabed (including cases where the samples of the presented data were collected), there was some dispersal of fine sediments. Of note in this context, samples collected from recently fed *Scarus psittacus* in controlled aquarium conditions (in clean, running seawater tank filtered to 1 µm) while confirming the patterns observed for grains 32 to 500 µm and >1000 µm, showed that fines may be slightly underestimated (~5%) in field collected samples (see Supplementary Figure 6-1).

6.5.1 Relative importance of sediment produced through bioerosion, reworking and endogenous carbonate production

While excavators are known to be the most significant contributors to the process of bioerosion and production of resultant new sediment (see Chapter 5) the main contributors to sediment reworking included both scraper (e.g. *Scarus psittacus* in the hardground and *Porites* bommie habitats, and *S. rubroviolaceus* in the nearshore lagoon) and excavator (e.g. *Chlorurus sordidus* in the eastern reefs and *C. strongylocephalus* in the rubble habitat) species. The proportion of sediment derived from bioerosion and from reworked existing sediment also varied among species and size classes of parrotfish and also differed between habitats because of the variability in sediment load (see supplementary Tables 6-14 to 6-19 for proportions of eroded to reworked sediment for different parrotfish species and sizes in each habitat). These differences between species and size classes, in terms of the proportion of sediment produced from bioerosion and sediment reworking, resulted in different patterns of inter-habitat rates of these processes. The highest sediment reworking rates were found in the eastern reef habitats because of the combined effects of high parrotfish density and high sediment load. Previous work has shown that high sediment loads can deter grazing by "herbivorous" fish (Bellwood & Fulton 2008) but there is also evidence that, in moderation, sediments do not deter parrotfish from feeding (Bonaldo & Bellwood 2011). The grain size of the sediment and the organic matter content of the EAM may act as an additional control on parrotfish bite rate (Gordon et al. 2016) but whether or not this can influence parrotfish species assemblages requires further study.

The quantity of sediment that parrotfish ingest per bite depends on the sediment load retained within the EAM, and overall habitat-scale sediment reworking rates depend on the species and sizes of parrotfish present in each habitat, and their respective feeding rates. At Vavvaru, the quantity of sediment in the EAM appeared to be influenced by position of the habitat on the platform, rather than algal turf length. Eastern reef habitats retained nearly double the amount of sediment as the western habitats (~0.02 compared to ~0.01 g cm^3), which may be caused by physical transport (wind and wave energy) of sediments from the more exposed atoll edge (west – north west) side of the platform, towards the atoll lagoon side (east - south east). Wave energy is likely consistently higher on the western side of the platform, and stronger monsoon winds (5.1 m s^{-1}) blow from the west during April to November (Kench et al. 2006). This may also be the reason for the observed shift of Vavvaru Island from an original more central position on the platform, to the south-east in recent decades (Perry et al. 2017). Along with other families such as the surgeonfish, sediment reworking can complement abiotic factors (Hubbard et al. 1990) as a substrate "cleaning agent" (Goatley & Bellwood 2010, Krone et al. 2011). In the eastern reef habitats, sediment reworking may be particularly important for clearing space to promote coral recruitment and sustain high percentage covers.

Total parrotfish sediment production varied markedly between reef habitats. Production rates were comparably high (>0.8 kg m^{-2} yr^{-1}) in the Rubble, NE reef and SE patch reef habitats, but because of its size, the Rubble habitat was the highest contributor of parrotfish derived sediment to the platform (45%). The high rate here was due to the relatively high abundance of large (>30 cm) excavator *Chlorurus strongylocephalus.* In this habitat, over 90% of the sediment produced was the result of bioerosion of reef framework. This is an important finding because it demonstrates that low coral cover habitats such as this could provide the greatest supply of sediment to reef islands in these settings. In contrast, over 34% of sediment produced in the eastern reef habitats was a result of the role of sediment reworking, primarily by the relatively higher density of scraping and small excavating species. In the context of sediment supply, this makes the rubble habitat a considerably greater source of new sediment to the platform compared to the eastern reef habitats.

The process of sediment reworking may contribute to the loss of sediment from the system by physicaly transporting and reducing the grain size of sediments (Bellwood 1996). This is partly because of active transport by parrotfish, but also because it causes fine sediments to become re-suspended, where they may be more susceptible to hydrodynamic transport (Bellwood 1996). The distance that these sediments travel depends on their grain size, shape and density, as well as the height that they are defecated from the seabed and local current regimes (Bellwood 1996, Kench & McLean 1996, Kench 1997, 1998). Previous work has estimated that fine sediments (<63 µm) suspended at 2 m above the seafloor could travel several hundred meters under gentle (~10 cm s^{-1}) current regimes before settling (Bellwood 1996). On a reef platform such as Vavvaru, which is only ~1000 m across, it is likely that much this material could be exported, particularly on the atoll-edge (west) side of the platform which experiences strong currents during changes in tidal state. Future work would benefit from examining the settling velocity of parrotfish derived sediments to make estimates of transport potential from different defecation heights. In addition, data on current direction and velocity at Vavvaru, complimented with experiments to examine the current velocity required to entrain sediments of different types and size fractions would help predict the fate of this material post-egestion (Kench & McLean 1996, Kench 1997, 1998). This will be particularly relevant for predicting the proportions of sediment retention and export from the reef under scenarios of projected future sea level rise, especially as many Indian Ocean coral reefs are struggling to keep pace (Perry et al. 2018). The increased water depth above the reef platform is likely to increase both current speeds and wave energy, and therefore increase the chance of hydrodynamic transport of sediments (Storlazzi et al. 2011).

In addition to ingested material, to our current knowledge, all marine teleost fish precipitate carbonate within their intestines as a result of continuously drinking seawater (Walsh et al. 1991, Wilson et al. 2009, Jennings & Wilson 2009). Some calcium is required for skeletal growth and cellular processes, but excess calcium uptake can cause the formation of renal stones and be detrimental to fish health (Wilson & Grosell 2003). To prevent this, teleosts secrete bicarbonate ions from intestinal epithelial cells, which bind to calcium (and magnesium) ions and produce a calcium carbonate precipitate with varying magnesium content (Salter et al. 2012, 2017). These fine grained carbonates are excreted with organic matter and other waste products back into the environment and may be preserved in carbonate sediments (Perry et al. 2011a). Unfed parrotfish in the present study did produce spheroid and rhombohedral carbonates endogenously, but no traces of these carbonates were found when examining sediments produced by wild feeding parrotfish under Scanning Electron Microscope (SEM). Parrotfish intestines have been reported to be acidic compared to most teleosts when feeding, with pH reaching as low as 6.2 in the anterior region of the intestine (Smith & Paulson 1974). These acidic conditions may inhibit carbonate precipitation, so it is unclear whether parrotfish produce new carbonate sediments endogenously when they are feeding or whether they have an alternative mechanism. This remains an interesting area of further study. It may be that parrotfish do produce amorphous phase carbonates, as suggested by Salter et al. (2012), but these are either dissolved quickly, or disperse rapidly upon entering the environment and so were not picked up when collecting faecal samples. If parrotfish do not produce carbonates within their intestines because of the acidic conditions, it poses an interesting biological question as to how they deal with excess calcium ingested. For the purposes of the present study, it was clear that endogenous carbonate production was unlikely to be a significant source of new sediment compared to that produced from eroded framework, and so it was not included in estimates of total sediment production.

6.5.2 Sediment transport and inter habitat variability in production of island grade sands

In the perimeter hardground, NE reef and SE patch reef habitats, *C. strongylocephalus, C. bicolor* and *S. rubroviolaceus* actively moved sediment off-slope. This resulted in the direct loss of 14%, 6% and 11% of the total sediment produced in each of these habitats respectively. This sediment loss exacerbated the importance of the interior rubble habitat as a key sediment supply to the platform as it is cut off from the atoll edge by the hardground habitat (the processes of sediment production and transport are summarised in Figure 6-12). Perimeter habitats may also be more susceptible to loss of sediment (and rubble) because of physical and hydrodynamic processes, such as wave energy and currents acting at the edge of the platform and reef slopes (Morgan & Kench 2012b, Morgan et al. 2016). In addition to the transport of sediment off-slope at the perimeter of the platform, fine sediments, particularly those <63 µm (silt grade sediments), are more likely to remain in suspension and be transported by hydrodynamic processes (Bellwood 1996). This may result in further export of fine (<63 µm) size fractions from the system because of the close proximity of these sediments to the platform edge. Excluding direct export, this could result in the loss of further ~4021 kg yr^{-1} (~12% of total parrotfish sediment production) from the hardground habitat, ~5870 kg yr^{-1} (~14% of total parrotfish sediment production) from the NE reef habitat and ~1356 kg yr^{-1} (~13% of total parrotfish sediment production) from the SE patch reef habitat.

Estimates of the quantity of different sediment size fractions that are produced on the Vavvaru platform (i.e. minus that directly exported off-slope) reveal that the rubble habitat is the dominant producer of 125 -1000 µm sediments, and also of coarse sands > 1000 µm. The eastern reef habitats are much smaller contributors of these size fractions due their relatively smaller area, and due to estimated transport of sediment off-slope, despite their high sediment production rates. Given that winds blowing from the west from April to November are stronger compared to those during December to March (Kench & Brander 2006) the rubble, and to a lesser extent the hardground and *Porites* bommie habitats, are likely to be especially important for sediment supply to

Vavvaru island, as the large volumes of sediment produced in these habitats are likely to be transported in a south easterly direction.

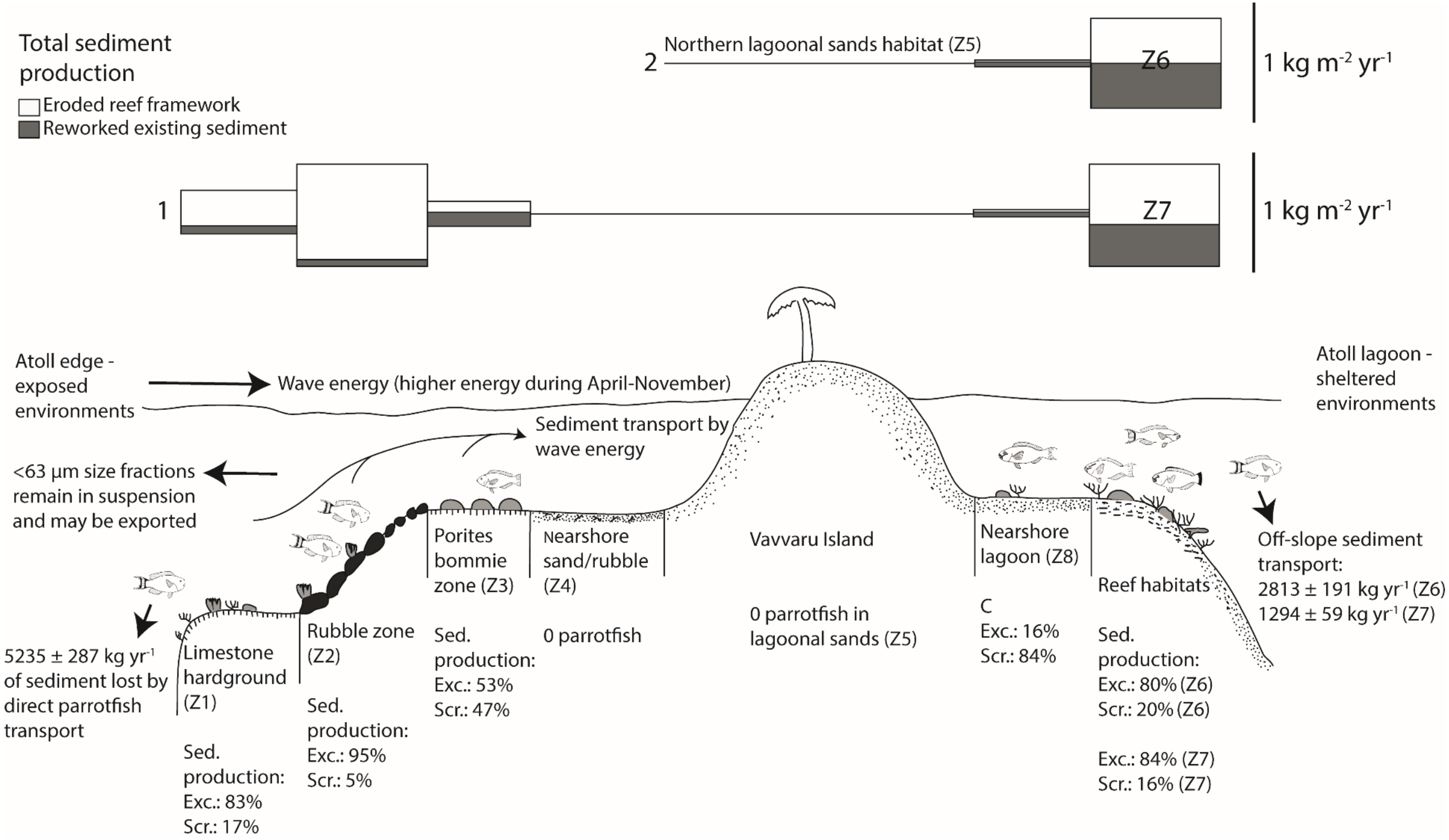


Figure 6-12 Summary of parrotfish sediment production over the Vavvaru reef platform.1 = Cross sections shown in diagram. 2 = habitats north of Vavvaru Island.

6.5.3 Wider Implications and directions for future research

The present study furthers our understanding of how habitat type can influence processes of parrotfish sediment production (i.e. bioeroded, reworked, or endogenously produced sediment). Understanding the controls on these processes can help us to predict how important parrotfish functional roles will respond to environmental disturbance. For example, large *C. strongylocephalus* have been shown to undergo major declines following fishing pressure in some regions (Bellwood et al. 2012). In habitats similar to the rubble and hardground habitats in the present study, this would have profound consequences for new sediment supply to the reef and any associated landforms. Another threat to reef fish assemblages, including parrotfish, is a loss of topographic complexity (Coker et al. 2012, Graham & Nash 2013, Graham 2014, Heenan et al. 2016, Darling et al. 2017, Richardson et al. 2017a, b). In the eastern reef habitats in the present study, the density of some of the most important sediment reworkers, *C. sordidus* and *S. niger*, is controlled by this structure. A loss of the structure in comparable habitats may cause declines in these species and the quantity of sediment they rework. As sediment reworking is thought to act as a substrate cleaning agent, decline in this function may lead to a reduction in coral recruitment success and the potential for habitat recovery (Goatley & Bellwood 2010, Krone et al. 2011).

While the present study has focussed on examining the variation in parrotfish functional roles among habitats, there is evidence to suggest that within habitat variability may also exist. For example, sediment load has been observed to influence parrotfish bite rates and as a result, may influence grazing, bioerosion and sediment production rates on different substrate types (Bonaldo & Bellwood 2011, Goatley et al. 2016). Within a habitat, sediment load may vary depending on the substrate characteristics and orientation and different species may also have preferences on which substrate types to feed on (Brandl & Bellwood 2014, 2016).

Questions also exist regarding shifts in grain size distribution with increasing fish size. In most species investigated, there was little difference in the grain sizes produced by fish of different size classes. However, in the species *S. frenatus*, a gradual shift from fine towards coarse size fractions with increasing fish size was observed. If this trend is apparent in more species (only 6 out of 15 parrotfish species are examined at Vavvaru alone) then fish size class distribution may influence the total quantity of different size fractions of sediment generated by whole parrotfish assemblages, which over larger scales, may influence the quantity of sediment that remains or is exported from the reef.

In terms of both bioerosion and sediment production, future work on parrotfish functional roles would benefit from quantifying “messy feeding”. The present, as well as other studies, assume that all material within the bite area is ingested, and that these ingestion rates directly correspond to the amount of sediment that parrotfish produce (Bellwood 1995b, Bruggemann et al. 1996, Bellwood et al. 2003, Alwany et al. 2009, Ong & Holland 2010, Morgan & Kench 2016a, Yarlett et al. 2018). However, there have not yet been any attempts to quantify the amount of eroded material or loose sediment that is disturbed, but not ingested. On occasion, excavator parrotfish were anecdotally observed to break off tips of branching corals, and drop the fragments onto the seabed. Parrotfish may therefore also produce coarser (gravel) grades of sediment through this process. In addition, we assume that the sediment that is ingested and triturated is egested in the same quantity. However, Smith & Paulson (1975) showed that anterior regions of the intestine in some parrotfish are acidic when feeding. It was proposed that this may be a mechanism to dissolve ingested carbonates to access additional nutritional resources. If this is the case, the quantity of sediment produced would be lower than the amount of carbonate ingested, and dissolution may further reduce the grain size of the sediment in the intestine. The extent of this dissolution may be influenced by the length of time the material spends in the intestine. Preliminary gut throughput estimates made during the present study suggest that this increases with fish size (weight), with a gut throughput time of ~25 – 30 mins for a parrotfish of ~2 g, and >2 hrs for a parrotfish of ~105 g (see Supplementary Table 6-37).

An acidic intestine may also prevent the formation of endogenous carbonates. While the present study shows that these carbonates were produced in starved fish, low gut pH has only been observed in feeding fish. When examining sediment samples produced by feeding parrotfish, no endogenous carbonate morphologies were observed. This does not necessarily mean they were not present or not produced, but it is a possibility. It is likely that fine size fractions, such as those produced endogenously, are underrepresented in the wild sediment samples collected because these grades of sediment are more likely to disperse and remain in suspension rather than fall to the substrate in pellets. It may also be possible that they were present in the collected sediment samples, but in such low quantities that they were not observed. Depending on the chemical composition, it may also be possible that any endogenous carbonates produced dissolve readily upon entering the environment, or during the sample processing stages (e.g. High Mg calcites are very soluble). Another possibility is that parrotfish have an alternative mechanism to deal with any excess calcium ingested, because of the acidic conditions within the gut. This may also be true in other families, such as surgeonfish, which are also understudied and do not appear to produce endogenous carbonates in aquarium conditions (unpublished observations).

Reef islands in atoll nations, such as the Maldives, are dependent on a continuous supply of sediment from reef sources (Perry et al. 2011b, Morgan & Kench 2014, 2016a, b). These islands are the only habitable land for the human populations in these nations, but the reefs supporting them are undoing dramatic change and degradation at an alarming rate. These changes, largely caused by climate change and exacerbated El Niño phenomena are having severe and immediate effects on reef carbonate and sediment budgets (Perry & Morgan 2017a, b). If these states persist over prolonged periods, the growth capacity of reefs and their associated sedimentary landforms will be severely hindered. Identifying the key sources of the right grades and types of sediment for reef island maintenance is an important first step towards predicting their response to ongoing environmental change. Parrotfish are known to be the most significant source of biologically derived sediment in the central Indian Ocean, and the present study has demonstrated that habitat condition and species assemblages can significantly influence their rates of new sediment production. Tracking the material from source to sink represents a challenging future question, along with its preservation potential following reports of reef sediment dissolution under projected future atmospheric carbon dioxide concentrations (Eyre et al. 2018).

Chapter 7 Thesis Key Findings, Discussion on Potential Impacts of Habitat Degradation and Fishing Pressure on Parrotfish Functional Roles and Directions for Future Work

Excavator parrotfish *Chlorurus microrhinos* at the municipal market, Pape’ete, Tahiti, French Polynesia. Photo credit: Robert T. Yarlett

7.1 Context

In this chapter, I summarise the key findings of the thesis so far, before building upon the results and understanding developed in this thesis and published literature to examine the outlook for parrotfish functional roles under environmental change scenarios. To extend current knowledge, this chapter discusses how different reef habitats may respond to these changes, and the implications of these responses for ecological and physical reef health. To answer research question 5 (on the impacts of environmental change on parrotfish functional roles), I focus specifically on the impacts of fishing pressure and loss of topographic complexity, as two very topical threats that coral reefs are facing and will likely continue to face in coming years. I address objective 9 of the thesis by making preliminary predictions of the impacts of these threats, thereby demonstrating how data presented in this thesis can be applied to future modelling and empirical studies to investigate the impact of disturbances on important parrotfish functional roles. From here, I suggest areas of future research into the functional roles of parrotfish on coral reefs.

7.2 Key Findings from the Present Work

7.2.1 Research Question 1: How does the rate of substrate bioerosion differ between parrotfish species and size classes in the Maldives?

This research question was addressed in chapter 4 for a range of common representative Maldivian parrotfish species. Excavators, particularly *Chlorurus strongylocephalus* (which eroded up to ~460 kg ind^{-1} yr^{-1}) had markedly higher bioerosion rates compared to scrapers, particularly at larger size classes. While this was expected, estimated bioerosion rates were considerably different to those reported for conspecifics in other regions (Bellwood 1995a, Bruggemann et al. 1996, Bellwood et al. 2003, Alwany et al. 2009, Ong & Holland 2010). This was thought to be partly because of environmental variability between regions, but also because of challenges associated with measuring parrotfish feeding metrics in the field, particularly grazing scar depth. Bioerosion rate was determined primarily by grazing scar volume and the proportion of bites that produced scars, both of which increased with fish size. Bite rate varied considerably between species (from 7.88 ± 0.63 bpm to 26.35 ± 1.42 bpm) and appeared to follow a bi-modal feeding cycle. This phenomenon has not been previously reported and its causes are uncertain. It is hypothesised that it may be caused by photoinhibition in food resources (cyanobacteria and potentially epilithic algae) and a resultant dip in nutritional quality at times of peak light intensity. However, the drivers of this pattern warrant further investigation.

7.2.2 Research Question 2: How do overall bioerosion rates and grazing pressures vary among reef habitats as a function of species assemblage and size structure?

This research question was addressed in chapter 5 for the habitats defined in chapter 3. In this chapter, bioerosion rate and grazing pressure was estimated for whole parrotfish communities across eight distinct reef habitats over an atoll edge reef platform. Six of the eight habitats supported parrotfish, and each of these had distinct species assemblages which appeared to be determined by topographic complexity and substrate type. Overall bioerosion rates varied markedly among habitats from 0 to 0.86 ± 0.11 kg m^{-2} yr^{-1} and was driven by the density of large (>30 cm) excavators. Overall parrotfish grazing pressure also varied considerably, but followed a different spatial pattern to that of bioerosion, revealing that these functional roles are not necessarily tightly coupled. This is thought to be because of the higher relative importance of scrapers and small size classes of parrotfish (<30 cm) in grazing. The importance of the different habitats for bioerosion (and resultant new sand generation) was dependent on the size of the habitat as well as overall bioerosion rate. The rubble habitat was the most important habitat for bioerosion, receiving nearly 55% of the total platform bioerosion despite making up <12% of the platform area. However, the highest grazing pressure occurred in the NE reef, where it is estimated that every m^{-2} of substrate is fully grazed every year by parrotfish.

7.2.3 Research Question 3: How do overall sediment production rates vary among reef habitats as a function of species assemblage and size structure, and what is the relative importance of new to reworked sediment?

This research question was addressed in chapter 6. Total sediment production rates varied markedly across the reef platform but were comparable in the three of the six habitats supporting parrotfish assemblages (the NE reef, SE patches and rubble habitats). In the western atoll-edge habitats, the sediment produced by parrotfish was predominantly comprised of new material derived from bioeroded reef substrate (>83%). In the eastern atoll-interior habitats, sediment reworking formed a more important part of the total sediment generated (>34% and up to ~75%). This was because of a higher density of scraping species, which were found to be important for sediment reworking but not for bioerosion. Endogenous carbonate production was also examined, but was thought to be insignificant compared to the quantities of sediment generated from the processes of bioerosion and sediment reworking because of the small volumes produced and questions around whether these carbonates are produced at all in feeding parrotfish.

7.2.4 Research Question 4: What are the characteristics (grain size and type) of sediment produced by different species and sizes of parrotfish, how does this influence the quantity of different sediment size fractions in different habitats and how does this material compare to that found on local reef islands?

This research question was addressed in chapter 6 which examined the grain size distribution and types of sediment generated by six common and representative species of Maldivian parrotfish. All species studied produced a wide range of sediment size fractions, from silt grade to coarse sands (<32 up to 2000 µm), but predominantly sands between 125-1000 µm. This material was comprised almost entirely of coral grains, with <20% made up of coralline algae, *Halimeda spp.,* mollusc shell fragments and Foraminifera. The sediment produced by parrotfish matches closely to the material found on local reef islands and beaches (Perry et al. 2015a).

7.3 Environmental Change and Parrotfish Functional Roles

Coral reefs are threatened globally by anthropogenic activities, and are undergoing dramatic changes at an alarming rate (Hughes et al. 2017a, b) Some of these activities can have direct impacts (e.g. fishing pressure, pollution, dredging, destructive fishing methods and sediment and nutrient inputs) and others can have indirect impacts (e.g. CO_2 emissions cause warming sea surface temperatures, exacerbated El Nino phenomena, and ocean acidification) on coral reefs (Hughes et al. 2003, Bellwood et al. 2004, Wilson et al. 2006, Hoey et al. 2016b, Hughes et al. 2017b, Eyre et al. 2018). These activities can influence reef benthic communities, water quality, topographic complexity and the abundance of different reef associated species. In many regions, parrotfish are directly fished from the reef for human consumption, and it is large excavating species that are often preferentially targeted (Bellwood et al. 2012).

Parrotfish assemblages are also influenced by reef habitat type. Variations in parrotfish assemblages occurs naturally over different reef habitats on healthy coral reefs because of the bottom-up controls of topographic complexity, substrate type and benthic community composition (as demonstrated in chapters 5 & 6; Chong-Seng et al. 2012, Nash et al. 2013, Tzadik & Appeldoorn 2013, Graham 2014, Darling et al. 2017, Richardson et al. 2017a). Natural and anthropogenic impacts can cause ecological and physical changes to these habitats, such as a loss of coral cover (e.g. after a coral bleaching event) and loss of structural complexity, which can happen rapidly following a physical disturbance such as a storm, or gradually through persistent bioerosion (Glynn 1997, Perry et al. 2014a). These changes to benthic community composition and structural complexity are likely to alter the associated parrotfish assemblages. As discussed in Chapter 5, different parrotfish assemblages can contribute differently to overall contributions to different functional roles. Changes to these natural assemblages may hence cause further changes to reef habitat condition because of the top-down influence that parrotfish have on reef habitats through their roles in bioerosion, grazing, sediment production, sediment reworking. The exact nature of this response may determine the likelihood of recovery from environmental disturbance.

7.3.1 Impacts of Fishing Pressure on Parrotfish Functional Roles

The direct extraction of parrotfish that occurs in many regions for human consumption is considered a major cause of reef degradation (Bellwood et al. 2004, 2012, Edwards et al. 2014, Taylor et al. 2015, Cinner et al. 2016). In the Indo-Pacific region, targeting of a select number of species can cause shifts in species dominance (Clua & Legendre 2008). The excavator species that are commonly targeted are large and slow growing, making them highly susceptible to overexploitation (Taylor & Choat 2014, Taylor et al. 2014). Even in areas of relatively low human population density, this targeted extraction can cause almost the complete removal of species such as *Bolbometopon muricatum* and large *Chlorurus spp.* (*C. microrhinos* in the Pacific or *C. strongylocephalus* in the Indian Ocean; Bellwood et al. 2011). This can be coupled with an increase of small excavator species, presumably because of reduced inter-species competition for food resources (e.g. *C. spilurus* in the Pacific or *C. sordidus* in the Indian Ocean; Bellwood et al. 2012). The abundance of scrapers was observed to remain relatively unchanged across this gradient. In terms of the effect of these community changes on overall parrotfish functional roles, it was demonstrated that bioerosion rates reduced by almost 100%, while the processes of grazing pressure and sediment reworking remained relatively resilient (unchanged) to these changes (Bellwood et al. 2012). However, coral reefs are complex environments made up of a variety of habitat types, each with their own distinctive role over the broader reef system (as demonstrated in chapters 5 & 6). It is unclear how different habitats will respond to the impacts of fishing pressure as this will likely depend on the relative differences in pre and post-fishing communities.

To answer this question would require empirical studies to measure parrotfish densities in different reef habitats over a gradient of fishing pressure, but preliminary predictions using results from the present study and trends reported in the literature can be made. These predictions can be used to generate hypotheses and set up future empirical and modelling work. Reefs in the Maldives have been used in this thesis to represent an unexploited system where parrotfish are not targeted by the commercial fishing industry. However, elsewhere in the Indo-Pacific, Bellwood et al. (2012) showed that the fishing pressure in areas of human population density as low as <50 people km^{-2} can be enough to result in the complete loss of large excavators. This appeared to result in 2.8 × increase in the abundance of small excavators with increasing human population density up to 200 people km^{-2}. Scrapers showed no significant change in abundance.

To investigate the potential impact of this level of fishing pressure (fishing pressure of a population density of 200 people km^{-2}) on Vavvaru reef habitats, a simple Excel based model was used to examine how the resultant changes in parrotfish assemblage would influence community level functional roles. This level of fishing pressure would be realistic given the Maldives has one of the highest population densities in the world (>1000 people km^{-2}). It was assumed that a shift in fishing pressure to reef species would result in complete removal of *Chlorurus strongylocephalus* and *Cetoscarus bicolor*. A 2.8 × increase in abundance was applied to small excavator *Chlorurus sordidus*, and it was assumed that there would be no change in abundance of scrapers. It was also assumed that only perimeter habitats, or habitats easily accessible by boat (the hardground, rubble, NE reef and SE patch reefs) would be under direct fishing pressure, especially as these are also the habitats that support communities of large excavators (see Chapter 5).

Under these assumptions, total parrotfish density actually increased (by ~20% in the hardground and rubble habitats, 60% in the SE patch reefs and 100% in the NE reef) in all habitats because of the opportunistic increase in small excavators. In reality, these increases are unlikely to be as extensive because small excavator increase has not been scaled to the original abundance of large excavators (i.e. if originally there was a very low relative abundance of large excavators, the abundance of small excavators may not increase as much as in areas where there was formally a high relative abundance of large excavators). However, the results generated still act as a good indicator of the potential impacts of targeting fishing pressure on large excavators. The predicted impact of such a change in Vavvaru habitats showed varied responses among both habitat types and the functional roles (bioerosion, grazing, sediment reworking and sediment production) examined (Figure 7-1).

7.3.1.1 Fishing impacts on bioerosion

Overall bioerosion rate showed a marked reduction in response to fishing pressure in the Hardground (0.35 kg m^{-2} yr^{-1} reduction), rubble (0.79 kg m^{-2} yr^{-1} reduction) and SE patch reef (0.41 kg m^{-2} yr^{-1} reduction) habitats. This is because of the substantial contribution of large excavators (*Chlorurus strongylocephalus* and *Cetoscarus* bicolor) to bioerosion in these habitats which are completely extracted under the assumptions of fishing pressure applied in the model. Under these scenarios, the predicted increase in abundance of small excavators is unlikely to compensate for the loss of large excavators. There was little change in bioerosion rate in the NE reef habitat because of the comparatively lower abundance (and therefore lower contribution to bioerosion) by large excavators. In this habitat, it is more likely that small excavators will be able to compensate for the loss of bioerosion caused by the extraction of large excavators.

7.3.1.2 Fishing impacts on grazing

Grazing pressure remained comparable in the hardground, rubble and SE patch reef habitats, but increased in the NE reefs (by 11.15 ha yr^{-1}) after applying fishing pressure assumptions to the model. Scrapers and small excavators are more important contributors to grazing compared to large excavators (see Chapter 5) and so appear to be able to compensate for the loss of grazing pressure by large excavators. The increase in grazing pressure in the NE reef is likely to be a result of assumptions applied regarding the increase of small excavators, and so may not be as extensive an increase as suggested in Figure 7-1.

7.3.1.3 Fishing impacts on sediment reworking

Fishing pressure appeared to have little effect on the role of sediment reworking. Slight increases in the amount of sediment reworked in the eastern reef habitats may occur because of the increase in small excavators, which have a faster feeding rate, but this increase is unlikely to be significant (the error bars overlap). For this functional role, small excavators are likely able to compensate for the extraction of large excavators from the system.

7.3.1.4 Fishing impacts on total sediment production

Overall sediment production remained comparable in the eastern reef habitats, but there was a marked reduction in the hardground (0.33 kg m^{-2} yr^{-1}) and rubble habitats (0.81 kg m^{-2} yr^{-1}). This is because of the importance of large excavators for bioerosion in these habitats (contributing over 90% to total parrotfish bioerosion, see Chapter 5) and the high relative importance of bioerosion compared to sediment reworking (bioerosion accounting for >83% of new sediment production) for total sediment production in these habitats. In the eastern reef habitats, a larger proportion of total parrotfish sediment production is derived from reworked material.

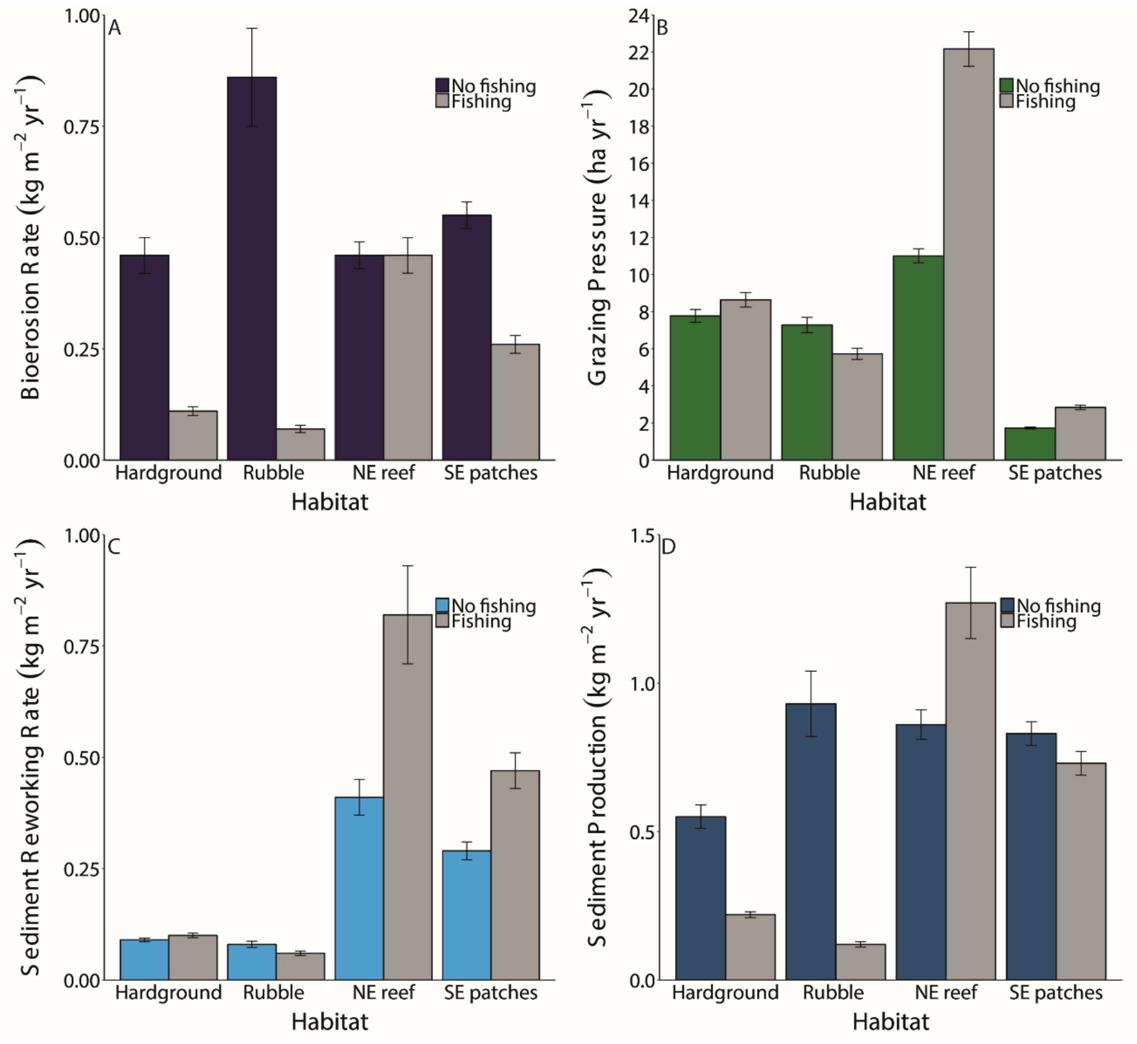


Figure 7-1 Impact of hypothetical fishing pressure on parrotfish functional roles Vavvaru perimeter habitats. Plots represent impact on A) Bioerosion rate, B) Grazing pressure, C) Sediment reworking, D) Total sediment production.

7.3.2 Impacts of fishing pressure summary

Of the functional roles examined, bioerosion appears to be the most susceptible to the impacts of fishing pressure, although this is more pronounced in the hardground and rubble habitats. As a result of reduced bioerosion in these western habitats, total sediment production is also severely affected. The hardground and rubble habitats are known to be two of the most important habitats in terms of biological sediment supply to the reef platform, so reduced bioerosion rates in these habitats would be likely to significantly limit the supply of material to the reef island. This would ultimately affect the capacity of the island to withstand physical erosion and track future projected sea level rise.

The increase in smaller scrapers would appear to compensate for the loss of large excavators in eastern reef habitats. However, it may not be realistic to expect increases in some functional roles (e.g. grazing and sediment reworking) in the eastern reef habitats, as responses of non-fished species are unlikely to be uniform in all habitats and community changes will likely depend on the original abundance of large excavators in these habitats. Although in comparison to bioerosion, these results demonstrate that the processes of grazing and sediment reworking may be more resilient to community change in these habitats.

As well as loss of large excavators, fishing pressure may have other impacts of parrotfish communities which are not factored into the calculations in the present study. For example, there may be a reduction in mean fish body size as a result of targeted extraction of large individuals (Taylor et al. 2015). However, this is relatively harder to predict, and will depend on the species preferentially removed and how specific the target catch is. It is also unclear whether mean size of non-fished species could increase in response to reduced competition for food resources. Another response to consider is the effect of fishing pressure on parrotfish sex ratios (Hawkins & Roberts 2003, O'Farrell et al. 2016). In most cases, the largest individuals in a population are also the terminal phase male parrotfish, so fishing pressure may have an influence spawning dynamics and parrotfish demographics.

Fishing closures and marine protected areas have, in some cases, allowed parrotfish populations to recover following fishing disturbance and with appropriate management, may even allow sustainable fisheries (McClanahan et al. 2007, 2016). Browsing parrotfish have also been observed to be susceptible to fishing (Edwards et al. 2014). Further work into this functional group is required to investigate how this influences the potential of the group to reverse shifts from coral to algal dominated reefs.

7.3.3 Predicting Impacts of Habitat Degradation on Parrotfish Functional Roles

In addition to the controls of fishing pressure, differences in the ecological and physical structure of coral reefs can also influence reef fish density, size and species richness (Friedlander & Parrish 1998, McClanahan & Arthur 2001, Gratwicke et al. 2005, Harborne et al. 2011, Heenan et al. 2016). Changes to algal cover, sediment load, live coral cover and reef structural complexity can therefore act as a bottom up control on fish assemblages and influence their density, biodiversity and ecosystem roles (Pratchett et al. 2011, Coker et al. 2012, Graham & Nash 2013, Nash et al. 2013). Many coral reefs are currently under severe threat from rising sea surface temperatures and exacerbated ENSO (El Niño Southern Oscillation) caused by climate change.

A particularly strong El Niño event that lasted from late 2015 until early 2017 caused widespread coral bleaching, and in many cases coral mortality, in all major reef building regions (Hughes et al. 2018). Reefs in the central Indian Ocean were affected by this event in mid-2016, and suffered comparable impacts to that of the 1998 El Niño event, with reports of up to 75% coral mortality, causing shifts from net positive to net negative carbonate budgetary states (Perry & Morgan 2017a, b). Loss of live coral has been shown to negatively impact recruitment of reef fish and will cause an immediate food shortage for obligate corallivores (Coker et al. 2012). However, the structural complexity provided by remaining dead coral skeletons can continue to provide habitat for many reef associated fish species after the bleaching event, until it collapses (Blackwood et al. 2012, Emslie et al. 2014).

For some parrotfish species, the increased substrate availability for feeding after bleaching events may allow growth of the population (Adam et al. 2011, Pratchett et al. 2011, Gilmour et al. 2013). However, persistent bioerosion and periodic physical disturbances will weaken and break down reef topographic complexity over time (Glynn 1988, 1997, Perry et al. 2013). With the loss of this structural complexity comes declines in reef fish abundance and diversity, including some parrotfish species (Tzadik & Appeldoorn 2013, Rogers et al. 2014, Darling et al. 2017). As shown in chapter 5, structural complexity is an essential habitat requirement for species such as *Scarus niger* and *Scarus viridifucatus*, and some generalist species (such as *Chlorurus sordidus*) are found to decrease in density with decreasing rugosity. It is important to understand how any changes to parrotfish assemblages that occur as a result of loss of habitat structure will influence the parrotfish functional roles.

Especially because these changes may have further implications for the reef environment and its recovery potential (Pratchett et al. 2014).

At the time of study, prior to the 2016 ENSO induced coral bleaching event, coral reefs in the Maldives were considered to be in good condition, including at the study site for the present work (Perry et al. 2017). Following the bleaching event, a study in early 2017 showed that reefs in the southern Maldives had very low coral cover but the reef structure remained (Perry & Morgan 2017a). There was also little change in parrotfish abundance (Perry & Morgan 2017a, b). Schuhmacher et al. (2005) observed that at 6 years following the 1998 bleaching event, persistent bioerosion had reduced a once three-dimensional Maldivian reef flat to a levelled rubble field. At 8 and 10 years after the bleaching event, Maldivian reefs were in a "regressive" phase, dominated by sand and rubble, but showed no sign of shifting to an algal dominated state (Lasagna et al. 2008, 2010). At about 10 years following the bleaching event, "young" stage growing reefs were observed, showing a road to recovery (Lasagna et al. 2010). Close monitoring of central Indian Ocean reefs will be required to monitor changes to these systems and to the reef fish assemblages to see how the recovery trajectory compares in the coming decades. Signs of phase shifts or delayed recruitment may be indicators of a prolonged degraded state and long term negative carbonate budgetary states.

The future trajectory of Maldivian reefs is also likely to vary spatially. Different reef habitat types, especially on atoll edge sites, which often have a more diverse array of habitats compared to atoll interior platforms, are likely to have suffered differing degrees of coral bleaching and mortality. These habitats may hence undergo different trajectories of degradation or recovery. For example, the hardground, rubble and *Porites* bommie habitats may be more resilient to the impacts of coral bleaching because these habitats had lower coral cover, fewer fragile branching coral species and more massive coral species (such as *Porites spp.*) which typically have a higher resilience to bleaching (Loya et al. 2001). The severe impacts are therefore more likely to occur on the eastern reef habitats, which have a higher percentage cover of branching *Acropora spp.,* can be more susceptible to bleaching and more easily broken down by physical disturbance, or persistent bioerosion (Schuhmacher et al. 2005).

Figure 7-2 shows anticipated impacts of loss of reef structural complexity on important parrotfish functional roles (bioerosion, grazing, sediment reworking and sediment production) in the main reef building habitats at Vavvaru (the NE reef and SE patches). It was assumed that with time, species that rely on the complex framework provided by these habitats (*Scarus niger* and *S.* viridifucatus – see chapter 5) would be lost, species that should a preference for rubble dominated habitats would increase to densities comparable to that of the rubble habitat, and that generalist species that were found in higher densities in the eastern reef habitats were likely to decline to densities comparable to that of the rubble habitat. Species that showed no strong association with rugosity or complex coral growth forms were assumed to remain at comparable densities.

Under these assumptions, total parrotfish density declined by ~70% in the NE reef habitat, and ~40% in the SE patch reefs habitat. The impact of this anticipated change in community varied considerably between functional roles and between habitats.

7.3.3.1 Impacts of habitat degradation on bioerosion

Bioerosion rate showed a potential minor reduction in both the NE reef and SE patch reef habitats, but this is unlikely to be significant. This is likely because the most significant contributors to bioerosion do not strongly associate high rugosity, structural complex habitats (see Chapter 5) and so this function is maintained when coral cover and structural complexity is lost.

7.3.3.2 Impacts of habitat degradation on grazing

Grazing pressure showed a marked reduction in the NE reef habitat (8.15 ha yr^{-1}). This is likely because of the marked reduction in *C. sordidus* and loss of *S. niger* in this habitat, which are the two highest contributors to grazing pressure (see Chapter 5). The decline of important grazers was not as severe in the SE patch reefs so this role showed only a slight decline in this habitat (0.85 ha yr^{-1}).

7.3.3.3 Impacts of habitat degradation on sediment reworking

Sediment reworking showed a comparable pattern to grazing pressure, with a marked reduction in the NE reef habitat (0.3 kg m^{-2} yr^{-1} reduction) and a potential slight reduction in the SE patch reefs. Again, the reduction observed in the NE reef habitat is because of the decline in the two most important sediment reworking species, *C. sordidus* and *S. niger*. The decline in important sediment reworking species is not as severe in the SE patch reefs and so the role of sediment reworking is not affected to the same extent.

7.3.3.4 Impacts of habitat degradation on total sediment production

Total sediment production rate showed a marked decline in the NE reef habitat (0.45 kg m^{-2} yr^{-1}). This reduction is because of the importance of sediment reworking in contributing to total parrotfish sediment production in this habitat (~47% of total sediment produced – see Chapter 6), so the decline in important sediment reworking species has a significant effect on total sediment production. Neither the roles of bioerosion or sediment reworking were as severely effected in the SE patch reefs, so total sediment production is expected to remain comparable after loss of structural complexity.

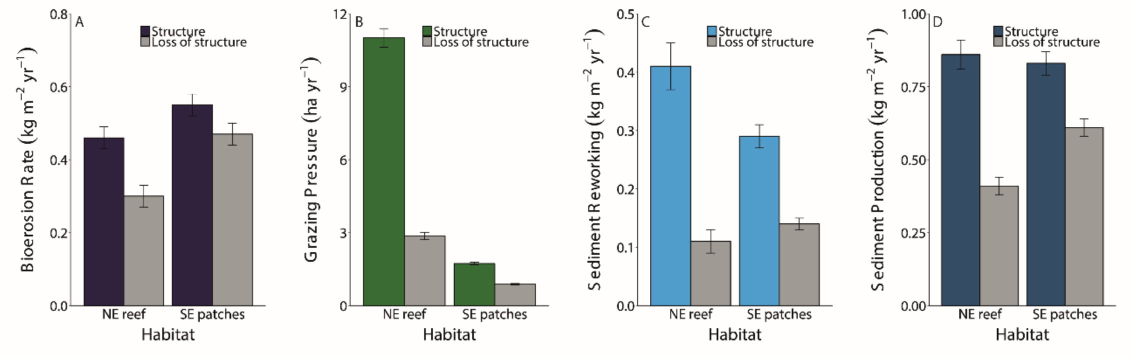


Figure 7-2 Predicted impact of loss of reef framework structural complexity on parrotfish functional roles in main Vavvaru reefal habitats (NE reef and SE patches): A) Bioerosion, B) Grazing pressure, C) Sediment reworking and D) Sediment production.

7.3.4 Impacts of habitat degradation summary

From the predictions in the present study, loss of structural complexity appears to primarily affect the roles of grazing and sediment reworking. In previous studies examining impacts of a loss of live coral cover but retention of reef structure, it has been found that parrotfish grazing on reefs in French Polynesia can prevent phase shifts to algal dominated states and promote coral recovery (Adam et al. 2011). The results of the present study suggest that loss of structural complexity may influence the capacity for parrotfish populations to prevent such shifts. This is because the loss of structure causes a reduction in the density of scraping and small excavator species, which are significant contributors to grazing pressure. This has been observed on heavily degraded Caribbean reefs, where the assemblage of herbivorous fish supported by the degraded habitats is able to maintain algal cover but not return the habitat to its previous low algal cover state (Paddack et al. 2006).

Large bioeroding species do not appear to rely on reef structure (likely because of a low risk of predation pressure – see Chapter 5) and so are likely to maintain their bioerosion rates in the eastern reef habitats after disturbance. However, if this state persists over prolonged time-scales (decades), the role of bioerosion may also be at risk. Graham et al. (2007) found a time-lag response following a loss of reef structural complexity whereby the reef supports large individuals but does not provide suitable habitat for juvenile recruitment. Within a few decades (large species of parrotfish live ~20 years), these large individuals may be lost either through natural mortality or fishing pressure, leaving the reef devoid of parrotfish and their functional roles. This emphasises the importance of protecting parrotfish nursery habitats, which may differ to the habitat requirements of adults (Hamilton et al. 2017).

The lower total sediment production rate in the NE reef is because of the importance of sediment reworking in this habitat, and the marked reduction observed in this role due to the reduced density of key scraping species. The impact of the changes to these functional roles on the reef system would likely be reduced coral recruitment success because of reduced removal of turf algae cover and loose sediment from substrate surfaces (Mumby 2006, Hughes et al. 2007, Mumby et al. 2007, Afeworki et al. 2013, Steneck et al. 2014). Although, these predictions are based purely on theory and are not definitive trajectories. Relative densities of different parrotfish species are likely to change as the habitats become less suitable for some, and more suitable for others. Interactions with other species may also play a part, particularly with regards to grazing pressure and sediment reworking, where surgeonfish are also likely to be significant contributors on Maldivian reefs, and may respond differently to habitat degradation compared to the parrotfish (Goatley & Bellwood 2010, Krone et al. 2011).

7.4 The synergistic effects of fishing pressure and habitat degradation

The impacts of fishing pressure and loss of structural complexity have so far been discussed separately, but many reefs over the Indo-Pacific region are subjected to both disturbances. The synergistic effects of both of these impacts is likely to be dire for parrotfish populations and maintaining their functional roles. While, overfishing is likely to cause declines in bioerosion rates, and resultant new sediment production in some habitats (Bellwood et al. 2012, present study), loss of structural complexity is more likely to reduce grazing pressure and sediment reworking.

The impacts on these functional roles may create negative feedback consequences for the health, and recovery potential of the reef system. The reductions in grazing pressure caused by loss of reef structure may result in excessive algal growth on coral reefs, which may further reduce grazing pressure (as algal turfs become too long for parrotfish grazing; Steneck et al. 2014), thereby preventing coral recruitment and smothering surviving corals. In addition, these uncropped algal turfs may retain higher sediment loads, especially if sediment reworking is reduced, which may further deter herbivorous fish from grazing (Afeworki et al. 2013, Adam et al. 2015, Goatley et al. 2016, Gordon et al. 2016). Reductions in bioerosion rate will further limit space for coral recruitment and also significantly reduce sediment supply to the reef and its associated sedimentary landforms (Perry et al. 2015a, Morgan & Kench 2016a). Over prolonged timescales, this may influence reef carbonate and sedimentary budgets, as well as the maintenance of reef islands and their capacity to keep pace with projected future sea level rise (Perry et al. 2011b, Perry et al. 2013). To protect these important functional roles for the reef system, efforts should be made to reduce direct extraction of large excavators, and where possible, prevent or reduce the structural decline of the reef framework. Some coral reefs have been observed to show signs of recovery from degraded states if free from chronic anthropogenic pressures, although this can take decades for heavily degraded reefs and require carefully planned fisheries restrictions (Gilmour et al. 2013, MacNeil et al. 2015).

7.4.1 Research Question 5: What are the potential impacts of fishing pressure and habitat degradation on the contributions of parrotfish communities to bioerosion, grazing, sediment production and sediment reworking, and what are the implications of this for the reef system?

This research question was addressed in the current chapter using data and analyses presented throughout this thesis and findings from the literature. Fishing pressure primarily impacts the role of parrotfish in bioerosion because it is typically large excavators that are extracted. However, the severity of the impact is habitat dependant and in some cases, small excavators may be able compensate for the removal of large excavators, presumably because of reduced competition for food resources. Habitat degradation, specifically the loss of structural complexity, primarily impacts grazing pressure and rates of sediment reworking. Again, the severity of the impact is habitat dependant. Total sediment production can also be reduced in some habitats by loss of structural complexity, where sediment reworking is a key contributor to sediment production. The synergistic impacts of fishing pressure and loss of structural complexity is likely to affect all four of the major parrotfish functional roles examined in this thesis. The consequences of this for reef environments is likely to be reduced coral recruitment, increase in macroalgae cover, reduced reef growth potential, and a reduced sediment supply to reef islands and beaches.

7.5 Recommendations for future research

7.5.1 Estimates of absolute reef fish density

Current estimates of fish biomass, the rate of fish extraction and extent of the functional roles played by fish in the world's oceans are full of uncertainties (Jennings & Collingridge 2015). Obtaining accurate and reliable fish density data is important for making community scale estimates of fish functional roles. For sedentary species that spend much of their time on the benthos or buried in sediment, obtaining an instantaneous density is relatively straight forward. However, mobile species represent a greater challenge because of their ability to move into and out of the survey area. Underwater Visual Census (UVC) is the most commonly used non-destructive methodology used to estimate reef fish abundance, but the methodology has a number of limitations (Lincoln Smith 1988, Harvey et al. 2001, 2004, Cappo et al. 2003, Watson et al. 2005, Langlois et al. 2006, Ward-Paige et al. 2010, Cheal et al. 2016).

In the present study, the rates of the processes examined were estimated by observing the number and types of parrotfish entering a fixed area of reef over a given time frame, rather than attempting to estimate abundance or biomass. This approach, using RUVs, matches the aims of the study to estimate the rates of important reef processes, RUVs have the advantages of being able to pause and check species ID and avoid influence of the observer on fish behaviour (Watson et al. 2005, Harborne et al. 2016). In addition, the error associated with estimating survey area is reduced when using RUV compared to UVC by having a fixed field of view of the camera and a physical marker to define the distance boundary. The survey area of RUVs may be influenced by the angle of the camera and topography of the seafloor so some error is still anticipated, but attempts were made to be consistent with camera set up to reduce this error. Where financially and logistically possible, using a well calibrated stereo-video set up would allow higher resolution fish body size estimates (Harvey & Shortis 1998, Harvey et al. 2001). In the present study, using RUVs was considered to appropriate for comparing estimating the rates of key parrotfish functional roles occurring in different reef habitats. However, this approach is unable to give a reliable estimate of fish absolute fish abundance.

Other metrics exist for analysing fish abundance data but were not considered suitable for use in the present study. A more commonly used metric for RUV surveys is MinCount (or MaxN), which records the maximum number of individuals in the field of view at any one time during a given sampling period (e.g. Ellis & DeMartini 1995, Watson et al. 2005), but interpreting fish densities per unit area from this is challenging (Schobernd et al. 2014). In contrast, MaxCount, where all individuals are counted during a sampling period (but without factoring for time), is prone to overestimating fish abundance (Conn 2011, Schobernd et al. 2014). An alternative metric, known as MeanCount (the mean number of individuals observed in a series of instantaneous still snapshots) may closely resemble true fish abundance (Schobernd et al. 2014), and may be a suitable metric to use where absolute fish abundance of common reef species is required (e.g. Cappo et al. 2003). However, as with all of these methodologies, much of the available data in the survey goes to waste as only relatively small proportions of the total video length are used. In doing this, rare but functionally important species could be missed from the survey. In the present study, all survey data was put to use, which enabled the detection of less common but functionally important species to be detected. For example, the author was not aware that *Cetoscarus bicolor* was present in the NE reef habitat, or that *S. russellii* was present at Vavvaru at all, until observed by RUV. Future research could therefore focus on increasing accuracy of estimates of reef fish abundance for cases where these data are required. Further advantages and disadvantages of common fish survey methods are summarised in Table 7-1.

Table 7-1 Advantages and disadvantages of commonly used fish survey methodology.

RUV (Single Video)	RUV (Stereo Video)	Underwater Visual Census (UVC)
Advantages		
Observer bias is minimised. Data are easily verifiable, and reproducible.	Observer bias is minimised. Data are easily verifiable, and reproducible.	All required data are collected during the survey with minimal post-survey processing time (unless survey is recorded).
Permanent record of data. Possible to pause and check species ID.	Permanent record of data. Possible to pause and check species ID.	Time and cost efficient. Requires only a dive slate and a transect line.

Can be baited or un-baited depending on study aims.	Can be baited or un-baited depending on study aims.	Survey can be recorded using a swimmable single, or stereo video system to create a permanent record that can; be re-watched for accurate species ID, improve area estimates and minimise observer bias.
Physical boundary of survey area due to restricted field of view.	Physical boundary of survey area due to restricted field of view.	Potential for large survey area to be covered
More likely to pick up shy/wary species compared to UVC.	More likely to pick up shy/wary species compared to UVC.	
Significantly longer survey time compared to UVC.	Significantly longer survey time compared to UVC.	
Ideal for both very shallow habitats (where it is difficult to observe fish without getting too close and disturbing them), very deep habitats and where extended survey periods are required (beyond recreational diving limits).	Ideal for both very shallow habitats (where it is difficult to observe fish without getting too close and disturbing them), very deep habitats and where extended survey periods are required (beyond recreational diving limits).	
	Accurate size measurements is calibrated correctly.	
Disadvantages		
Vertical structures on the reef can obscure view	Vertical structures on the reef can obscure view.	Observers must be well trained in species ID, and undertaking many simultaneous tasks induces observer error and bias.
Only coarse size estimates (10-15cm size classes) can be made reliably using scale bars or lasers.	Complicated set up and calibration required to use accurately for size estimates.	No physical boundary of the transect line, potentially resulting in an 82% underestimate or 194% overestimate of survey area (Harvey, 2004), effecting density estimates. Although this can be improved if video recorded.
Only a small area is surveyed per video if stationary, therefore thorough replication is needed to take into account intra-habitat variability and species with small home ranges.	Only a small area is surveyed per video if stationary, therefore thorough replication across habitats is needed to take into account intra-habitat variability and species with small home ranges.	No permanent record of survey, unless recorded.

Extensive post-survey data processing time and risks of under or overestimating abundance estimates depending on the analytical techniques used.	Extensive post-survey data processing time and risks of under or overestimating abundance estimates depending on the analytical techniques used.	Observer variability makes UVCs difficult to verify, unless recorded.
Can be difficult to determine depth of field.	Very expensive compared to other survey methods due to the specialist calibration equipment and software required, specific camera models and frame set up, and analytical software (http://www.seagis.com.au/). Although there have been attempts to use cheaper camera models to help reduce the cost of this (Letessier et al. 2015).	Fish may be attracted or wary of observer. The risk of causing flight behaviour is particularly high in shallow water.
		Less likely to pick up shy/wary species compared to stationary video methods.
		Comparatively very short survey time.

7.5.2 Bi-modal feeding cycle

A previously unreported bi-modal feeding cycle was found in all species examined in the present study. In previous studies, data have been fitted with quadratic curves, or pooled into time categories, thereby either fitting a set defined pattern or presenting the data in a way that reduces resolution of the best fit curve (Bruggemann et al. 1994a, Bellwood 1995a, Fox & Bellwood 2007, Bonaldo & Bellwood 2008, Lokrantz et al. 2008, Alwany et al. 2009, Ong & Holland 2010, Bejarano et al. 2013). By fitting a LOESS regression to the raw bite rate data, the bimodal pattern became apparent. Further confidence in this pattern has been found in very high resolution “soundscape” datasets (Timothy Trichas, personal communication). Currently, the environmental drivers behind this phenomenon are unknown, but it is hypothesised that it may be due to photoinhibition and a resultant dip in nutritional quality in food resources (cyanobacteria, and potentially epilithic algae). Understanding the environmental drivers behind parrotfish bite rates and feeding cycles is important because the rates and patterns have a major influence on the functional roles of parrotfish.

7.5.3 Synergistic impacts of multiple environmental stressors on reef fish assemblages and their functional roles

Preliminary attempts to anticipate the impacts of two types of environmental change (fishing pressure and loss of structural complexity) were presented earlier in this chapter based on reports from the literature and analyses presented in chapter 5. However, to accurately model these processes would require more data on a few currently understudied areas of parrotfish biology, including; species life history data, inter-species interactions and a more detailed understanding of the influence of food resource availability (particularly cyanobacteria) on parrotfish distribution. In terms of habitat degradation, the bleaching event of 2016 now presents an opportunity to monitor changes to Maldivian coral reef habitats, and their associated fish assemblages. In these studies, data from this thesis can be applied to estimate the changes that this degradation causes to parrotfish functional roles. Perry & Morgan (2017a, b) have begun this monitoring processes on reefs in the Southern Maldives at 6 months and 12 months after the bleaching event. While coral cover reduced dramatically, the reef structure remained at this stage so parrotfish assemblages have changed very little. Continued monitoring will be required to track changes in the reef structure and the associated impacts on the parrotfish assemblages.

7.5.4 Endogenous carbonate production by parrotfish and possible alternatives-hypotheses

Chapter 6 of this thesis presented a preliminary insight into the importance of endogenous carbonate production in the context of total sediment production by parrotfish. While this process of carbonate sediment production was thought to be insignificant in terms of sediment supply to reef environments, there are a number of further interesting research questions with regards to whether or not parrotfish produce endogenous carbonates when they are feeding, and if not, what alternative mechanisms do parrotfish have to prevent excessive calcium uptake?

Firstly, it is known that metabolic rate can influence carbonate production, but there are no approaches to correct for fish that are inactive and non-feeding (both of which are known to reduce metabolic rate) in aquarium conditions (Jobling 1981, Wilson et al. 1996, 2009, Perry et al. 2011a). The observations in the present thesis, and indeed many studies, are therefore likely to represent a significant underestimate of endogenous carbonate production, but to what extent is uncertain.

Despite this idea of underestimated production, parrotfish represent an interesting study group because of their unique gut chemistry. Smith & Paulson (1974) observed acidic gut pH in anterior region of the intestine of feeding parrotfish, and also carbonic anhydrase production in parrotfish intestines (Smith et al. 1975). It was proposed that parrotfish dissolve carbonates within their intestines in order to access additional nutritional resources within the carbonate substrates that they erode and ingest. This may also be the case for other herbivorous fish groups such as surgeonfish, which did not appear to produce carbonates at all in aquarium conditions, unless these were immediately dissolved (Yarlett & Salter unpublished data). The parrotfish observed in the present study in carbonate production experiments were unfed, and were likely to have a more alkaline gut pH (Smith & Paulson 1974).

From a sediment supply point of view, the question around endogenous carbonate production in parrotfish and surgeonfish is important because these groups make up very high percentages of overall fish biomass on many Indo-Pacific coral reefs. However, these are the groups where data are severely lacking. From a biological perspective, these groups are interesting because it is possible that they represent the first known exceptions to the currently accepted view that all marine teleost fish produce carbonates endogenously as a by-product of osmoregulation. If this is the case, it poses questions as to how parrotfish (and surgeonfish) deal with excess calcium ingested, and prevent the formation of renal stones. It may be that carbonate are only produced in the posterior regions of the intestine in parrotfish, or it may be possible that they have evolved an alternative mechanism of dealing with excess calcium ions. One such hypothesis is that these ions are dealt with in the mucus coating that parrotfish produce at night, but this requires further investigation.

7.5.5 Parrotfish sediment production and its fate within the reef system

The present work presents the grain size distribution and grain type of parrotfish at a reef platform in the central Maldives. This material has been shown to be comparable to the dominant grain sizes found on local reef islands. While it is difficult to trace sediment from source to sink, it is assumed based on the quantities of the appropriate grain sizes produced that parrotfish are major sources of island grade material. While the size range of grains produced is not expected to change significantly among species and regions, it is possible that the sediment can further reduce in grain size upon entering the environment. Recent research has shown how susceptible reef sediments can be to dissolution under projected future trajectories of ocean pH (Eyre et al. 2018). Questions remain around both the current preservation potential of parrotfish-derived sediments on coral reefs, and its preservation potential in coming decades. Dissolution of this material could have negative implications for the long term sediment supply to and maintenance of reef associated sedimentary landforms.

Scarus frenatus (terminal phase) enjoying a good clean at Vavvaru. Photo credit: Kate E. Philpot.

References

Adam MS (2006) Country Review: Maldives. In De Young C (ed) Review of the state of world marine capture and fisheries management: Indian Ocean. Rome. Foof and Agricultural Organisation of the United Nations, p 383-391

Adam TC, Kelley M, Ruttenberg BI, Burkepile DE (2015) Resource partitioning along multiple niche axes drives functional diversity in parrotfishes on Caribbean coral reefs. Oecologia 179:1173–1185

Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC, Bernardi G (2011) Herbivory, connectivity, and ecosystem resilience: Response of a coral reef to a large-scale perturbation. PLoS One 6:e23717

Afeworki Y, Bruggemann JH, Videler JJ (2011) Limited flexibility in resource use in a coral reef grazer foraging on seasonally changing algal communities. Coral Reefs 30:109–122

Afeworki Y, Zekeria ZAZ, Videler JJJ, Bruggemann JH (2013) Food intake by the parrotfish Scarus ferrugineus varies seasonally and is determined by temperature, size and territoriality. Mar Ecol Prog Ser 489:213–224

Alvarez-Filip L, Gill J a., Dulvy NK (2011) Complex reef architecture supports more small-bodied fishes and longer food chains on Caribbean reefs. Ecosphere 2:doi:10.1890/ES11-00185.1

Alwany M a., Thaler E, Stachowitsch M (2009) Parrotfish bioerosion on Egyptian Red Sea reefs. J Exp Mar Bio Ecol 371:170–176

Aswani S, Sabetian A (2010) Implications of Urbanization for Artisanal Parrotfish Fisheries in the Western Solomon Islands. Conserv Biol 24:520–530

Bejarano S, Golbuu Y, Sapolu T, Mumby PJP (2013) Ecological risk and the exploitation of herbivorous reef fish across Micronesia. Mar Ecol Prog Ser 482:197–215

Bejarano S, Jouffray JB, Chollett I, Allen R, Roff G, Marshell A, Steneck R, Ferse SCA, Mumby PJ (2017) The shape of success in a turbulent world: wave exposure filtering of coral reef herbivory. Funct Ecol 31:1312–1324

Bell JD, Ratner BD, Stobutzki I, Oliver J (2006) Addressing the coral reef crisis in developing countries. Ocean Coast Manag 49:976–985

Bellwood DR (1988) The juvenile colour patterns of two scarus species from the western Pacific: S. prasiognathosand S. tricolor (Pisces: Scaridae). J Nat Hist 22:1677–1682

Bellwood DR (1994) A phylogenetic study of the parrotfish family Scaridae (Pisces: Labroidea), with a revision of genera. Rec Aust Museum, Suppl 20:1–86

Bellwood DR (1995b) Patterns of bioerosion and sediment release by parrotfishes (family Scaridae) on the Great Barrier. Mar Ecol Prog Ser 117:127–136

Bellwood DR (1995a) Direct estimate of bioerosion by two parrotfish species, Chlorurus gibbus and C. sordidus, on the Great Barrier Reef, Australia. Mar Biol 121:419–429

Bellwood DR (1996) Production and reworking of sediment by parrotfishes (family Scaridae) on the Great Barrier Reef, Australia. Mar Biol 125:795–800

Bellwood DR, Choat JH (1990) A functional analysis of grazing in parrotfishes (family Sacaridae): the ecological implications. Enviromental Biol Fishes 28:189–214

Bellwood DR, Fulton CJ (2008) Sediment-mediated suppression of herbivory on coral reefs: Decreasing resilience to rising sea levels and climate change? Limnol Oceanogr 53:2695–2701

Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems : resilience and ecosystem function on coral reefs. Ecol Lettters 6:281–285

Bellwood DR, Hoey AS, Hughes TP (2012) Human activity selectively impacts the ecosystem roles of parrotfishes on coral reefs. Proc R Soc B Biol Sci 279:1621–1629

Bellwood DR, Hughes TP, Folke C, Nystrom M (2004) Confronting the coral reef crisis. Nature 429:827–833

Bellwood DR, Hughes TP, Hoey AS (2006) Sleeping Functional Group Drives Coral-Reef Recovery. Curr Biol 16:2434–2439

Birkeland C, Dayton PK (2005) The importance in fishery management of leaving the big ones. Trends Ecol Evol 20:356–358

Blackwood JC, Hastings A, Mumby PJ (2012) The effect of fishing on hysteresis in Caribbean coral reefs. Theor Ecol 5:105–114

Blott SJ, Pye K (2001) Gradistat: A Grain Size Distribution and Statistics Package for the Analysis of Unconcolidated Sediments. Earth Surf Process Landforms 26:1237–1248

Bonaldo RM, Bellwood DR (2008) Size-dependent variation in the functional role of the parrotfish Scarus rivulatus on the Great Barrier Reef, Australia. Mar Ecol Prog Ser 360:237–244

Bonaldo RM, Bellwood DR (2009) Dynamics of parrotfish grazing scars. Mar Biol 156:771–777

Bonaldo RM, Bellwood DR (2011) Spatial variation in the effects of grazing on epilithic algal turfs on the Great Barrier Reef, Australia. Coral Reefs 30:381–390

Bonaldo RM, Hoey AS, Bellwood DR (2014) The ecosystem roles of parrotfishes on tropical reefs. Oceanogr Mar Biol An Annu Rev 52:81–132

Bonaldo RM, Krajewski JP, Sazima C, Sazima I (2006) Foraging activity and resource use by three parrotfish species at Fernando de Noronha

Archipelago, tropical West Atlantic. Mar Biol 149:423–433

Box SJ, Mumby PJ (2007) Effect of macroalgal competition on growth and survival of juenile Caribbean corals. Mar Ecol Prog Ser 342:139–149

Bozec Y-M, O'Farrell S, Bruggemann JH, Luckhurst BE, Mumby PJ (2016) Tradeoffs between fisheries harvest and the resilience of coral reefs. Proc Natl Acad Sci 113:4536–4541

Bozec YM, Yakob L, Bejarano S, Mumby PJ (2013) Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. Oikos 122:428–440

Braithwaite CJR (1973) Settling behaviour related to sieve analysis of skeletal sands. Sedimentology 20:251–262

Brandl SJ, Bellwood DR (2014) Individual-based analyses reveal limited functional overlap in a coral reef fish community. J Anim Ecol 83:661–670

Brandl SJ, Bellwood DR (2016) Microtopographic refuges shape consumer-producer dynamics by mediating consumer functional diversity. Oecologia 182:203–217

Bruggemann JH, Begeman J, Bosma E, Verburg P, Breeman A (1994b) Foraging by the stoplight parrotfish Sparisoma viride II. Intake and assimilation of food, protein and energy. Mar Ecol Prog Ser 106:57–71

Bruggemann JH, Kessel AMA van, Rooij JMJ van, Breeman AMA (1996) Bioerosion and sediment ingestion by the caribbean parrotfish Scarus vetula and Sparisoma viride: Implications of fish size, feeding mode and habitat use. Mar Ecol Prog Ser 134:59–71

Bruggemann JH, Kuyper MWM, Breeman A (1994c) Comparative-Analysis of Foraging and Habitat Use By the Sympatric Caribbean Parrotfish Scarus-Vetula and Sparisoma-Viride (Scaridae). Mar Ecol Ser 112:51–66

Bruggemann J, van Oppen M, Breeman A (1994a) Foraging by the stoplight parrotfish Sparisoma viride. I. Food selection in different, socially determined habitats. Mar Ecol Prog Ser 106:41–55

Cappo M, Harvey EB, Malcolm HC, Speare P (2003) Potential of Video Techniques To Monitor Diversity , Abundance and Size of Fish in Studies of Marine Protected Areas. Aquat Prot Areas-what Work bests how do we know:455–464

Carassou L, Léopold M, Guillemot N, Wantiez L, Kulbicki M (2013) Does Herbivorous Fish Protection Really Improve Coral Reef Resilience? A Case Study from New Caledonia (South Pacific). PLoS One 8

Cardwell JR, Liley NR (1991) Hormonal control of sex and color change in the stoplight parrotfish, Sparisoma viride. Gen Comp Endocrinol 81:7–20

Carlson PM, Davis K, Warner RR, Caselle JE (2017) Fine-scale spatial patterns of parrotfish herbivory are shaped by resource availability. Mar Ecol Prog Ser 577:165–176

Carr A, Tibbetts IR, Kemp A, Truss R, Drennan J (2006) Inferring Parrotfish (Teleostei: Scaridae) Pharyngeal Mill Function From Dental Morphology, Wear, and Microstructure. J Morphol 267:1147–1156

Carté BK (1996) Potential of Marine Biomedical Natural Products research and medical applications. Oxford Journals 46:271–286

Chazottes V, Chevillotte V, Dufresne A (2004) Characteristics of the particulate production by the sea urchin Echinometra mathaei on Indo-Pacific reefs: influence of coral communities and implications on the sedimentary dynamics. Geobios 37:13–22

Cheal AJ, Emslie MJ, Macneil MA, Miller I, Sweatman HPA (2016) Spatial variation in the functional characteristics of herbivorous fish communities and the resilience of coral reefs. Ecol Appl 23:174–188

Cheal A, Emslie M, Miller I, Sweatman H (2012) The distribution of herbivorous fishes on the Great Barrier Reef. Mar Biol 159:1143–1154

Cheetham MD, Keene AF, Bush RT, Sullivan LA, Erskine WD (2008) A comparison of grain-size analysis methods for sand-dominated fluvial sediments. Sedimentology 55:1905–1913

Chen L (2002) Post-settlement diet shift of Chlorurus sordidus and Scarus schlegeli (Pisces: Scaridae). Zool Stud 41:47–58

Choat JH, klanten OS, Herwerden L Van, Robertson DR, Clements KD (2012) Patterns and processes in the evolutionary history of parrotfishes (Family Labridae). Biol J Linn Soc 107:529–557

Chong-Seng KM, Mannering TD, Pratchett MS, Bellwood DR, Graham NAJ (2012) The influence of coral reef benthic condition on associated fish assemblages. PLoS One 7:1–10

Cinner JE, Huchery C, MacNeil MA, Graham NAJ, Mcclanahan TR, Maina J, Maire E, Kittinger JN, Hicks CC, Mora C, Allison EH, D'Agata S, Hoey A, Feary DA, Crowder L, Williams ID, Kulbicki M, Vigliola L, Wantiez L, Edgar G, Stuart-Smith RD, Sandin SA, Green AL, Hardt MJ, Beger M, Friedlander A, Campbell SJ, Holmes KE, Wilson SK, Brokovich E, Brooks AJ, Cruz-Motta JJ, Booth DJ, Chabanet P, Gough C, Tupper M, Ferse SCA, Sumaila UR, Mouillot D (2016) Bright spots among the world's coral reefs. Nature 535:416–419

Clements KD, German DP, Piché J, Tribollet AD, Howard Choat J (2016) Integrating ecological roles and trophic resources on coral reefs: multiple lines of evidence identify parrotfishes as microphages. Biol J Linn Soc:doi:10.1111/bij.12914

Clua E, Legendre P (2008) Shifting dominance among Scarid species on reefs representing a gradient of fishing pressure. Aquat Living Resour 21:339–348

Coker DJ, Graham N a. J, Pratchett MS (2012) Interactive effects of live coral and structural complexity on the recruitment of reef fishes. Coral Reefs 31:919–927

Conn PB (2011) An evaluation and power analysis of fishery independent reef fish sampling in the Gulf of Mexico and U.S. South Atlantic. :38 p

Cooper C a, Whittamore JM, Wilson RW (2010) Ca2+-driven intestinal HCO(3)(-) secretion and CaCO3 precipitation in the European flounder in vivo: influences on acid-base regulation and blood gas transport. Am J Physiol Regul Integr Comp Physiol 298:R870-6

Cordeiro CAMM, Mendes TC, Harborne AR, Ferreira CEL (2015) Spatial distribution of nominally herbivorous fishes across environmental gradients on Brazilian rocky reefs. J Fish Biol 89:939–958

Cowman PF, Bellwood DR, Herwerden L van (2009) Dating the evolutionary origins of wrasse lineages (Labridae) and the rise of trophic novelty on coral reefs. Mol Phylogenet Evol 52:621–631

D'Agata S, Mouillot D, Wantiez L, Friedlander AM, Kulbicki M, Vigliola L (2016) Marine reserves lag behind wilderness in the conservation of key functional roles. Nat Commun 7:10.1038/ncomms12000

D'Angelo C, Wiedenmann J (2014) Impacts of nutrient enrichment on coral reefs: New perspectives and implications for coastal management and reef survival. Curr Opin Environ Sustain 7:82–93

Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK (2017) Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36:561–575

Davis K, Carlson PM, Bradley D, Warner RR, Caselle JE (2017) Predation risk influences feeding rates but competition structures space use for a common Pacific parrotfish. Oecologia 184:139–149

Done TJ (1992) Phase-Shifts in Coral-Reef Communities and Their Ecological Significance. Hydrobiologia:121–132

Done TJ, Ogden J, Wiebe W, Rosen B (1996) Biodiversity and Ecosystem Function of Coral Reefs. In: Mooney H, Cushman J, E M, Sala O, Schilze E-D (eds) Functional Roles of Biodiversity: A Global Perspective. John Wiley & Sons Ltd, Michigan, p 393–429

Donner SD, Potere D (2007) The Inequity of the Global Threat to Coral Reefs. Bioscience 57:214–215

Eakin CM (1996) A model comparison of calcium carbonate budgets before and after the. Coral Reefs 15:109–119

Eakin CM (2001) A tale of two ENSO events: carbonate budgets and the influence of two warming disturbances and intervening variability, Uva Island, Panama. 69:171–186

Edwards CB, Friedlander a M, Green AG, Hardt MJ, Sala E, Sweatman HP, Williams ID, Zgliczynski B, Sandin S a, Smith JE (2014) Global assessment of the status of coral reef herbivorous fishes : evidence for fishing effects Global assessment of the status of coral reef herbivorous fishes : evidence for fishing effects. Proc R Soc B:7–11

Ellis DM, DeMartini EE (1995) Evaluation of a video camera technique for indexing abundances of juvenile pink snapper, Pristipomoides filamentosus, and other Hawaiian insular shelf fishes. Fish Bull 93:67–77

Emslie MJ, Cheal AJ, Johns KA (2014) Retention of habitat complexity minimizes disassembly of reef fish communities following disturbance: A large-scale natural experiment. PLoS One 9

Eyre BD, Cyronak T, Drupp P, Carlo EH De, Sachs JP, Andersson AJ (2018) Coral reefs will transition to net dissolving before end of century. 911:908–911

Ferrario F, Beck MW, Storlazzi CD, Micheli F, Shepard CC, Airoldi L (2014) The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nat Commun 5:3794

Ford MR, Kench PS (2012) The durability of bioclastic sediments and implications for coral reef deposit formation. Sedimentology 59:830–842

Fox RJ, Bellwood DR (2007) Quantifying herbivory across a coral reef depth\rgradient. Mar Ecol Prog Ser 339:49–59

Friedlander AM, Brown EK, Jokiel PL, Smith WR, Rodgers KS (2003) Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. Coral Reefs 22:291–305

Friedlander AM, Parrish JD (1998) Habitat characteristics affecting fish assemblages on a Hawaiian coral reef. J Exp Mar Biol Ecol 224:1–30

Frydl P, Stearn CW (1978) Rate of Bioerosion by Parrotfish in Barbados Reef Environments. SEPM J Sediment Res Vol. 48:1149–1157

Fulton CJ, Bellwood DR (2004) Wave exposure, swimming performance, and the structure of tropical and temperate reef fish assemblages. Mar Biol 144:429–437

Fulton CJ, Bellwood DR, Wainwright PC (2001) The relationship between swimming ability and habitat use in wrasses (Labridae). Mar Biol 139:25–33

Gilmour JP, Smith LD, Heyward AJ, Baird AH, Pratchett MS (2013) Recovery of an Isolated Coral Reef System Following Sever Disturbance. Science 340:69–71

Gischler E, Zingeler D (2002) The origin of carbonate mud in isolated carbonate platforms of Belize, Central America. Int J Earth Sci 91:1054–1070

Glynn PW (1988) El Niño warming, coral mortality and reef framework destruction by Echinoid bioerosion in the eastern pacific. Galaxea 7:129–160

Glynn PW (1997) Bioerosion and coral-reef growth: a dynamic balance. Life death coral reefs:68–95

Goatley CHR, Bellwood DR (2010) Biologically mediated sediment fluxes on coral reefs: Sediment removal and off-reef transportation by the surgeonfish Ctenochaetus striatus. Mar Ecol Prog Ser 415:237–245

Goatley CHR, Bonaldo RM, Fox RJ, Bellwood DR (2016) Sediments and herbivory as sensitive indicators of coral reef degradation. Ecol Soc 21

Gordon SE, Goatley CHR, Bellwood DR (2016) Low-quality sediments deter grazing by the parrotfish Scarus rivulatus on inner-shelf reefs. Coral Reefs 35:285–291

Graham NAJ (2014) Habitat complexity: Coral structural loss leads to fisheries declines. Curr Biol 24:R359–R361

Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. Coral Reefs 32:315–326

Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Robinson J, Bijoux JP, Daw TM (2007) Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. Conserv Biol 21:1291–1300

Gratwicke B, Speight MR, Road SP (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. J Fish Biol 66:650–667

Green AL, Bellwood DR (2009) Monitoring Functional Groups of Herbivorous Reef Fishes as Indicators of Coral Reef Resilience A practical guide for coral reef managers in the Asia Pacific Region. Gland, Siwtzerland

Grosell M, Wood CM, Wilson RW, Bury NR, Hogstrand C, Rankin C, Jensen FB (2004) Bicarbonate secretion plays a role in chloride and water absorption of the European flounder intestine. AJP Regul Integr Comp Physiol 288:R936–R946

Grutter AS, Rumney JG, Sinclair-Taylor T, Waldie P, Franklin CE (2011) Fish mucous cocoons: the “mosquito nets” of the sea. Biol Lett 7:292–294

Gygi R (1975) *Sparisoma viride* (Bonnaterre), the stoplight Parrotfish), a major sediment producer on coral reefs of Bermuda? Ecolgae Geol Helv:327–359

Hamilton RJ, Almany GR, Brown CJ, Pita J, Peterson NA, Howard Choat J (2017) Logging degrades nursery habitat for an iconic coral reef fish. Biol Conserv 210:273–280

Hamilton RJ, Almany GR, Stevens D, Bode M, Pita J, Peterson NA, Choat JH (2016) Hyperstability masks declines in bumphead parrotfish (Bolbometopon muricatum) populations. Coral Reefs 35:751–763

Harborne a R (2013) The ecology, behaviour and physiology of fishes on coral reef flats, and the potential impacts of climate change. J Fish Biol 83:417–47

Harborne A, Mumby P, Kennedy E, Ferrari R (2011) Biotic and multi-scale abiotic controls of habitat quality: their effect on coral-reef fishes. Mar Ecol Prog Ser 437:201–214

Harborne AR, Selwyn JD, Lawson JM, Gallo M (2016) Environmental drivers of diurnal visits by transient predatory fishes to Caribbean patch reefs. J Fish

Biol 90:265–282

Harborne AR, Talwar B, Brooks EJ (2015) The conservation implications of spatial and temporal variability in the diurnal use of Bahamian tidal mangrove creeks by transient predatory fishes. Aquat Conserv Mar Freshw Ecosyst 26:202–211

Harvey ES, Fletcher D, Shortis MR (2001) A comparison of the precision and accuracy of estimates of reef-fish lengths made by divers and a stereo-video system. Fish Bull 99:63–71

Harvey E, Fletcher D, Shortis M, Kendrick GA (2004) Citation: Harvey, E, Fletcher, D, Shortis, M and Kendrick, G 2004, “A comparison of underwater visual distance estimates made by scuba divers and a stereo-video system: Implications for underwater visual census of reef fish abundance”, Marine and Freshwat. Mar Freshw Res 55:573–580

Harvey ES, Shortis MR (1998) Calibration Stability of an Underwater Stereo Video System : Implications for Measurement Accuracy and Precision. Mar Technol Soc J 32:3–17

Hawkins JP, Roberts CM (2003) Effects of fishing on sex-changing Caribbean parrotfishes. Biol Conserv 115:213–226

Heenan A, Hoey AS, Williams GJ, Williams ID (2016) Natural bounds on herbivorous coral reef fishes. Proc R Soc B Biol Sci 283:20161716

Hixon MA, Beets JP (1993) Predation, Prey Refuges, and the Structure of Coral-Reef Fish Assemblages. Ecol Monogr 63:77–101

Hoegh-Guldberg O (1998) Climate Change, coral bleaching and the future of the world’ s coral reefs. Ove Hoegh-Guldberg.

Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. Coral Reefs 27:37–47

Hoey AS, Bellwood DR (2011) Suppression of herbivory by macroalgal density: A critical feedback on coral reefs? Ecol Lett 14:267–273

Hoey AS, Feary DA, Burt JA, Vaughan G, Pratchett MS, Berumen ML (2016a) Regional variation in the structure and function of parrotfishes on Arabian reefs. Mar Pollut Bull 105:524–531

Hoey A, Howells E, Johansen J, Hobbs J-P, Messmer V, McCowan D, Wilson S, Pratchett M (2016b) Recent Advances in Understanding the Effects of Climate Change on Coral Reefs. Diversity 8:12

Howard KG, Claisse JT, Clark TB, Boyle K, Parrish JD (2013) Home range and movement patterns of the Redlip Parrotfish (Scarus rubroviolaceus) in Hawaii. Mar Biol 160:1583–1595

Hubbard DK, Miller AI, David A, Islands USV (1990) Production and cycling of calcium carbonate in a shelf-edge reef system (St. Croix, U.S. Virgin Islands): Apllications to the nature of reef systems in the fossil record. Framework 60:335–360

Hughes TP (1994) Catastrophes, Phase Shifts, and Large-Scale Degradation of a Caribbean Coral Reef. Science 265:1547–1551

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, Lough JM, Marshall P, Nyström M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301:929–933

Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, Leemput IA Van De, Lough JM, Morrison TH, Palumbi SR, Nes EH Van, Scheffer M (2017b) Coral reefs in the Anthropocene. Nature 546:82–90

Hughes TP, Bellwood DR, Folke C, Steneck RS, Wilson J (2005) New paradigms for supporting the resilience of marine ecosystems. Trends Ecol Evol 20:380–386

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs JPA, Hoogenboom MO, Kennedy E V., Kuo CY, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017a) Global warming and recurrent mass bleaching of corals. Nature 543:373–377

Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschaniwskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. Curr Biol 17:360–365

Hutchings PA (1986) Biological destruction of coral reefs. Coral Reefs 4:239–252

Jackson JBC, Donovan MK, Cramer KL, Lam W (2014) Status and Trends of Caribbean Coral Reefs : 1970-2012. Glob Coral Reef Monit Network, IUCN, Gland Switz:306

Jackson JBC, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Lenihan HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. Science 293:629–637

Jayewardene D (2009) A factorial experiment quantifying the influence of parrotfish density and size on algal reduction on Hawaiian coral reefs. J Exp Mar Bio Ecol 375:64–69

Jennings S, Collingridge K (2015) Predicting consumer biomass, size-structure, production, catch potential, responses to fishing and associated uncertainties in the world’s marine ecosystems. PLoS One 10:1–28

Jennings S, Wilson RW (2009) Fishing impacts on the marine inorganic carbon cycle. J Appl Ecol 46:976–982

Jobling M (1981) The Influences of Feeding on the Metabolic-Rate of Fishes - a Short Review. J Fish Biol 18:385–400

Johansson CL, Leemput IA van de, Depczynski M, Hoey AS, Bellwood DR (2013) Key herbivores reveal limited functional redundancy on inshore coral reefs. Coral Reefs 32:963–972

Kench PS (1997) Contemporary sedimentation in the Cocos (Keeling) Islands, Indian Ocean: interpretation using settling velocity analysis. Sediment Geol 114:109–130

Kench PS (1998) A currents of removal approach for interpreting carbonate sedimentary processes. Mar Geol 145:197–223

Kench PS, Brander RW (2006) Response of reef island shorelines to seasonal climate oscillations: South Maalhosmadulu atoll, Maldives. J Geophys Res Earth Surf 111:1–12

Kench PS, Cowell PJ (2000) Variations in sediment production and implications for atoll island stability under rising sea level. Proc Ninth Int Coral Reef Symp Bali, 23-27 Oct 2000, 2:1181–1186

Kench PS, McLean RF (1996) Hydraulic characteristics of bioclastic deposits: New possibilities for environmental interpretation using settling velocity fractions. Sedimentology 43:561–570

Kench PS, McLean RF, Brander RW, Nichol SL, Smithers SG, Ford MR, Parnell KE, Aslam M (2006) Geological effects of tsunami on mid-ocean atoll islands: The Maldives before and after the Sumatran tsunami. Geology 34:177–180

Kench PS, McLean RF, Nichol SL (2005) New model of reef-island evolution: Maldives, Indian Ocean. Geology 33:145–148

Kennedy E V., Perry CT, Halloran PR, Iglesias-Prieto R, Schönberg CHLL, Wisshak M, Form AU, Carricart-Ganivet JP, Fine M, Eakin CM, Mumby PJ (2013) Avoiding coral reef functional collapse requires local and global action. Curr Biol 23:912–918

Kiene W (1985) Biological destruction of experimental coral substrates at Lizard island, Great Barrier Reef, Australia. Proc 5th Int Coral Reef Symp

Komyakova V, Munday PL, Jones GP (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. PLoS One 8:e83178

Krone R, Paster M, Schuhmacher H (2010) Effect of the surgeonfish Ctenochaetus striatus (Acanthuridae) on the processes of sediment transport and deposition on a coral reef in the Red Sea. Facies 57:215–221

Krone R, Paster M, Schuhmacher H (2011) Effect of the surgeonfish Ctenochaetus striatus (Acanthuridae) on the processes of sediment transport and deposition on a coral reef in the Red Sea. Facies 57:215–221

Langlois TJ, Chabanet P, Pelletier D (2006) Baited Underwater Video for Assessing Reef Fish Populations. Fish 118:53–57

Lasagna R, Albertelli G, Colantoni P, Morri C, Bianchi CN (2010) Ecological stages of Maldivian reefs after the coral mass mortality of 1998. Facies 56:1–11

Lasagna R, Albertelli G, Giovannetti E, Grondona M, Milani A, Morri C, Bianchi CN (2008) Status of Maldivian reefs eight years after the 1998 coral mass mortality. Chem Ecol 24:67–72

Letessier TB, Juhel JB, Vigliola L, Meeuwig JJ (2015) Low-cost small action cameras in stereo generates accurate underwater measurements of fish. J Exp Mar Bio Ecol 466:120–126

Lincoln Smith M (1988) Effects of observer swimming speed on sample counts of temperate rocky reef fish assemblages . Mar Ecol Prog Ser 43:223–231

Lokrantz J, Nyström M, Thyresson M, Johansson C (2008) The non-linear relationship between body size and function in parrotfishes. Coral Reefs 27:967–974

Long SP, Humphries S (1994) Photoinhibition of photosynthesis in nature. Annu Rev Plant Physiol Plant Mol Biol 45:633–662

Loya Y, Sakai K, Yamazato K, Nakano, Sambali, Woesik R Van (2001) Coral bleaching: the winners and the losers. Ecol Lett 4:122–131

Lugo-Fernández A, Roberts HH, Suhayda JN (1998) Wave transformations across a caribbean fringing-barrier Coral Reef. Cont Shelf Res 18:1099–1124

MacNeil MA, Graham NAJ, Cinner JE, Wilson SK, Williams ID, Maina J, Newman S, Friedlander AM, Jupiter S, Polunin NVC, Mcclanahan TR (2015) Recovery potential of the world's coral reef fishes. Nature 520:341–344

McAfee ST, Morgan SG (1996) Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. Mar Biol 125:427–437

McClanahan TR (2011) Coral reef fish communities in management systems with unregulated fishing and small fisheries closures compared with lightly fished reefs - Maldives vs. Kenya. Aquat Conserv Mar Freshw Ecosyst 21:186–198

McClanahan TR (1994) Coral Reefs effects of fishing , substrate complexity , and sea urchins. Coral Reefs 13:231–241

McClanahan TR (1995) A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. Ecol Modell 80:1–19

McClanahan TR, Arthur R (2001) the Effect of Marine Reserves and Habitat on Populations of East African Coral Reef Fishes. Ecol Appl 11:559–569

McClanahan TR, Maina JM, Graham NAJ, Jones KR (2016) Modeling Reef Fish Biomass, Recovery Potential, and Management Priorities in the Western Indian Ocean. PLoS One 11:e0154585

McClanahan TR, Nicholas A. J, Graham, Calnan JM, Macneil MA (2007) Toward Pristine Biomass: Reef Fish Recovery in Coral Reef Marine Protected Areas in Kenya. Ecol Appl 17:1055–1067

McManus JW, Meñez LAB, Kesner-Reyes KN, Vergara SG, Ablan MC (2000) Coral reef fishing and coral-algal phase shifts: Implications for global reef status. ICES J Mar Sci 57:572–578

McManus JW, Polsenberg JF (2004) Coral-algal phase shifts on coral reefs: Ecological and environmental aspects. Prog Oceanogr 60:263–279

Micheli F, Mumby PJ, Brumbaugh DR, Broad K, Dahlgren CP, Harborne AR, Holmes KE, Kappel C V., Litvin SY, Sanchirico JN (2014) High vulnerability of ecosystem function and services to diversity loss in Caribbean coral reefs. Biol Conserv 171:186–194

Millero FJ (2007) The Marine Inorganic Carbon Cycle. Chem Rev 107:308–341

Milliman JD, Troy PJ, Balch WM, Adams AK, Li YH, Mackenzie FT (1999) Biologically mediated dissolution of calcium carbonate above the chemical lysocline? Deep Res Part I Oceanogr Res Pap 46:1653–1669

Moberg FF, Folke C (1999) Ecological goods and services of coral reef ecosystems. Ecol Econ 29:215–233

Mora C, Aburto-Oropeza O, Ayala-Bocos A, Ayotte PM, Banks S, Bauman AG, Beger M, Bessudo S, Booth DJ, Brokovich E, Brooks A, Chabanet P, Cinner JE, Cortés J, Cruz-Motta JJ, Cupul-Magaña A, DeMartini EE, Edgar GJ, Feary DA, Ferse SCA, Friedlander AM, Gaston KJ, Gough C, Graham NAJ, Green A, Guzman H, Hardt M, Kulbicki M, Letourneur Y, Ĺpez-Pérez A, Loreau M, Loya Y, Martinez C, Mascareñas-Osorio I, Morove T, Nadon MO, Nakamura Y, Paredes G, Polunin NVC, Pratchett MS, Reyes Bonilla H, Rivera F, Sala E, Sandin SA, Soler G, Stuart-Smith R, Tessier E, Tittensor DP, Tupper M, Usseglio P, Vigliola L, Wantiez L, Williams I, Wilson SK, Zapata FA (2011) Global human footprint on the linkage between biodiversity and ecosystem functioning in reef fishes. PLoS Biol 9

Morgan KM, Kench PS (2012a) Skeletal extension and calcification of reef-building corals in the central Indian Ocean. Mar Environ Res 81:78–82

Morgan KM, Kench PS (2012b) Export of reef-derived sediments on Vabbinfaru reef platform, Maldives. In: proceedings of the 12th International Coral Reef Sympoisum,. Cairns, Australia, p 1A Reef and Reef Island Geomorphology

Morgan KM, Kench PS (2014) A detrital sediment budget of a Maldivian reef platform. Geomorphology 222:122–131

Morgan KM, Kench PS (2016a) Parrotfish erosion underpins reef growth, sand talus development and island building in the Maldives. Sediment Geol 341:50–57

Morgan KM, Kench PS (2016b) Reef to island sediment connections on a Maldivian carbonate platform: using benthic ecology and biosedimentary depositional facies to examine island-building potential. Earth Surf Process Landforms 41:1815–1825

Morgan KM, Perry CT, Smithers SG, Johnson JA, Gulliver P (2016) Transitions in coral reef accretion rates linked to intrinsic ecological shifts on turbid-zone nearshore reefs. Geology 44:995–998

Morse JW, Gledhill DK, Millero FJ (2003) CaCO3 precipitation kinetics in waters from the Great Bahama Bank: Implications for the relationship between Bank hydrochemistry and whitings. Geochim Cosmochim Acta 67:2819–2826

Mumby PJ (2006) The Impact of Exploiting Grazers (Scaridae) on the Dynamics of Caribbean Coral Reefs. Ecol Appl 16:747–769

Mumby PJ (2009) Herbivory versus corallivory: are parrotfish good or bad for Caribbean coral reefs? Coral Reefs 28:683–690

Mumby PJ (2016) Stratifying herbivore fisheries by habitat to avoid ecosystem overfishing of coral reefs. Fish Fish 17:266–278

Mumby PJ, Dahlgren CP, Harborne AR, Kappel C V, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006) Fishing, trophic cascades, and the process of grazing on coral reefs. Science 311:98–101

Mumby PJ, Harborne AR (2010) Marine reserves enhance the recovery of corals on Caribbean reefs. PLoS One 5:e8657

Mumby PJ, Harborne AR, Williams J, Kappel C V., Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG (2007) Trophic cascade facilitates coral recruitment in a marine reserve. Proc Natl Acad Sci 104:8362–8367

Mumby PPJ, Steneck RSR, Edwards AJA, Ferrari R, Coleman R, Harborne AAR, Gibson JPJ (2012) Fishing down a Caribbean food web relaxes trophic cascades. Mar Ecol Prog Ser 445:13–24

Mumby PJ, Wabnitz CCC (2002) Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. Environ Biol Fishes 63:265–279

Nanami A (2016) Parrotfish grazing ability: interspecific differences in relation to jaw-lever mechanics and relative weight of adductor mandibulae on an Okinawan coral reef. PeerJ 4:e2425

Nash KL, Graham NAJ, Januchowski-Hartley FA, Bellwood DR (2012) Influence of habitat condition and competition on foraging behaviour of parrotfishes. Mar Ecol Prog Ser 457:113–124

Nash KL, Graham NAJ, Wilson SK, Bellwood DR (2013) Cross-scale Habitat Structure Drives Fish Body Size Distributions on Coral Reefs. Ecosystems 16:478–490

Neumann AC (1966) Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, Cliona lampa. Limnol Oceanogr 11:92–108

Newman MJH, Paredes GA, Sala E, Jackson JBC (2006) Structure of Caribbean coral reef communities across a large gradient of fish biomass. Ecol Lett 9:1216–1227

Newton K, Côté IM, Pilling GM, Jennings S, Dulvy NK (2007) Current and Future Sustainability of Island Coral Reef Fisheries. Curr Biol 17:655–658

O'Farrell S, Harborne AR, Bozec YM, Luckhurst BE, Mumby PJ (2015) Protection of functionally important parrotfishes increases their biomass but fails to deliver enhanced recruitment. Mar Ecol Prog Ser 522:245–254

O'Farrell S, Luckhurst BE, Box SJ, Mumby PJ (2016) Parrotfish sex ratios recover rapidly in Bermuda following a fishing ban. Coral Reefs 35:421–425

Ogden JC (1977) Carbonate sediment production by parrot fish and sea urchins on Caribbean reefs. Am Assoc Pet Geol Stud Geol **4**:281-288

Oksanen J, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlinn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2017) Vegan: Community Ecology Package. R package version 2.4-5

Ong L, Holland KN (2010) Bioerosion of coral reefs by two Hawaiian parrotfishes: Species, size differences and fishery implications. Mar Biol 157:1313–1323

Paddack MJ, Cowen RK, Sponaugle S (2006) Grazing pressure of herbivorous coral reef fishes on low coral-cover reefs. Coral Reefs 25:461–472

Perry CT, Alvarez-Filip L, Graham NAJ, Mumby PJ, Wilson SK, Kench PS, Manzello DP, Morgan KM, Slamgen ABA, Thomson DP, Januchowski-Hartley F, Smithers SG, Steneck RS, Carlton R, Edinger EN, Enochs IC, Estrada-Saldívar N, Haywood MDE, Kolodziej G, Murphy GN, Pérez-Cervantes E, Suchley A, Valentino L, Boenish R, Wilson M, Macdonald C (2018) Loss of coral reef growth capacity to track future increases in sea level. Nature 558:396-400

Perry CT, Edinger EN, Kench PS, Murphy GN, Smithers SG, Steneck RS, Mumby PJ (2012) Estimating rates of biologically driven coral reef framework production and erosion: A new census-based carbonate budget methodology and applications to the reefs of Bonaire. Coral Reefs 31:853–868

Perry CT, Hepburn LJ (2008) Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: Taphonomic signatures of reef accretion and reef depositional events. Earth-Science Rev 86:106–144

Perry CT, Kench PS, O’Leary MJ, Morgan KM, Januchowski-Hartley F (2015a) Linking reef ecology to island building: Parrotfish identified as major producers of island-building sediment in the Maldives. Geology 43:503–506

Perry CT, Kench PS, Smithers SG, Riegl B, Yamano H, O’Leary MJ (2011b) Implications of reef ecosystem change for the stability and maintenance of coral reef islands. Glob Chang Biol 17:3679–3696

Perry CT, Morgan KM (2017b) Post-bleaching coral community change on southern Maldivian reefs: is there potential for rapid recovery? Coral Reefs 36:1189–1194

Perry CT, Morgan KM (2017a) Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. Sci Rep 7:1–9

Perry CT, Morgan KM, Yarlett RT (2017) Reef Habitat Type and Spatial Extent as Interacting Controls on Platform-Scale Carbonate Budgets. Front Mar Sci 4:1–13

Perry CT, Murphy GN, Graham NAJ, Wilson SK, Januchowski-Hartley FA, East H (2015b) Remote coral reefs can sustain high growth potential and may match future sea-level trends. Sci Rep 5:4–11

Perry CT, Murphy GN, Kench PS, Edinger EN, Smithers SG, Steneck RS, Mumby PJ (2014b) Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential. Proc R Soc B Biol Sci 281:20142018–20142018

Perry CT, Murphy GN, Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ (2013) Caribbean-wide decline in carbonate production threatens coral reef growth. Nat Commun 4:1402

Perry CT, Salter MA, Harborne AR, Crowley SF, Jelks HL, Wilson RW (2011) Fish as major carbonate mud producers and missing components of the tropical carbonate factory. Proc Natl Acad Sci 108:3865–3869

Perry CT, Smithers SG, Kench PS, Pears B (2014a) Impacts of Cyclone Yasi on nearshore, terrigenous sediment-dominated reefs of the central Great Barrier Reef, Australia. Geomorphology 222:92–105

Perry CT, Spencer T, Kench PS (2008) Carbonate budgets and reef production states: A geomorphic perspective on the ecological phase-shift concept. Coral Reefs 27:853–866

Pisapia C, Burn D, Yoosuf R, Najeeb A, Anderson KD, Pratchett MS (2016) Coral recovery in the central Maldives archipelago since the last major mass-bleaching, in 1998. Sci Rep 6:1–10

Pörtner HO, Langenbuch M, Reipschläger A (2004) Biological Impact of Elevated Ocean CO 2 Concentrations: Lessons from Animal Physiology and Earth History. J Oceanogr 60:705–718

Pratchett MS, Hoey AS, Wilson SK (2014) Reef degradation and the loss of critical ecosystem goods and services provided by coral reef fishes. Curr Opin Environ Sustain 7:37–43

Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ (2011) Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. Diversity 3:424–452

Richardson LE, Graham NAJ, Hoey AS (2017b) Cross-scale habitat structure driven by coral species composition on tropical reefs. Sci Rep 7:1–11

Richardson LE, Graham NAJ, Pratchett MS, Hoey AS (2017a) Structural complexity mediates functional structure of reef fish assemblages among coral habitats. Environ Biol Fishes 100:193–207

Risk MJ, Sluka R (2000) The Maldives: A Nation of Atolls. In: McClanahan TR, Sheppard, CRC, Obura DO (eds) Coral Reefs of the Indian Ocean: Their Ecology and Conservation. Oxford University Press, Ney York, p 325-352

Robertson RD, Choat JH (1974) Protogynous hermaphroditism and social systems in Labrid fish. In: Proceedings of the Second International Coral Reef Symposium. Brisbane, p 217–225

Robertson R, Warner RR (1978) Sexual patterns in the labroid fishes of the Western Caribbean, II, the parrotfishes (Scaridae). Smithson Contrib to Zool:1–26

Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. Curr Biol 24:1000–1005

Rotjan RD, Lewis SM (2005) Selective predation by parrotfishes on the reef coral Porites astreoides. Mar Ecol Prog Ser 305:193–201

Rotjan RDR, Lewis SMS (2008) Impact of coral predators on tropical reefs. Mar Ecol Prog Ser 367:73–91

Ruckelshaus M, Doney SC, Galindo HM, Barry JP, Chan F, Duffy JE, English CA, Gaines SD, Grebmeier JM, Hollowed AB, Knowlton N, Polovina J, Rabalais NN, Sydeman WJ, Talley LD (2013) Securing ocean benefits for society in the face of climate change. Mar Policy 40:154–159

Russ GR, Questel SLA, Rizzari JR, Alcala AC (2015) The parrotfish–coral relationship: refuting the ubiquity of a prevailing paradigm. Mar Biol 162:2029–2045

Salter MA, Harborne AR, Perry CT, Wilson RW (2017) Phase heterogeneity in carbonate production by marine fish influences their roles in sediment generation and the inorganic carbon cycle. Sci Rep 7:1–15

Salter MA, Perry CT, Wilson RW (2012) Production of mud-grade carbonates by marine fish: Crystalline products and their sedimentary significance.

Sedimentology 59:2172–2198

Schobernd ZH, Bacheler NM, Conn PB, Trenkel V (2014) Examining the utility of alternative video monitoring metrics for indexing reef fish abundance. Can J Fish Aquat Sci 71:464–471

Schuhmacher H, Loch K, Loch W, See WR (2005) The aftermath of coral bleaching on a Maldivian reef - A quantitative study. Facies 51:80–92

Scoffin T. P (1992) Taphonomy of coral reefs: a review. Coral Reefs 11:57–77

Scoffin T. P, Stearn CWW, D. B, Frydl P, Hawkins CMM, I.G. H, MacGeachy J. K, Boucher D, Frydl P, Hawkins CMM, Hunter IG, MacGeachy J. K, D. B, I.G. H (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados: Part II, Erosion, sediments and internal structure. Bull Mar Sci 30:475–508

Shephard KL (1994) Functions for fish mucus. Rev Fish Biol Fish 4:401–429

Smith RL, Paulson AC (1974) Food Transit Times and Gut pH in Two Pacific Parrotfishes. Source: Copeia 1974:796–799

Smith RL, Paulson AC (1975) Carbonic Anhydrase in Some Coral Reef Fishes: Adaptation To Carbonate Ingestion? Comp Biochem Physiol 50:131–134

Smith RL, Paulson AC, Smth RL, Paulson AC (1975) Carbonic Anhydrase in Some Coral Reef Fishes : Adaptation To Carbonate Ingestion ? Comp Biochem Physiol 50:0–3

Song C, Woodcock C, Seto K (2001) Classification and change detection using Landsat TM data: when and how to correct atmospheric effects? Remote Sens Environ 75:230–244

Stearn CW, Scoffin T. P, Martindale W (1977) Calcium carbonate budget of a fringing reef on the west coast of Barbados. Bull Mar Sci 27:479–510

Steneck RS, Arnold SN, Mumby PJ (2014) Experiment mimics fishing on parrotfish: Insights on coral reef recovery and alternative attractors. Mar Ecol Prog Ser 506:115–127

Storlazzi CD, Elias E, Field ME, Presto MK (2011) Numerical modelling of the impact of sea-level rise on fringing coral reef hydrodynamics and sediment transport. Coral Reefs 30:83-96

Takahashi S, Murata N (2008) How do environmental stresses accelerate photoinhibition? Trends Plant Sci 13:178–182

Taylor BM, Choat JH (2014) Comparative demography of commercially important parrotfish species from Micronesia. J Fish Biol 84:383–402

Taylor BM, Houk P, Russ GR, Choat JH (2014) Life histories predict vulnerability to overexploitation in parrotfishes. Coral Reefs 33:869–878

Taylor BM, Lindfield SJ, Choat JH (2015) Hierarchical and scale-dependent effects of fishing pressure and environment on the structure and size distribution of parrotfish communities. Ecography (Cop) 38:520–530

Tzadik OE, Appeldoorn RS (2013) Reef structure drives parrotfish species composition on shelf edge reefs in La Parguera, Puerto Rico. Cont Shelf Res 54:14–23

Videler H, Geertjes GJ, Videler JJ (1999) Biochemical characteristics and antibiotic properties of the mucous envelope of the queen parrotfish. J Fish Biol 54:1124–1127

Walsh PJ, Blackwelder P, Gill KA, Danulat E, Mommsen TP (1991) Carbonate deposits in marine fish intestines: A new source of biomineralization. Limnol Oceanogr 36:1227–1232

Ward-Paige C, Flemming JM, Lotze HK (2010) Overestimating fish counts by non-instantaneous visual censuses: Consequences for population and community descriptions. PLoS One 5:1–9

Watson DL, Harvey ES, Anderson MJ, Kendrick GA (2005) A comparison of temperate reef fish assemblages recorded by three underwater stereo-video techniques. Mar Biol 148:415–425

Watson DL, Harvey ES, Fitzpatrick BM, Langlois TJ, Shedrawi G (2010) Assessing reef fish assemblage structure: How do different stereo-video techniques compare? Mar Biol 157:1237–1250

Welsh JQ, Goatley CHR, Bellwood DR (2013) The ontogeny of home ranges: evidence from coral reef fishes. Proc R Soc B Biol Sci 280:20132066–20132066

Wentworth CK (1922) A scale of grade and class terms for clastic sediments. J Geol 30:377-392

Westneat MW, Alfaro ME (2005) Phylogenetic relationships and evolutionary history of the reef fish family Labridae. Mol Phylogenet Evol 36:370–390

Whittamore JM, Cooper CA, Wilson RW (2010) HCO3- secretion and CaCO3 precipitation play major roles in intestinal water absorption in marine teleost fish in vivo. Am J Physiol Regul Integr Comp Physiol 298:R877-86

Wilson SK, Fisher R, Pratchett MS, Graham N a. J, Dulvy NK, Turner R a., Cakacaka a., Polunin NVC, Rushton SP (2008) Exploitation and habitat degradation as agents of change within coral reef fish communities. Glob Chang Biol 14:2796–2809

Wilson R, Gilmour K, Henry R, Wood C (1996) Intestinal base excretion in the seawater-adapted rainbow trout: a role in acid-base balance? J Exp Biol 199:2331–2343

Wilson SK, Graham NAJ, Pratchett MS, Jones GP, Polunin NVC (2006) Multiple disturbances and the global degradation of coral reefs: Are reef fishes at risk or resilient? Glob Chang Biol 12:2220–2234

Wilson RW, Grosell M (2003) Intestinal bicarbonate secretion in marine teleost fish - Source of bicarbonate, pH sensitivity, and consequences for whole animal acid-base and calcium homeostasis. Biochim Biophys Acta - Biomembr 1618:163–174

Wilson RW, Millero FJ, Taylor JR, Walsh PJ, Christensen V, Jennings S, Grosell M (2009) Contribution of fish to the marine inorganic carbon cycle. Science (80-) 323:359–362

Wilson RW, Wilson JM, Grosell M (2002) Intestinal bicarbonate secretion by marine teleost fish - why and how? Biochim Biophys Acta-Biomembranes 1566:182–193

Worm B, Barbier EB, Beaumont N, Duffy JE, Folke C, Halpern BS, Jackson JBC, Lotze HK, Micheli F, Palumbi SR, Sala E, Selkoe KA, Stachowicz JJ, Watson R (2006) Impacts of biodiversity loss on ocean ecosystem services. Science (80-) 314:787–790

Yarlett RT, Perry CT, Wilson RW, Philpot KE (2018) Constraining species-size class variability in rates of parrotfish bioerosion on Maldivian coral reefs: implications for regional-scale bioerosion estimates. Mar Ecol Prog Ser 590:155–169

Zemke-White WL, Choat JH, Clements KD (2002) A re-evaluation of the diel feeding hypothesis for marine herbivorous fishes. Mar Biol 141:571–579

Appendices

Chapter 4 Supplementary Data

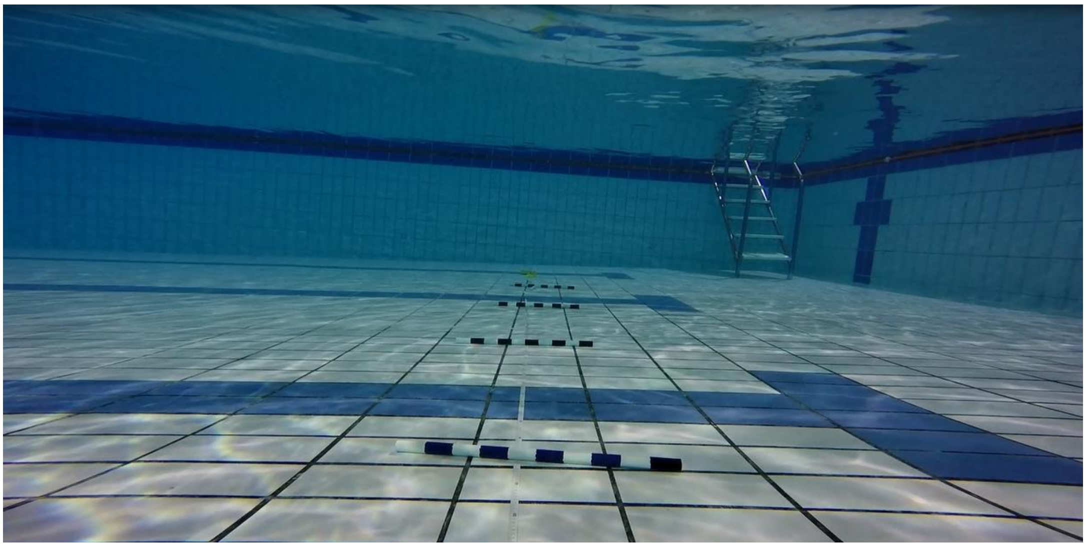
Supplementary Table 4-1 Mean bite rates (bpm) for Initial and Terminal life phases for the six study species (standard error presented in brackets).

Species	**Initial**	**Terminal**
Chlorurus sordidus	19.91 (± 1.23)	14.94 (± 1.06)
Chlorurus strongylocephalus	9.79 (± 0.79)	6.94 (± 1.16)
Scarus rubroviolaceus	9.69 (± 1.35)	9.39 (± 1.24)
Scarus frenatus	12.86 (± 1.18)	14.82 (± 1.60)
Scarus niger	25.10 (± 2.16)	27.08 (± 1.92)
Scarus psittacus	29.98 (± 2.38)	

Chapter 5 Supplementary Data and Information

Aim

The aim of the pilot study was to test how accurately the length of objects can be categorised into 10 or 15 cm size intervals using a single camera mounted onto a frame, with a series of calibration bars.



Methods

The pilot study was carried out at the Pyramids Leisure Centre on the 11th Dec 2015, when the pool was closed to the public. A Go-Pro Series 4 was mounted horizontally onto a PVC frame and deployed onto the bottom of the pool. A measuring tape was laid out from directly under the camera up to 4 m in front. Four 50 cm scale bars with 5 cm increments were deployed at 1, 2, 3 and 4 m in front of the camera. This calibration set up was recorded for approximately the first minute of the video, where the scale bars were raised and lowered in the water column. The scale bars and tape measure were then removed. Fifty pieces of PVC pipe ranging in size from 5 – 50 cm (approximate size range of parrotfish) were then swam through the video frame at a range of angles and distances. The pieces were cut to random sizes by Neville England and were unknown the observer. The pieces were labelled and swam through the video in a specified order so to be able to match each pipe to its known size post-analysis.

During the video analysis, an overlay was made to show the position and size of the scales and increments once the scale bars had been removed. These needed to be removed in the field to avoid causing any disruption to natural fish feeding or behaviour. The size of each of the pipes was then estimated and compared to the known size category post analysis.

Results

The pipes were estimated into the correct 10 cm size category with an 82% accuracy. Of the 9 pipes identified incorrectly, 5 of the 9 were borderline sizes (i.e. within 2cm of the boundary), and only 2 were more than 5 cm out. The incorrect measurements were generally where the pipe was head on, or at a difficult angle to judge from the video. By categorising the pipies into a 15 cm size, accuracy increased to 96%. The 15 cm size category was therefore chosen for use in the study.

Notes

- Avoid measuring fish towards the edges of the field of view due to distortions caused by the fish eye effect.

- Measurements are most accurate when the pipe is directly in front and perpendicular to the camera.
- Use both the scale bar in front and behind the fish when making size estimates for fish within located within the two.

Supplementary Table 5-1 Parrotfish density in Hardground habitat

	Ind/m^2/min			
Initial Phase	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	7.01112E-05 ± 5.25387E-05	0.003303 ± 0.00096	0	0
Chlorurus strongylocephalus	0	0	0.000299 ± 0.000182	0.000171348 ± 9.48622E-05
Chlorurus enneacanthus	0	2.06E-05 ± 2.06E-05	0	0
Scarus frenatus	0	0.002667 ± 0.001591	0	0
Scarus rubroviolaceus	0.000541331 ± 0.000289921	0.002662 ± 0.000774	0.001024 ± 0.00032	0
Scarus psittacus	0.008991669 ± 0.005048645	0.006134 ± 0.00173	0	0
Scarus niger	0	0	0	0
Scarus tricolor	0	0.00305 ± 0.000739	0.000344 ± 0.000236	0
Scarus scaber	0	0	0	0
Scarus prasiognathos	0	0	0	0.000120289 ± 0.000120289
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0.001864 ± 0.000867	0.000142 ± 9.71E-05	0
Hipposcarus harid	0	0	0	0
Cetoscarus bicolor	0	0	0	3.23172E-05 ± 3.23172E-05
Calotomus carolinus	2.01189E-05 ± 2.01189E-05	0.001258 ± 0.000275	0	0
Terminal Phase				
Chlorurus sordidus	0	0.000989 ± 0.000173	0.00152 ± 0.000652	0
Chlorurus strongylocephalus	0	0	8.58E-05 ± 6.05E-05	0.000816565 ± 0.000370648
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0.000494 ± 0.000228	0.000295479 ± 0.000255277
Scarus rubroviolaceus	0	0	0.000144 ± 6.29E-05	0.001120075 ± 0.000514395
Scarus psittacus	0	0.002241 ± 0.000978	0	0
Scarus niger	0	2.06E-05 ± 1.93E-05	0	0
Scarus tricolor	0	6.84E-05 ± 3.45E-05	0.002217 ± 0.000723	0
Scarus scaber	0	7.06E-05 ± 4.93E-05	0.00031 ± 0.000148	0
Scarus prasiognathos	0	0	0	0.001430848 ± 0.000644693
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0.000243 ± 0.000126	0
Hipposcarus harid	0	0	0.000152 ± 8.35E-05	0.000204151 ± 0.000105725
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	7.19E-05 ± 4.97E-05	0	0
Juveniles				
All species	2.01189E-05 ± 2.01189E-05			

Supplementary Table 5-2 Parrotfish density in Rubble habitat

	Ind/m^2/min			
Initial	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.001933 ± 0.001424	0.006262 ± 0.002681	0	0
Chlorurus strongylocephalus	0	0	0.003147 ± 0.001687	0.001384 ± 0.00128
Chlorurus enneacanthus	0	0.00012 ± 0.000116	0	0
Scarus frenatus	0.000193 ± 0.000106	0.003034 ± 0.001023	0.000713 ± 0.000631	0
Scarus rubroviolaceus	0.000524 ± 0.000507	0.00183 ± 0.000706	0.000251 ± 0.000145	0
Scarus psittacus	0.004505 ± 0.002444	0.004161 ± 0.002121	0	0
Scarus niger	0	0.000328 ± 0.000243	0	0
Scarus tricolor	0	9.05E-05 ± 8.76E-05	0	0
Scarus scaber	0	0.001622 ± 0.000837	5.98E-05 ± 5.79E-05	0
Scarus prasiognathos	0	6.02E-05 ± 5.83E-05	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	6.02E-05 ± 5.83E-05	0
Cetoscarus bicolor	0	0	0	0.000445 ± 0.000328
Calotomus carolinus	0	0.001601 ± 0.001498	0	0
Terminal				
Chlorurus sordidus	0	0.000181 ± 0.000101	0.000866 ± 0.00072	0
Chlorurus strongylocephalus	0	0	0.000125 ± 8.51E-05	0.000582 ± 0.000238
Chlorurus enneacanthus	0	0	9.05E-05 ± 9.05E-05	0
Scarus frenatus	0	6.89E-05 ± 6.89E-05	0.002545 ± 0.001125	0.001421 ± 0.001056
Scarus rubroviolaceus	0	0	0.000181 ± 0.000181	0.001244 ± 0.000337
Scarus psittacus	0	0.000803 ± 0.000803	0	0
Scarus niger	0	0.000161 ± 0.000161	0.000251 ± 0.000179	0
Scarus tricolor	0	0.000468 ± 0.000223	0.000147 ± 0.000102	0
Scarus scaber	0	0	0.001724 ± 0.000665	0
Scarus prasiognathos	0	0	8.03E-05 ± 8.03E-05	0.001083 ± 0.000837
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	6.02E-05 ± 6.02E-05	0.000181 ± 0.000181
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles				
All species	0.000178 ± 0.000121			

Supplementary Table 5-3 Parrotfish density in *Porites* bommie habitat

	Ind/m^2/min			
Initial	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.002411 ± 0.001214	0.009447 ± 0.002705	0	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0.001923 ± 0.001574	0.009119 ± 0.003646	0.000197 ± 0.000106	0
Scarus frenatus	0	0.001402 ± 0.000455	0.00017 ± 0.000117	0
Scarus rubroviolaceus	0.001204 ± 0.000576	0.00968 ± 0.003658	0.002262 ± 0.000509	4.57E-05 ± 4.57E-05
Scarus psittacus	0.027027 ± 0.007021	0.015601 ± 0.004209	0.000469 ± 0.000469	0
Scarus niger	0	0	0	0
Scarus tricolor	0	0.001951 ± 0.000682	0.000116 ± 0.000116	0
Scarus scaber	6.28E-05 ± 6.28E-05	0.002749 ± 0.000703	5.78E-05 ± 5.78E-05	0
Scarus prasiognathos	0	0.000292 ± 0.00019	0.000654 ± 0.000309	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	4.62E-05 ± 4.62E-05	0	0
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0.000104 ± 7.11E-05	0	0
Terminal				
Chlorurus sordidus	0	0.000379 ± 0.000264	0.000439 ± 0.000309	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0	0.002462 ± 0.001306	0.003622 ± 0.001779	0
Scarus frenatus	0	0	0.000521 ± 0.000196	0.000163 ± 0.000111
Scarus rubroviolaceus	0	0	0.000265 ± 0.000153	0.0007 ± 0.00036
Scarus psittacus	0	0.001027 ± 0.000254	0	0
Scarus niger	0	0	0	0
Scarus tricolor	0	0.000131 ± 9.41E-05	0.000762 ± 0.000583	0
Scarus scaber	0	8.88E-05 ± 8.88E-05	0.001191 ± 0.000337	0.000153 ± 0.000153
Scarus prasiognathos	0	0	0.000137 ± 0.000137	0.000212 ± 0.000115
Scarus viridifucatus	0	0	4.57E-05 ± 4.57E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	9.39E-05 ± 9.39E-05	0.00039 ± 0.000343
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	4.57E-05 ± 4.57E-05	0
Juveniles				
All species	0.037039 ± 0.022613			

Supplementary Table 5-4 Parrotfish density in Nearshore lagoon habitat

	Ind/m^2/min			
Initial	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	5.27973E-05 ± 5.27973E-05	0.000274 ± 0.000239	0	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0	0
Scarus rubroviolaceus	0	0.00078 ± 0.000432	0.000566 ± 0.000367	0
Scarus psittacus	0	0.000183 ± 0.000126	0	0
Scarus niger	0	7.96E-05 ± 7.96E-05	0	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0	0	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0	0
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Terminal				
Chlorurus sordidus	0	0.000756 ± 0.000342	0	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0	0
Scarus rubroviolaceus	0	0	0.001502 ± 0.000537	3.5E-05 ± 3.5E-05
Scarus psittacus	0	0.000478 ± 0.00031	0	0
Scarus niger	0	0.000822 ± 0.000507	0	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0	0.000732 ± 0.000357	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	3.9E-05 ± 3.9E-05	7.96E-05 ± 7.96E-05
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles				
All species	0			

Supplementary Table 5-5 Parrotfish density in NE reef habitat

	Ind/m^2/min			
Initial	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.034167 ± 0.006628	0.08008 ± 0.014443	0	0
Chlorurus strongylocephalus	0	5.32E-05 ± 5.32E-05	0.000127 ± 8.84E-05	0
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0.002328 ± 0.001507	0.000928 ± 0.000466	0	0
Scarus rubroviolaceus	0	5.18E-05 ± 5.18E-05	5.32E-05 ± 5.32E-05	0
Scarus psittacus	0.017306 ± 0.00681	0.006746 ± 0.002988	0	0
Scarus niger	0.005756 ± 0.001458	0.015681 ± 0.002525	0	0
Scarus tricolor	0	5.32E-05 ± 5.32E-05	0	0
Scarus scaber	0.000254 ± 0.000127	0.001227 ± 0.000491	0	0
Scarus prasiognathos	4.08E-05 ± 4.08E-05	0.001642 ± 0.000883	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0	0
Cetoscarus bicolor	0	0	0.000112 ± 8.17E-05	0.000738 ± 0.000391
Calotomus carolinus	0	0.000713 ± 0.00036	0	0
Terminal				
Chlorurus sordidus	0	0.014284 ± 0.002098	0.00526 ± 0.001321	0
Chlorurus strongylocephalus	0	0	0.000117 ± 8E-05	0.000175 ± 9.7E-05
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0.001068 ± 0.000653	4.08E-05 ± 4.08E-05
Scarus rubroviolaceus	0	0	0.000115 ± 8.49E-05	0.000105 ± 0.000105
Scarus psittacus	0	0.005002 ± 0.002149	0	0
Scarus niger	0	0.009781 ± 0.003061	0.002033 ± 0.000989	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	5.32E-05 ± 5.32E-05	0.000342 ± 0.000266	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0.001781 ± 0.000448	3.49E-05 ± 3.49E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0	7.06E-05 ± 4.81E-05
Cetoscarus bicolor	0	0	0	0.000282 ± 0.000129
Calotomus carolinus	0	7.53E-05 ± 5.14E-05	5.32E-05 ± 5.32E-05	0
Juveniles				
All species	0.016191 ± 0.008185			

Supplementary Table 5-6 Parrotfish density in SE patches habitat

	Ind/m^2/min			
Initial	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.004624 ± 0.00204	0.02342 ± 0.007534	0	0
Chlorurus strongylocephalus	0	0.001045 ± 0.000835	0.000642 ± 0.000516	0
Chlorurus enneacanthus	0	0.000129 ± 9.48E-05	0	0
Scarus frenatus	0.008069 ± 0.002406	0.005091 ± 0.002232	0.000161 ± 0.000111	0
Scarus rubroviolaceus	0	0.000309 ± 0.000139	0.000526 ± 0.000195	0
Scarus psittacus	0.002993 ± 0.001649	0.002203 ± 0.000997	0	0
Scarus niger	0.00195 ± 0.000829	0.00484 ± 0.002482	0	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0.001528 ± 0.00099	0	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	8.18E-05 ± 5.58E-05	0.000341 ± 0.0003	0
Cetoscarus bicolor	0	0	0.000385 ± 0.000187	0.000219 ± 0.000108
Calotomus carolinus	0	0.000436 ± 0.000345	0	0
Terminal				
Chlorurus sordidus	0	0.01153 ± 0.003237	0.00544 ± 0.001242	0
Chlorurus strongylocephalus	0	0	0.001093 ± 0.000415	0.00086 ± 0.000277
Chlorurus enneacanthus	0	0.000265 ± 0.000216	3.98E-05 ± 3.85E-05	0
Scarus frenatus	0	0	0.005813 ± 0.000959	0.00095 ± 0.000427
Scarus rubroviolaceus	0	0	0.000199 ± 0.00012	0.0015 ± 0.000298
Scarus psittacus	0	0.002311 ± 0.001431	0	0
Scarus niger	0	0.004541 ± 0.001268	0.001057 ± 0.000522	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0.000244 ± 0.000138	0.025026 ± 0.023828	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0.000319 ± 0.000239	3.98E-05 ± 3.85E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	8.18E-05 ± 5.4E-05	0.000156 ± 0.000104
Cetoscarus bicolor	0	0	0	0.000112 ± 7.73E-05
Calotomus carolinus	0	0	0	0
Juveniles				
All species	0.001417 ± 0.00057			

Supplementary Table 5-7 Overall parrotfish bioerosion rates the Hardground habitat

Hardground (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	3.26057E-05 ± 1.06256E-05	0.009488 ± 0.001712	0.020667 ± 0.003139	0
Chlorurus strongylocephalus	0	0	0.093653 ± 0.018281	0.291364 ± 0.032635
Chlorurus enneacanthus	0	5.39E-05 ± 2.53E-05	0	0
Scarus frenatus	0	0.000533 ± 9.64E-05	0.000529 ± 6.74E-05	0.000238 ± 5.4E-05
Scarus rubroviolaceus	1.42218E-05 ± 5.47225E-06	0.000132 ± 1.96E-05	0.003011 ± 0.000527	0.002474 ± 0.000412
Scarus psittacus	0.001895801 ± 0.000416483	0.011954 ± 0.001753	0	0
Scarus niger	0	2.31E-05 ± 7.46E-06	0	0
Scarus tricolor	0	0.002922 ± 0.000349	0.002771 ± 0.000348	0
Scarus scaber	0	1.75E-05 ± 4.06E-06	0.000432 ± 7.5E-05	0
Scarus prasiognathos	0	0	0	0.00149 ± 0.000164
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0.000629 ± 0.000113	0.000489 ± 7E-05	0
Hipposcarus harid	0	0	0.00014 ± 2.19E-05	0.000316 ± 5.47E-05
Cetoscarus bicolor	0	0	0	0.01661 ± 0.00463
Calotomus carolinus	0	0	0	0
Juveniles	5.28563E-07 ± 3.51711E-07	0	0	0

Supplementary Table 5-8 Overall parrotfish bioerosion rates in Rubble habitat

Rubble (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.00062 ± 0.000222	0.006563 ± 0.001522	0.007718 ± 0.002436	0
Chlorurus strongylocephalus	0	0	0.346223 ± 0.070068	0.393562 ± 0.084954
Chlorurus enneacanthus	0	0.000122 ± 5.72E-05	0.000806 ± 0.000302	0
Scarus frenatus	4.16E-06 ± 1.4E-06	0.000528 ± 7.12E-05	0.002347 ± 0.000293	0.001024 ± 0.000209
Scarus rubroviolaceus	5.36E-06 ± 3.57E-06	4.2E-05 ± 6.82E-06	0.000522 ± 0.000133	0.001939 ± 0.000271
Scarus psittacus	0.00038 ± 8.1E-05	0.003224 ± 0.000585	0	0
Scarus niger	0	0.000213 ± 5.79E-05	0.000163 ± 4.16E-05	0
Scarus tricolor	0	0.000244 ± 4.51E-05	9.56E-05 ± 2.39E-05	0
Scarus scaber	0	0.000276 ± 5.19E-05	0.001285 ± 0.000152	0
Scarus prasiognathos	0	1.02E-05 ± 3.36E-06	5.78E-05 ± 1.55E-05	0.000781 ± 0.000165
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	8.67E-05 ± 2.33E-05	0.00013 ± 3.49E-05
Cetoscarus bicolor	0	0	0	0.089056 ± 0.019313
Calotomus carolinus	0	0	0	0
Juveniles	1.82E-06 ± 8.56E-07	0	0	0

Supplementary Table 5-9 Overall parrotfish bioerosion rates in *Porites* bommie

Porites bommie (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.000774 ± 0.000196	0.01014 ± 0.001787	0.003913 ± 0.001065	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0.000617 ± 0.000236	0.01163 ± 0.002595	0.034074 ± 0.00675	0
Scarus frenatus	0	0.000241 ± 3.19E-05	0.000498 ± 5.47E-05	0.000117 ± 2.23E-05
Scarus rubroviolaceus	1.24E-05 ± 4.34E-06	0.000222 ± 3.51E-05	0.00306 ± 0.000456	0.001164 ± 0.000241
Scarus psittacus	0.002286 ± 0.000293	0.010846 ± 0.001322	0	0
Scarus niger	0	0	0	0
Scarus tricolor	0	0.00091 ± 0.000119	0.00057 ± 0.00016	0
Scarus scaber	1.35E-06 ± 7.54E-07	0.000483 ± 5.64E-05	0.0009 ± 9.15E-05	0.00011 ± 2.95E-05
Scarus prasiognathos	0	4.97E-05 ± 1.11E-05	0.000583 ± 7.35E-05	0.000153 ± 2.39E-05
Scarus viridifucatus	0	0	3.3E-05 ± 8.84E-06	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	7.86E-06 ± 2.58E-06	6.76E-05 ± 1.81E-05	0.000281 ± 6.7E-05
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	0.000379 ± 0.000162	0	0	0

Supplementary Table 5-10 Overall parrotfish bioerosion rates in NE reef habitat

NE reef (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.01096 ± 0.001611	0.096112 ± 0.013585	0.046862 ± 0.00621	0
Chlorurus strongylocephalus	0	0.001437 ± 0.000525	0.025833 ± 0.004546	0.034977 ± 0.005804
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	5.02E-05 ± 1.89E-05	0.000158 ± 2.85E-05	0.000769 ± 0.000133	2.94E-05 ± 7.89E-06
Scarus rubroviolaceus	0	1.19E-06 ± 4.2E-07	0.000204 ± 5.65E-05	0.000163 ± 6.22E-05
Scarus psittacus	0.001461 ± 0.000239	0.00763 ± 0.001051	0	0
Scarus niger	0.000386 ± 5.18E-05	0.011123 ± 0.00106	0.00132 ± 0.000246	0
Scarus tricolor	0	2.32E-05 ± 7.5E-06	0	0
Scarus scaber	5.46E-06 ± 1.67E-06	0.000218 ± 3.41E-05	0.000247 ± 5.24E-05	0
Scarus prasiognathos	8.8E-07 ± 4.9E-07	0.000279 ± 5.32E-05	0	0
Scarus viridifucatus	0	0.000303 ± 3.52E-05	2.51E-05 ± 6.74E-06	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0	5.09E-05 ± 9.65E-06
Cetoscarus bicolor	0	0	0.011827 ± 0.003093	0.203372 ± 0.028357
Calotomus carolinus	0	0	0	0
Juveniles	0.000166 ± 6.09E-05	0	0	0

Supplementary Table 5-11 Overall parrotfish bioerosion rates in SE patches habitat

SE patches (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.001483 ± 0.000341	0.035597 ± 0.005576	0.048467 ± 0.006243	0
Chlorurus strongylocephalus	0	0.028229 ± 0.008398	0.13313 ±0.020455	0.172145 ± 0.019775
Chlorurus enneacanthus	0	0.000402 ± 0.000151	0.000355 ± 0.000133	0
Scarus frenatus	0.000174 ± 3.75E-05	0.000866 ± 0.000141	0.004304 ± 0.000351	0.000685 ± 9.5E-05
Scarus rubroviolaceus	0	7.09E-06 ± 1.26E-06	0.000877 ± 0.000147	0.002342 ± 0.00029
Scarus psittacus	0.000253 ± 5.33E-05	0.002932 ± 0.000556	0	0
Scarus niger	0.000131 ± 2.39E-05	0.004098 ± 0.000551	0.000687 ± 0.000133	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0.000302 ± 5.93E-05	0.00058 ± 9E-05	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	5.43E-05 ± 1.41E-05	2.87E-05 ± 7.69E-06	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	1.39E-05 ± 3.23E-06	0.000305 ± 6.06E-05	0.000113 ± 2.16E-05
Cetoscarus bicolor	0	0	0.040748 ± 0.007603	0.066154 ± 0.008654
Calotomus carolinus	0	0	0	0
Juveniles	1.45E-05 ± 4.5E-06	0	0	0

Supplementary Table 5-12 Overall parrotfish bioerosion rates in Nearshore lagoon

N.shore Lagoon (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	1.69E-05 ± 7.8E-06	0.001049 ± 0.000226	0	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0	0
Scarus rubroviolaceus	0	1.79E-05 ± 3.76E-06	0.0025 ± 0.000491	5.47E-05 ± 2.08E-05
Scarus psittacus	0	0.000429 ± 7.8E-05	0	0
Scarus niger	0	0.000394 ± 7.86E-05	0	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0	0.000528 ± 7.6E-05	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	2.81E-05 ± 7.54E-06	5.74E-05 ± 1.54E-05
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	0	0	0	0

Supplementary Table 5-13 Overall parrotfish grazing pressure in Hardground habitat

Hardground (m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	46.03 ± 11.22	5878.46 ± 482.34	5221.60 ± 557.86	0
Chlorurus strongylocephalus	0	0	2644.12 ± 371.72	8303.05 ± 805.59
Chlorurus enneacanthus	0	33.37 ± 7.13	0	0
Scarus frenatus	0	1227.64 ± 167.20	807.44 ± 87.13	362.49 ±69.78
Scarus rubroviolaceus	67.62 ± 19.44	479.25 ± 60.85	1886.34 ± 308.79	1288.82 ± 199.30
Scarus psittacus	6705.79 ± 934.44	23166.52 ± 2960.95	0	0
Scarus niger	0	44.79 ± 12.43	0	0
Scarus tricolor	0	5663.73 ± 581.95	7599.16 ± 773.14	0
Scarus scaber	0	40.30 ± 7.05	658.73 ± 96.95	0
Scarus prasiognathos	0	0	0	2273.69 ± 212.33
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	1448.19 ± 196.56	746.68 ± 90.53	0
Hipposcarus harid	0	0	213.04 ± 28.35	481.85 ± 70.74
Cetoscarus bicolor	0	0	0	473.33 ± 114.30
Calotomus carolinus	0	0	0	0
Juveniles	2.51 ± 1.25	0	0	0

Supplementary Table 5-14 Overall parrotfish grazing pressure in Rubble habitat

Rubble ($m^{-2}\ yr^{-1}$)	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	1226.74 ± 328.83	5698.34 ± 600.97	2732.88 ± 606.63	0
Chlorurus strongylocephalus	0	0	13699.69 ± 1996.70	15718.43 ± 2939.05
Chlorurus enneacanthus	0	105.82 ± 22.59	285.58 ± 75.15	0
Scarus frenatus	45.15 ± 8.21	1703.18 ± 173.01	5018.58 ± 531.37	2188.97 ± 379.51
Scarus rubroviolaceus	35.73 ± 17.77	213.02 ± 29.65	458.30 ± 109.06	1415.25 ± 183.97
Scarus psittacus	1885.10 ± 254.69	8755.46 ± 1384.35	0	0
Scarus niger	0	579.85 ± 135.30	626.79 ± 129.46	0
Scarus tricolor	0	663.17 ± 105.29	367.43 ± 74.37	0
Scarus scaber	0	890.36 ± 126.24	2748.53 ± 276.00	0
Scarus prasiognathos	0	33.04 ± 8.17	123.63 ± 28.10	1668.90 ± 299.66
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	185.45 ± 42.15	278.17 ± 63.22
Cetoscarus bicolor	0	0	0	3556.81 ± 668.16
Calotomus carolinus	0	0	0	0
Juveniles	12.13 ± 4.27	0	0	0

Supplementary Table 5-15 Overall parrotfish grazing pressure in *Porites* bommie habitat

Porites bommie (m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	1282.28 ± 243.32	7377.48 ± 591.16	1160.87 ± 222.30	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	1022.72 ± 293.15	8461.67 ± 858.60	10109.66 ± 1408.67	0
Scarus frenatus	0	650.27 ± 65.06	891.86 ± 83.05	209.89 ± 33.79
Scarus rubroviolaceus	69.10 ± 18.13	945.34 ± 127.82	2251.42 ± 314.04	712.21 ± 136.66
Scarus psittacus	9497.12 ± 772.08	24683.37 ± 2621.02	0	0
Scarus niger	0	0	0	0
Scarus tricolor	0	2070.35 ± 233.03	1836.00 ± 417.36	0
Scarus scaber	12.30 ± 3.72	1305.29 ± 114.86	1611.96 ± 138.87	197.36 ± 44.86
Scarus prasiognathos	0	134.26 ± 22.60	1044.81 ± 111.55	273.76 ± 36.26
Scarus viridifucatus	0	0	59.03 ± 13.42	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	21.24 ± 5.25	121.19 ± 27.54	502.97 ± 101.67
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	2116.06 ± 677.52	0	0	0

Supplementary Table 5-16 Overall parrotfish grazing pressure in NE reef habitat

NE reef (m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	11616.00 ± 1277.13	44708.95 ± 2873.93	8890.00 ± 828.68	0
Chlorurus strongylocephalus	0	49.19 ± 11.91	547.61 ± 69.40	748.38 ± 107.58
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	291.77 ± 59.64	272.80 ± 37.09	881.39 ± 129.20	33.70 ± 7.66
Scarus rubroviolaceus	0	3.23 ± 0.98	95.80 ± 24.85	63.91 ± 22.58
Scarus psittacus	3879.68 ± 403.25	11102.49 ± 1332.29	0	0
Scarus niger	1025.33 ± 93.03	16188.14 ± 1326.85	2718.84 ± 410.21	0
Scarus tricolor	0	33.81 ± 9.39	0	0
Scarus scaber	31.77 ± 5.26	376.49 ± 44.42	282.64 ± 50.91	0
Scarus prasiognathos	5.12 ± 1.55	482.82 ± 69.23	0	0
Scarus viridifucatus	0	523.76 ± 45.91	28.80 ± 6.55	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0	58.28 ± 9.37
Cetoscarus bicolor	0	0	250.72 ± 47.21	4351.44 ± 525.58
Calotomus carolinus	0	0	0	0
Juveniles	591.44 ± 162.48	0	0	0

Supplementary Table 5-17 Overall parrotfish grazing pressure in SE patches habitat

SE patches (m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	443.08 ± 76.09	4666.63 ± 332.43	2591.15 ± 234.74	0
Chlorurus strongylocephalus	0	272.26 ± 53.65	795.33 ± 88.01	1038.01 ± 103.29
Chlorurus enneacanthus	0	52.65 ± 9.02	18.96 ± 4.99	0
Scarus frenatus	284.98 ± 33.30	421.99 ± 51.73	1389.53 ± 96.14	221.00 ± 25.99
Scarus rubroviolaceus	0	5.43 ± 0.83	116.24 ± 18.22	258.07 ± 29.66
Scarus psittacus	189.07 ± 25.30	1202.26 ± 198.70	0	0
Scarus niger	97.91 ± 12.11	1680.80 ± 194.30	398.56 ± 62.39	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	146.89 ± 21.77	187.37 ± 24.62	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	26.46 ± 5.16	9.26 ± 2.10	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	6.78 ± 1.19	98.42 ± 16.58	36.35 ± 5.90
Cetoscarus bicolor	0	0	243.43 ± 32.71	398.90 ± 45.20
Calotomus carolinus	0	0	0	0
Juveniles	14.59 ± 3.38	0	0	0

Supplementary Table 5-18 Overall parrotfish grazing pressure in Nearshore Lagoon

N.shore lagoon (m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	18.93 ± 6.53	514.58 ± 50.34	0	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0	0
Scarus rubroviolaceus	0	51.32 ± 9.22	1240.30 ± 228.01	22.55 ± 7.97
Scarus psittacus	0	658.43 ± 104.30	0	0
Scarus niger	0	604.82 ± 103.76	0	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0	637.56 ± 77.82	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	33.96 ± 7.72	69.31 ± 15.75
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	0	0	0	0

Chapter 6 Supplementary Data

Supplementary Table 6-1 Sediment reworking rates (kg m^{-2} yr^{-1}) for the six representative parrotfish species in each habitat (factoring for differences in sediment load among habitats).

Hardground	**<15 cm**	**16 to 30 cm**	**31 to 45 cm**	**>46 cm**
Chlorurus sordidus	1.22 ± 0.45	1.70 ± 0.42	6.05 ± 1.76	N/A
Chlorurus strongylocephaus	0.46 ± 0.17	3.31 ± 0.90	8.03 ± 2.24	15.34 ± 4.15
Scarus rubroviolaceus	0.13 ± 0.07	0.22 ± 0.07	2.04 ± 0.91	2.19 ±0.82
Scarus frenatus	0.45 ± 0.15	1.05 ± 0.29	2.96 ± 0.76	2.96 ± 0.76
Scarus niger	0.64 ± 0.18	2.28 ± 0.69	4.79 ± 1.47	N/A
Scarus psittacus	0.80 ± 0.21	3.38 ± 1.09	N/A	N/A
Rubble				
Chlorurus sordidus	1.52 ± 0.68	2.12 ± 0.77	7.57 ± 2.97	N/A
Chlorurus strongylocephaus	0.58 ± 0.27	4.14 ± 1.57	10.04 ± 3.86	19.17 ± 7.27
Scarus rubroviolaceus	0.16 ± 0.09	0.28 ± 0.12	2.54 ± 1.31	2.73 ± 1.25
Scarus frenatus	0.56 ± 0.24	1.32 ± 0.50	3.69 ± 1.37	3.69 ± 1.37
Scarus niger	0.80 ± 0.31	2.85 ± 1.15	5.99 ± 2.42	N/A
Scarus psittacus	1.00 ± 0.37	4.23 ± 1.77	N/A	N/A
***Porites* bommie**				
Chlorurus sordidus	1.52 ± 0.69	2.12 ± 0.78	7.57 ± 3.01	N/A
Chlorurus strongylocephaus	0.58 ± 0.27	4.14 ± 1.59	10.04 ± 3.92	19.17 ± 7.37
Scarus rubroviolaceus	0.16 ±0.09	0.28 ± 0.12	2.54 ± 1.33	2.73 ± 1.26
Scarus frenatus	0.56 ± 0.24	1.32 ± 0.51	3.69 ± 1.39	3.69 ± 1.39
Scarus niger	0.80 ± 0.31	2.85 ± 1.16	5.99 ± 2.46	N/A
Scarus psittacus	1.00 ± 0.38	4.23 ± 1.79	N/A	N/A
NE reef				
Chlorurus sordidus	2.89 ± 2.21	4.03 ± 2.89	14.37 ± 10.53	N/A
Chlorurus strongylocephaus	1.10 ± 0.85	7.87 ± 5.70	19.08 ± 13.89	36.43 ± 26.41
Scarus rubroviolaceus	0.31 ± 0.26	0.53 ± 0.40	4.84 ± 3.90	5.19 ± 4.00
Scarus frenatus	1.07 ±0.80	2.50 ± 1.82	7.02 ± 5.06	7.02 ± 5.06
Scarus niger	1.52 ± 1.11	5.41 ± 3.99	11.38 ± 8.41	N/A
Scarus psittacus	1.91 ± 1.37	8.04 ± 6.00	N/A	N/A
SE patch reefs				
Chlorurus sordidus	3.65 ± 1.86	5.09 ± 2.19	18.16 ± 8.30	N/A
Chlorurus strongylocephaus	1.39 ± 0.72	9.94 ± 4.43	24.10 ± 10.85	46.02 ± 20.49
Scarus rubroviolaceus	0.39 ± 0.24	0.67 ± 0.32	6.11 ± 3.47	6.56 ± 3.37
Scarus frenatus	1.35 ± 0.65	3.16 ± 1.42	8.87 ± 3.88	8.87 ± 3.88
Scarus niger	1.91 ± 0.87	6.83 ± 3.18	14.37 ± 6.73	N/A
Scarus psittacus	2.41 ± 1.05	10.15 ± 4.86	N/A	N/A
Nearshore lagoon				
Chlorurus sordidus	3.20 ± 1.34	4.45 ± 1.42	15.89 ± 5.62	N/A
Chlorurus strongylocephaus	1.22 ± 0.52	8.69 ± 2.94	21.09 ± 7.27	40.26 ± 13.61
Scarus rubroviolaceus	0.34 ± 0.19	0.59 ± 0.23	5.34 ± 2.61	5.74 ± 2.44
Scarus frenatus	1.18 ± 0.45	2.76 ± 0.95	7.76 ± 2.55	7.76 ± 2.55
Scarus niger	1.67 ± 0.58	5.98 ±2.18	12.57 ± 4.62	N/A
Scarus psittacus	2.11 ± 0.69	8.88 ± 3.39	N/A	N/A

Supplementary Table 6-2 Sediment reworking contributions- Hardground

Hardground (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	5.35428E-05 ± 1.38811E-05	0.006839 ± 0.00065	0.006074 ± 0.000718	0
Chlorurus strongylocephalus	0	0	0.003076 ±0.000483	0.009659 ±0.001055
Chlorurus enneacanthus	0	3.88E-05 ± 9.61E-06	0	0
Scarus frenatus	0	0.001428 ± 0.000218	0.000939 ± 0.000116	0.000422 ± 9.26E-05
Scarus rubroviolaceus	7.86591E-05 ± 2.33232E-05	0.000558 ± 7.66E-05	0.002194 ± 0.000374	0.001499 ± 0.000246
Scarus psittacus	0.007800982 ± 0.001242015	0.02695 ± 0.003733	0	0
Scarus niger	0	5.21E-05 ± 1.59E-05	0	0
Scarus tricolor	0	0.006589 ± 0.000742	0.00884 ± 0.000984	0
Scarus scaber	0	4.69E-05 ± 9.18E-06	0.000766 ± 0.000129	0
Scarus prasiognathos	0	0	0	0.002645 ± 0.000282
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0.001685 ± 0.000256	0.000869 ± 0.00012	0
Hipposcarus harid	0	0	0.000248 ± 3.76E-05	0.000561 ± 9.39E-05
Cetoscarus bicolor	0	0	0	0.000551 ± 0.00015
Calotomus carolinus	0	0	0	0
Juveniles	2.92341E-06 ± 1.49903E-06	0	0	0

Supplementary Table 6-3 Sediment reworking contributions- Rubble

Rubble (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.001273 ± 0.000452	0.005912 ± 0.001075	0.002836 ± 0.000955	0
Chlorurus strongylocephalus	0	0	0.014214 ± 0.003232	0.016309 ± 0.004863
Chlorurus enneacanthus	0	0.00011 ± 4.04E-05	0.000296 ± 0.000118	0
Scarus frenatus	4.68E-05 ± 1.2E-05	0.001767 ± 0.000282	0.005207 ± 0.000913	0.002271 ± 0.000652
Scarus rubroviolaceus	3.71E-05 ± 2.15E-05	0.000221 ± 4.33E-05	0.000476 ± 0.000138	0.001468 ± 0.00025
Scarus psittacus	0.001956 ± 0.000439	0.009084 ± 0.002033	0	0
Scarus niger	0	0.000602 ± 0.000207	0.00065 ± 0.000196	0
Scarus tricolor	0	0.000688 ± 0.000161	0.000381 ± 0.000113	0
Scarus scaber	0	0.000924 ± 0.000206	0.002852 ± 0.000474	0
Scarus prasiognathos	0	3.43E-05 ± 1.33E-05	0.000128 ± 4.83E-05	0.001732 ± 0.000515
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0.000192 ± 7.24E-05	0.000289 ± 0.000109
Cetoscarus bicolor	0	0	0	0.00369 ± 0.001106
Calotomus carolinus	0	0	0	0
Juveniles	1.26E-05 ± 5.17E-06	0	0	0

Supplementary table 6-4 Sediment reworking contributions- *Porites* bommie

Porites bommie (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.001588 ± 0.000399	0.009136 ± 0.001262	0.001438 ± 0.000417	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0.001266 ± 0.000481	0.010478 ± 0.001834	0.012519 ± 0.002645	0
Scarus frenatus	0	0.000805 ± 0.000127	0.001104 ± 0.00017	0.00026 ± 6.93E-05
Scarus rubroviolaceus	8.56E-05 ± 2.62E-05	0.001171 ± 0.000223	0.002788 ± 0.000475	0.000882 ± 0.000222
Scarus psittacus	0.01176 ± 0.001588	0.030566 ± 0.004595	0	0
Scarus niger	0	0	0	0
Scarus tricolor	0	0.002564 ± 0.000425	0.002274 ± 0.000755	0
Scarus scaber	1.52E-05 ± 6.49E-06	0.001616 ± 0.000224	0.001996 ± 0.000285	0.000244 ± 9.2E-05
Scarus prasiognathos	0	0.000166 ± 4.4E-05	0.001294 ± 0.000229	0.000339 ± 7.44E-05
Scarus viridifucatus	0	0	7.31E-05 ± 2.75E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	2.63E-05 ± 1.02E-05	0.00015 ± 5.65E-05	0.000623 ± 0.000208
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	0.00262 ± 0.00098	0	0	0

Supplementary table 6-5 Sediment reworking contributions- NE reef

NE reef (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.042744 ± 0.010447	0.16452 ± 0.035502	0.032713 ± 0.008495	0
Chlorurus strongylocephalus	0	0.000181 ± 0.000131	0.002015 ± 0.000743	0.002754 ± 0.00119
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0.001074 ± 0.000543	0.001004 ± 0.000402	0.003243 ± 0.001508	0.000124 ± 8.94E-05
Scarus rubroviolaceus	0	1.19E-05 ± 8.9E-06	0.000353 ± 0.000173	0.000235 ± 0.000181
Scarus psittacus	0.014276 ± 0.004728	0.040855 ± 0.012229	0	0
Scarus niger	0.003773 ± 0.00098	0.059569 ± 0.012986	0.010005 ± 0.003969	0
Scarus tricolor	0	0.000124 ± 9.19E-05	0	0
Scarus scaber	0.000117 ± 4.79E-05	0.001385 ± 0.000481	0.00104 ± 0.000594	0
Scarus prasiognathos	1.88E-05 ± 1.41E-05	0.001777 ± 0.00075	0	0
Scarus viridifucatus	0	0.001927 ± 0.000497	0.000106 ± 7.64E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0	0.000214 ± 0.000109
Cetoscarus bicolor	0	0	0.000923 ± 0.000505	0.016012 ± 0.005811
Calotomus carolinus	0	0	0	0
Juveniles	0.002176 ± 0.001017	0	0	0

Supplementary Table 6-6 Sediment reworking contributions- SE patches

SE patches (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.007308 ± 0.001855	0.076969 ± 0.011082	0.042737 ± 0.006741	0
Chlorurus strongylocephalus	0	0.004491 ± 0.001632	0.013118 ± 0.002613	0.01712 ± 0.003147
Chlorurus enneacanthus	0	0.000868 ± 0.000301	0.000313 ± 0.000143	0
Scarus frenatus	0.0047 ± 0.000876	0.00696 ± 0.001551	0.022918 ± 0.003059	0.003645 ± 0.000827
Scarus rubroviolaceus	0	8.95E-05 ± 2.18E-05	0.001917 ± 0.0004	0.004256 ± 0.000714
Scarus psittacus	0.003118 ± 0.000808	0.019829 ± 0.005253	0	0
Scarus niger	0.001615 ± 0.000355	0.027722 ± 0.005386	0.006574 ± 0.001715	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0.002423 ± 0.000652	0.00309 ± 0.000783	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0.000436 ± 0.000155	0.000153 ± 6.7E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0.000112 ± 3.55E-05	0.001623 ± 0.000528	0.0006 ± 0.000188
Cetoscarus bicolor	0	0	0.004015 ± 0.000971	0.006579 ± 0.001377
Calotomus carolinus	0	0	0	0
Juveniles	0.000241 ± 6.99E-05	0	0	0

Supplementary Table 6-7 Sediment reworking contributions- Nearshore lagoon

Nearshore lagoon (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	7.3E-05 ± 3.06E-05	0.001984 ± 0.000291	0	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0	0
Scarus rubroviolaceus	0	0.000198 ± 4.52E-05	0.004782 ± 0.001006	8.69E-05 ± 3.7E-05
Scarus psittacus	0	0.002539 ± 0.000514	0	0
Scarus niger	0	0.002332 ± 0.000527	0	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0	0.002458 ± 0.000435	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0.000131 ± 4.31E-05	0.000267 ± 8.8E-05
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	0	0	0	0

Supplementary Table 6-8 Hardground Total sediment production

Hardground (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	8.61E-05 ± 1.74811E-05	0.016327 ± 0.001831	0.026741 ± 0.00322	0
Chlorurus strongylocephalus	0	0	0.096729 ± 0.018288	0.301024 ± 0.032652
Chlorurus enneacanthus	0	9.27E-05 ± 2.71E-05	0	0
Scarus frenatus	0	0.001961 ± 0.000238	0.001469 ± 0.000134	0.000659 ± 0.000107
Scarus rubroviolaceus	9.29E-05 ± 2.39566E-05	0.00069 ± 7.91E-05	0.005205 ± 0.000646	0.003974 ± 0.00048
Scarus psittacus	0.009697 ± 0.001309984	0.038904 ± 0.004124	0	0
Scarus niger	0	7.52E-05 ± 1.75E-05	0	0
Scarus tricolor	0	0.009511 ± 0.00082	0.011611 ± 0.001044	0
Scarus scaber	0	6.44E-05 ± 1E-05	0.001198 ± 0.000149	0
Scarus prasiognathos	0	0	0	0.004135 ± 0.000326
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0.002314 ± 0.00028	0.001358 ± 0.000139	0
Hipposcarus harid	0	0	0.000387 ± 4.36E-05	0.000876 ± 0.000109
Cetoscarus bicolor	0	0	0	0.01716 ± 0.004633
Calotomus carolinus	0	0	0	0
Juveniles	3.45E-06 ± 1.53973E-06	0	0	0

Supplementary Table 6-9 Rubble Total sediment production

Rubble (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.001893 ± 0.000503999	0.012475 ± 0.001863	0.010553 ± 0.002616	0
Chlorurus strongylocephalus	0	0	0.360437 ± 0.070143	0.409871 ± 0.085093
Chlorurus enneacanthus	0	0.000232 ± 7.01E-05	0.001103 ± 0.000324	0
Scarus frenatus	5.1E-05 ± 1.20884E-05	0.002295 ± 0.000291	0.007554 ± 0.000959	0.003295 ± 0.000685
Scarus rubroviolaceus	4.24E-05 ± 2.18233E-05	0.000263 ± 4.38E-05	0.000997 ± 0.000192	0.003407 ± 0.000369
Scarus psittacus	0.002336 ± 0.000446384	0.012308 ± 0.002116	0	0
Scarus niger	0	0.000815 ± 0.000215	0.000813 ± 0.000201	0
Scarus tricolor	0	0.000932 ± 0.000167	0.000477 ± 0.000115	0
Scarus scaber	0	0.0012 ± 0.000212	0.004137 ± 0.000498	0
Scarus prasiognathos	0	4.45E-05 ± 1.37E-05	0.000186 ± 5.07E-05	0.002512 ± 0.000541
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0.000279 ± 7.61E-05	0.000419 ± 0.000114
Cetoscarus bicolor	0	0	0	0.092747 ± 0.019345
Calotomus carolinus	0	0	0	0
Juveniles	1.44E-05 ± 5.23861E-06	0	0	0

Supplementary Table 6-10 Porites bommie Total sediment production

Porites bommie (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.002361 ± 0.0004451	0.019276 ± 0.002188	0.00535 ± 0.001144	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0.001883 ± 0.00053625	0.022109 ± 0.003177	0.046592 ± 0.00725	0
Scarus frenatus	0	0.001046 ± 0.000131	0.001602 ± 0.000179	0.000377 ± 7.28E-05
Scarus rubroviolaceus	9.79E-05 ± 2.6575E-05	0.001393 ± 0.000226	0.005848 ± 0.000659	0.002046 ± 0.000327
Scarus psittacus	0.014047 ± 0.001615	0.041412 ± 0.004781	0	0
Scarus niger	0	0	0	0
Scarus tricolor	0	0.003473 ± 0.000441	0.002844 ± 0.000772	0
Scarus scaber	1.66E-05 ± 6.53E-06	0.002099 ± 0.000231	0.002896 ± 0.000299	0.000355 ± 9.66E-05
Scarus prasiognathos	0	0.000216 ± 4.54E-05	0.001877 ± 0.00024	0.000492 ±7.81E-05
Scarus viridifucatus	0	0	0.000106 ± 2.89E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	3.42E-05 ± 1.05E-05	0.000218 ±5.93E-05	0.000904 ± 0.000219
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	0.002999 ± 0.00099318	0	0	0

Supplementary Table 6-11 NE reef Total sediment production

NE reef (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.053704 ± 0.010571	0.260632 ± 0.038012	0.079576 ± 0.010523	0
Chlorurus strongylocephalus	0	0.001618 ± 0.000541	0.027848 ± 0.004607	0.037731 ± 0.005925
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0.001124 ± 0.000544	0.001162 ± 0.000403	0.004013 ± 0.001514	0.000153 ± 8.98E-05
Scarus rubroviolaceus	0	1.31E-05 ± 8.91E-06	0.000556 ± 0.000182	0.000399 ± 0.000191
Scarus psittacus	0.015737 ± 0.004734	0.048485 ± 0.012274	0	0
Scarus niger	0.004159 ± 0.000981	0.070692 ± 0.013029	0.011325 ± 0.003976	0
Scarus tricolor	0	0.000148 ± 9.22E-05	0	0
Scarus scaber	0.000122 ± 4.79E-05	0.001603 ± 0.000482	0.001287 ± 0.000597	0
Scarus prasiognathos	1.97E-05 ± 1.41E-05	0.002056 ± 0.000752	0	0
Scarus viridifucatus	0	0.00223 ± 0.000499	0.000131 ± 7.67E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0	0.000265 ± 0.00011
Cetoscarus bicolor	0	0	0.01275 ± 0.003134	0.219385 ± 0.028947
Calotomus carolinus	0	0	0	0
Juveniles	0.002342 ± 0.001019	0	0	0

Supplementary Table 6-12 SE patch reefs Total sediment production

SE patch reefs (kg m^{-2} yr^{-1})	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	0.008791 ± 0.001886	0.112566 ± 0.012405	0.091204 ± 0.009187	0
Chlorurus strongylocephalus	0	0.03272 ± 0.008555	0.146248 ± 0.020622	0.189265 ± 0.020024
Chlorurus enneacanthus	0	0.00127 ± 0.000337	0.000667 ±0.000195	0
Scarus frenatus	0.004874 ± 0.000876	0.007826 ± 0.001557	0.027222 ± 0.003079	0.00433 ± 0.000833
Scarus rubroviolaceus	0	9.66E-05 ± 2.18E-05	0.002794 ± 0.000426	0.006598 ± 0.00077
Scarus psittacus	0.003371 ± 0.00081	0.022761 ± 0.005282	0	0
Scarus niger	0.001746 ± 0.000356	0.03182 ± 0.005414	0.00726 ± 0.00172	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0.002724 ± 0.000655	0.003671 ± 0.000788	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0.000491 ± 0.000155	0.000181 ± 6.74E-05	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0.000126 ± 3.57E-05	0.001928 ± 0.000531	0.000712 ± 0.000189
Cetoscarus bicolor	0	0	0.044763 ± 0.007665	0.072734 ± 0.008763
Calotomus carolinus	0	0	0	0
Juveniles	0.000255 ± 7.01E-05	0	0	0

Supplementary Table 6-13 Nearshore lagoon Total sediment production

Nearshore lagoon (kg $m^{-2} yr^{-1}$)	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Chlorurus sordidus	8.99414E-05 ± 3.15594E-05	0.003033 ± 0.000368	0	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0	0
Scarus rubroviolaceus	0	0.000216 ± 4.54E-05	0.007282 ± 0.00112	0.000142 ± 4.25E-05
Scarus psittacus	0	0.002968 ± 0.00052	0	0
Scarus niger	0	0.002726 ± 0.000533	0	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0	0.002986 ± 0.000441	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0.000159 ± 4.38E-05	0.000325 ± 8.93E-05
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	0	0	0	0

Supplementary Table 6-14 Hardground % of total sediment reworked

Hardground	1 to 15	16 to 30	31 to 45	46 to 60
Chlorurus sordidus	62	42	23	0
Chlorurus strongylocephalus	0	0	3	3
Chlorurus enneacanthus	0	42	0	0
Scarus frenatus	0	73	64	64
Scarus rubroviolaceus	85	81	42	38
Scarus psittacus	80	69	0	0
Scarus niger	0	69	0	0
Scarus tricolor	0	69	76	0
Scarus scaber	0	73	64	0
Scarus prasiognathos	0	0	0	64
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	73	64	0
Hipposcarus harid	0	0	64	64
Cetoscarus bicolor	0	0	0	3
Calotomus carolinus	0	0	0	0
Juveniles	85	0	0	0

Supplementary table 6-15 Rubble % of total sediment reworked

Rubble	1 to 15	16 to 30	31 to 45	46 to 60
Chlorurus sordidus	67	47	27	0
Chlorurus strongylocephalus	0	0	4	4
Chlorurus enneacanthus	0	47	27	0
Scarus frenatus	92	77	69	69
Scarus rubroviolaceus	87	84	48	43
Scarus psittacus	84	74	0	0
Scarus niger	0	74	80	0
Scarus tricolor	0	74	80	0
Scarus scaber	0	77	69	0
Scarus prasiognathos	0	77	69	69
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	69	69
Cetoscarus bicolor	0	0	0	4
Calotomus carolinus	0	0	0	0
Juveniles	87	0	0	0

Supplementary Table 6-16 *Porites* bommie % of total sediment reworked

Porites bommie	**1 to 15**	**16 to 30**	**31 to 45**	**46 to 60**
Chlorurus sordidus	67	47	27	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	67	47	27	0
Scarus frenatus	0	77	69	69
Scarus rubroviolaceus	87	84	48	43
Scarus psittacus	84	74	0	0
Scarus niger	0	0	0	0
Scarus tricolor	0	74	80	0
Scarus scaber	92	77	69	69
Scarus prasiognathos	0	77	69	69
Scarus viridifucatus	0	0	69	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	77	69	69
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	87	0	0	0

Supplementary Table 6-17 NE reef % of total sediment reworked

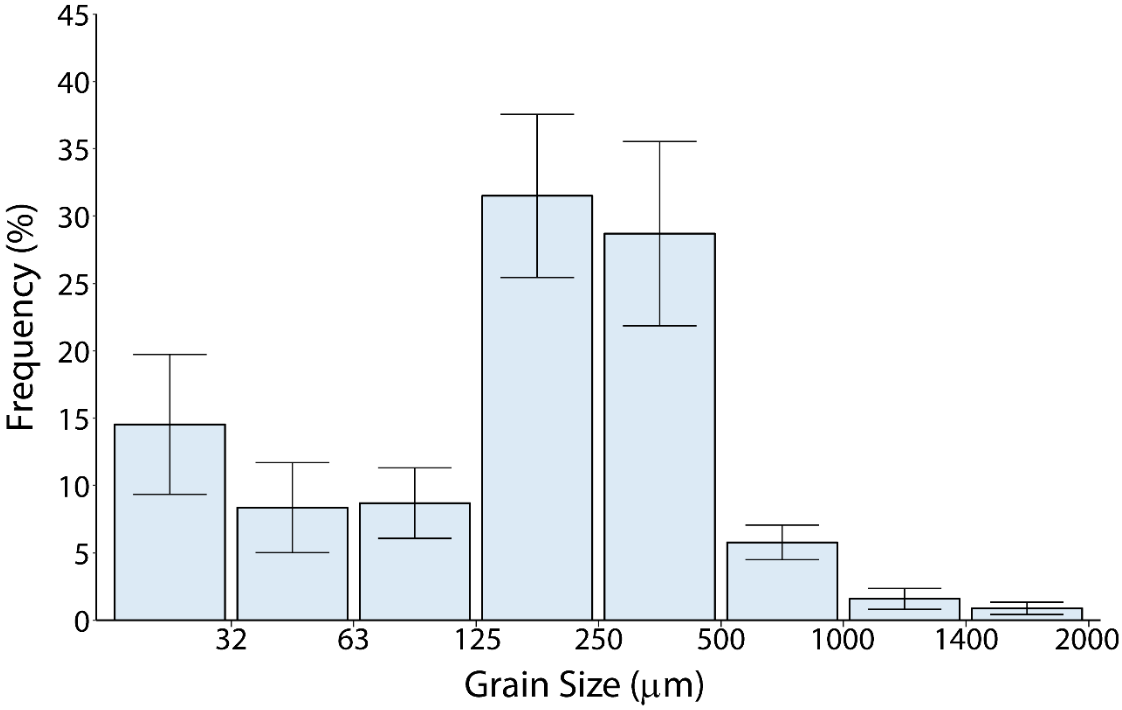
% reworked	**1 to 15**	**16 to 30**	**31 to 45**	**46 to 60**
Chlorurus sordidus	80	63	41	0
Chlorurus strongylocephalus	0	11	7	7
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	96	86	81	81
Scarus rubroviolaceus	0	91	63	59
Scarus psittacus	91	84	0	0
Scarus niger	91	84	88	0
Scarus tricolor	0	84	0	0
Scarus scaber	96	86	81	0
Scarus prasiognathos	96	86	0	0
Scarus viridifucatus	0	86	81	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	0	81
Cetoscarus bicolor	0	0	7	7
Calotomus carolinus	0	0	0	0
Juveniles	93	0	0	0

Supplementary Table 6-18 SE patch reefs % of total sediment reworked

SE patch reefs	1 to 15	16 to 30	31 to 45	46 to 60
Chlorurus sordidus	83	68	47	0
Chlorurus strongylocephalus	0	14	9	9
Chlorurus enneacanthus	0	68	47	0
Scarus frenatus	96	89	84	84
Scarus rubroviolaceus	0	93	69	65
Scarus psittacus	93	87	0	0
Scarus niger	93	87	91	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	89	84	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	89	84	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	89	84	84
Cetoscarus bicolor	0	0	9	9
Calotomus carolinus	0	0	0	0
Juveniles	94	0	0	0

Supplementary Table 6-19 Nearshore lagoon % of total sediment reworked

Nearshore	1 to 15	16 to 30	31 to 45	46 to 60
Chlorurus sordidus	81	65	0	0
Chlorurus strongylocephalus	0	0	0	0
Chlorurus enneacanthus	0	0	0	0
Scarus frenatus	0	0	0	0
Scarus rubroviolaceus	0	92	66	61
Scarus psittacus	0	86	0	0
Scarus niger	0	86	0	0
Scarus tricolor	0	0	0	0
Scarus scaber	0	0	82	0
Scarus prasiognathos	0	0	0	0
Scarus viridifucatus	0	0	0	0
Scarus russelii	0	0	0	0
Hipposcarus harid	0	0	82	82
Cetoscarus bicolor	0	0	0	0
Calotomus carolinus	0	0	0	0
Juveniles	0	0	0	0



Supplementary Figure 6-1 Grain size distribution of sediment produced by recently feeding <15 cm *Scarus psittacus* in aquarium conditions. The grain size distribution is comparable to that of sample collected in the field, but suggest that % of fines <32 μm may be underestimated in field samples.

Supplementary Table 6-20: Percentage of sediment size fractions produced by different size classes of *Chlorurus sordidus*

Grain Size µm	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
32	4.96 ± 1.02	8.13 ± 1.24	6.02 ± 1.30	N/A
63	5.55 ± 0.71	8.30 ± 0.95	6.87 ± 1.11	N/A
125	9.81 ± 1.30	14.28 ± 1.11	12.09 ± 0.95	N/A
250	18.93 ± 1.91	21.91 ± 1.07	22.36 ± 1.89	N/A
500	29.62 ± 1.34	26.71 ± 1.50	30.32 ± 1.70	N/A
1000	26.31 ± 2.94	19.40 ± 2.64	21.99 ± 1.81	N/A
1400	2.73 ± 1.20	0.90 ± 0.61	0.36 ± 0.23	N/A
2000	2.09 ± 2.09	0.38 ± 0.38	0	N/A

Supplementary Table 6-21: Percentage of sediment size fractions produced by different size classes of *Chlorurus strongylocephalus*

Grain Size µm	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
32	N/A	7.74 ± 1.82	3.18 ± 0.74	6.37 ± 2.40
63	N/A	6.99 ± 1.21	4.70 ± 1.04	6.09 ± 1.59
125	N/A	12.23 ± 1.57	11.94 ± 1.65	11.37 ± 2.09
250	N/A	21.43 ± 1.75	27.95 ± 3.14	21.24 ± 1.75
500	N/A	29.10 ± 1.83	32.64 ± 2.72	28.36 ± 2.97
1000	N/A	21.72 ± 3.36	18.73 ± 3.00	24.62 ± 4.51
1400	N/A	0.48 ± 0.48	0.31 ± 0.31	1.60 ± 0.68
2000	N/A	0.31 ± 0.31	0.56 ± 0.56	0.35 ± 0.35

Supplementary Table 6-22: Percentage of sediment size fractions produced by different size classes of *Scarus frenatus*

Grain Size µm	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
32	8.21 ± 0.92	9.21 ± 1.32	4.71 ± 0.78	4.46 ± 0.85
63	11.98 ± 0.53	9.48 ± 1.13	6.26 ± 1.22	6.11 ± 1.14
125	20.84 ± 0.89	16.61 ± 1.34	12.84 ± 2.18	12.12 ± 1.16
250	26.77 ± 1.70	25.22 ± 1.30	23.97 ± 2.99	24.55 ± 1.03
500	20.42 ± 1.07	24.38 ± 1.79	26.26 ± 3.04	31.84 ± 1.46
1000	11.79 ± 1.77	14.98 ± 1.47	17.58 ± 1.67	19.66 ± 1.95
1400	0	0.06 ± 0.04	7.62 ± 7.62	0.98 ± 0.69
2000	0	0.06 ± 0.06	0.76 ± 0.76	0.29 ± 0.29

Supplementary Table 6-23: Percentage of sediment size fractions produced by different size classes of *Scarus niger*

Grain Size µm	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
32	9.40 ± 2.92	7.96 ± 2.05	7.93 ± 1.77	N/A
63	9.90 ± 2.37	7.77 ± 1.38	8.74 ± 1.60	N/A
125	17.40 ± 1.55	13.43 ± 1.43	16.60 ± 1.52	N/A
250	24.57 ± 1.64	21.18 ± 1.67	28.12 ± 2.17	N/A
500	23.85 ± 3.18	25.81 ± 1.93	25.64 ± 1.60	N/A
1000	14.00 ± 2.87	21.62 ± 3.09	12.86 ± 4.11	N/A
1400	0.35 ± 0.19	1.94 ± 0.76	0.11 ± 0.11	N/A
2000	0.53 ± 0.53	0.31 ± 0.21	0	N/A

Supplementary Table 6-24: Percentage of sediment size fractions produced by different size classes of *Scarus psittacus*

Grain Size µm	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
32	1.99 ± 1.14	9.21 ± 1.09	N/A	N/A
63	3.65 ± 1.23	8.93 ± 0.55	N/A	N/A
125	8.94 ± 1.80	12.58 ± 2.53	N/A	N/A
250	25.44 ± 2.76	23.54 ± 0.26	N/A	N/A
500	36.77 ± 2.70	29.78 ± 1.40	N/A	N/A
1000	23.21 ± 4.22	15.96 ± 0.32	N/A	N/A
1400	0	0	N/A	N/A
2000	0	0	N/A	N/A

Supplementary Table 6-25: Percentage of sediment size fractions produced by different size classes of *Scarus rubroviolaceus*

Grain Size µm	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
32	3.21 ± 1.20	6.36 ± 1.71	2.88 ± 0.51	3.39 ± 0.28
63	3.82 ± 0.97	7.29 ± 1.97	3.61 ± 0.56	4.47 ± 0.34
125	5.79 ± 1.21	11.96 ± 2.76	8.46 ± 1.46	9.65 ± 0.71
250	21.05 ± 3.06	25.23 ± 1.03	21.55 ± 1.98	21.25 ± 1.58
500	38.96 ± 2.74	32.48 ± 3.99	33.60 ± 2.82	31.87 ± 0.69
1000	25.88 ± 4.11	16.52 ± 2.60	27.84 ± 2.35	26.17 ± 2.09
1400	1.30 ± 0.65	0.17 ± 0.11	1.81 ± 1.05	1.85 ± 0.69
2000	0	0	0.26 ± 0.26	1.36 ± 0.88

Supplementary Table 6-26: Percentage of sediment size fractions produced by *Scarus psittacus in aquarium conditions*

Grain Size	1 to 15 cm
32	14.53 ± 5.20
63	8.35 ± 3.34
125	8.69 ± 2.62
250	31.50 ± 6.06
500	28.70 ± 6.84
1000	5.77 ± 1.29
1400	1.58 ± 0.77
2000	0.88 ± 0.46

Supplementary Table 6-27: Grain types produced by different size classes of *Chlorurus sordidus.* CCA = Crustose Coralline Algae

Grain Type	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
Coral	91.13	78.74	92.19	N/A
Halimeda spp.	6.73	12.93	3.75	N/A
CCA	0.92	5.46	0.00	N/A
Mollusca	1.22	2.01	2.50	N/A
Foraminifera	0.00	0.00	0.31	N/A
Unidentified	0.00	0.86	1.25	N/A

Supplementary Table 6-28: Grain types produced by different size classes of *Chlorurus strongylocephalus.* CCA = Crustose Coralline Algae

Grain Type	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
Coral	N/A	97.83	95.67	93.60
Halimeda spp.	N/A	0.00	1.00	3.66
CCA	N/A	2.17	2.33	2.44
Mollusca	N/A	0.00	0.00	0.00
Foraminifera	N/A	0.00	0.00	0.30
Unidentified	N/A	0.00	1.00	0.00

Supplementary Table 6-29: Grain types produced by different size classes of *Scarus frenatus..* CCA = Crustose Coralline Algae

Grain Type	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Coral	95.51	97.85	87.57	96.71
Halimeda spp.	1.40	1.53	1.16	0.00
CCA	2.25	0.31	4.34	1.52
Mollusca	0.56	0.00	4.91	0.51
Foraminifera	0.00	0.31	2.02	1.27
Unidentified	0.28	0.00	0.00	0.00

Supplementary Table 6-30: Grain types produced by different size classes of *Scarus niger..* CCA = Crustose Coralline Algae

Grain Type	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Coral	98.60	97.39	95.02	N/A
Halimeda spp.	0.23	0.65	0.93	N/A
CCA	0.47	0.98	2.18	N/A
Mollusca	0.23	0.65	1.25	N/A
Foraminifera	0.47	0.33	0.31	N/A
Unidentified	0.00	0.00	0.31	N/A

Supplementary Table 6-31: Grain types produced by different size classes of *Scarus psittacus..* CCA = Crustose Coralline Algae

Grain Type	**1 to 15 cm**	**16 to 30 cm**	**31 to 45 cm**	**46 to 60 cm**
Coral	96.60	92.05	N/A	N/A
Halimeda spp.	0.85	0.66	N/A	N/A
CCA	2.55	4.97	N/A	N/A
Mollusca	0.00	1.66	N/A	N/A
Foraminifera	0.00	0.66	N/A	N/A
Unidentified	0.00	0.00	N/A	N/A

Supplementary Table 6-32: Grain types produced by different size classes of *Scarus psittacus*.. CCA = Crustose Coralline Algae

Grain Type	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
Coral	96.60	92.05	N/A	N/A
Halimeda spp.	0.85	0.66	N/A	N/A
CCA	2.55	4.97	N/A	N/A
Mollusca	0.00	1.66	N/A	N/A
Foraminifera	0.00	0.66	N/A	N/A
Unidentified	0.00	0.00	N/A	N/A

Supplementary Table 6-33: Grain types produced by different size classes of *Scarus rubroviolaceus*.. CCA = Crustose Coralline Algae

Grain Type	1 to 15 cm	16 to 30 cm	31 to 45 cm	46 to 60 cm
Coral	100.00	100.00	92.90	97.78
Halimeda spp.	0.00	0.00	2.16	0.28
CCA	0.00	0.00	3.40	1.39
Mollusca	0.00	0.00	0.93	0.00
Foraminifera	0.00	0.00	0.31	0.28
Unidentified	0.00	0.00	0.31	0.28

Supplementary Table 6-34: Sediment load within the epilithic algal matrix in each Vavvaru habitat (g cm^{-3} ± SE)

Habitat	Sediment Load (g cm^{-3} ± SE)
Z1 – Hardground	0.008 ± 0.001
Z2 – Rubble	0.01 ± 0.003
Z3 – *Porites* bommie	0.01 ± 0.003
Z6 – NE reef	0.019 ± 0.013
Z7 – SE patches	0.024 ± 0.009
Z8 – Nearshore lagoon	0.021 ± 0.005

Supplementary Table 6-35: Grain size distributions (% per size fraction) of sediments retained within the epilithic algal matrix in each Vavvaru habitat.

Habitat	**Z1**	**Z2**	**Z3**	**Z6**	**Z7**	**Z8**
32	10.51 ± 2.42	9.20 ± 1.96	4.32 ± 1.38	8.26 ± 2.10	7.26 ± 2.32	4.39 ± 1.07
63	12.91 ± 1.79	10.00 ± 1.41	5.60 ± 1.05	12.76 ± 3.29	8.06 ± 2.41	6.73 ± 0.65
125	17.10 ± 2.01	15.13 ± 1.13	11.57 ± 0.44	28.39 ± 3.36	18.25 ± 1.96	21.69 ± 2.08
250	18.91 ± 3.03	27.97 ± 1.63	29.40 ± 2.67	30.83 ± 3.25	33.91 ± 3.38	36.44 ± 1.67
500	18.40 ± 2.28	27.12 ± 2.24	33.90 ± 0.91	14.90 ± 4.27	24.82 ± 3.54	22.23 ± 3.41
1000	18.98 ± 5.12	10.46 ± 1.73	14.58 ± 1.91	4.40 ± 1.19	6.55 ± 0.15	6.64 ± 1.72
1400	0.66 ± 0.66	0.08 ± 0.08	0.21 ± 0.09	0.06 ± 0.06	0.14 ± 0.07	0.51 ± 0.43
2000	0.82 ± 0.82	0.03 ± 0.03	0.41 ± 0.33	0.40 ± 0.24	0.16 ± 0.16	1.38 ± 1.23
2800	1.11 ± 1.11	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.83 ± 0.42	0.00 ± 0.00

Supplementary Table 6-36: Percent contribution of grain types found in EAM sediments in each Vavvaru habitat. CCA = Crustose Coralline Algae

Grain Type	**Z1**	**Z2**	**Z3**	**Z6**	**Z7**	**Z8**
Coral	97.94	94.06	98.31	96.78	97.10	97.55
Halimeda	0.88	1.65	0.56	0.80	1.61	1.22
CCA	0.00	1.65	0.56	0.00	0.97	0.92
Mollusca	0.88	1.98	0.28	1.88	0.00	0.00
Foraminifera	0.29	0.00	0.28	0.27	0.32	0.31
Unidentified	0.00	0.00	0.00	0.27	0.00	0.00

Supplementary Table 6-37: Parrotfish gut throughout times. Estimates were made by holding parrotfish in aquarium conditions unfed for at least 48 hours to clear stomach contents. Food (coral rubble) was then added to the tank. A Go Pro Hero 4 was mounted on top of the tank and gut throughput was estimated from the time that foraging first commenced and the time of the first defecation were recorded.

Species	**Fish weight (g)**	**Throughput time (mins)**
Scarus psittacus	2.15	30.58
Scarus psittacus	2.14	26.23
Scarus psittacus	2.04	25.97
Scarus psittacus	4.51	47.47
Scarus psittacus	4.88	49.93
Scarus psittacus	5.44	57.33
Scarus psittacus	5.57	57.65
Scarus psittacus	8.72	64.48
Chlorurus sordidus	105	136.08
Chlorurus sordidus	90	97.08