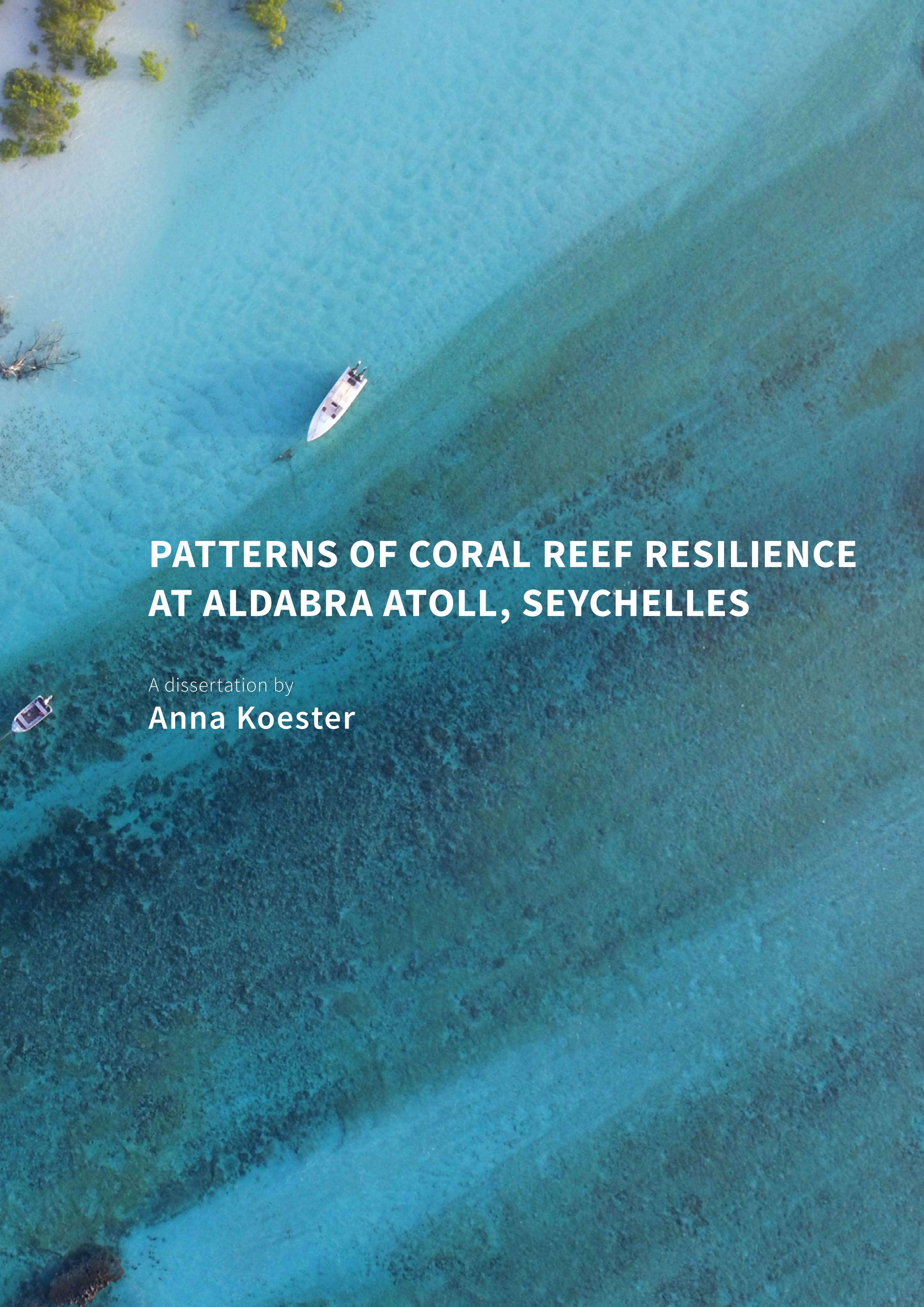


PATTERNS OF CORAL REEF RESILIENCE AT ALDABRA ATOLL, SEYCHELLES

A dissertation by

Anna Koester

PATTERNS OF CORAL REEF RESILIENCE AT ALDABRA ATOLL, SEYCHELLES

A dissertation by

Anna Koester

submitted in partial fulfilment of the requirements for obtaining a Doctoral Degree in Science (Dr. rer. nat.) at the University of Bremen, Faculty of Biology and Chemistry

Supervisor:
Prof. Dr. Christian Wild

Reviewers:
1. Prof. Dr. Christian Wild
2. Prof. Dr. Marko Rohlfs

The work contained within this dissertation took place between 1st July 2017 and 30th October 2020 at the Center for Environmental Research and Sustainable Technology (UFT) at the University of Bremen, Germany.

Date of PhD colloquium 19th November 2020

Table of Contents

Chapter N°1

General Introduction

Chapter N°2

Early trajectories of benthic coral reef communities following the 2015/16 coral bleaching event at remote Aldabra Atoll, Seychelles

Chapter N°3

Coral recruit and juvenile abundance indicate rapid post-bleaching recovery at remote Aldabra Atoll, Seychelles

Chapter N°4

Coral bleaching has little short-term impact on reef fishes at remote Aldabra Atoll, Seychelles

Chapter N°5

General Discussion

Abstract

Climate change-induced coral bleaching events are increasing in frequency and severity, threatening the persistence of coral reefs worldwide. With diminishing time frames for recovery between such events, improving our understanding of coral reef resilience is critical. Remote, well protected coral reefs such as those at Aldabra Atoll (Seychelles) serve as unique natural laboratories to study reef resilience in absence of direct anthropogenic stressors like eutrophication and overfishing. Using spatiotemporal monitoring data of benthic and fish communities in combination with in-situ water temperature measurements, this thesis assesses how Aldabra's coral reef system responded to and recovered from the 2014–2017 global coral bleaching event. Immediately following the bleaching, hard coral cover decreased by 51–62% on Aldabra's seaward reefs at shallow (5 m) and deep (15 m) water depths, but inside its semi-enclosed lagoon (< 3 m water depth), coral mortality was lower (34%), likely due to three-fold higher daily water temperature variability there. Primarily driven by herbivores, Aldabra's fish abundance increased by > 120% following the bleaching event. Although there were substantial fluctuations in fish abundance and biomass throughout the study period, pre- and post-bleaching values were similar. During the four years post-bleaching (2016–2019), hard coral cover on the deeper seaward reefs did not change; turf algae and the calcifying macroalgae *Halimeda* remained the dominant taxa there. In shallow water, however, hard coral cover in 2019 reached 54–68% (seaward reefs) and 93% (lagoon) of pre-bleaching coral cover. Independent of water depth, coral juvenile abundance more than doubled over the period 2016–2019 at all locations, whilst coral larvae settlement was one order of magnitude higher inside the lagoon compared to the seaward reef. The results of this thesis highlight the substantial natural variation in bleaching susceptibility and recovery driven by environmental conditions. High daily water temperature variability and water flow in Aldabra's lagoon is likely to confer lower bleaching-induced mortality. As the early recovery of hard coral cover was predominantly driven by the growth of remnant colonies, slower recovery rates on the seaward reefs are likely due to slower coral growth at depth and higher wave exposure. The rapid increase in coral juvenile abundance indicate that reef recovery will speed up substantially also on Aldabra's seaward reefs. These recovery trajectories are likely to be connected to the high abundance of herbivores at Aldabra, which limit turf algae cover, thus promoting coral growth and the survival of coral juveniles. While coral reefs at remote, strictly protected locations may not be less susceptible to bleaching-induced hard coral mortality, post-bleaching recovery can be rapid in absence of local anthropogenic stressors. Nevertheless, while local management of coral reef systems is crucial to support their recovery from mass coral bleaching events, immediate action to tackle the root cause of the climate crisis is indispensable to preserve even the world's most strictly protected and remote coral reefs.

9 Zusammenfassung

Der durch den Klimawandel verursachte Anstieg der Häufigkeit und Intensität von Korallenbleichen bedroht den Fortbestand von Korallenriffen weltweit. Ein besseres Verständnis über die Widerstandsfähigkeit von Korallenriffen ist daher von entscheidender Bedeutung. Abgelegene, gut geschützte Korallenriffe wie die vom Aldabra Atoll (Seychellen), wo direkte anthropogene Stressfaktoren wie Eutrophierung und Überfischung keine Rolle spielen, dienen als natürliche Laboratorien zur Untersuchung der Widerstandsfähigkeit von Korallenriffen. Unter Verwendung von Lang- und Kurzzeitmonitoringdaten des Riffbenthos der Fischgemeinschaften und der Wassertemperaturen zeigt diese Arbeit, wie Aldabra’s Riffe auf die globale Korallenbleiche von 2014–2017 reagiert haben und sich seither davon erholen. Unmittelbar nach der Bleiche nahm die Hartkorallenbedeckung an Aldabra‘s seewärtigen Riffen im flachen (5 m) und tieferen (15 m) Wasser um 51–62% ab. Innerhalb der Lagune (< 3 m Wassertiefe) war die Korallensterblichkeit jedoch geringer (34%), was wahrscheinlich auf die dreifach höheren täglichen Wassertemperaturschwankungen dort zurückzuführen ist. Die Anzahl an Fischen nahm nach der Bleiche um > 120% zu. Dieser Anstieg wurde hauptsächlich von Herbivoren verursacht. In den vier Jahren nach der Bleiche (2016–2019) veränderte sich die Hartkorallenbedeckung der tiefen seewärtigen Riffe nicht; Fadenalgen und die kalkbildenden Makroalgen *Halimeda* blieben dort die dominierenden Taxa. Im Flachwasser erreichte die Hartkorallenbedeckung im Jahr 2019 jedoch 54–68% (seewärtige Riffe) und 93% (Lagune) der Korallenbedeckung aus der Zeit vor der Bleiche. Unabhängig von der Wassertiefe hat sich die Anzahl von Jung-Korallen im Zeitraum 2016–2019 an allen Standorten mehr als verdoppelt, während die Besiedlung durch Korallenlarven innerhalb der Lagune um eine Größenordnung höher war als am seewärtigen Riff. Die Ergebnisse dieser Arbeit unterstreichen die erheblichen umweltbedingten Unterschiede im Einfluss von Korallenbleichen und der nachfolgenden Erholung. Die hohe tägliche Temperaturschwankung und die Wasserströmung in Aldabra‘s Lagune führt wahrscheinlich zu einer geringeren Korallensterblichkeit während einer Bleiche. Da die frühe Erholung der Hartkorallenbedeckung vor allem durch das Wachstum von überlebenden Kolonien angetrieben wurde, sind langsamere Erholungsraten an den seewärtigen Riffen vermutlich auf langsameres Korallenwachstum in der Tiefe und in höherer Wellenexposition zurückzuführen. Die rasche Zunahme in der Anzahl an Jung-Korallen deutet aber darauf hin, dass sich die Erholung auch an den seewärtigen Riffen von Aldabra erheblich beschleunigen wird. Diese Beobachtungen stehen wahrscheinlich im Zusammenhang mit der hohen Anzahl von herbivoren Fischen, die die Fadenalgenbedeckung begrenzen und so das Korallenwachstum und das Überleben der Jung-Korallen fördern. Während Korallenriffe an abgelegenen, streng geschützten Standorten nicht weniger anfällig für eine durch Bleiche verursachte Hartkorallensterblichkeit sind, kann deren Erholung sehr rasch erfolgen. Auch wenn Management von lokalen Stressfaktoren entscheidend ist, um die Erholung von Korallenriffen nach Korallenbleichen zu unterstützen, sind sofortige Maßnahmen zur Bekämpfung der Grundursache der Klimakrise unerlässlich, um selbst die am strengsten geschützten und abgelegensten Korallenriffe der Welt zu erhalten.

11 Acknowledgements

Aldabra Atoll is a truly magical place that has left me in absolute awe every time I had the chance to set foot on it. Far away from the next inhabited land, with the vastness of the Indian Ocean in between, being isolated and at the mercy of nature – this evokes a feeling of freedom in me. For some this may seem strange; living on an isolated atoll for several months with a small group of people, without the chance to just leave, may appear as the opposite of a free lifestyle. Immersed in nature, living on a beach, seeing all these shades of the crystal clear blue water and meeting Aldabra's charismatic native inhabitants is an experience that humbled me and made me wish this feeling could somehow be bottled and used to treat the greed that is driving our world. I am privileged, one of few lucky people that got the chance to experience a place like Aldabra and could not have dreamed about a better research project to pursue my PhD.

There are many people I would like to thank for their involvement and support throughout this PhD journey. First off, Christian Wild – thank you for providing me with the opportunity to do this research, for developing the project with me, helping with the bureaucratic matters in a refreshingly pragmatic way, for supporting and guiding me throughout the entire research project, your quick feedback, open door and fast replies, for training me to see the big picture in my research as well as your optimism and your encouragement to see the glass half full and not half empty! I also want to thank everyone else I met at the Uni Bremen who helped me along the way. Valentina Migani, thank you for your help with the statistics and R coding, I learned a LOT from you and am truly grateful I had your support, that I could meet you so often and ask all my silly questions; I really enjoyed working with you and discussing the project with you. Amanda Ford, thank you for all your input and our discussion sessions at the beginning of my PhD and all these email conversations and your support and feedback after you have left Bremen. I am very glad that our science discussions at the beginning turned into friendship! I also had interesting discussions with and got very helpful feedback from Sebastian Ferse. Thank you for your fast replies, constructive comments, new ideas and for being part of my examination panel! I also want to thank everyone at the AG Wild and especially my office colleagues Ameris Contreras, Arjen Tilstra and Yusuf El-Khaled for advice, support, discussions and happy chats at work and my student Cesc Gordó Vilaseca for his assistance. Finally, a very big thank you goes to Marko Rohlfs for examining my thesis and agreeing to do this so quickly and to Wilhelm Hagen, Inae Kim-Frommherz and Lisa Zimmermann for agreeing to be panel members for my defence.

My PhD research would not have happened without all the people from the Seychelles Islands Foundation (SIF). First of all, I want to thank Frauke Fleischer-Dogley (CEO) and Nancy Bunbury (Director of Research and Conservation) for taking me on as marine research volunteer on Aldabra in 2016. This was the chance of a lifetime and paved the way to my PhD project. I want to thank you for giving me the opportunity to return to Aldabra as a researcher and for all your support, advice and motivation along the way. Especially you Nancy have supported me throughout these years. You trained me to become a better writer, always gave extremely helpful feedback, are incredibly motivating and encouraging, provided moral support and were always available when I needed your help (especially in these crazy last weeks!). I really enjoy working with and learning from you and hope this will long continue!

I am also extremely thankful to all the SIF staff. As most of the data I used in my project is derived from SIF's long-term marine monitoring programme, there are many people who contributed to, and provided the basis of the research in my thesis. Jude Brice (Island Manager), thank you for all the logistical support during the fieldwork, for brainstorming and finding solutions to problems and for your fantastic drone pictures that I used for my thesis! April Burt aka AJB (former Aldabra Science Coordinator), working with you on Aldabra has just always been delightful! You are an excellent team leader and a wonderful person to discuss science and hang out with. Thank you for your help, advice and your incredibly contagious determination. Cheryl Sanchez (former Aldabra Science Coordinator), thank you for always making everything possible and for leading my coral larvae settlement study so competently when I was not there! You have been massively helpful and supportive during my field stays and I really enjoyed working and diving with you! Philip Haupt, who led the development and implementation of the amazing Aldabra Reef Monitoring programme, which broke new ground in Aldabra's long research history, and the first two intensive seasons of data collection: thank you for the early discussions we had about my research, your positivity and your helpful advice during my PhD!

Although I can't name everybody here, a huge thank you goes to all Aldabra staff members for their contribution to the data collection, field work and support, specifically: Marvin Roseline, Joel Bonne, Ella Nancy, Leeroy Estrale, Ronny Marie, Terence Mahoune, Jennifer Apoo, Trevor Henriette, Jake Letori, Lorraine Cook, Janske van de Crommenacker, Alain Banane, Jeremy Raguain, Germano Soru, Jessica Moumou (thank you for analysing all the tiles!), Jilani Suleman, Julio Agricole, Luke A'Bear, Matt Waller and Diane Ernesta. I also want to thank all the staff at SIF's head office for their support and contribution, specifically Rowana Walton for benthic photo analysis of season 2 photos, Christina Quanz for organising research supplies for me and Bernadette Julie for taking care of all the visa matters!

There are many people I did not meet or work directly with, but I am very grateful to for data collection during the Aldabra Reef Monitoring programme: Heather Richards, Daig Romain, Karen Chong-Seng, Tom Mannering, Shiira Padayachy, Rebecca Fillipin, Stephanie Marie, Sheril de Commarmond, Marcus Dubel, Ervin Estico, Giovanni Rose, Samuel Basset and Shane Brice. Furthermore, thanks go to Anthony Bernard and Nick Riddin

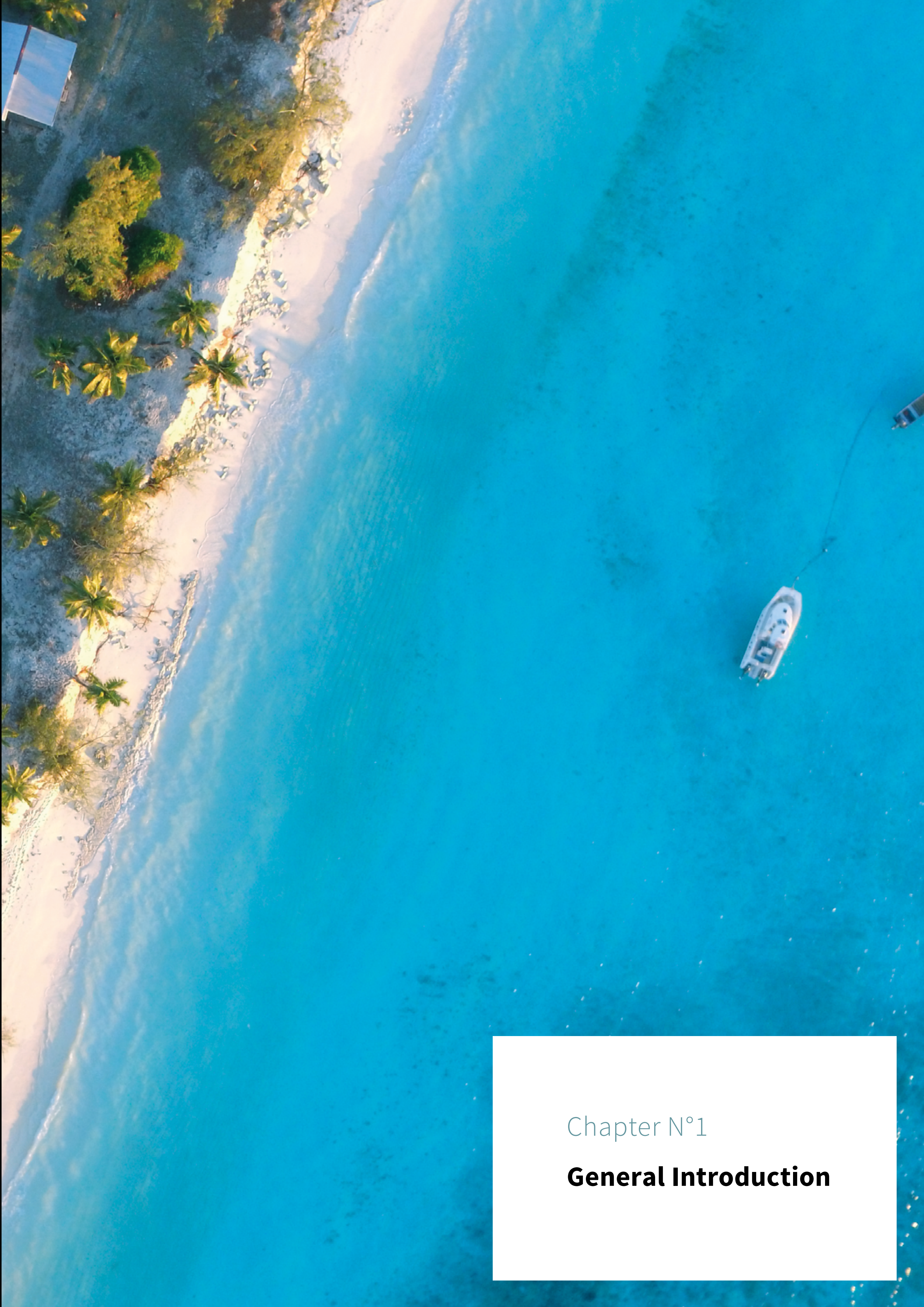
(South African Institute for Aquatic Biodiversity) and all SIF staff for establishing the permanent benthic transects at Aldabra as well as Rebecca Klaus for valuable advice on survey methodology and Fernando Cagua for helping to set up the photo analysis procedures.

Finally, I want to thank all the people in my life that supported me throughout my undertakings, the trips abroad and everything that led up to and through my PhD.

Zunächst möchte ich meiner Familie danken, denn ohne sie wäre ich nicht dort wo ich jetzt bin. Mama, Frauke, Bernd, Jörg und natürlich Papa, ihr habt mich alle auf diesem Weg begleitet und ihn mir auch bereitet. Ihr habt mich immer ermutigt, wenn es mal geschwankt hat und mich wissen lassen, dass ich es hinbekomme. Danke.

My friends: Franzi, Anna (who long knew that one day she'd call me Dr. Koester!) and Marie – thank you for your friendship and your support throughout all these years and your encouragement that massively helped me along the way. Naomi, thank you for being a great friend, for your optimism, hugs, dinners, walks and weekend trips to get me outside. I am very glad I met you here in Bremen! I also want to thank my (former) flatmates Hail, Ahmad, Lucas, Marko and Judith for making our house feel like home. Especially Judith: I can't thank you enough for all your help and your support, specifically in these last weeks and with my thesis design. Living with you is great and I am very glad I can call you my friend. Thank you!

Lastly, I want to thank my pti Marvin. You supported me from the beginning to the end, on Aldabra during fieldwork, and most importantly during the hard times when I was in Bremen. You encouraged me, listened to my worries, cheered me up and gave me advice. Thank you for always being there for me and for sitting with me through this difficult time.



Chapter N°1

General Introduction

Coral reefs: value and threats

Coral reefs exist within a narrow belt across the world's tropical oceans, where local climate, marine chemistry, ocean currents, and biology combine to provide suitable conditions for reef-building hard corals (Burke et al. 2011). Hard corals (Order: Scleractinia) have skeletons built from calcium carbonate, which form the physical structure of coral reefs and the basis for one of the most biodiverse and productive ecosystems on earth (Burke et al. 2011). Globally, coral reefs provide not only critical habitat for ca. 70,000 known species (Fisher et al. 2015), but also essential ecosystem goods and services to approximately one-eighth of the world's human population in terms of food, livelihood and shoreline protection (Burke et al. 2011).

Despite their importance, coral reefs are rapidly degrading and disappearing in response to numerous anthropogenic impacts. Overfishing and destructive fishing practices, coastal development, pollution and eutrophication through coastal sediment and nutrient runoff can profoundly change the structure and functioning of coral reef systems (Bellwood et al. 2004; Hughes et al. 2007) and has caused widespread reef degradation for centuries (Pandolfi et al. 2003). Climate change impacts exert further stress, including increased storm frequency, ocean acidification (IPCC 2014) and thermal stress-induced coral bleaching (Hughes et al. 2018a).

Coral bleaching is a stress response triggered by prolonged periods of water temperature anomalies (Hoegh-Guldberg 1999), solar irradiance (Brown et al. 1994; Anthony et al. 2007), eutrophication (Nagelkerken 2006; Pogoreutz et al. 2017) or sedimentation (Fisher et al. 2019), during which corals lose their endosymbiotic algae (dinoflagellates of the family Symbiodiniaceae), which provide the majority of energy to most reef corals (Anthony and Fabricius 2000). Prolonged bleaching depletes the coral's energy supply and reserves, leading to reduced growth and reproduction, and ultimately death, as consequence. While coral bleaching itself is a natural phenomenon and not always lethal (Suggett and Smith 2011), its increasing frequency and intensity over regional scales (> 1000 km) is caused by global warming and associated thermal stress (Hughes et al. 2018a). Between the 1980s and 2016, median time intervals between severe bleaching events have reduced from 27 to < 6 years (Hughes et al. 2018a), and the most recent three global coral bleaching events recorded to date occurred within a window of only 20 years (1997–1998, 2010, 2014–2017), causing widespread coral mortality worldwide (Hughes et al. 2017a; Eakin et al. 2019). As recovery windows between major bleaching events are projected to narrow even further, strengthening knowledge and understanding of coral reef responses and resilience has become crucial for their conservation, as well as that of the biodiversity they harbour and the ecosystem services they provide.

Coral reef resilience

Ecological resilience can be described as the magnitude of disturbance an ecosystem can absorb while maintaining essentially the same functions (Holling 1973; McClanahan et al. 2012). Applied to coral reefs, this usually refers to their ability to return to coral-dominated states following disturbances. When resilience is lost or the disturbance exceeds the resilience capacity, reefs can drastically change in community composition and structure ('phase shifts'; Nyström et al. 2008). This often constitutes the loss of hard corals and (sometimes long-lasting) increases of other benthic organisms (e.g., macroalgae, Done 1992; Wilkinson 2004; Graham et al. 2015; turf algae, Jouffray et al. 2014; cyanobacteria, Albert et al. 2012; sponges or soft corals, Norström et al. 2009), i.e. benthic states that are less desirable (Folke et al. 2004) and support lower levels of biodiversity and ecosystem functions. Changes may not always manifest in the increasing dominance of other benthic organisms, but may result in novel coral community compositions that differ profoundly in function (Graham et al. 2014; McWilliam et al. 2020).

Two important aspects of coral reef resilience are: (a) the ability to resist change or survive a disturbance, i.e. resistance/susceptibility; and (b) the ability to recover from disturbance and return to the pre-disturbance condition, i.e. recovery (Nyström et al. 2008; McClanahan et al. 2012). While resilience is more complex than this, these two aspects are tangible and relevant for ecosystem management (Nyström et al. 2008; McClanahan et al. 2012) and are thus key concepts of my thesis. As hard coral susceptibility and recovery to disturbance vary on multiple levels, with complex interdependencies (Nyström et al. 2008), the central theme of my thesis focusses on aspects considered most relevant to climate change-induced coral bleaching.

A coral reefs' susceptibility to and recovery from coral bleaching and mortality differs depending on its ecosystem composition, and can be further influenced by environmental conditions and the presence and type of anthropogenic disturbances (Table 1.1, Table 1.2). For example, branching corals (e.g. *Acropora*, *Pocillopora*) are typically more susceptible to bleaching and show higher post-bleaching mortality than massive corals (e.g. *Porites*; Marshall and Baird 2000; Loya et al. 2001; Hoey et al. 2016; Fox et al. 2019), whilst specific environmental conditions may reduce or increase susceptibility (Table 1.1). High frequency temperature variability is a key driver for increased thermal stress tolerance of corals (Donner 2011; Oliver and Palumbi 2011; Safaie et al. 2018), while increased solar radiation (e.g. shallow water, no cloud cover) can exacerbate it (Anthony et al. 2007). Local anthropogenic stress, such as pollution, improper sewage treatment or coastal development (e.g. causing sedimentation) can increase coral's susceptibility to bleaching-induced mortality and reduce their ability to recover (D'Angelo and Wiedenmann 2014; Fisher et al. 2019; Table 1.1, Table 1.2). Reef recovery is directly driven by the growth of remnant coral colonies and coral recruitment (Diaz-Pulido et al. 2009; Gilmour et al. 2013; Graham et al. 2015), both of which are positively influenced by herbivory, which reduces the negative effects of turf and macroalgae (Arnold et al. 2010; Smith et al. 2016; Johns et al. 2018; Table 1.2). Fishing and the direct removal of herbivores can thus reduce the potential for reefs to recover, with sedimentation and eutrophication further compromising recovery (Carilli et al. 2009).

While many of these susceptibility- and recovery-influencing factors are natural (e.g. depth, temperature variability, water flow/ocean currents), the majority are associated with local or global anthropogenic disturbances. The reduction of local human stressors is therefore a key component to managing coral reefs for resilience in the face of climate change (McClanahan et al. 2012; Flower et al. 2017).

Table 1.1: Factors influencing the susceptibility of coral reefs to thermal stress-induced coral bleaching and mortality. Symbols indicate primarily positive effects, i.e. reducing susceptibility to bleaching (+), negative effects, i.e. increasing susceptibility (−) or both (+ −), depending on context.

Susceptibility factor	**Effect**	**Explanation and references**
Coral taxa	+ −	Differences in coral physiology affects thermal tolerance and bleaching susceptibility varies among taxa (Baird et al. 2009; Mizerek et al. 2018)
Coral morphology	+ −	Branching corals are typically more susceptible than massive ones, due to reduced mass transfer of toxic by-products produced by endosymbionts during heat stress (van Woesik et al. 2012; Darling et al. 2013; Mizerek et al. 2018)
Thermotolerance of endosymbionts	+ −	Differential thermal tolerance of endosymbionts affects bleaching prevalence of corals (Rowan 2004; Sampayo et al. 2008)
Thermal stress	−	Magnitude of thermal stress, combining duration and temperature, e.g. measured as degree heating weeks (DHW), from ‘no stress’ to ‘severe bleaching and mortality likely’ (Liu et al. 2013)
Temperature variability	+	Exposure to high temperature variability can acclimatise corals to temperature anomalies and reduce their susceptibility to heat stress (Oliver and Palumbi 2011; Safaie et al. 2018)
Water flow	+	High water flow increases the mass transfer of toxic by-products produced by endosymbionts during heat stress and can lower bleaching prevalence (Nakamura and van Woesik 2001)
Upwelling and internal waves	+	Waves can reduce heat stress by modulating heat accumulation in the water column (Riegl and Piller 2003; Sheppard 2009; Chollett et al. 2010; Wyatt et al. 2020)
Light exposure	−	Light can exacerbate thermal stress by damaging the photosynthetic system of endosymbionts, e.g. at shallow depths (Lesser and Farrell 2004; Anthony et al. 2007; Brown and Dunne 2008)
Turbidity (natural or anthropogenically induced)	+ −	Suspended particles can reduce (through shading from light, as energy source for coral) or enhance (smothering) effects of thermal stress (Anthony et al. 2007; Cacciapaglia and van Woesik 2016; Morgan et al. 2017; Fisher et al. 2019)
Nutrients	−	Nutrient enrichment can exacerbate thermal stress but this can vary among coral species, morphology, type and level of nutrients and local context (D’Angelo and Wiedenmann 2014; DeCarlo et al. 2020)
Physical anthropogenic impacts	−	Coral mining, dredging, ship groundings, trampling or diving can increase the susceptibility of corals to thermal stress but this varies with scale and frequency of the disturbance (Hawkins and Roberts 1992; Chabanet et al. 2005; Fox et al. 2005)

Table 1.2: Factors influencing the recovery of coral reefs from thermal stress-induced coral bleaching and mortality. Symbols indicate primarily positive effects (+), negative effects (−) or both (+ −), depending on context.

Recovery factor	Effect	Explanation and references
Abundance of mature colonies	+	Mature remnant colonies can increase coral coverage by re-growth, which is a key aspect of reef recovery; they can also provide propagules for reef replenishment, although this is often delayed as the reproductive capacity is usually low after bleaching. (Riegl 2002; Burt et al. 2008; Diaz-Pulido et al. 2009; Riegl and Purkis 2009)
Coral growth	+	Re-growth of remnant colonies, particularly of fast-growing, branching and plating species. These are, however, more susceptible to bleaching mortality. Taxa less susceptible to bleaching are usually slow-growing (Diaz-Pulido et al. 2009; Gilmour et al. 2013)
Coral recruitment	+	Coral recruitment is key driver for recovery as it replenishes the reef with new individuals (Mumby and Harborne 2010; Gilmour et al. 2013; Graham et al. 2015)
Connectivity	+	Supply of coral larvae from less impacted locations may promote recovery at degraded sites (Mumby and Hastings 2008; Elmhirst et al. 2009; Jones et al. 2009; Graham et al. 2011).
Type and abundance of algae	+ −	Crustose coralline algae (CCA) can consolidate substrate and can enhance coral larvae settlement; turf algae (if not cropped short) and macroalgae can inhibit larvae settlement, impact the survival of coral recruits and directly compete with adult corals through allopathy and trapped sediments that can smother corals (Arnold et al. 2010; O'Leary et al. 2012; Mumby et al. 2013; Johns et al. 2018; Yadav et al. 2018)
Herbivory	+	The presence of a diverse guild of herbivores and high herbivore biomass can reduce turf and macroalgae cover and increase CCA cover (Hughes et al. 2007; Lokrantz et al. 2008; Mumby and Harborne 2010; O'Leary et al. 2012; Graham et al. 2015; Smith et al. 2016)
Substrate availability	+	Stable and suitable substrate is important for coral recruitment and recovery, while unconsolidated rubble can hinder recovery (O'Leary et al. 2012; Chong-Seng et al. 2014)
Light availability	+	Light availability affects growth rates, e.g. coral growth and recovery may be slower due to light attenuation at deeper water depths (Huston 1985; Pratchett et al. 2015; Robinson et al. 2019)
Wave exposure	−	Fast-growing coral taxa (e.g. branching corals) are less common on reefs with high wave exposure, which may slow recovery in these areas (Done 1982; Gove et al. 2015; Williams et al. 2015; Robinson et al. 2019)
Fishing pressure	−	Fishing can affect species interactions and trophic cascades of fish communities which can have top-down effects on benthic communities and coral recovery. Direct removal of herbivorous fish can reduce herbivorous pressure, allowing macro- and turf algae to proliferate (Wilson et al. 2010; Graham et al. 2015, 2017)
Sedimentation	−	Sediments can smother corals and limit larvae settlement and survival of recruits (Acevedo et al. 1989; Rogers 1990; Crabbe and Smith 2005)
Nutrients	−	Nutrient enrichment can decrease recovery but studies note the difficulty to separate pure nutrient effects from sedimentation and overfishing (Connell et al. 1997; Hughes et al. 2003; Fabricius 2005; Carilli et al. 2009); seabird nutrients have positive effect on CCA cover and herbivorous fish, promoting recovery (Benkwitt et al. 2019)

Research gaps

Approximately 58% of the world's coral reefs are located within 30 min travel time from the nearest human settlement, while 25% are within 4 h from the nearest major market (Maire et al. 2016). The overwhelming majority of coral reefs is therefore subject to stressors that influence (a) reef condition *per se*, and (b) their susceptibility to and recovery potential from climate change impacts.

Reducing local stressors, for example nutrient enrichment, sedimentation and overfishing, should facilitate the management of coral reefs for resilience to climate change impacts, but there is still considerable debate on the effectiveness of this approach. Whilst managing local anthropogenic stressors is still widely considered to increase reef resilience (e.g. Sandin et al. 2008; Carilli et al. 2009; McClanahan et al. 2012; Graham et al. 2013; Flower et al. 2017), others argue that this approach has little value (e.g. Côté and Darling 2010; Bruno and Valdivia 2016; Bruno et al. 2019). Research into reef resilience has seen vast progress from early theoretical frameworks (Obura 2005; Nyström et al. 2008) towards more applied (Obura and Grimsditch 2009; McClanahan et al. 2012; Flower et al. 2017) and empirical work (Bayraktarov et al. 2013; Graham et al. 2015; Hughes et al. 2017b). Nevertheless, the need for more data from a wider array of locations and environments to better understand ecosystem functioning and reef resilience processes under varying conditions has been repeatedly highlighted (Nyström et al. 2008; Graham et al. 2011; Pandolfi 2015; Flower et al. 2017; Lam et al. 2017; Mumby 2017).

Some of the most valuable sites for understanding coral reef functioning and resilience are in remote locations, which provide critical baseline information with which the influence of anthropogenic impacts on reef resilience can be better understood (Sandin et al. 2008). Indeed, the 1998/99 global coral bleaching event, and the unprecedented bleaching event of 2014–2017 caused mass mortality of corals even at the most remote and best protected reefs worldwide (Gilmour et al. 2013; Heron et al. 2017; Sheppard et al. 2017; Hughes et al. 2018b; Cerutti et al. 2020), indicating that reducing local impacts is not a panacea for reducing bleaching susceptibility and subsequent mortality during extreme thermal stress events. Assessing pre- and post-bleaching coral reef trajectories at such locations is thus crucial to improve our understanding of the recovery potential of reef systems and how this varies. Such information is critical not only with regards to managing local stressors at reefs elsewhere, but also for alternative strategies to conserve the world's corals reefs (e.g. reef restoration, assisted evolution).

Only 3.7% of the oceans are under ‘very low impact’ from cumulative local and global anthropogenic stressors (Halpern et al. 2008; see also Guan et al. 2020), and many of the coral reefs in these areas do not have accumulated data on coral reef trajectories before and after bleaching events. Opportunities to study this in detail are therefore limited, but detailed monitoring of these relatively undisturbed sites is essential to provide scientists and managers with appropriate baseline information, with which success and failure of reef conservation strategies can be assessed.

An ideal site for such research is Aldabra Atoll in the Seychelles. The atoll has been well protected and managed for almost 50 years, hosts a very small team of staff as its only human residents, and comprehensive long-term marine monitoring programme is in place that allows to track climate change induced changes to its coral reef ecosystem.

Study site: Aldabra Atoll, natural laboratory and ecological benchmark

Aldabra Atoll, in the Western Indian Ocean, is a raised coral atoll that consists of a ring of four main islands that span 34 × 14.5 km around its large lagoon (155 km$^{2)}$. It is part of the Seychelles Archipelago, which consists of 115 islands and atolls that are scattered across its 1,400,000 km^2 exclusive economic zone (Kawaley 1998; Fig. 1.1). More than 99% of the Seychelles’ population (98,000) lives on the granitic ‘Inner Islands’ in the north-east of the archipelago, whilst the ‘Outer Islands’ (coralline islands and atolls) in the south and south-west are not or only scarcely populated (Seychelles National Bureau of Statistics 2020). Aldabra is located more than 400 km north (Madagascar) and 700 km east (Tanzania) from the nearest inhabited land, and more than 1000 km from the Seychelles’ main island of Mahé (Fig. 1.1).

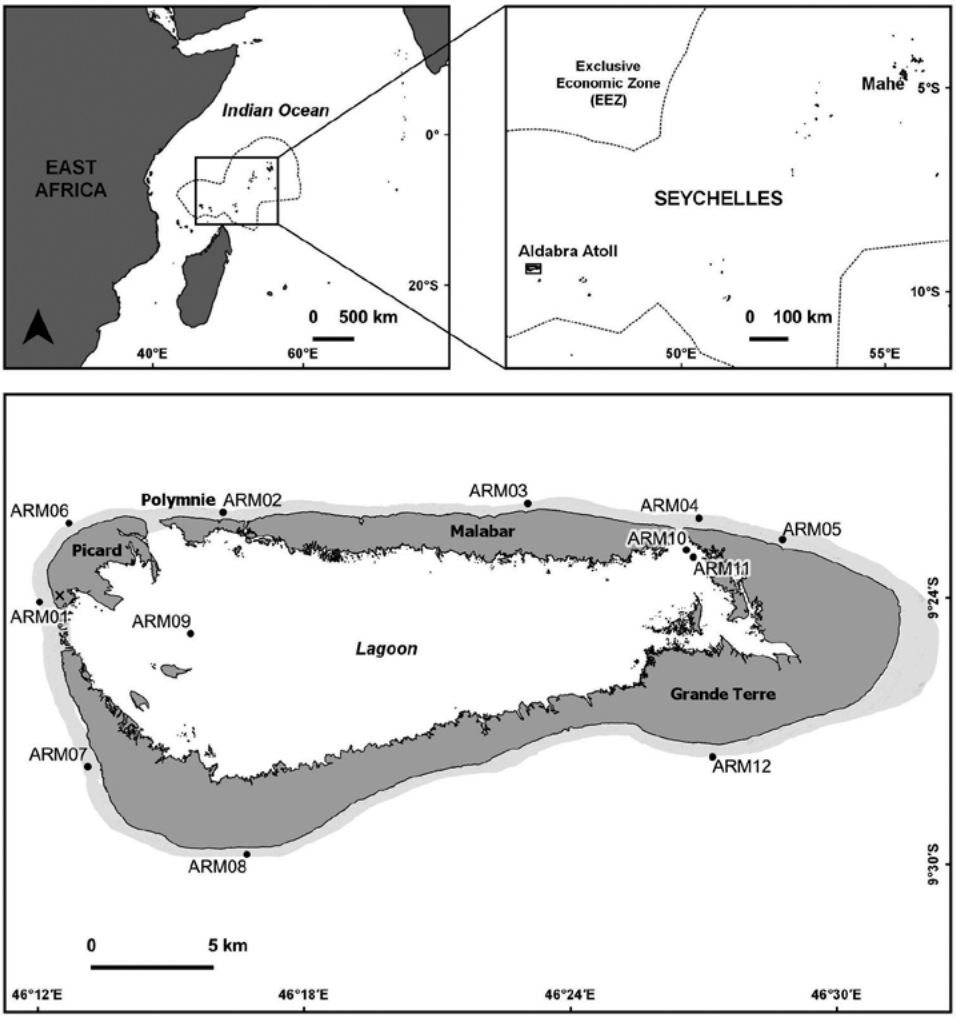


Figure 1.1: Location of Aldabra Atoll in the Western Indian Ocean and the Seychelles (top) and its four main islands (bottom). The black cross on Picard island indicates the location of the research station (see Figure 1.2). Black dots indicate the permanent marine monitoring sites of the Aldabra Reef Monitoring programme used in this research. The light grey shading around Aldabra indicates its seaward reefs.

Due to Aldabra's isolation, it's scarcity of freshwater and distance from trade routes, human settlement has only ever been temporary (Stoddart 1971), and mainly for the exploitation of giant tortoises, sea turtles, fish and timber (Stoddart 1968a, 1971). From 1965 until Seychelles' independence in 1976, Aldabra was part of the British Indian Ocean Territory and in 1966, was proposed as a site for a military air staging-post to be set up in conjunction with the United States of America (Stoddart 1968b). Following international protests and interventions by the Royal Society of London to protect Aldabra for its outstanding biodiversity and value to science (Stoddart 1968b), plans for the military base were abandoned in 1967 and instead shifted to Diego Garcia in the Chagos Archipelago (Lunn 2019).

Following the scientific campaign and the set-up of Aldabra's first research station by the Royal Society of London (Stoddart 1968b, 1971), management of Aldabra was taken over by the Seychelles Islands Foundation (SIF), a public trust established under presidential decree in 1979. In 1981, Aldabra was designated as a Special Reserve (the highest level of national protection under Seychelles' legislation), which covers an area of 2559 km^2 since 2018 (439 km^2 prior to that; Seychelles Islands Foundation 2016). In 1982, Aldabra was inscribed as a UNESCO World Heritage Site (UNESCO 2020); it is also an International Endemic Bird Area since 2001 (BirdLife International 2020) and a Ramsar Wetland of International Importance since 2010 (Ramsar Convention Secretariat 2010). More recently Aldabra has been designated as part of the IOSEA Network of Sites of Importance for Marine Turtles (2014; CMS Secretariat 2020), a Platinum level Blue Park (2019; Marine Conservation Institute 2020) and an International Marine Mammal Area (2020; Marine Mammal Protected Areas Task Force 2020). SIF's management incorporates international research collaborations, upholding and improving the protection measures on the atoll, and practical conservation interventions including re-introductions of native species (Šúr et al. 2013), eradications of invasive alien species (Bunbury et al. 2018, 2019) and ecosystem rehabilitation activities (Burt et al. 2020). To enable management, monitoring and research of Aldabra's terrestrial and marine ecosystems, SIF maintains a small research station (Figure 1.2; minimum 94% solar powered since 2012; Quanz et al. 2013) with ca. 10–20 staff. Whilst it is a no-take protected area, a small and strictly regulated subsistence fishery for SIF's staff, using handline and troll fishing, is permitted (Seychelles Islands Foundation 2016).

Figure 1.2: SIF research station on Picard island at Aldabra Atoll (photo: Jude Brice).

Due to its isolation and long history of protection, Aldabra represents a natural laboratory and ecological benchmark to study natural ecosystem processes and the effects of climate change on a variety of habitats and organisms in near absence of local anthropogenic impacts. Although there is a long and fairly consistent track record of monitoring and research of its terrestrial ecosystems, scientific inquiry of its marine habitats has been relatively low between the departure of the Royal Society in the 1970s and the first global coral bleaching event in 1998, which caused 38–66% hard coral mortality at Aldabra (Spencer et al. 2000; Teleki et al. 2000).

The 1998 bleaching event spurred the formation of the first marine monitoring programme at Aldabra (Aldabra Marine Programme, AMP), a research initiative affiliated with the Cambridge University Coastal Research Unit (Teleki et al. 1999). The AMP established the first permanent survey sites for long-term, routine marine monitoring, primarily to track coral reef recovery following the 1998 bleaching event (Teleki et al. 1999). Surveys of Aldabra's benthic and fish communities were conducted in 1999 and annually between 2001 and 2005 and found relatively slow hard coral recovery, although the fish communities appeared to remain intact (Teleki et al. 1999; Stobart et al. 2001, 2002a, 2002b; Downing et al. 2003, 2005; Buckley et al. 2004). After returning a final time in 2008, the onset of piracy in the area prevented further AMP field activities from 2009 (Burt and Walton 2017). Some of the AMP data (1999–2005) is available as collated summary figures given in the reports (openly available at www.aldabra.org).

In 2013, before the most recent global coral bleaching event in 2015/2016, SIF established the Aldabra Reef Monitoring (ARM) programme (Haupt 2013). SIF based the ARM survey design on the previous AMP surveys, with modifications to the survey depths to improve SCUBA diver safety (permanent survey sites [Fig. 1.1] established at shallow water depths at 5 m and 15 m vs. 10 m and 20 m) and survey efficiency (Haupt 2013). Since then, SIF research staff have annually monitored Aldabra's reef benthos, fish communities and water temperature and the programme has therefore tracked changes to Aldabra's coral reef ecosystem following the 2015/2016 coral bleaching event.

This thesis sets out to synthesise the results of the past six reef monitoring years at Aldabra to advance our understanding on reef resilience and to provide future research and management recommendations for Aldabra and beyond.

Thesis research questions

The overarching research question for this thesis is:

How does the minimally disturbed, well-protected coral reef ecosystem of Aldabra Atoll respond to and recover from mass coral bleaching in absence of direct anthropogenic stressors?

To address this main question, the following sub-questions are asked:

1. How does coral bleaching susceptibility vary across coral genera, coral life stages and natural environmental gradients at Aldabra?

2. How does coral reef recovery at Aldabra vary across coral genera, coral life stages and natural environmental gradients?

3. What is the response of Aldabra's reef fish communities to the effects of coral bleaching and changes to the benthic reef community?

4. Which factors may facilitate or mitigate susceptibility and recovery at Aldabra?

Approach and thesis structure

My thesis focusses on examining reef recovery using the remote and relatively undisturbed atoll of Aldabra, in the Seychelles as model study site. The research incorporates: (a) long-term coral reef monitoring data (benthos, fish, water temperature); and (b) short-term coral larvae settlement data. The thesis is composed of five chapters, including three data chapters in the form of stand-alone manuscripts written for peer-reviewed journals which are either published (Chapter 2), in review (Chapter 3) or in preparation (Chapter 4) at the time of writing. Each chapter assesses a different aspect of susceptibility to and recovery from the 2015/2016 global coral bleaching event at Aldabra, which together build a detailed and valuable picture of the atoll's reef trajectories through and resilience to bleaching (Figure 1.3). This first chapter serves as a general introduction, while the fifth chapter synthesises the findings of all the data chapters in a general discussion.

In **Chapter 2, 'Early trajectories of benthic coral reef communities following the 2015/16 coral bleaching event at remote Aldabra Atoll, Seychelles'**, we initially address research questions 1 and 2 and assess benthic community changes following the bleaching event and how this varied across three major reef areas that are subject to different environmental conditions. This chapter specifically focusses on the reef coverage of six major benthic groups (hard corals, soft corals, crustose coralline algae, turf algae, calcifying macroalgae) and the most abundant hard coral genera. To start to address research question 4, we assess changes across water depths and evaluate water temperature variability as potential factors of spatial differences in bleaching susceptibility. This chapter provides an important basis for the next two chapters.

In **Chapter 3, 'Coral recruit and juvenile abundance indicate rapid post-bleaching recovery at remote Aldabra Atoll, Seychelles',** we address research questions 1, 2 and 4. We assessed temporal and spatial differences in the abundance and composition of coral juveniles following the bleaching event and combined this with additional assessments of hard coral reproduction, which has not been studied before in the Seychelles Outer Islands. This chapter therefore specifically assesses a major component of coral reef recovery: coral recruitment.

In **Chapter 4, 'Coral bleaching has little short-term impact on reef fishes at remote Aldabra Atoll, Seychelles',** we address research question 3 and assess changes in fish abundance and biomass of fish functional groups in response to the bleaching-induced changes in the benthic community composition. Fish communities, and in particularly herbivorous fish, play an important role for post-disturbance reef recovery. This chapter therefore returns to question 4 (factor: herbivory) and complements and extends the findings of the previous two chapters.

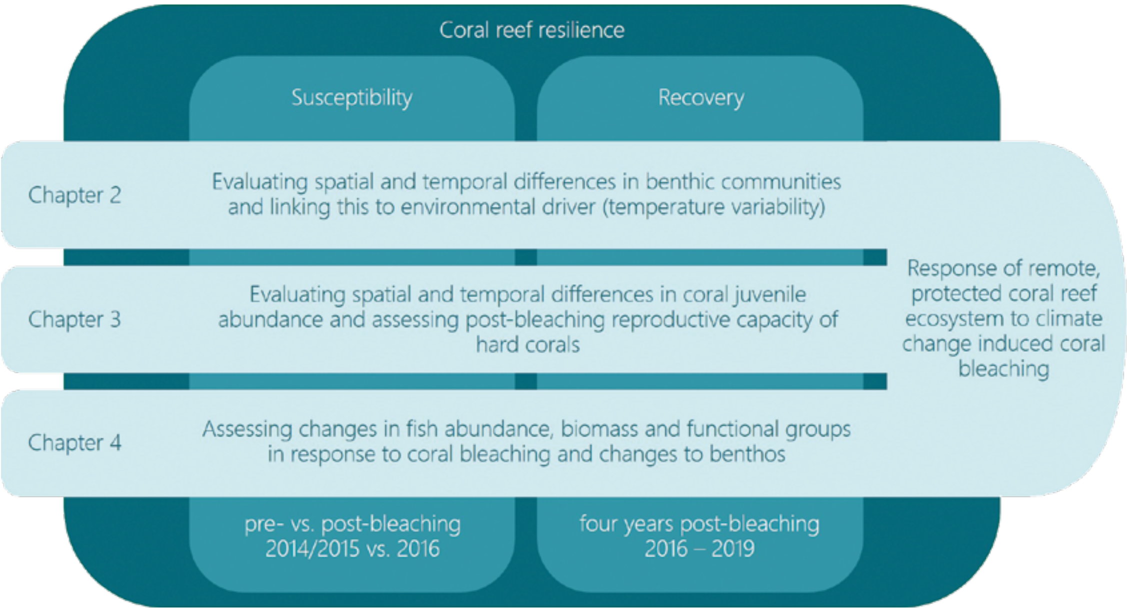


Figure 1.3: Overview of the three research-based chapters included in this thesis.

Contribution of candidate to each research-based chapter

The contributions of the candidate to each research-based chapter of this thesis (Chapters 2–4) are given as percent of the total workload per task (Table 1.3). Each contributing author listed in the chapters was involved in the development following the first draft.

Table 1.3: Contribution of the candidate to each research-based chapter per task.

Task	Chapter 2	Chapter 3	Chapter 4
Concept and design	50%	60%	70%
Data collection	60%	40%	20%
Data analysis and interpretation	70%	80%	70%
Preparation of figures and tables	70%	100%	100%
Drafting of the manuscript	100%	100%	100%

References

Acevedo R, Morelock J, Olivieri RA (1989) Modification of coral reef zonation by terrigenous sediment stress. Palaios 4:92–100

Albert S, Dunbabin M, Skinner M (2012) Benthic Shift in a Solomon Island's lagoon: corals to cyanobacteria. In: Yellowlees D., Hughes T.P. (eds) Proceedings of the 12th International Coral Reef Symposium. Cairns, Australia, pp 9–13

Anthony KRN, Connolly SR, Hoegh-Guldberg O (2007) Bleaching, energetics, and coral mortality risk: Effects of temperature, light, and sediment regime. Limnol Oceanogr 52:716–726

Anthony KRN, Fabricius KE (2000) Shifting roles of heterotrophy and autotrophy in coral energetics under varying turbidity. J Exp Mar Bio Ecol 252:221–253

Arnold SN, Steneck R, Mumby P (2010) Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105

Baird AH, Bhagooli R, Ralph PJ, Takahashi S (2009) Coral bleaching: the role of the host. Trends Ecol Evol 24:16–20

Bayraktarov E, Pizarro V, Eidens C, Wilke T, Wild C (2013) Bleaching susceptibility and recovery of Colombian Caribbean corals in response to water current exposure and seasonal upwelling. PLoS One 8:e80536

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

Benkwitt CE, Wilson SK, Graham N (2019) Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. Glob Chang Biol 25:2619–2632

BirdLife International (2020) Important Bird Areas factsheet: Aldabra Special Reserve. http://datazone.birdlife.org/site/factsheet/aldabra-special-reserve-iba-seychelles

Brown BE, Dunne RP (2008) Solar radiation modulates bleaching and damage protection in a shallow water coral. Mar Ecol Prog Ser 362:99–107

Brown BE, Dunne RP, Scoffin TP, Letissier MDA (1994) Solar damage in intertidal corals. Mar Ecol Prog Ser 105:219–230

Bruno JF, Côté IM, Toth LT (2019) Climate change, coral Loss, and the curious case of the parrotfish paradigm: why don't marine protected areas improve reef resilience? Ann Rev Mar Sci 11:307–334

Bruno JF, Valdivia A (2016) Coral reef degradation is not correlated with local human population density. Sci Rep 6:29778

Buckley R, Stobart B, Downing N, Teleki K (2004) Aldabra Marine Programme Phase V. Report on the 2004 Aldabra Marine Programme research. Cambridge Coastal Research Unit, Department of Geography, University of Cambridge.

Bunbury N, von Brandis R, Currie JC, van de Crommenacker J, Accouche W, Birch D, Chong-Seng L, Doak N, Haupt P, Haverson P, Jean-Baptiste M, Fleischer-Dogley F (2018) Late stage dynamics of a successful feral goat eradication from the UNESCO World Heritage site of Aldabra Atoll, Seychelles. Biol Invasions 20:1735–1747

Bunbury N, Haverson P, Page N, Agricole J, Angell G, Banville P, Constance A, Friedlander J, Leite L, Mahoune T, Melton-Durup E, Moumou J, Raines K, van de Crommenacker J, Fleischer-Dogley F (2019) Five eradications, three species, three islands: overview, insights and recommendations from invasive bird eradications in the Seychelles. In: Veitch C.R., Clout M.N., Martin A.R., Russel J.C., West C.J. (eds) Proceedings of the International Conference on Island Invasives 2017. IUCN, Gland, Switzerland, pp 282–288

Burke L, Reytar K, Spalding M, Perry A (2011) Reefs at risk revisited. World Resources Institute. Washington, DC.

Burt AJ, Raguain J, Sanchez C, Brice J, Fleischer-Dogley F, Goldberg R, Talma S, Syposz M, Mahony J, Letori J, Quanz C, Ramkalawan S, Francourt C, Capricieuse I, Antao A, Belle K, Zillhardt T, Moumou J, Roseline M, Bonne J, Marie R, Constance E, Suleman J, Turnbull LA (2020) The costs of removing the unsanctioned import of marine plastic litter to small island states. Sci Rep 10:14458

Burt AJ, Walton R (2017) Aldabra Reef Monitoring Planning Protocoll v. 1.0. Seychelles Islands Foundation.

Burt J, Bartholomew A, Usseglio P (2008) Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates. Mar Biol 154:27–36

Cacciapaglia C, van Woesik R (2016) Climate-change refugia: Shading reef corals by turbidity. Glob Chang Biol 22:1145–1154

Carilli JE, Norris RD, Black BA, Walsh SM, McField M (2009) Local stressors reduce coral resilience to bleaching. PLoS One 4:e6324

Cerutti J, Burt AJ, Haupt P, Bunbury N, Mumby P, Schaepman-Strub G (2020) Impacts of the 2014–2017 global bleaching event on a protected remote atoll in the Western Indian Ocean. Coral Reefs 39:15–26

Chabanet P, Adjeroud M, Andréfouët S, Bozec YM, Ferraris J, Garcìa-Charton JA, Schrimm M (2005) Human-induced physical disturbances and their indicators on coral reef habitats: A multi-scale approach. Aquat Living Resour 18:215–230

Chollett I, Mumby P, Cortés J (2010) Upwelling areas do not guarantee refuge for coral reefs in a warming Ocean. Mar Ecol Prog Ser 416:47–56

Chong-Seng K, Graham N, Pratchett M (2014) Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33:449–461

CMS Secretariat (2020) IOSEA Marine Turtles Site Network. https://www.cms.int/iosea-turtles/en/activities/site-network

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461

Côté IM, Darling ES (2010) Rethinking ecosystem resilience in the face of climate change. PLoS Biol 8:e1000438

Crabbe MJC, Smith DJ (2005) Sediment impacts on growth rates of Acropora and Porites corals from fringing reefs of Sulawesi, Indonesia. Coral Reefs 24:437–441

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, McClanahan TR, Côté IM (2013) Life histories predict coral community disassembly under multiple stressors. Glob Chang Biol 19:1930–1940

DeCarlo TM, Gajdzik L, Ellis J, Coker DJ, Roberts MB, Hammerman NM, Pandolfi JM, Monroe AA, Berumen ML (2020) Nutrient-supplying ocean currents modulate coral bleaching susceptibility. Sci Adv 6:1–8

Diaz-Pulido G, McCook LJ, Dove S, Berkelmans R, Roff G, Kline DI, Weeks S, Evans RD, Williamson DH, Hoegh-Guldberg O (2009) Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. PLoS One 4:e5239

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1:95–107

Done TJ (1992) Phase shifts in coral reef communities and their ecological significance. Hydrobiologia 247:121–132

Donner SD (2011) An evaluation of the effect of recent temperature variability on the prediction of coral bleaching events. Ecol Appl 21:1718–1730

Downing N, Buckley R, Stobart B, Leclair L, Teleki K (2005) Reef fish diversity at Aldabra Atoll, Seychelles, during the five years following the 1998 coral bleaching event. Philos Trans R Soc A Math Phys Eng Sci 363:257–261

Downing N, Stobart B, Buckley R, Leclair L, Teleki K (2003) The State of the Reef: Five Years after Bleaching. Aldabra Marine Programme Phase IV Report. Cambridge Coastal Research Unit, Department of Geography, University of Cambridge.

Eakin CM, Sweatman HPA, Brainard RE (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38:539–545

Elmhirst T, Connolly SR, Hughes TP (2009) Connectivity, regime shifts and the resilience of coral reefs. Coral Reefs 28:949–957

Fabricius K (2005) Effects of terrestrial runoff on the ecology of corals and coral reefs: Review and synthesis. Mar Pollut Bull 50:125–146

Fisher R, Bessell-Browne P, Jones RJ (2019) Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. Nat Commun 10:2346

Fisher R, O'Leary RA, Low-Choy S, Mengersen K, Knowlton N, Brainard RE, Caley MJ (2015) Species richness on coral reefs and the pursuit of convergent global estimates. Curr Biol 25:500–505

Flower J, Ortiz JC, Chollett I, Abelson A, Castro-Sanguino C, Hock K, Lam V, Mumby P (2017) Interpreting coral reef monitoring data: A guide for improved management decisions. Ecol Indic 72:848–869

Folke C, Carpenter S, Walker B, Scheffer M, Elmqvist T, Gunderson L, Holling CS (2004) Regime shifts, resilience, and biodiversity in ecosystem management. Annu Rev Ecol Evol Syst 35:557–581

Fox HE, Mous PJ, Pet JS, Muljadi AH, Caldwell RL (2005) Experimental assessment of coral reef rehabilitation following blast fishing. Conserv Biol 19:98–107

Fox MD, Carter AL, Edwards C, Takeshita Y, Johnson MD, Petrovic V, Amir CG, Sala E, Sandin S, Smith J (2019) Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. Coral Reefs 38:701–712

Gilmour J, Smith LD, Heyward AJ, Baird AH, Pratchett M (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71

Gove JM, Williams G, McManus MA, Clark SJ, Ehses JS, Wedding LM (2015) Coral reef benthic regimes exhibit non-linear threshold responses to natural physical drivers. Mar Ecol Prog Ser 522:33–48

Graham N, Bellwood DR, Cinner JE, Hughes TP, Norström A V., Nyström M (2013) Managing resilience to reverse phase shifts in coral reefs. Front Ecol Environ 11:541–548

Graham N, Chong-Seng K, Huchery C, Januchowski-Hartley FA, Nash KL (2014) Coral reef community composition in the context of disturbance history on the Great Barrier Reef, Australia. PLoS One 9:e101204

Graham N, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:1–17

Graham N, McClanahan TR, MacNeil MA, Wilson SK, Cinner JE, Huchery C, Holmes TH (2017) Human Disruption of Coral Reef Trophic Structure. Curr Biol 27:231–236

Graham N, Nash KL, Kool JT (2011) Coral reef recovery dynamics in a changing world. Coral Reefs 30:283–294

Guan Y, Hohn S, Wild C, Merico A (2020) Vulnerability of global coral reef habitat suitability to ocean warming, acidification and eutrophication. Glob Chang Biol 26:5646–5660

Halpern BS, Walbridge S, Selkoe KA, Kappel C V., Micheli F, D’Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A Global Map of Human Impact on Marine Ecosystems. Science 319:948–952

Haupt P (2013) Bridging the survey implementation gap, and piloting new sustainable marine monitoring methods for Aldabra. Unpublished report for Seychelles Islands Foundation.

Hawkins JP, Roberts CM (1992) Effects of recreational SCUBA diving on fore-reef slope communities of coral reefs. Biol Conserv 62:171–178

Heron SF, Eakin CM, Douvere F, Anderson KD, Day JC, Geiger E, Hoegh-Guldberg O, van Hooidonk R, Hughes TP, Marshall PA, Obura D (2017) Impacts of Climate Change on World Heritage Coral Reefs: A First Global Scientific Assessment. UNESCO World Heritage Centre, Paris

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world’s coral reefs. Mar Freshw Res 50:839–866

Hoey A, Howells E, Johansen JL, Hobbs JPA, Messmer V, McCowan DM, Wilson SK, Pratchett M (2016) Recent advances in understanding the effects of climate change on coral reefs. Diversity 8:1–22

Holling CS (1973) Resilience and stability of ecological systems. Annu Rev Ecol Syst 4:1–23

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 J, Graham N, Harrison H, Hobbs JPA, Hoey A, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018a) 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 S, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson J, Kleypas J, Lough J, Marshall PA, Nyström M, Palumbi S, 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, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017a) Coral reefs in the Anthropocene. Nature 546:82–90

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

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey A, Hoogenboom M, Liu G, McWilliam MJ, Pears RJ, Pratchett M, Skirving WJ, Stella JS, Torda G (2018b) Global warming transforms coral reef assemblages. Nature 556:492–496

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

Huston M (1985) Variation in coral growth rates with depth at Discovery Bay, Jamaica. Coral Reefs 4:19–25

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, R.K. Pachauri and L.A. Meyer (eds.)]. IPCC, Geneva, Switzerland, 151 pp.

Johns KA, Emslie MJ, Hoey A, Osborne K, Jonker MJ, Cheal AJ (2018) Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9:e02349

Jones GP, Almany GR, Russ GR, Sale PF, Steneck RS, Van Oppen MJH, Willis BL (2009) Larval retention and connectivity among populations of corals and reef fishes: History, advances and challenges. Coral Reefs 28:307–325

Jouffray J-B, Nyström M, Norström A V., Williams ID, Wedding LM, Kittinger JN, Williams G (2014) Identifying multiple coral reef regimes and their drivers across the Hawaiian archipelago. Philos Trans R Soc B Biol Sci 370:20130268

Kawaley I (1998) Implications of the Exclusive Economic Zone and EEZ management for Seychelles, a small midocean Island commonwealth territory. Ocean Dev Int Law 29:225–264

Lam V, Doropoulos C, Mumby P (2017) The influence of resilience-based management on coral reef monitoring: A systematic review. PLoS One 12:e0172064

Lesser MP, Farrell JH (2004) Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. Coral Reefs 23:367–377

Liu G, Rauenzahn J, Heron SF, Eakin C, Skirving W, Christensen T, Strong A, Li J (2013) NOAA Technical Report NESDIS 143. NOAA Coral Reef Watch 50 km satellite sea surface temperature-based decision support system for coral bleaching management.

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

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

Lunn J (2019) Disputes over the British Indian Ocean Territory: December 2019 update. UK parliament briefing paper. House of Commons Library, UK.

Maire E, Cinner J, Velez L, Huchery C, Mora C, Dagata S, Vigliola L, Wantiez L, Kulbicki M, Mouillot D (2016) How accessible are coral reefs to people? A global assessment based on travel time. Ecol Lett 19:351–360

Marine Conservation Institute (2020) Aldabra Atoll Special Reserve. https://marine-conservation.org/blueparks/awardees/aldabra/

Marine Mammal Protected Areas Task Force (2020) Aldabra Atoll IMMA. https://www.marinemammalhabitat.org/portfolio-item/aldabra-atoll/

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163

McClanahan TR, Donner SD, Maynard J, MacNeil MA, Graham N, Maina J, Baker AC, Alemu I. JB, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E, Mumby P, Paddack MJ, Selig ER, van Woesik R (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. PLoS One 7:e42884

McWilliam MJ, Pratchett M, Hoogenboom M, Hughes TP (2020) Deficits in functional trait diversity following recovery on coral reefs. Proc R Soc B Biol Sci 287:20192628

Mizerek TL, Baird AH, Madin JS (2018) Species traits as indicators of coral bleaching. Coral Reefs 37:791–800

Morgan KM, Perry CT, Johnson JA, Smithers SG (2017) Nearshore turbid-zone corals exhibit high bleaching tolerance on the Great Barrier Reef following the 2016 ocean warming event. Front Mar Sci 4:224

Mumby P (2017) Embracing a world of subtlety and nuance on coral reefs. Coral Reefs 36:1003–1011

Mumby P, Bejarano S, Golbuu Y, Steneck R, Arnold SN, van Woesik R, Friedlander A (2013) Empirical relationships among resilience indicators on Micronesian reefs. Coral Reefs 32:213–226

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

Mumby P, Hastings A (2008) The impact of ecosystem connectivity on coral reef resilience. J Appl Ecol 45:854–862

Nagelkerken I (2006) Relationship between anthropogenic impacts and bleaching-associated tissue mortality of corals in Curaçao (Netherlands Antilles). Rev Biol Trop 54:31–43

Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301–304

Norström A V., Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral-macroalgal phase shifts. Mar Ecol Prog Ser 376:293–306

Nyström M, Graham NAJ, Lokrantz J, Norström A V. (2008) Capturing the cornerstones of coral reef resilience: Linking theory to practice. Coral Reefs 27:795–809

O'Leary JK, Potts DC, Braga JC, McClanahan TR (2012) Indirect consequences of fishing: Reduction of coralline algae suppresses juvenile coral abundance. Coral Reefs 31:547–559

Obura D, Grimsditch G (2009) Resilience Assessment of coral reefs – Assessment protocol for coral reefs, focusing on coral bleaching and thermal stress. IUCN working group on Climate Change and Coral Reefs. IUCN, Gland, Switzerland

Obura DO (2005) Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. Estuar Coast Shelf Sci 63:353–372

Oliver T, Palumbi S (2011) Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30:429–440

Pandolfi JM (2015) Incorporating Uncertainty in Predicting the Future Response of Coral Reefs to Climate Change. Annu Rev Ecol Evol Syst 46:281–303

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, Warner RR, Jackson JBC (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301:955–958

Pogoreutz C, Rädecker N, Cárdenas A, Gärdes A, Voolstra CR, Wild C (2017) Sugar enrichment provides evidence for a role of nitrogen fixation in coral bleaching. Glob Chang Biol 23:3838–3848

Pratchett M, Anderson KD, Hoogenboom M, Widman E, Baird AH, Pandolfi JM, Edmunds PJ, Lough JM (2015) Spatial, temporal and taxonomic variation in coral growth - implications for the structure and function of coral reef ecosystems. In: Hughes R.N., Hughes D.J., Smith I.P., Dale A.C. (eds) Oceanography and marine biology: An annual review. CRC Press, pp 215–295

Quanz C, Bunbury N, Fleischer-Dogley F (2013) Improving the sustainable operation of a world heritage site: increasing energy efficiency and implementing a renewable energy system on Aldabra Atoll, Seychelles. PARKS 19:47–58

Ramsar Convention Secreteriat (2010) Ramsar Sites Information Service. https://rsis.ramsar.org/ris/1887?language=en

Riegl B (2002) Effects of the 1996 and 1998 positive sea-surface temperature anomalies on corals, coral diseases and fish in the Arabian Gulf (Dubai, UAE). Mar Biol 140:29–40

Riegl B, Piller WE (2003) Possible refugia for reefs in times of environmental stress. Int J Earth Sci 92:520–531

Riegl B, Purkis SJ (2009) Model of coral population response to accelerated bleaching and mass mortality in a changing climate. Ecol Modell 220:192–208

Robinson JPW, Wilson SK, Graham N (2019) Abiotic and biotic controls on coral recovery 16 years after mass bleaching. Coral Reefs 38:1255–1265

Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. Mar Ecol Prog Ser 62:185–202

Rowan R (2004) Thermal adaptation in reef coral symbionts. Nature 430:742

Safaie A, Silbiger NJ, McClanahan TR, Pawlak G, Barshis DJ, Hench JL, Rogers JS, Williams G, Davis KA (2018) High frequency temperature variability reduces the risk of coral bleaching. Nat Commun 9:1671

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. PNAS 105:10444–10449

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and Degradation of Coral Reefs in the Northern Line Islands. PLoS One 3:e1548

Seychelles Islands Foundation (2016) Aldabra Atoll Management Plan 2016.

Seychelles National Bureau of Statistics (2020) Population statistics. https://www.nbs.gov.sc/

Sheppard C (2009) Large temperature plunges recorded by data loggers at different depths on an Indian Ocean atoll: Comparison with satellite data and relevance to coral refuges. Coral Reefs 28:399–403

Sheppard C, Sheppard A, Mogg A, Bayley D, Dempsey AC, Roache R, Turner J, Purkis S (2017) Coral Bleaching and Mortality in the Chagos Archipelago. Atoll Res Bull 2017:1–26

Smith JE, Brainard R, Carter A, Grillo S, Edwards C, Harris J, Lewis L, Obura D, Rohwer F, Sala E, Vroom PS, Sandin S (2016) Re-evaluating the health of coral reef communities: baselines and evidence for human impacts across the central pacific. Proc R Soc B 283:1–9

Spencer T, Teleki K, Bradshaw C, Spalding MD (2000) Coral bleaching in the southern Seychelles during the 1997–1998 Indian Ocean warm event. Mar Pollut Bull 40:569–586

Stobart B, Buckley R, Downing N, Callow M, LeClair L, Teleki K (2002a) Extending the survey eastward. Aldabra Marine Programme phase III Report. Cambridge Coastal Research Unit. Department of Geography, University of Cambridge.

Stobart B, Buckley R, Leclair L, Teleki K, Downing N, Souter D, Callow M (2002b) Aldabra: Monitoring the path to recovery. In: Lindén O., Souter D., Wilhelmsson D., Obura D. (eds) Coral Degradation in the Indian Ocean: Status Report 2002. CORDIO, Department of Biology and Environmental Science, University of Kalmar, Kalmar, pp 232–247

Stobart B, Buckley R, LeClair L, Teleki K, Downing N, Souter D, Callow M (2001) Aldabra: Monitoring the path to recovery. Aldabra Marine Programme Phase II Report. Cambridge Coastal Research Unit. Department of Geography, University of Cambridge.

Stoddart DR (1968a) The Conservation of Aldabra. Geogr J 134:471–485

Stoddart DR (1968b) The Aldabra affair. Biol Conserv 1:63–69

Stoddart DR (1971) Settlement, development and conservation of Aldabra. Philos Trans R Soc London B, Biol Sci 260:611–628

Suggett DJ, Smith DJ (2011) Interpreting the sign of coral bleaching as friend vs. foe. Glob Chang Biol 17:45–55

Šúr M, van de Crommenacker J, Bunbury N (2013) Assessing effectiveness of reintroduction of the flightless Aldabra rail on Picard Island, Aldabra Atoll, Seychelles. Conserv Evid 10:80–84

Teleki K, Downing N, Stobart B, Buckley R (1999) Aldabra Marine Programme Phase I Report. Cambridge Coastal Research Unit, Department of Geography, University of Cambridge. Cambridge Coastal Research Unit

Teleki K, Downing N, Stobart B, Buckley R (2000) The status of the Aldabra Atoll coral reefs and fishes following the 1998 coral bleaching event. In: Souter D., Obura D., Lindén O. (eds) Coral reef degradation in the Indian Ocean: Status Report 2000. CORDIO, Department of Biology and Environmental Science, University of Kalmar, Kalmar, pp 114

UNESCO (2020) Aldabra Atoll. https://whc.unesco.org/en/list/185/

Wilkinson C (2004) Status of Coral Reefs of the World: 2004. Global Coral Reef Monitoring Network. Australian Institute of Marine Science,

Williams G, Gove J, Eynaud Y, Zgliczynski BJ, Sandin S (2015) Local human impacts decouple natural biophysical relationships on Pacific coral reefs. Ecography 38:751–761

Wilson SK, Fisher R, Pratchett M, Graham N, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC (2010) Habitat degradation and fishing effects on the size structure of coral reef fish communities. Ecol Appl 20:442–451

van Woesik R, Irikawa A, Anzai R, Nakamura T (2012) Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. Coral Reefs 31:633–639

Wyatt ASJ, Leichter JJ, Toth LT, Miyajima T, Aronson RB, Nagata T (2020) Heat accumulation on coral reefs mitigated by internal waves. Nat Geosci 13:28–34

Yadav S, Alcoverro T, Arthur R (2018) Coral reefs respond to repeated ENSO events with increasing resistance but reduced recovery capacities in the Lakshadweep archipelago. Coral Reefs 37:1245–1257

Chapter N°2

Early trajectories of benthic coral reef communities following the 2015/16 coral bleaching event at remote Aldabra Atoll, Seychelles

Anna Koester, Valentina Migani, Nancy Bunbury,
Amanda Ford, Cheryl Sanchez, Christian Wild

This work has been published in *Scientific Reports 10:17034*
https://doi.org/10.1038/s41598-020-74077-x

Abstract

Documenting post-bleaching trajectories of coral reef communities is crucial to understand their resilience to climate change. We investigated reef community changes following the 2015/16 bleaching event at Aldabra Atoll, where direct human impact is minimal. We combined benthic data collected pre- (2014) and post-bleaching (2016–2019) at 12 sites across three locations (lagoon, 2 m depth; seaward west and east, 5 and 15 m depth) with water temperature measurements. While seaward reefs experienced relative hard coral reductions of 51–62%, lagoonal coral loss was lower (–34%), probably due to three-fold higher daily water temperature variability there. Between 2016 and 2019, hard coral cover did not change on deep reefs which remained dominated by turf algae and *Halimeda*, but absolute cover on shallow reefs increased annually by 1.3% (east), 2.3% (west) and 3.0% (lagoon), reaching, respectively, 54%, 68% and 93% of the pre-bleaching cover in 2019. Full recovery at the shallow seaward locations may take at least five more years, but remains uncertain for the deeper reefs. The expected increase in frequency and severity of coral bleaching events is likely to make even rapid recovery as observed in Aldabra's lagoon too slow to prevent long-term reef degradation, even at remote sites.

Introduction

Climate change-induced coral bleaching events are increasing in frequency and severity, threatening the persistence of coral reef ecosystems worldwide. Global warming reduced the time frames between bleaching events from 27 years in the early 1980s to 5.9 years in 2016 (Hughes et al. 2018a) and recovery windows are predicted to shorten even further as severe bleaching events are expected to occur annually on 90% of the world's coral reefs by 2055 (Van Hooidonk et al. 2014). In this context, assessing post-disturbance reef trajectories is crucial to understand which conditions favour reef recovery (Graham et al. 2015; Robinson et al. 2019).

The metric most widely used to assess reef recovery is the return time of coral cover to pre-disturbance values, hereafter 'coral recovery' (Graham et al. 2011; Johns et al. 2014). Coral recovery rates are influenced by various environmental and physical factors, e.g. water depth (Mumby et al. 2001; Furby et al. 2013), light intensity (Mumby et al. 2001), nutrient levels (Grottoli et al. 2006), water flow (Nakamura and Van Woesik 2001) and temperature variability (Oliver and Palumbi 2011; Safaie et al. 2018). Furthermore, as bleaching susceptibility and rebound potential of corals varies on multiple levels (e.g. among taxa; Marshall and Baird 2000; Stimson et al. 2002; within taxa; Edmunds 1994; Mizerek et al. 2018; across coral growth forms; Darling et al. 2013; among symbiont type; Rowan 2004; Sampayo et al. 2008), coral recovery is typically faster than the return to pre-disturbance coral community composition, hereafter 'reassembly' (Johns et al. 2014). Reassembly is a critical aspect of reef recovery, ensuring that the coral community's traits and functions are restored (Johns et al. 2014). Speed of coral recovery and reassembly varies substantially among reefs (Johns et al. 2014; Adjeroud et al. 2018; Gouezo et al. 2019) and regions (Graham et al. 2011), underlining the complex nature of reef recovery processes.

Reef recovery relies on the growth and propagation of surviving colonies and coral recruitment (Gilmour et al. 2013; Chong-Seng et al. 2014; Graham et al. 2015) which is influenced by abiotic and biotic conditions and anthropogenic disturbance. High wave exposure, for example, limits coral growth and coral larvae settlement (Gove et al. 2015), while coral recruitment and survival can be enhanced by herbivores that control algal turf and fleshy macroalgae and promote crustose coralline algae (CCA) growth (Smith et al. 2010; Yadav et al. 2016; Johns et al. 2018). These natural drivers of recovery may be disrupted by direct human stressors such as overfishing of herbivores and/or nutrient enrichment, favouring algal proliferation and impeding or preventing reef recovery. This implies that, despite substantial variation in coral recovery and reassembly, both can be promoted through targeted management of direct anthropogenic disturbance (Anthony et al. 2015).

Consequently, coral reefs removed from direct human stressors serve as a baseline to assess the natural recovery potential in the face of the exacerbating effects of climate change and diminishing time frames for reef recovery. Understanding the variation in bleaching impact and recovery trajectories at such sites can provide crucial information for regional marine spatial planning and climate policies (Sandin et al. 2008). Aldabra Atoll in the Western Indian Ocean (WIO) offers the opportunity to examine bleaching impacts and subsequent reef trajectory dynamics under minimal direct human disturbance (Stobart et al. 2005; Friedlander et al. 2015). Designated as a Special Reserve, the highest level of national protection, under Seychelles' legislation in 1981, and inscribed as a UNESCO World Heritage Site in 1982, Aldabra's marine ecosystem has been protected from commercial fishing pressure for almost 40 years, and human-driven nutrient inputs are absent. Nevertheless, coral bleaching events have caused high coral mortality at Aldabra in 1998/1999 (38% and 66% on the seaward reef at 10 m and 20 m water depth, respectively; Norström et al. 2009) and in 2015/2016 (35% in the lagoon at 2 m water depth; 54% at 5 m and 55% at 15 m water depth on the seaward reef; Cerutti et al. 2020).

Here we utilise a unique 5-year data set that covers the aftermath of a major global coral bleaching event at a remote reef system with minimal local human impact. Following the findings of Cerutti et al. (2020) that bleaching induced coral mortality was lower at Aldabra's lagoon than at the seaward reef after the 2015/16 coral bleaching (35% vs. 55% loss), we examine early post-bleaching reef trajectories at Aldabra Atoll in the context of spatial variations in bleaching impact by: (1) assessing changes of benthic communities across locations between 2014 (pre-bleaching) and 2016 (post-bleaching) and quantifying daily water temperature variability to explore whether this links to spatial differences in bleaching impact (Safaie et al. 2018), and (2) evaluating the post-bleaching trajectories (recovery/stability/degradation) of the benthic communities at these locations between 2016 and 2019. We use our results to outline expected future prospects for Aldabra's reefs and the implications for remote reefs elsewhere.

Study site

Aldabra (46°20’E, 9°24’S), managed by a Public Trust, the Seychelles Islands Foundation (SIF), since 1979, is an elevated coral atoll in the southwest of the Seychelles archipelago spanning 34 × 14.5 km (Fig. 2.1). Two distinct seasons govern Aldabra’s climate; the south-east trade winds from April to November create a dry and cooler climate whilst the north-west monsoon from November/December to March generates wet and warmer conditions. Aldabra’s large lagoon (196 km^2) is encircled by four main islands and subject to a 2–3 m tidal range (Farrow and Brander 1971). The north-east, east and south-east parts of Aldabra are exposed to strong winds and high wave energy, whilst the north-west and west are relatively sheltered (Taylor 1971). Because of this contrasting level of exposure, we divided Aldabra’s reefs into three locations: seaward western, seaward eastern and lagoonal reefs (contrasting with Cerutti et al. 2020, who did not make the distinction between west and east at the seaward reef).

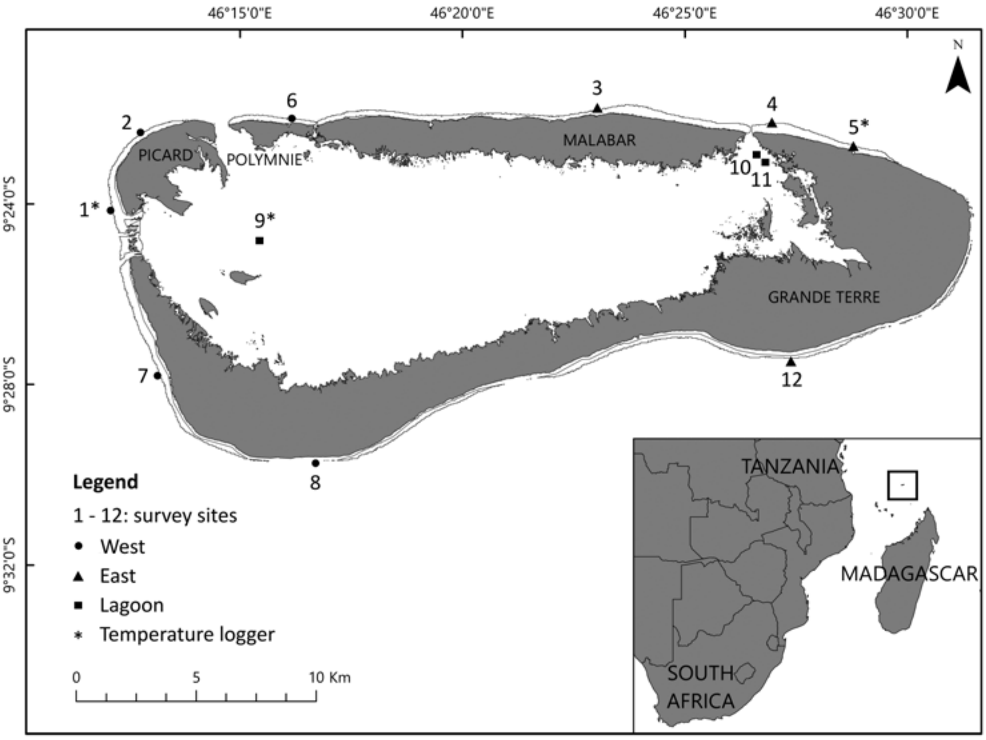


Figure 2.1: Location of Aldabra Atoll in the Western Indian Ocean (inset) with its four main islands, 12 survey sites at the seaward west (five sites), east (four sites) and in the lagoon (three sites) and three temperature logger sites (modified from Cerutti et al. 2020).

During the 2014–2017 Global Scale Coral Bleaching Event (Eakin et al. 2019), Aldabra’s reefs experienced continuous bleaching risk between December 2015 and June 2016. Satellite derived sea surface temperature reached a maximum of 30.7 °C in March 2016, resulting in a peak degree heating weeks (DHW; Liu et al. 2013) value of 3.4 °C-weeks (Cerutti et al. 2020; but note that the NOAA Aldabra virtual station is located ca. 55 km north-east of Aldabra: 46°50’E, 9°00’S).

Data collection

Benthic data was collected from 12 permanent study sites (Fig. 2.1) once prior to bleaching, and four times post-bleaching. We refer to the survey periods as follows: (1) 2014 (pre-bleaching; data collected Dec 2014–Jan 2015), (2) 2016 (1st year post-bleaching; Dec 2016), (3) 2017 (2nd year post-bleaching; Dec 2017), (4) 2018 (3rd year post-bleaching; Dec 2018–Jan 2019) and (5) 2019 (4th year post-bleaching, Nov 2019–Jan 2020).

Of the 12 study sites, permanently marked transects are located at 5 and 15 m water depth at nine seaward survey sites (n = 18 seaward transects) and at ca. 2 m water depth at three sites in the lagoon (n = 3 lagoonal transects; Fig. 2.1). All permanent transects are 50 m long, follow the depth contour, and are parallel to the shoreline. In 2014, two transect sections at 0–10 m and 20–30 m were surveyed on each permanent transect. During all post-bleaching surveys, increased availability of resources allowed an additional section to be surveyed on each permanent transect at 40–50 m. Along each section, benthic photoquadrats were collected on both sides of the tape measure with a GoPro camera attached to a 70 × 50 cm PVC frame at 70 cm height (pre-bleaching: GoPro Hero-3 Silver, 11 megapixels; post-bleaching: GoPro Hero-4 Silver and GoPro Hero-5 Black, 12 megapixels).

Water temperature data was obtained from three Onset loggers (HOBO U22-001) deployed between 2015 and 2018 at three of the permanent sites representing conditions in the lagoon (Site 9, 2 m water depth), shallow west (Site 1, 5 m) and shallow east (Site 5, 5 m; Fig. 2.1). Water temperature was recorded every 30 min with an accuracy of ± 0.2°C (Onset Computer Corporation 2012).

Data processing and statistical analysis

R version 3.6.1 (R Core Team 2019) was used for statistical analysis. All graphs were created with the *ggplot2* package (Wickham 2016). Benthic photos were analysed using Coral Point Count with Excel extensions (CPCe; Kohler and Gill 2006) by identifying the benthos at 16 randomly assigned points per image as described by Cerutti et al. (2020). This yielded a total of 179,247 points (excluding points on photoquadrat frame, transect tape or shadow) across all survey years. Five major categories were assigned for benthic cover analysis: hard coral, soft coral, turf algae, CCA and *Halimeda* spp. (hereafter '*Halimeda*'), which was by far the most dominant macroalga on Aldabra's reefs. Fleshy macroalgae was not included as a category in the analysis as its mean cover was low across all locations and years (0–1.5%), except in 2018 at the deep eastern reefs (9.8%) where a seasonal *Caulerpa racemosa* bloom was recorded in Dec 2018 which had subsided by Feb 2019 (Supplementary Table S7), For the coral community, nine taxonomic categories were chosen following Cerutti et al. (2020) whereby the category 'Acroporidae (excluding *Isopora palifera*)' was replaced by *Acropora* and *Montipora* for more detailed analysis: *Acropora* (branching, plating and encrusting growth forms combined), *Montipora* (encrusting), *I. palifera*, Merulinidae, branching *Po-*

rites (also includes digitate growth forms), massive *Porites*, other hard corals, *Rhytisma*, and other soft corals. To assess changes of the selected categories across locations between 2014 and 2016 (bleaching impact), the mean percent benthic cover of two transect sections was used as a response variable due to no third transect sections being conducted in 2014. To evaluate changes at these locations between 2016 and 2019 (post-bleaching trajectories), the mean percent benthic cover of three transect sections was included as a response variable.

Generalised Estimating Equations (GEE – 'geeglm' function, *geepack* package: Halekoh et al. 2006) with auto-regressive correlation structure were used to test for differences in the benthic and coral cover categories across time (bleaching impact: 2014, 2016; post-bleaching trajectory: 2016, 2017, 2018, 2019) and location (lagoon, west, east) at shallow (2m, 5m) and deep (15m) water depth. Fixed explanatory variables included year, location, and their interactive effect (i.e. model structures: Year × Location; Location + Year; Location; Year). Survey site was set as a random factor to correct for pseudo-replication (transects sections). To correct for non-normality of the response variable (percentage benthic cover), we used different error distributions and link functions that best fitted the models and depended on the nature of the data (see Supplementary Tables S1–S4 for further details). We validated the models by running Generalised Linear Models first ('glm' function, R *stats* package: R Core Team 2019) and checking the residual distribution to see if the assumption of homogeneity of variance, normality and leverage were met. We then also checked the Pearson residual distribution for the GEE models. We used a post-hoc analysis based on least square means with Bonferroni adjustment (*'lsmean'* function, lsmean package: Lenth 2016) to identify pairwise differences between the variables in significant interactive models (Year x Location). Due to many low values of *Rhytisma* (shallow and deep) and all coral categories at deep locations between 2016 and 2019, models of post-bleaching trajectories had a poor fit and these categories could not be tested statistically.

To further assess reef recovery, we calculated: (1) the annual rate of change in absolute hard coral cover increase (Coté et al. 2006) and (2) an estimate of years remaining (from 2019) until hard coral cover reaches pre-bleaching levels (see equations 1 and 2 in Supplementary Material). Acknowledging the latter as an extremely simplified projection that assumes a linear increase in hard coral cover, we applied both calculations only to those locations where hard coral cover had increased significantly between 2016 and 2019 (i.e. according to GEE analysis).

To assess which hard coral categories contributed most to overall hard coral cover increase (where it was significant according to GEE analysis), we calculated the absolute change in percentage cover between 2016 and 2019 for each hard coral category. Based on this, we calculated the contribution of each coral category to overall hard coral cover increase.

To visualise coral community trajectories, non-metric multidimensional scaling (nMDS) based on Bray-Curtis dissimilarity matrices of the coral community (using percent cover) was performed ('metaMDS' function, *vegan* package: Oksanen et al. 2013). Only coral categories covering ≥ 5% of any transect section were included in the analysis. All other categories were combined into 'other hard corals' and 'other soft corals' (note that these categories contain different taxa to 'other hard corals' and 'other soft corals' in the GEE analysis). To display which coral and major benthic categories correlated with the community differences, significant correlation vectors were overlaid on nMDS plots ('envfit' function).

To assess daily water temperature regimes, overlapping time series of temperature data logged at the three monitored sites (Sites 1, 5 and 9) were selected (Feb 2015 and Nov 2018). Due to technical issues there were data gaps of 1-week (2–9 Apr 2015) and 5-months (12 Dec 2016–5 May 2017) for Site 1 and a data gap of 3-weeks for Site 9 (10 Dec 2016–1 Jan 2017). At Site 5, data was only available from Feb 2015 to Apr 2017 due to logger loss. Across the entire period, a minimum of 809 days remained for each logger (Site 9: 1353; Site 1: 1248, Site 5: 809) from which annual mean daily temperature (mean, maximum, minimum) and temperature variability (range, coefficient of variation) was calculated. To test for differences in these measures between sites, two-sided t-tests were conducted for each combination (i.e. Site 1 vs. Site 9; Site 1 vs. Site 5; Site 5 vs. Site 9) with Bonferroni adjustment applied to *p*-values to correct for multiple comparisons.

Aldabra's coral recovery in global context

To gain perspective on how Aldabra's reef recovery fits into the global context, a table of studies reporting reef recovery was compiled (Supplementary Table S6) and the annual rate of change in absolute hard coral cover (equation 1 in Supplementary Material; Coté et al. 2006) was calculated for each reef. Studies were drawn from Baker et al. (2008) and Graham et al. (2011) and supplemented by more recent literature. Only studies reporting uninterrupted recovery from bleaching events were included; i.e. where no additional acute disturbance (e.g. bleaching, storm, *Acanthaster* outbreak) was reported within the recovery period.

Benthic community change directly after bleaching

Overall, between Dec 2014 and Dec 2016, Aldabra's reefs experienced 53% and 92% reductions of hard and soft corals, respectively. Hard coral reduction, however, was only significant on the seaward reefs, where losses were substantially higher than inside the lagoon (lagoon: −34%, west shallow: −56%; east shallow: −62%, west and east deep; −51%; Fig. 2.2a, Supplementary Table S1). In the lagoon, mean daily water temperature range was more than three times higher than the ranges recorded at the shallow seaward reefs (Table 2.1, Fig. 2.3). Soft coral cover declined by 91–92% at all locations (Fig. 2.2b, g), but absolute losses were considerably lower inside the lagoon as soft coral cover there was already < 2% in 2014 (compared to 7–26% at the seaward reefs). At the lagoon and west, CCA and turf algae increased (CCA, lagoon: 5–14%, shallow west: 4–12%, deep west: 1–9%; turf algae, lagoon: 46–57%, shallow west: 48–59%, deep west: 30–62%), together comprising 70% of the benthos at these locations in 2016 (Fig. 2.2c–i). While calcareous green alga *Halimeda* only increased at the shallow west and the lagoon (from ca. 1% to 6% cover), it remained most abundant at the east (25–29% cover in 2016) and together with CCA and turf algae (i.e. all algae groups combined) comprised 70–81% of the benthos there in 2016 (Fig. 2.2c-j).

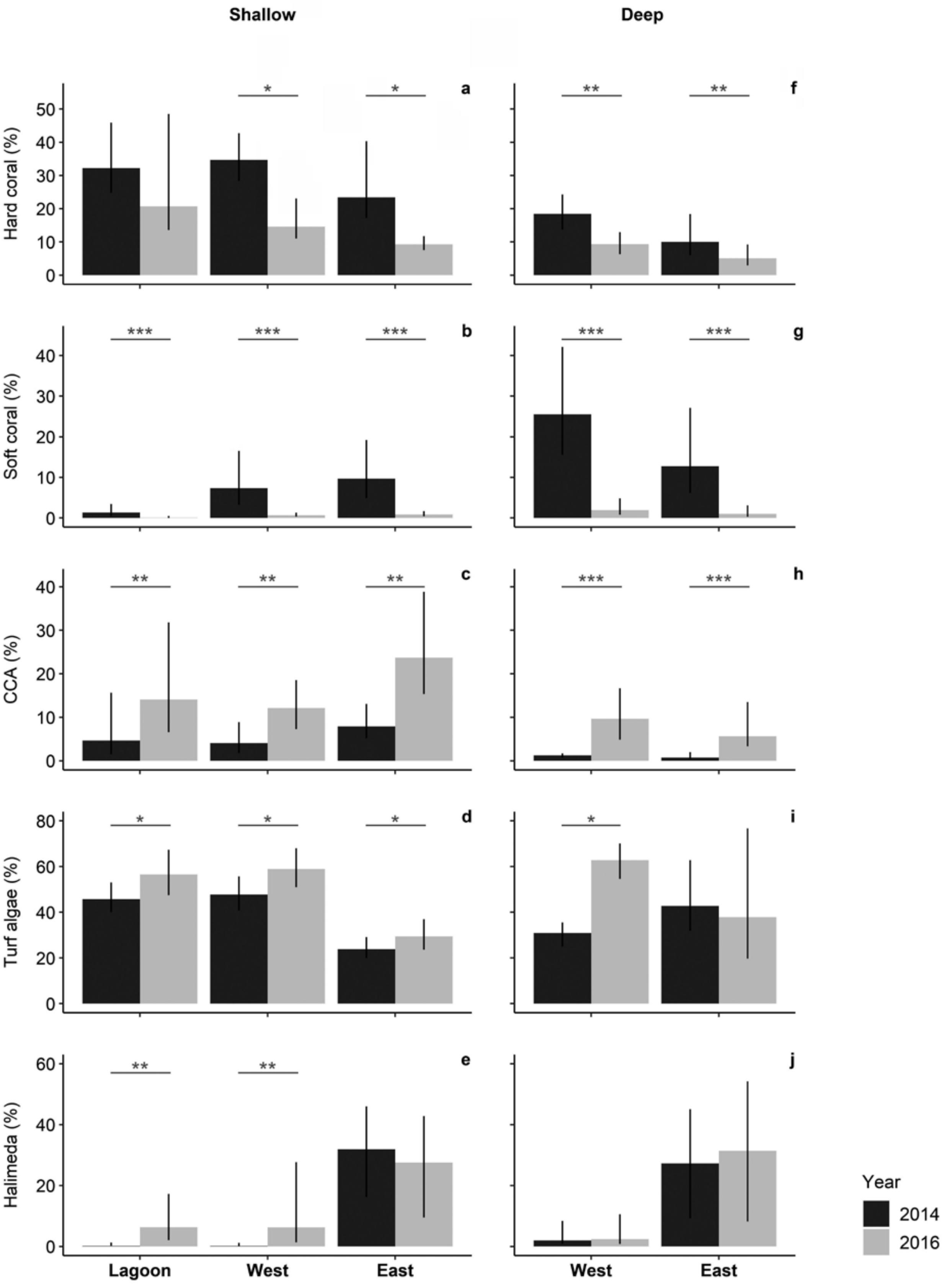


Figure 2.2: Mean cover of major benthic groups at shallow (a–e) and deep locations (f–j) between 2014 and 2016 at Aldabra (transect sections: lagoon n = 6, west n = 10 per depth, east n = 8 per depth). Bars represent back-transformed estimates of GEE analysis with 95% confidence interval. Significant differences across years are indicated with asterisks (* $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$).

Table 2.1: Differences in mean daily water temperatures (mean, mean maximum, mean minimum) and daily mean temperature variability (range, CV: coefficient of variation of mean) of three shallow reef sites in the lagoon and the seaward west and east of Aldabra during Feb 2015–Nov 2018 (see also Supplementary Figure S2).

	Daily temperature (° C)						t-test								
Site	Site 9 (Lagoon)		Site 1 (West)		Site 5 (East)		Site 9 vs. Site 1			Site 1 vs. Site 5			Site 9 vs. Site 5		
Measure	Mean	SD	Mean	SD	Mean	SD	dF	t	*p*	dF	t	*p*	dF	t	*p*
Mean	27.47	1.71	27.13	1.66	27.24	1.79	729.4	2.7	**< 0.05**	728.7	0.8	>0.05	726.2	1.8	> 0.05
Max.	28.77	1.96	27.45	1.78	27.59	1.82	723.7	9.5	**< 0.001**	729.7	1.0	>0.05	726.1	8.5	**< 0.001**
Min.	26.26	1.34	26.67	1.66	26.83	1.70	706.7	3.7	**< 0.001**	729.5	1.2	>0.05	700.1	5.0	**< 0.001**
Range	2.45	0.77	0.77	0.25	0.75	0.27	436.8	39.4	**< 0.001**	719.0	1.2	>0.05	456.0	39.4	**< 0.001**
CV	3.44	1.11	1.82	0.69	1.76	0.75	609.1	23.7	**< 0.001**	725.1	1.2	>0.05	639.0	24.0	**< 0.001**

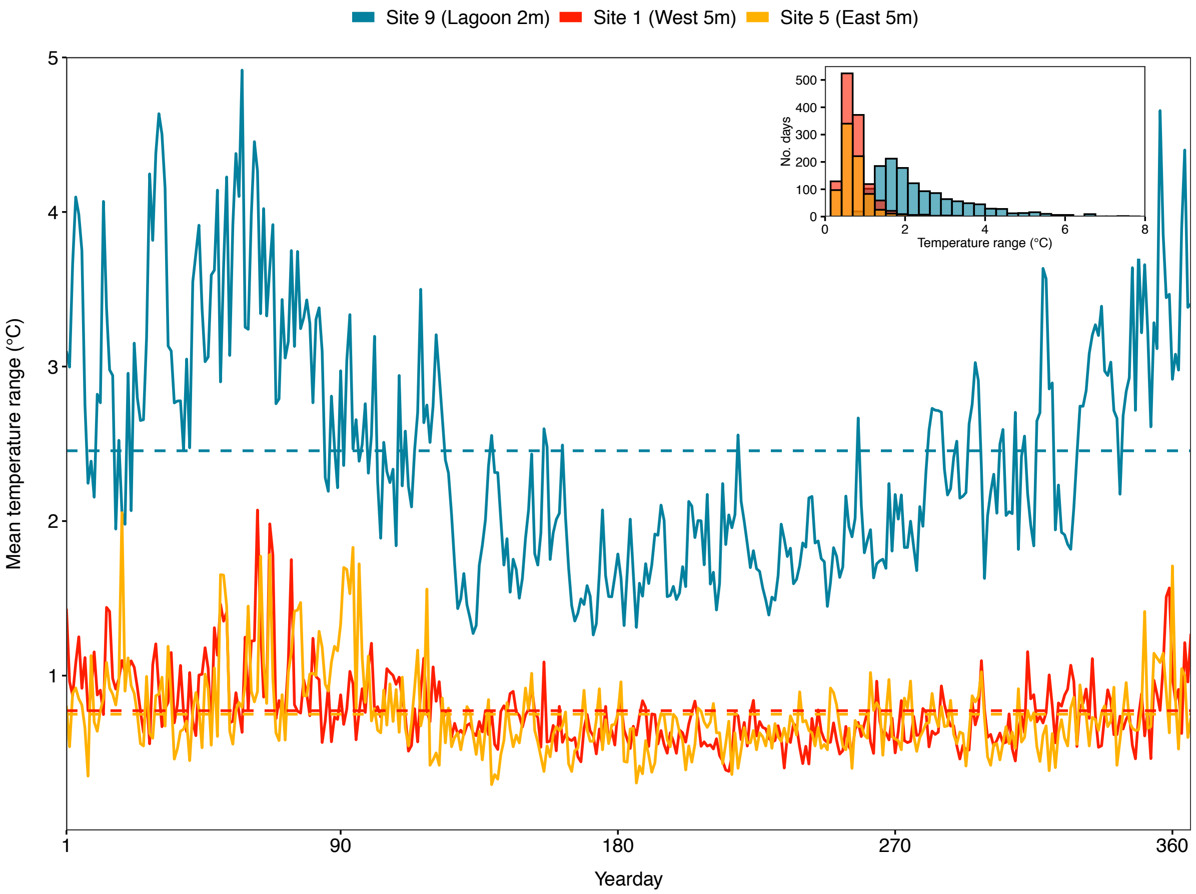


Figure 2.3: Mean *in-situ* water temperature ranges (°C) at three representative sites in the lagoon and at the seaward east and west of Aldabra. Solid lines indicate daily mean ranges calculated from temperature records obtained in 30-min intervals between February 2015 and November 2018 (see methods). Dashed lines represent mean daily temperature range within the study period. Inset shows the same data as histogram, representing the number of days during which a given temperature range was recorded at each site.

Cover of all coral taxa declined significantly between 2014 and 2016 (except for ‘other hard corals’ and *Isopora palifera*, the latter of which slightly increased at the shallow east during 2014–2016) but absolute losses varied across locations (Supplementary Table S2, Supplementary Fig. S1). *Acropora* and *Montipora* were most affected at the shallow west and east, dropping from 2–5% cover in 2014 to ≤ 0.7% cover in 2016, a relative reduction of 84–99%. Although relative losses of 83–95% were also recorded for both taxa at the deep locations and the lagoon, absolute losses there were lower, as cover of these taxa was already low in 2014 (deep locations: 0.4–1.7%; lagoon: 0.6–0.9%). Branching *Porites* experienced a relative decline of 83–99% at the seaward reefs (1–4% cover in 2014; < 0.1% cover in 2016), but retained 50% of pre-bleaching cover at the lagoon (6% in 2014, 3% in 2016). Of all taxa, the highest absolute losses were recorded for *Rhytisma* at the seaward west where it reduced from 8% and 26% cover (shallow and deep, respectively) in 2014 to < 0.1% cover at both depths in 2016.

Post-bleaching trajectories

Except for soft coral cover, which did not change at any location between 2016 and 2019, trajectories of benthic groups varied across locations (Fig. 2.4, Supplementary Table S3). By 2019, mean hard coral cover had increased at all shallow locations to 13%, 23% and 30% at the east, west and lagoon, respectively (Fig. 2.4a), equating to 54% (east), 68% (west) and 93% (lagoon) of the pre-bleaching hard coral cover. The absolute annual rate of change in hard coral cover was 1.3%, 2.3% and 3.0% at the east, west and lagoon, respectively (Table 2.2). From 2019, the projected time until hard coral cover has fully recovered to pre-bleaching levels (2014) is 0.7, 4.8 and 8.5 years at the lagoon, west and east, respectively (Table 2.2). These are conservative estimates as hard coral cover gains until 2019 were non-linear and accelerated over time (e.g. 1.6–2.0 times higher from 2018 to 2019, than from 2017 to 2018, and 2016 to 2017). Simultaneously with hard coral cover increase, turf algae reduced to below pre-bleaching levels by 2018 (east: 28–18%, west: 64–40%, lagoon: 60–38%; Fig. 2.3d). However, while benthic communities at the shallow west and lagoon were no longer turf algae-dominated by 2018, and CCA cover remained unchanged during 2016–2019, CCA cover dropped at the shallow east during 2016–2019 (27–11%), with turf algae and *Halimeda* covering 18%–21% and 45%–50% of the shallow eastern benthos in 2017, 2018 and 2019, respectively (Fig. 2.4c–e).

At the deep locations hard coral cover did not change between 2016 and 2019 (Fig. 2.4f). Although turf algae cover decreased between 2016 and 2018, it still covered 51% of the western benthos in 2019 (Fig. 2.4i), 70% more than pre-bleaching. At the east, turf algae cover remained below pre-bleaching levels but, similar to the shallow east, *Halimeda* and turf algae combined dominated the benthos at 53–61% and 9–23% cover between 2017 and 2019, respectively (Fig. 2.4i, j).

Table 2.2: Absolute percentage increase in mean hard coral cover at Aldabra's shallow locations between 2016 and 2019 and projected time remaining from 2019 for full hard coral recovery (values obtained from back-transformed estimates of GEE analysis). Asterisks indicate significant increase between years (see Fig. 4a). Note that these were only calculated for locations where hard coral cover significantly increased based on the GEE analysis.

Location	Absolute hard coral cover increase (%)				Annual rate of change	Predicted years until full recovery[a]
	2016/17	2017/18	2018/19	2016/19		
Lagoon	2.1	2.6	4.2	9.0*	3.0	0.7
West (shallow)	1.6	2.0	3.2	6.9*	2.3	4.8
East (shallow)	0.9	1.1	1.8	3.9*	1.3	8.5

[a] Based on annual rate of change and assumes linear increase

Montipora was the only hard coral genus that increased significantly between 2016 and 2019 (Supplementary Table S4, Supplementary Fig. S3). Although the absolute cover of *Montipora* was relatively low in 2019 at all shallow locations (< 3.5%), its increase contributed ca. 39% to the overall hard coral cover increase at the shallow west and east during 2016–2019 (Supplementary Table S5). The increase of 'other hard corals', albeit statistically not significant, contributed 38% (shallow east) and 29% (shallow west) to overall hard coral cover increase. In the lagoon, branching *Porites* and 'other hard corals' contributed most to overall hard coral cover increase between 2016 and 2019 (36% and 33%, respectively) although increases were not statistically significant. Although overall soft coral cover did not increase at any location, *Rhytisma* covered 7.0% of the benthos at the deep west in 2019 (vs. not being recorded in 2016), while remaining < 1.5% at all other locations (Supplementary Fig. S3).

In terms of coral community composition (Fig. 2.5), in the lagoon, where bleaching-induced coral mortality was lowest and the magnitude of hard coral recovery was highest, coral community composition transitioned back to pre-bleaching assemblages between 2016 and 2019. Less pronounced than in the lagoon, western communities also showed returning transitions towards pre-bleaching assemblages, even at the deep reefs.

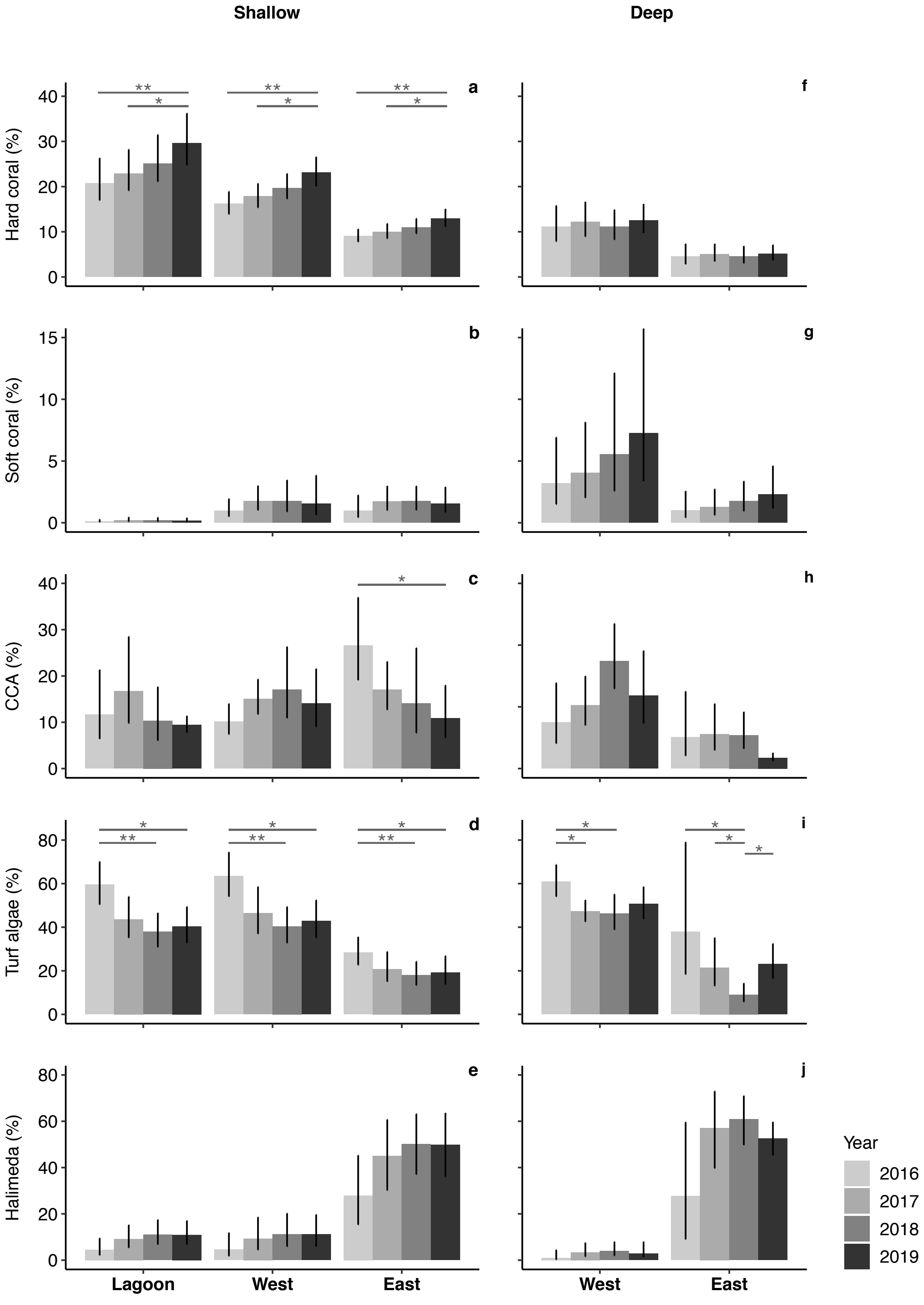


Figure 2.4: Mean cover of major benthic groups at shallow (a–e) and deep locations (f–j) between 2016 and 2019 at Aldabra (transect sections: lagoon n = 9, west n = 15 per depth, east n = 12 per depth). Bars represent back-transformed estimates of GEE analysis with 95% confidence interval. Significant differences across years are indicated with asterisks (* $p < 0.5$; ** $p < 0.01$).

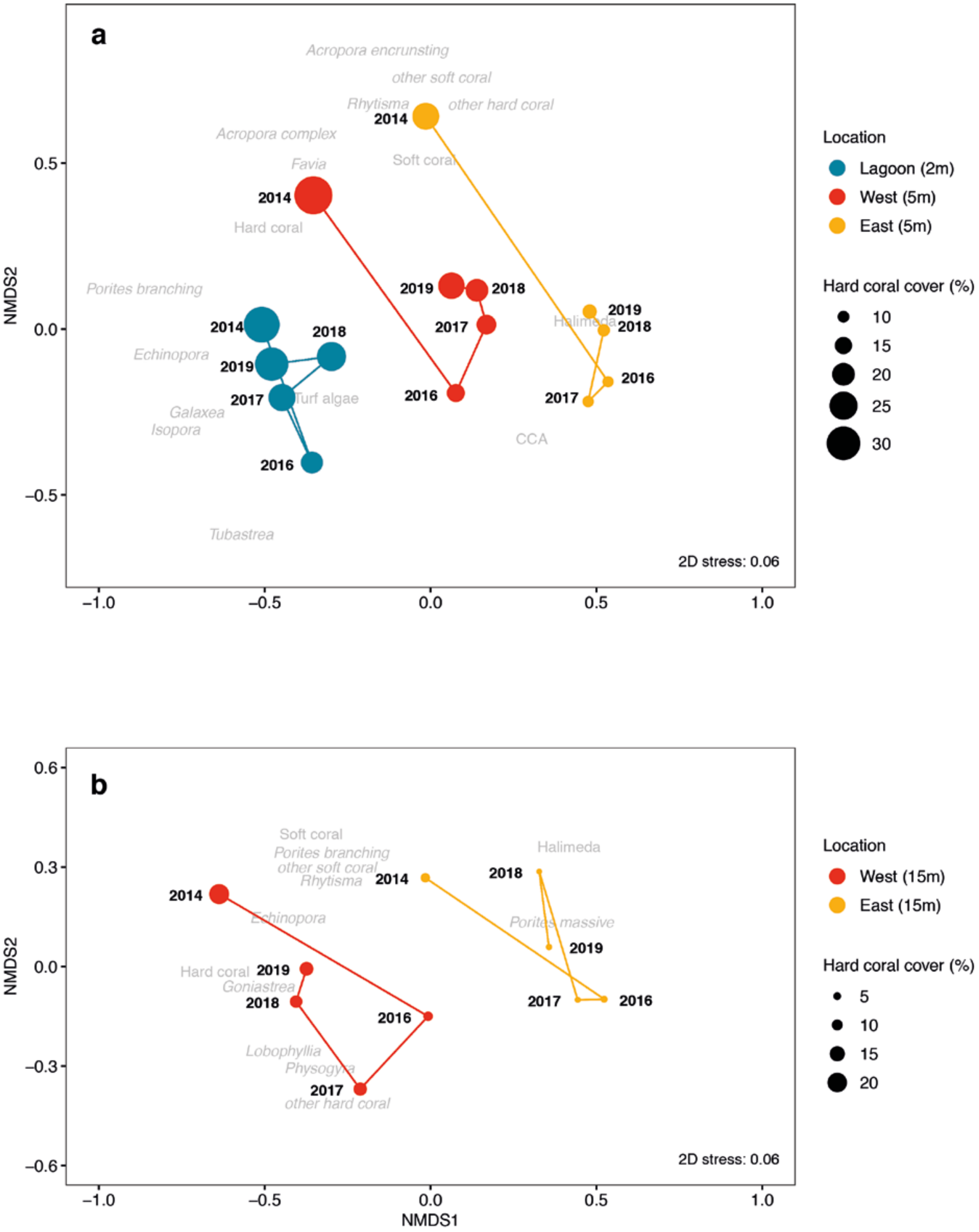


Figure 2.5: Non-metric multidimensional scaling (nMDS) of coral communities between 2014 and 2019 at Aldabra's shallow (a) and deep (b) locations. Vectors connecting years display directional change of coral community composition at each location. Benthic and coral (italics) groups driving differences among locations and years displayed in grey. Scaled points indicate mean percent hard coral cover per location per year. Note that 'other hard corals' and 'other soft corals' contain different taxa than in the GEE analysis.

Discussion

Spatial variation in coral mortality following bleaching

Spatial variation in the extent of bleaching-induced hard coral mortality was clearly evident at Aldabra (see also Cerutti et al. 2020). Hard coral loss on the seaward reefs ranged between 51% and 62% and was only marginally lower at 15 m compared to 5 m water depth, indicating that corals in deeper water were as susceptible to heat stress as those in the shallows. This contrasts with other studies in which shallow coral communities suffered substantially higher post-bleaching mortality than deeper ones (e.g. Marshall and Baird 2000), but appears similar to observations in the Chagos Archipelago following the 1998 bleaching event (Sheppard et al. 2008). In Aldabra's lagoon, hard coral loss (34%) was considerably lower than on seaward reefs (51–62%). A lower reduction of hard coral cover inside Aldabra's lagoon was also observed following the 1998/99 bleaching event (Stobart et al. 2002), although no data is available for comparison. Within our study's time frame, mean daily temperature variability was three-fold higher in the lagoon than on the seaward reefs, which has been proposed to result in inherently higher heat stress tolerance of hard corals and thus lower bleaching mortality (Donner 2011; Oliver and Palumbi 2011; Safaie et al. 2018). Lagoon corals may also have been protected from UV radiation as a result of UV-absorbing leachate from seagrass leaves being steeped inside the lagoon (Iluz et al. 2008) or due to light attenuation from suspended particles (Woesik et al. 2012; Morgan et al. 2017). Seagrass beds can be found in the vicinity of the lagoonal study reefs (Hamylton et al. 2018) and (in comparison to the seaward reefs) turbidity in the lagoon was noted to be relatively high during surveys at slack high tide (pers. obs. Dec 2016, 2017, 2018, A.K.). Both mechanisms could result in reduced irradiance intensity experienced by corals, acting as additional buffers against thermal stress (but see Fisher et al. 2019). Furthermore, the high amount of suspended particulate material may allow corals to derive nutrients by heterotrophic feeding, contributing to higher bleaching survival when symbiont-acquired nutrients are low or entirely lacking (Grottoli et al. 2006; Palardy et al. 2008).

Across all locations, *Acropora* and *Montipora* consistently exhibited the highest susceptibility and suffered extensive losses following the bleaching event. Both genera are amongst the most susceptible hard corals to bleaching (Marshall and Baird 2000; Hoey et al. 2016; Fox et al. 2019) while massive *Porites*, as found elsewhere (Loya et al. 2001; Pratchett et al. 2013), appeared resistant. However, the atoll-wide resistance of *I. palifera* and the location-specific resistance of branching *Porites* are striking (see also Cerutti et al. 2020). Whilst I. *palifera* remained abundant at the shallow western and lagoonal reefs, branching *Porites* (at Aldabra e.g. *P. cylindrica, P. harrisoni, P. monticulosa, P. profundus* and *P. rus*, which can exhibit branching or digitate growth forms; Friedlander et al. 2015) suffered substantially lower mortality in the lagoon and remained relatively abundant there post-bleaching. Although it is currently unknown whether different species of branching *Porites* were present at Aldabra's seaward reefs and in the lagoon, it is reasonable to suggest that adaptation to the variable lagoon environment was conducive to lower bleaching susceptibility and mortality.

Post-bleaching trajectories

Aldabra's reef trajectories in the three post-bleaching years varied substantially across locations. In 2019, hard coral cover at the shallow west (23%) and the lagoon (30%) reached 68% and 93% of the pre-bleaching cover, respectively (vs. 15% and 21% hard coral cover in 2016, i.e. 44% and 65% of pre-bleaching cover, respectively), and by 2018, benthic communities were no longer dominated by turf algae. Although coral recovery also occurred at the shallow east (from 9% hard coral cover, i.e. 38% of pre-bleaching cover in 2016 to 13% hard coral cover, i.e. 54% of pre-bleaching cover in 2019), *Halimeda* remained the single most dominant benthic group. There was no coral recovery at the deep locations, with reefs remaining dominated by turf algae (west) and *Halimeda* (east) between 2016 and 2019.

Coral recovery was particularly fast inside Aldabra's lagoon, almost reaching pre-bleaching levels within three years. It is possible that a large proportion of hard corals in the lagoon experienced only partial mortality and were able to rapidly regrow post-bleaching. This seems especially likely because the coral community composition also nearly reassembled to pre-bleaching levels by 2019. Survival and growth of remnant coral colonies is an important component in reef recovery, specifically in the first few years post-disturbance when the reproductive capacity of corals may be low (Golbuu et al. 2007; Diaz-Pulido et al. 2009; Gilmour et al. 2013). This process is particularly important for isolated reefs that rely on coral recruitment from local sources as was reported from the remote Scott Reef, Australia (Gilmour et al. 2013) and the Inner Seychelles (Graham et al. 2015). In both cases, recovery following the 1998/99 bleaching event was slow for 7–10 years but then increased exponentially with increasing recruitment capacity. Given that recovery of Aldabra's seaward reefs following the 1998/99 bleaching event was slow until 2005 (Buckley et al. 2004; after which no further records are available), but coral cover had reached high levels by 2014, coral recruitment from local sources is likely important. The coral community in Aldabra's lagoon may be critical for the long-term recovery of Aldabra's reef system, with the potential to boost recovery at the seaward reefs. Nevertheless, information on the connectivity within Aldabra's reefs as well as to other reefs in the region is limited (but see Crochelet et al. 2016) and research is needed in this area.

At both the lagoon and shallow west, the trajectories of turf algae and CCA following the bleaching event indicate a critical component of reef recovery (Fox et al. 2019). Although the post-bleaching increase in CCA cover may be an artefact of the two-dimensional survey method employed here (i.e. where the loss of canopy forming corals may simply have increased the visibility of CCA underneath; Goatley and Bellwood 2011), its stable cover in all post-bleaching years may benefit recovery processes. CCA can promote reef recovery by stabilising the reef framework (Smith et al. 2016) and enhancing coral larvae settlement (Yadav et al. 2016; Johns et al. 2018), whereas turf algae, often the first benthic group to grow over dead coral substrate following disturbance (Diaz-Pulido and McCook 2002; Gilmour et al. 2013; Gouezo et al. 2019; Head et al. 2019), can aggressively compete with adult corals through smothering and allelopathy (Smith et al. 2016), and can inhibit coral larval settlement (Ford et al. 2018; Johns et al. 2018) and the survival of coral recruits (Arnold et al. 2010). The rapid proliferation of turf algae following bleaching events can thus be detrimental to hard coral recovery. At Aldabra's shallow reefs, however, turf algae cover was reduced to pre-bleaching levels within two years after bleaching (by 2018). This rapid reduction and the general lack of fleshy macroalgae across Aldabra's reefs indicate high grazing pressure. Indeed, Aldabra hosts the highest biomass of herbivorous fish in the Seychelles (Friedlander et al. 2015) and herbivory may actually have facilitated an increase in CCA (Smith et al. 2016) following the bleaching event. Both herbivory and CCA abundance may be positively influenced by nutrient input of the guano from Aldabra's numerous seabird populations (Šúr et al. 2013), as was recently shown at the Chagos Archipelago (Benkwitt et al. 2019).

At the shallow east and the deep reefs, recovery is likely restricted by abiotic conditions. Robinson et al. (2019) found that coral recovery in the Inner Seychelles following the 1997/98 bleaching event was prolonged with increasing water depth and wave exposure which was attributed to lower coral growth rates, e.g. due to increased light attenuation at depth (Huston 1985; Pratchett et al. 2015). In terms of wave exposure, coral community composition is naturally shaped along wave energy gradients (Done 1982; Gove et al. 2015; Williams et al. 2015). Branching (i.e. usually fast-growing) hard corals are less likely to occur where wave energy is high, which ultimately prolongs the time for hard coral recovery in those areas (Robinson et al. 2019). These abiotic conditions likely reflect the lack of hard coral recovery at Aldabra's deep reefs (depth) and the lower magnitude of recovery at the shallow east (wave exposure). Although Aldabra's deep western reefs remain dominated by turf algae, hard coral recovery can still occur in the long term. However, as already noted by Drew (1977) and Stobart et al. (2002), there is a prominent gradient of decreasing coral cover and increasing *Halimeda* cover from the western towards the eastern seaward reefs, attributed to an increase in hydrodynamic energy. *Halimeda* was already present in high abundance on Aldabra's eastern reefs pre-bleaching and remained unchanged until 2016. However, by 2017 it became the single most dominant benthic category in the east, reaching up to 61% of overall benthic cover by 2018, potentially further constraining coral recovery there.

Hard coral recovery following disturbance is often driven by *Acropora* and *Pocillopora* (Bruno et al. 2001; Arthur et al. 2006; Hagan and Spencer 2008; Robinson et al. 2019; Sheppard and Sheppard 2019; Wilson et al. 2019), but also other taxa such as *Porites*, *Montipora*, *Isopora*, *Galaxea* and *Pavona* are named in the literature (Brown and Suharsono 1990; Bruno et al. 2001; McClanahan et al. 2005; Guzman and Cortés 2007; Hagan and Spencer 2008). At Aldabra's lagoon, hard coral cover increase was largely due to the contributions of branching *Porites* and 'other hard corals'. Many taxa that exhibit branching growth forms are characterised by life history traits that favour fast growth and wide dispersal, and are therefore often the first to recover at recently disturbed habitats. However, at the seaward reefs, most taxa that exhibit branching growth forms remained scarce during 2016–2019, with encrusting *Montipora* and 'other hard corals' contributing most to the early overall hard coral recovery. Previously, fast recovery of encrusting *Montipora* was associated with higher wave exposure (Gouezo et al. 2019), which may explain why it is mainly found at Aldabra's seaward locations.

Due to different bleaching susceptibility and recovery potential of coral taxa, overall hard coral recovery can be accompanied by a shift in coral community composition (Burt et al. 2008; Johns et al. 2014; but examples for reassembly also exist: Burt et al. 2008; Gilmour et al. 2013; Johns et al. 2014). Such community shifts can alter the ecological functions of a reef and their response to future disturbance (Johns et al. 2014). At Aldabra, coral communities in the lagoon recovered and reassembled almost completely within three years and also the western communities showed reassembly trajectories until 2019. The lower post-bleaching mortality of branching *Porites* in the lagoon and its relative contribution to overall hard coral recovery possibly indicates location-specific resilience, which may also have been important for the rapid return to pre-bleaching coral community composition there. As reef recovery is ongoing at Aldabra's seaward reefs, however, it is possible that further taxa emerge which could dominate hard coral recovery, particularly if coral recruitment speeds up coral recovery (Gilmour et al. 2013; Graham et al. 2015).

Furthermore, in contrast to the lagoon, pre-bleaching coral communities at the seaward reefs were not only characterized by hard corals. Soft corals also constituted an important component at the seaward reefs prior to the bleaching event and community reassembly there also depends on soft coral recovery. Overall soft coral recovery was negligible during 2016–2019, however, *Rhytisma* covered 7% of the benthos at the deep west in 2019, albeit not being recorded in 2016. This is similar to observations at Aldabra following the 1998 bleaching event where *Rhytisma* increased at 10 m water depth from zero to 8% cover by 2002, i.e. during the same time frame as studied here (Buckley et al. 2004; Stobart et al. 2005). The subsequent increase to 26% cover by 2004 and the slow hard coral recovery caused reason to suggest Aldabra's reefs had undergone a shift from hard to soft coral dominance (Norström et al. 2009). It is possible that *Rhytisma* rapidly re-gains its previous abundance, with potential negative implications for hard coral recovery, but unlike implied previously (Norström et al. 2009; Ateweberhan et al. 2013), the high abundance of *Rhytisma* has been restricted to Aldabra's deep western reefs and does not affect the entire reef system.

Aldabra's reef recovery in context

Overall annual rate of change in absolute hard coral cover at Aldabra's shallow reefs was 2.2% over three years (Supplementary Table S6), similar to values reported for reefs within and outside no-take marine protected areas in Kenya (2.3% over three years), the Maldives (2.3% over four years) and Palau (2.1% over eight years). Higher annual increases during similar recovery time frames were reported from Alphonse Atoll, Seychelles (2.9% over two years) and the Lakshadweep Islands (3.5% over three years), both of which are unprotected. In the Inner Seychelles, overall hard coral cover increased annually by 1.8% over nine years (including reefs within and outside no-take marine protected areas) and at the remote Chagos Archipelago, cover increased annually by 2.6% over 11 years. However, looking at individual reefs regardless of location and level of protection, 56% of the annual rates of change provided in Supplementary Table S6 fall within the range reported for Aldabra's reefs (1.3–3.0%), with 21% and 23% of the values falling below or above that range, respectively (Supplementary Figure S4). Hard coral cover increase at Aldabra's shallow reefs, in terms of annual rate of change, was therefore not exceptionally low or high in comparison to reefs elsewhere.

Graham et al. (2011) reviewed global recovery rates following various acute disturbances and found a mean annual rate of 3.56% coral cover increase, with a range from 0.13% to 12.49%. However, rates were lowest in fully protected areas (0.8% vs. 4.0% in open areas) and varied depending on post-disturbance coral cover (between 2% and 4%). It was proposed that because protected areas promote higher coral cover (provided they are undisturbed), they are more susceptible to disturbances such as coral bleaching and may lose a higher proportion of corals than unprotected areas (the authors noted however, that enforcement or compliance could not be standardised among the assessed protected areas). Arguing that recovery dynamics are likely nonlinear and may be faster where disturbances have opened up more space for coral recruitment, recovery from high to medium coral loss (in their study 6–20% post-disturbance cover) may be faster than from extreme (< 5% post-disturbance cover) and small losses (21–30% post-disturbance cover; Graham et al. 2011). Our results do not match these findings (i.e. at Aldabra, recovery rate was highest where coral loss was lowest), probably because the early recovery at Aldabra observed here, particularly in the lagoon, is likely driven by the growth of remnant coral colonies rather than coral recruitment. Furthermore, in contrast to the studies used by Graham et al. (2011), full recovery is not realised at all of Aldabra's locations due to the short recovery time frame studied here. These discrepancies show that post-disturbance recovery measured by hard coral cover increase alone misses the complexities of this process (Graham et al. 2011) and reduces the meaningfulness of comparisons if no context is provided.

The return of coral cover and coral community composition to pre-disturbance values can provide this context and are useful indicators. For example, Aldabra's lagoon nearly completely recovered its pre-bleaching hard coral cover within three years, matched by only two other reefs in our comparison within a similar time frame for recovery (Vipingo and Kanamai in Kenya, both unprotected; Supplementary Table S6). However, despite these often being the best indicators at data scarce locations (if available at all) it is important to acknowledge that longer-term effects of reef degradation may be masked and that reef state immediately pre-disturbance is likely not the ideal baseline (i.e. shifting baselines; Hughes et al. 2011).

Future prospects for Aldabra's reefs

Despite its remoteness and strict protection, Aldabra's reefs were significantly impacted by the 2015/16 bleaching event, joining other remote reef systems such as the Chagos Archipelago (Head et al. 2019) and the northern Great Barrier Reef (Hughes et al. 2018b) that suffered extensive bleaching-induced coral mortality. Nevertheless, we show that Aldabra's lagoon rapidly recovered its pre-bleaching coral cover and reassembled to its pre-bleaching coral community composition within three years. While at the shallow seaward reefs, coral recovery is predicted to take ca. 5–9 more years (if there is no major bleaching event), it is likely prolonged at the deep reefs.

Our results add to the work of Cerutti et al. (2020) in providing locally important baseline information for ongoing coral reef research, ultimately feeding into Aldabra's management and corroborating its protective status. On the global level, our study adds to previous work conducted at remote reefs (e.g. Gilmour et al. 2013; Sheppard et al. 2008), advancing the knowledge of coral bleaching impact and recovery in the absence of direct human disturbance. With an expected increase in the magnitude and frequency of mass bleaching events (Van Hooidonk et al. 2014), intervals between major events will become too short for adequate reef recovery, and reef locations where bleaching impact has been low so far, are likely to become more vulnerable to temperature stress. Our research underlines the need for drastic measures to reduce greenhouse gas emissions, alongside continued reduction and management of local human disturbance to conserve the world's coral reefs.

References

Adjeroud M, Kayal M, Iborra-Cantonnet C, Vercelloni J, Bosserelle P, Liao V, Chancerelle Y, Claudet J, Penin L (2018) Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. Sci Rep 8:9680

Anthony KRN, Marshall PA, Abdulla A, Beeden R, Bergh C, Black R, Eakin CM, Game ET, Gooch M, Graham N, Green AL, Heron SF, van Hooidonk R, Knowland C, Mangubhai S, Marshall N, Maynard J, Mcginnity P, Mcleod E, Mumby P, Nyström M, Obura D, Oliver J, Possingham HP, Pressey RL, Rowlands GP, Tamelander J, Wachenfeld DR, Wear S (2015) Operationalizing resilience for adaptive coral reef management under global environmental change. Glob Chang Biol 21:48–61

Arnold SN, Steneck R, Mumby P (2010) Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105

Arthur R, Done TJ, Marsh H, Harriott VJ (2006) Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands. Coral Reefs 25:427–440

Ateweberhan M, Feary DA, Keshavmurthy S, Chen A, Schleyer MH, Sheppard C (2013) Climate change impacts on coral reefs: Synergies with local effects, possibilities for acclimation, and management implications. Mar Pollut Bull 74:526–539

Baker AC, Glynn PW, Riegl B (2008) Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. Estuar Coast Shelf Sci 80:435–471

Benkwitt CE, Wilson SK, Graham N (2019) Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. Glob Chang Biol 25:2619–2632

Brown BE, Suharsono (1990) Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. Coral Reefs 8:163–170

Bruno JF, Siddon C, Witman J, Colin P, Toscano M (2001) El Niño related coral bleaching in Palau, Western Caroline Islands. Coral Reefs 20:127–136

Buckley R, Stobart B, Downing N, Teleki K (2004) Aldabra Marine Programme Phase V. Report on the 2004 Aldabra Marine Programme research. Cambridge Coastal Research Unit

Burt J, Bartholomew A, Usseglio P (2008) Recovery of corals a decade after a bleaching event in Dubai, United Arab Emirates. Mar Biol 154:27–36

Cerutti J, Burt AJ, Haupt P, Bunbury N, Mumby P, Schaepman-Strub G (2020) Impacts of the 2014-2017 global bleaching event on a protected remote atoll in the Western Indian Ocean. Coral Reefs 39:15–26

Chong-Seng K, Graham N, Pratchett M (2014) Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33:449–461

Coté IM, Gardner TA, Hutchinson DJ, Watkinson AR (2006) New approaches to estimating recent ecological change on coral reefs. In: Coté I.M., Reynolds J.R. (eds) Coral Reef Conservation. Cambridge University Press, Cambridge, pp 293–313

Crochelet E, Roberts J, Lagabrielle E, Obura D, Petit M, Chabanet P (2016) A model-based assessment of reef larvae dispersal in the Western Indian Ocean reveals regional connectivity patterns — potential implications for conservation policies. Reg Stud Mar Sci 7:159–167

Darling ES, McClanahan TR, Côté IM (2013) Life histories predict coral community disassembly under multiple stressors. Glob Chang Biol 19:1930–1940

Diaz-Pulido G, McCook L (2002) The fate of bleached corals: Patterns and dynamics of algal recruitment. Mar Ecol Prog Ser 232:115–128

Diaz-Pulido G, McCook L, Dove S, Berkelmans R, Roff G, Kline DI, Weeks S, Evans RD, Williamson DH, Hoegh-guldberg O (2009) Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. PLoS One

Done TJ (1982) Patterns in the distribution of coral communities across the central Great Barrier Reef. Coral Reefs 1:95–107

Donner SD (2011) An evaluation of the effect of recent temperature variability on the prediction of coral bleaching events. Ecol Appl 21:1718–1730

Drew E (1977) A photographic survey down the seaward reef-front of Aldabra Atoll. Atoll Res Bull 193:1–17

Eakin CM, Sweatman HPA, Brainard RE (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38:539–545

Edmunds PJ (1994) Evidence that reef-wide patterns of coral bleaching may be the result of the distribution of bleaching-susceptible clones. Mar Biol 121:137–142

Farrow GE, Brander KM (1971) Tidal studies on Aldabra. Philos Trans R Soc London B 260:93–121

Fisher R, Bessell-Browne P, Jones RJ (2019) Synergistic and antagonistic impacts of suspended sediments and thermal stress on corals. Nat Commun 10:2346

Ford AK, Eich A, McAndrews RS, Mangubhai S, Nugues MM, Bejarano S, Moore BR, Rico C, Wild C, Ferse SCA (2018) Evaluation of coral reef management effectiveness using conventional versus resilience-based metrics. Ecol Indic 85:308–317

Fox MD, Carter AL, Edwards C, Takeshita Y, Johnson MD, Petrovic V, Amir CG, Sala E, Sandin S, Smith J (2019) Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. Coral Reefs 38:701–712

Friedlander A, Ballesteros E, Beets J, Brown BE, Fay JM, Haupt P, Henning B, Rose P, Sala E (2015) Biodiversity and ecosystem health of the Aldabra Group, southern Seychelles: Scientific report to the government of Seychelles.

Furby KA, Bouwmeester J, Berumen ML (2013) Susceptibility of central Red Sea corals during a major bleaching event. Coral Reefs 32:505–513

Gilmour J, Smith LD, Heyward AJ, Baird AH, Pratchett M (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71

Goatley CHR, Bellwood DR (2011) The Roles of Dimensionality, Canopies and Complexity in Ecosystem Monitoring. PLoS One 6:e27307

Golbuu Y, Victor S, Penland L, Idip D, Emaurois C, Okaji K, Yukihira H, Iwase A, van Woesik R (2007) Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. Coral Reefs 26:319–332

Gouezo M, Golbuu Y, Fabricius K, Olsudong D, Mereb G, Nestor V, Wolanski E, Harrison PL, Doropoulos C (2019) Drivers of recovery and reassembly of coral reef communities. Proc R Soc B 286:20182908

Gove JM, Williams GJ, McManus MA, Clark SJ, Ehses JS, Wedding LM (2015) Coral reef benthic regimes exhibit non-linear threshold responses to natural physical drivers. Mar Ecol Prog Ser 522:33–48

Graham N, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97

Graham N, Nash KL, Kool JT (2011) Coral reef recovery dynamics in a changing world. Coral Reefs 30:283–294

Grottoli AG, Rodrigues LJ, Palardy JE (2006) Heterotrophic plasticity and resilience in bleached corals. Nature 440:1186–1189

Guzman HM, Cortés J (2007) Reef recovery 20 years after the 1982-1983 El Niño massive mortality. Mar Biol 151:401–411

Hagan AB, Spencer T (2008) Reef resilience and change 1998-2007, Alphonse Atoll, Seychelles. 388–392

Halekoh U, Højsgaard S, Yan J (2006) The R package geepack for generalized estimating equations. J Stat Softw 15:1–11

Hamylton S, Hagan A, Bunbury N, Fleischer-Dogley F, Spencer T (2018) Mapping the lagoon at Aldabra Atoll, Western Indian Ocean. Atoll Res Bull 619:45–59

Head C, Bayley DT., Rowlands G., Roche R, Tickler D., Roger A., Koldewey H, Turner J, Andradi-Brown DA (2019) Coral bleaching impacts from back-to-back 2015–2016 thermal anomalies in the remote central Indian Ocean. Coral Reefs 38:605–618

Hoey A, Howells E, Johansen JL, Hobbs JPA, Messmer V, McCowan DM, Wilson SK, Pratchett M (2016) Recent advances in understanding the effects of climate change on coral reefs. Diversity 8:1–22

Van Hooidonk R, Maynard JA, Manzello D, Planes S (2014) Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. Glob Chang Biol 20:103–112

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 J, Graham N, Harrison H, Hobbs JPA, Hoey A, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

Hughes TP, Bellwood DR, Baird AH, Brodie J, Bruno JF, Pandolfi JM (2011) Shifting baselines, declining coral cover, and the erosion of reef resilience: Comment on Sweatman et al. (2011). Coral Reefs 30:653–660

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey A, Hoogenboom M, Liu G, McWilliam MJ, Pears RJ, Pratchett M, Skirving WJ, Stella JS, Torda G (2018b) Global warming transforms coral reef assemblages. Nature 556:492–496

Huston M (1985) Variation in coral growth rates with depth at Discovery Bay, Jamaica. Coral Reefs 4:19–25

Iluz D, Vago R, Chadwick NE, Hoffman R, Dubinsky Z (2008) Seychelles Lagoon Provides Corals with a Refuge from Bleaching. Res Lett Ecol 2008:1–4

Johns KA, Emslie MJ, Hoey A, Osborne K, Jonker MJ, Cheal AJ (2018) Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9:e02349

Johns KA, Osborne KO, Logan M (2014) Contrasting rates of coral recovery and reassembly in coral communities on the Great Barrier Reef. Coral Reefs 33:553–563

Kohler KE, Gill SM (2006) Coral Point Count with Excel extensions (CPCe): a visual basic program for the determination of coral and substrate coverage using random point count methodology. Comput Geosci 32:1259–1269

Lenth R V. (2016) Least-squares means: The R package lsmeans. J Stat Softw 69:1–33

Liu G, Rauenzahn J, Heron SF, Eakin C, Skirving W, Christensen T, Strong A, Li J (2013) NOAA Technical Report NESDIS 143. NOAA Coral Reef Watch 50 km satellite sea surface temperature-based decision support system for coral bleaching management.

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

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163

McClanahan TR, Maina J, Starger CJ, Herron-Perez P, Dusek E (2005) Detriments to post-bleaching recovery of corals. Coral Reefs 24:230–246

Mizerek TL, Baird AH, Madin JS (2018) Species traits as indicators of coral bleaching. Coral Reefs 37:791–800

Morgan KM, Perry CT, Johnson JA, Smithers SG (2017) Nearshore turbid-zone corals exhibit high bleaching tolerance on the Great Barrier Reef following the 2016 ocean warming event. Front Mar Sci 4:224

Mumby P, Chisholm JRM, Edwards AJ, Clark CD, Roark EB, Andrefouet S, Jaubert J (2001) Unprecedented bleaching-induced mortality in *Porites* spp. at Rangiroa Atoll, French Polynesia. Mar Biol 139:183–189

Nakamura T, Van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301–304

Norström A V., Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral-macroalgal phase shifts. Mar Ecol Prog Ser 376:293–306

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Wagner H (2013) Package vegan: community ecology package 2.5-1.

Oliver T, Palumbi SR (2011) Do fluctuating temperature environments elevate coral thermal tolerance? Coral Reefs 30:429–440

Onset Computer Corporation (2012) HOBO Water Temp Pro v2 (U22-001) Manual.

Palardy JE, Rodrigues LJ, Grottoli AG (2008) The importance of zooplankton to the daily metabolic carbon requirements of healthy and bleached corals at two depths. J Exp Mar Bio Ecol 367:180–188

Pratchett M, Anderson KD, Hoogenboom M, Widman E, Baird AH, Pandolfi JM, Edmunds PJ, Lough JM (2015) Spatial, temporal and taxonomic variation in coral growth - implications for the structure and function of coral reef ecosystems. In: Hughes R.N., Hughes D.J., Smith I.P., Dale A.C. (eds) Oceanography and marine biology: An annual review. CRC Press, pp 215–295

Pratchett M, McCowan D, Maynard JA, Heron SF (2013) Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. PLoS One 8:1–10

R Core Team (2019) R: A Language and Environment for Statistical Computing.

Robinson JPW, Wilson SK, Graham N (2019) Abiotic and biotic controls on coral recovery 16 years after mass bleaching. Coral Reefs 38:1255–1265

Rowan R (2004) Thermal adaptation in reef coral symbionts. Nature 430:742

Safaie A, Silbiger NJ, McClanahan TR, Pawlak G, Barshis DJ, Hench JL, Rogers JS, Williams GJ, Davis KA (2018) High frequency temperature variability reduces the risk of coral bleaching. Nat Commun 9:1671

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. PNAS 105:10444–10449

Sandin SA, Smith J, DeMartini EE, Dinsdale EA, Donner SD, Friedlander A, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and degradation of coral reefs in the Northern Line Islands. PLoS One 3:e1548; 10.1371/journal.pone.0001548

Sheppard C, Harris A, Sheppard A (2008) Archipelago-wide coral recovery patterns since 1998 in the Chagos Archipelago, central Indian Ocean. Mar Ecol Prog Ser 362:109–117

Sheppard C, Sheppard A (2019) British Indian Ocean Territory (Chagos Archipelago). In: Sheppard C. (eds) World Seas: an Environmental Evaluation. Volume II: The Indian Ocean to the Pacific. Academic Press, pp 237–252

Smith J, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Smith JE, Brainard R, Carter A, Grillo S, Edwards C, Harris J, Lewis L, Obura D, Rohwer F, Sala E, Vroom PS, Sandin S (2016) Re-evaluating the health of coral reef communities: baselines and evidence for human impacts across the central pacific. Proc R Soc B 283:1–9

Stimson J, Sakai K, Sembali H (2002) Interspecific comparison of the symbiotic relationship in corals with high and low rates of bleaching-induced mortality. Coral Reefs 21:409–421

Stobart B, Buckley R, Leclair L, Teleki K, Downing N, Souter D, Callow M (2002) Aldabra: Monitoring the path to recovery. In: Lindén O., Souter D., Wilhelmsson D., Obura D. (eds) Coral Degradation in the Indian Ocean: Status Report 2002. CORDIO, Department of Biology and Environmental Science, University of Kalmar, Kalmar, pp 232–247

Stobart B, Teleki K, Buckley R, Downing N, Callow M (2005) Coral recovery at Aldabra Atoll, Seychelles: five years after the 1998 bleaching event. Philos Trans R Soc A Math Phys Eng Sci 363:251–255

Šúr M, Bunbury N, Van De Crommenacker J (2013) Frigatebirds on Aldabra Atoll: population census, recommended monitoring protocol and sustainable tourism guidelines. Bird Conserv Int 23:214–220

Taylor JD (1971) Intertidal zonation at Aldabra Atoll. Philos Trans R Soc London B 260:173–213

Wickham H (2016) ggplot2 - Elegant graphics for data analysis (2nd edition). J Stat Softw 77:3–5

Williams G, Gove J, Eynaud Y, Zgliczynski BJ, Sandin S (2015) Local human impacts decouple natural biophysical relationships on Pacific coral reefs. Ecography 38:751–761

Wilson SK, Robinson JPW, Chong-Seng K, Robinson J, Graham N (2019) Boom and bust of keystone structure on coral reefs. Coral Reefs 38:625–635

Woesik R, Houk P, Isechal AL, Idechong JW, Victor S, Golbuu Y (2012) Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. Ecol Evol 2:2474–2484

Yadav S, Rathod P, Alcoverro T, Arthur R (2016) “Choice” and destiny: the substrate composition and mechanical stability of settlement structures can mediate coral recruit fate in post-bleached reefs. Coral Reefs 35:211–222

Supplementary Material

Table S1: Bleaching impact on benthic categories. Effect of location (western seaward, eastern seaward, lagoon) and year (2014, 2016) on selected benthic categories at shallow and deep reefs. Degrees of freedom (dF), chi-square-value ($\chi2$) and *p*-value obtained from GEE model comparisons with ANOVA (type I). Where two error distributions are shown, grey coloured text corresponds to the analysis of deep locations. Significance levels: * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant: $p > 0.05$. CCA = crustose coralline algae.

			shallow			deep		
Category	Error distribution (link function)	Fixed factor	dF	$\chi2$	*p*	dF	$\chi2$	*p*
Hard coral	Gamma (inverse) Gamma (log)	Location	2	3.6	ns	1	4.0	*
		Year	1	10.9	***	2	7.5	**
		Location:Year	2	6.21	*	2	1.2	ns
Soft coral	Gamma (log)	Location	2	10.1	**	1	1.8	ns
		Year	1	31.6	***	2	27.9	***
		Location:Year	2	2.3	ns	2	1.5	ns
CCA	Gamma (log)	Location	2	5.6	ns	1	0.6	ns
		Year	1	11.9	**	2	33.9	***
		Location:Year	2	1.6	ns	2	0.3	ns
Turf algae	Gamma (log)	Location	2	40.6	***	1	>0.0	ns
		Year	1	5.6	*	2	3.2	ns
		Location:Year	2	2.3	ns	2	4.5	*
Halimeda	Binomial (logit)	Location	2	14.9	***	1	11.4	***
		Year	2	0.1	ns	2	>0.0	ns
		Location:Year	1	13.2	**	2	1.9	ns

Table S2: Bleaching impact on coral categories. Effect of location (western seaward, eastern seaward, lagoon) and year (2014, 2016) on selected coral categories at shallow and deep reefs. Degrees of freedom (dF), chi-square-value ($\chi 2$) and p-value obtained from GEE model comparisons with ANOVA (type I). Where two error distributions are shown, grey coloured text corresponds to the analysis of deep locations. Significance levels: * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant: $p > 0.05$.

Category	Error distribution (link function)	Fixed factor	shallow			deep		
			dF	$\chi 2$	*p*	dF	$\chi 2$	*p*
Acropora	Gamma (log)	Location	2	13.5	***	1	3.9	*
		Year	1	31.6	***	1	17.1	***
		Location:Year	2	1	ns	1	1.6	ns
Montipora	Gamma (log)	Location	2	14.5	***	1	0.7	ns
		Year	1	14.2	***	1	31.5	***
		Location:Year	2	2.9	ns	1	0.1	ns
Isopora palifera	Gamma (log)	Location	2	10.2	**	1	0.5	ns
		Year	1	1	ns	1	0.1	ns
		Location:Year	2	12.9	**	1	0.3	ns
Merulinidae	Gamma (log)	Location	2	7.9	*	1	9.2	**
		Year	1	8.9	**	1	10.6	**
		Location:Year	2	0.2	ns	1	>0.0	ns
Porites massive	Gamma (log) Gamma (inverse)	Location	2	2.3	ns	1	3.2	ns
		Year	1	0.7	ns	1	0.0	ns
		Location:Year	2	1.2	ns	1	6.7	*
Porites branching	Gamma (log)	Location	2	61.2	***	1	1.6	ns
		Year	1	143	***	1	16.2	***
		Location:Year	2	99.9	***	1	>0.0	ns
other hard corals	Binomial (logit)	Location	2	1.2	ns	1	2.4	ns
		Year	1	3.7	ns	1	1.8	ns
		Location:Year	2	2.8	ns	1	0.3	ns
Rhytisma	Gamma (inverse) Gamma (log)	Location	2	122	***	1	9.0	**
		Year	1	6.1	*	1	925	***
		Location:Year	2	5.7	ns	1	8.0	**
other soft corals	Gamma (log)	Location	2	13.3	**	1	0.7	ns
		Year	1	19.6	***	1	6.9	**
		Location:Year	2	0.4	ns	1	0.6	ns

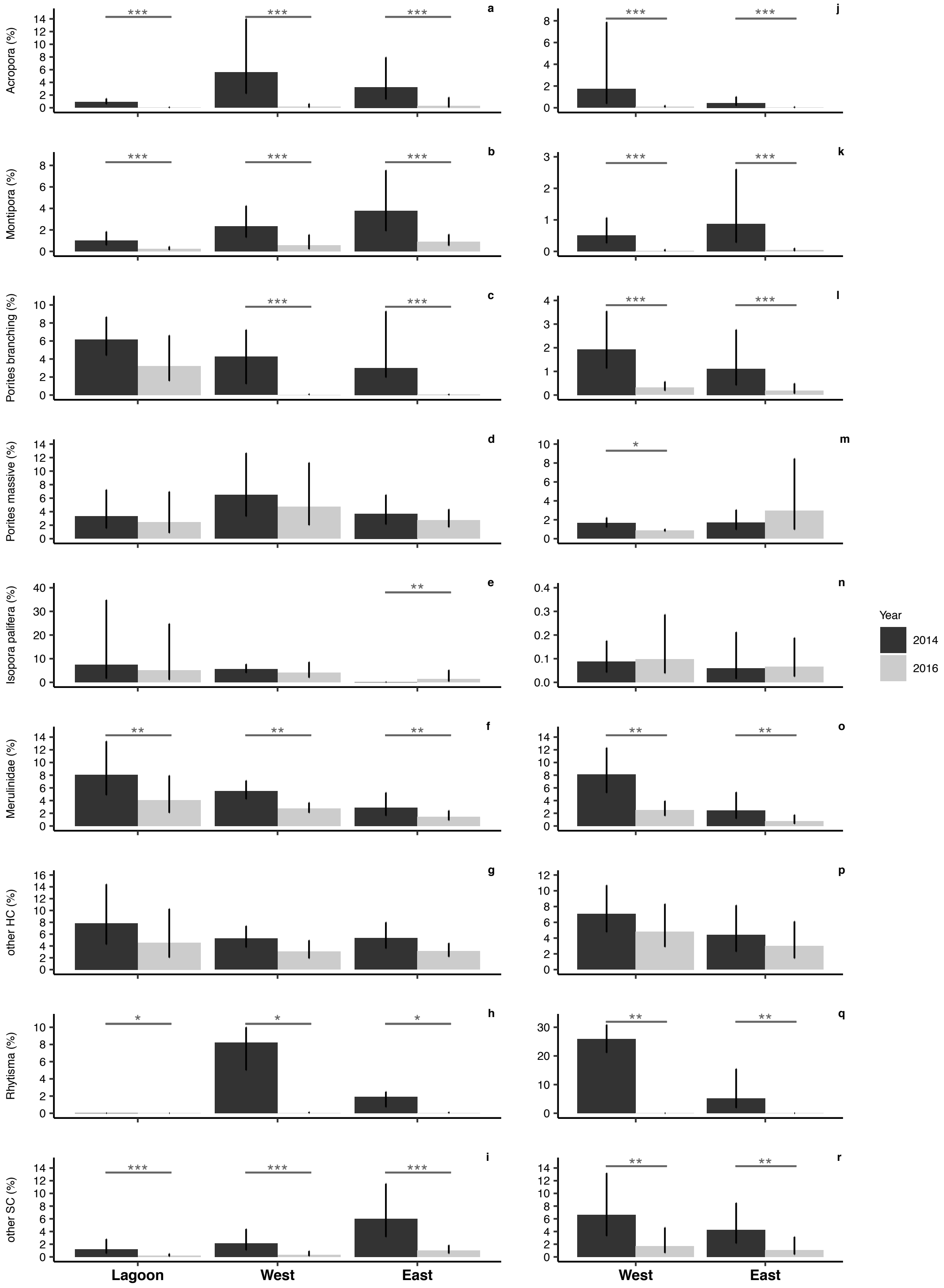


Figure S1: Mean cover of coral taxa at shallow (a–i) and deep locations (j–r) between 2014 and 2016 at Aldabra (transect sections: lagoon n = 6, west n = 10 per depth, east n = 8 per depth). Bars represent back–transformed estimates of GEE analysis with 95% confidence interval. Significant differences across years are indicated with asterisks (* $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$)

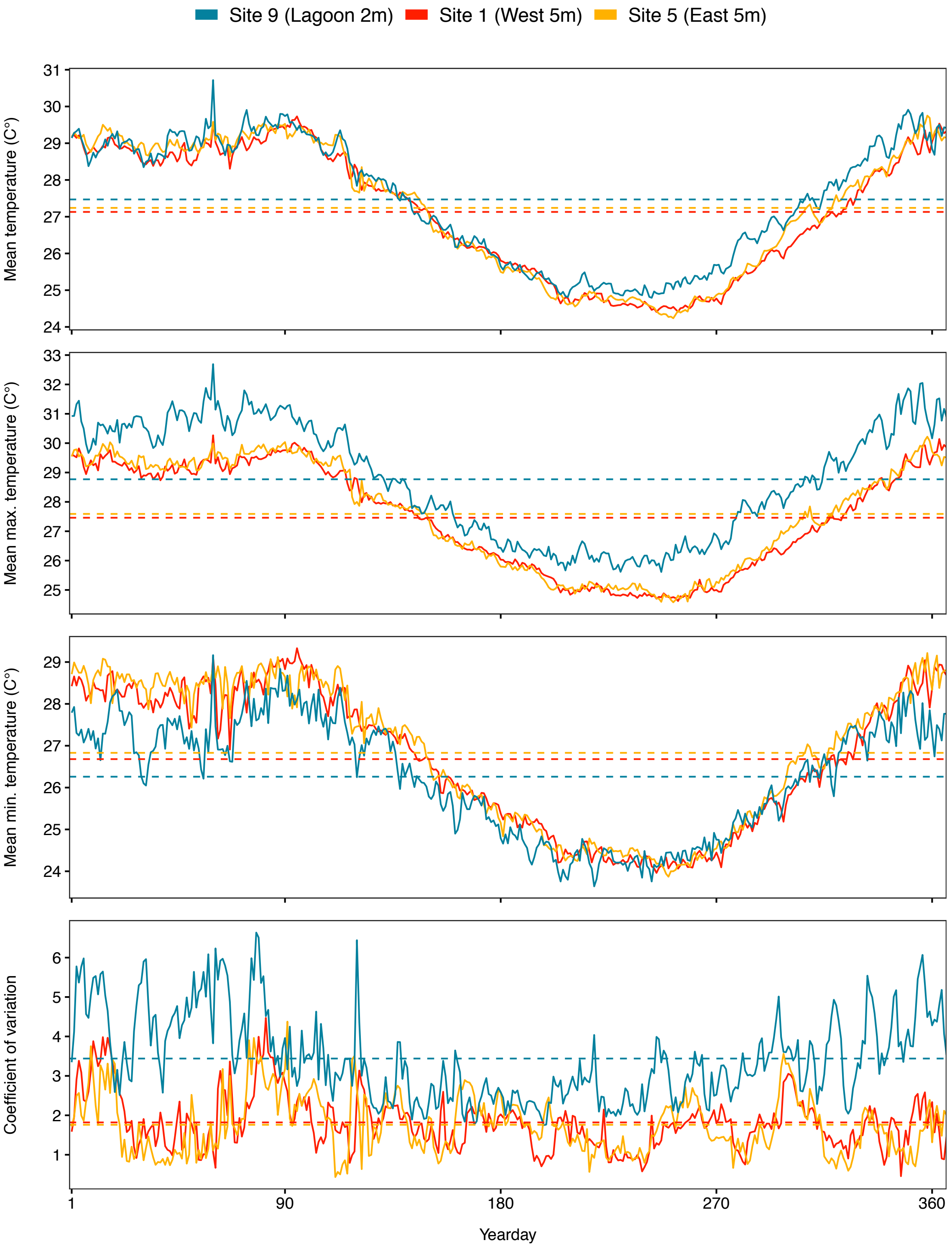


Figure S2: Annual mean daily water temperature (mean, maximum, minimum) and coefficient of variation at three representative sites in the lagoon and at the seaward west and east of Aldabra. Solid lines indicate daily means calculated from temperature records obtained in 30−min intervals between February 2015 and November 2018 (see methods). Dashed lines represent the mean within the study period.

Table S3: Post-bleaching trajectories of benthic categories. Effect of location (western seaward, eastern seaward, lagoon) and year (2016, 2017, 2018, 2019) on selected benthic categories at shallow and deep reefs. Degrees of freedom (dF), chi-square-value ($\chi2$) and p-value obtained from GEE model comparisons with ANOVA (type I). Significance levels: * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant: $p > 0.05$. CCA = crustose coralline algae.

			shallow			deep		
Category	Error distribution (link function)	Fixed factor	dF	$\chi2$	p	dF	$\chi2$	p
Hard coral	Gamma (log)	Location	2	97.2	***	1	28.4	***
		Year	3	15.2	**	3	0.5	ns
		Location:Year	6	1.1	ns	3	3.2	ns
Soft coral	Gamma (log)	Location	2	36	***	1	11.1	***
		Year	3	2.3	ns	3	3.0	ns
		Location:Year	6	5.2	ns	3	3.3	ns
CCA	Gamma (log)	Location	2	3.4	ns	1	16	**
		Year	3	3.4	ns	3	6.1	ns
		Location:Year	6	14.4	*	3	10.0	ns
Turf algae	Gamma (log)	Location	2	34.7	***	1	29.7	***
		Year	3	19.7	***	3	9.5	*
		Location:Year	6	4.6	ns	3	10.3	*
Halimeda	Binomial (logit)	Location	2	72.9	***	1	85.3	***
		Year	3	4.9	ns	3	4.6	ns
		Location:Year	6	3.0	ns	3	5.3	ns

Table S4: Post-bleaching trajectories of coral categories. Effect of location (western seaward, eastern seaward, lagoon) and year (2016, 2017, 2018, 2019) on selected coral categories at shallow reefs. Degrees of freedom (dF), chi-square-value ($\chi 2$) and p-value obtained from GEE model comparisons with ANOVA (type I). Significance levels: * $p < 0.5$; ** $p < 0.01$; *** $p < 0.001$; ns = not significant: $p > 0.05$. All categories from deep locations and *Rhytisma* from shallow locations had poor model fit and could not be tested statistically.

Category	Error distribution (link function)	Fixed factor	dF	χ2	*p*
Acropora	Binomial (logit)	Location	2	6.7	*
		Year	3	0.4	ns
		Location:Year	6	3.8	ns
Montipora	Binomial (logit)	Location	2	14.2	***
		Year	3	16.5	***
		Location:Year	6	2.1	ns
Isopora palifera	Binomial (logit)	Location	2	10.2	**
		Year	3	1.1	ns
		Location:Year	6	0.3	ns
Merulinidae	Binomial (logit)	Location	2	10.1	**
		Year	3	1.4	ns
		Location:Year	6	3.3	ns
Porites massive	Binomial (logit)	Location	2	9.6	**
		Year	3	>0.0	ns
		Location:Year	6	0.3	ns
Porites branching	Binomial (logit)	Location	2	69.6	***
		Year	3	5.6	ns
		Location:Year	6	0.1	ns
other hard corals	Binomial (logit)	Location	2	10.2	**
		Year	3	5.1	ns
		Location:Year	6	3.4	ns
other soft corals	Binomial (logit)	Location	2	4.3	ns
		Year	3	2.2	ns
		Location:Year	6	6.1	ns

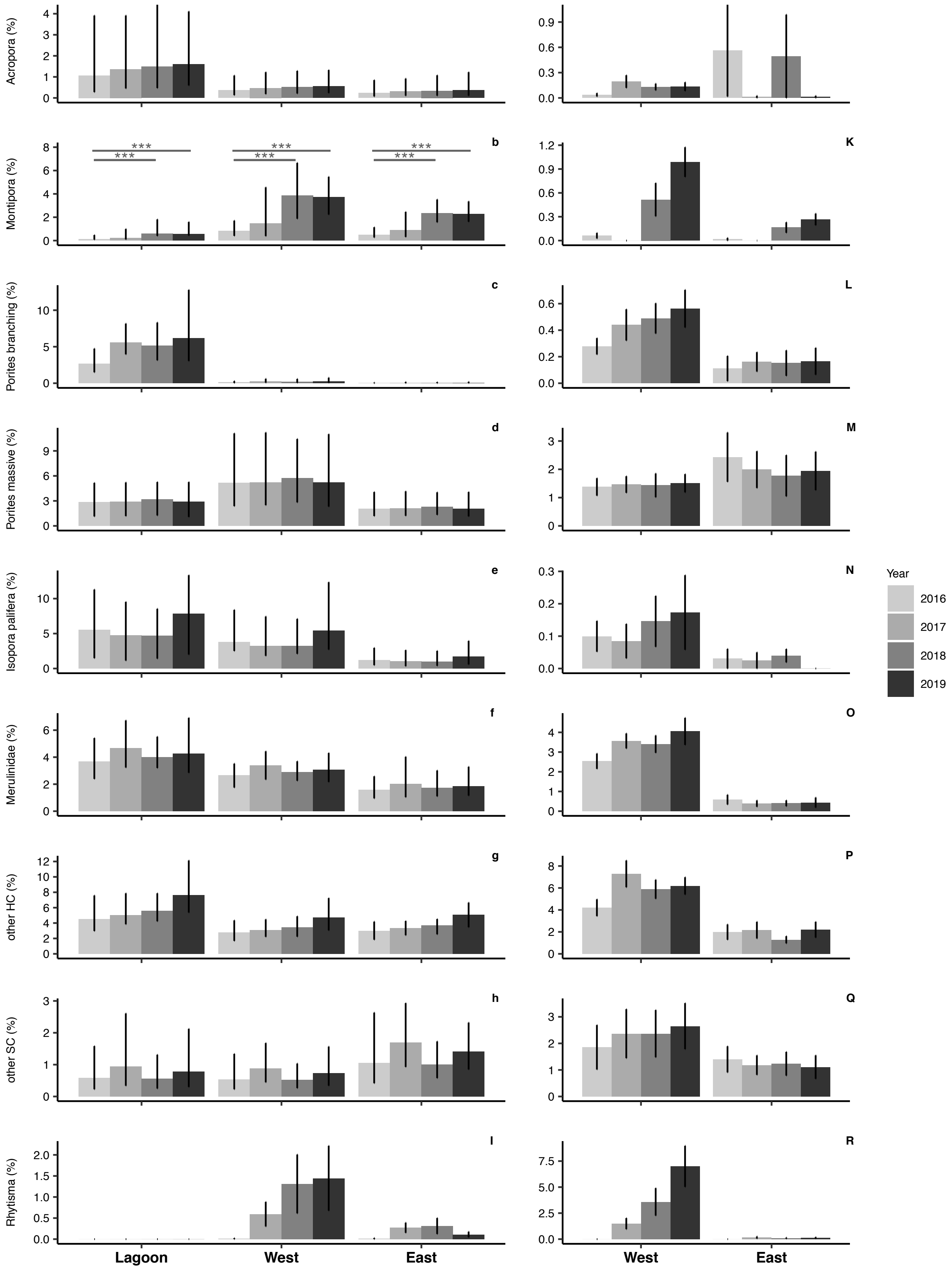


Figure S3: Mean cover of coral taxa at shallow (a–I) and deep locations (J–R) between 2016 and 2019 at Aldabra (transect sections: lagoon n = 9, west n = 15 per depth, east n = 12 per depth). Bars in plots a–h represent back–transformed estimates of GEE analysis with 95% confidence interval. Significant differences across years are indicated with asterisks (*** $p < 0.001$). Categories in plots I–R were not statistically tested due to poor model fit and are displayed as mean cover (± SE).

Table S5: Absolute percentage change in mean cover of coral taxa between 2016–2019 at Aldabra's shallow locations and the percent contribution to the change in overall hard coral cover. Taxa are sorted in descending order based on their contribution to overall change in hard coral cover. Note that values were obtained from back-transformed estimates of GEE analysis as displayed in Fig. S3, overall values displayed here (*) therefore slightly deviate from those obtained from GEE analysis of overall hard coral cover as displayed in Figure 2.4 and Table 2.2.

		Mean cover (%)		Absolute	Contribution to	Cumulated
Location	Taxa	2016	2019	Change (%)	overall change (%)	contribution (%)
Lagoon	*Porites* branching	2.68	6.35	3.67	36.06	36.06
	other hard coral	4.77	8.15	3.38	33.18	69.24
	Isopora palifera	4.18	5.34	1.15	11.32	80.56
	Merulinidae	3.61	4.46	0.85	8.34	88.91
	Montipora	0.20	0.84	0.64	6.32	95.23
	Acropora	1.05	1.58	0.53	5.16	100.39
	Porites massive	2.44	2.40	-0.04	-0.39	100.00
	Overall*	18.93	29.11	10.19	100.00	
West shallow	*Montipora*	0.83	3.50	2.67	39.38	39.38
	other hard coral	2.72	4.71	1.99	29.36	68.75
	Isopora palifera	4.63	5.90	1.27	18.72	87.47
	Merulinidae	2.48	3.07	0.59	8.71	96.18
	Acropora	0.37	0.56	0.19	2.77	98.95
	Porites branching	0.10	0.25	0.15	2.23	101.18
	Porites massive	5.23	5.15	-0.08	-1.18	100.00
	Overall*	16.37	23.14	6.78	100.00	
East shallow	other hard coral	2.78	4.81	2.03	43.76	43.76
	Montipora	0.55	2.32	1.78	38.31	82.07
	Merulinidae	1.57	1.95	0.38	8.19	90.26
	Isopora palifera	1.19	1.53	0.34	7.37	97.63
	Acropora	0.24	0.37	0.12	2.65	100.28
	Porites branching	0.01	0.03	0.02	0.36	100.65
	Porites massive	2.20	2.17	-0.03	-0.65	100.00
	Overall*	8.54	13.18	4.64	100.00	

Table S6: Post-bleaching hard coral recovery of 52 reefs at 11 locations worldwide. Overall values at each location are grand means obtained from reef level data (unless given in reference). Locations are sorted in ascending order by number of recovery years.

Location (bleaching event)	Pre-bleaching mean cover (%)	First record post-bleaching		Last record post-bleaching		No recovery years	Recovery (%)[b]	Annual rate of change (%)	Dominant recovery taxa	Level of protection (year of designation)
		Year	Mean cover (%)	Year	Mean cover (%)					
Alphonse Atoll, Seychelles (1997/98)[1]	20-40	2001	17.9	2003	23.7	2	56.5-113	2.9	Pcp, Acr, Por ms	
East (5–15 m)	n.a.	—"—	18.2	—"—	22.2	—"—	n.a.	2.0	n.a.	
West (5–15 m)	—"—	—"—	17.6	—"—	25.2	—"—	—"—	3.8	—"—	
Aldabra Atoll, Seychelles (2015/16)[a]	30.2	2016	15.4	2019	22.0	3	71.4	2.2		Special Reserve (1981)
Lagoon (2 m)	32.3	—"—	21.0	—"—	30.0	—"—	92.9	3.0	Por br	—"—
Seaward west (5 m)	34.1	—"—	16.2	—"—	23.1	—"—	67.7	2.3	Mon	—"—
Seaward east (5 m)	24.1	—"—	9.1	—"—	12.9	—"—	53.6	1.3	Mon	—"—
Kenya (1997/98)[2,3]	31.3	1999	10.7	2002	17.7	3	56.4	2.3		
Malindi (lagoon, 2 m)	45.0	—"—	9.0	—"—	17.0	—"—	37.8	2.7	Por br, Pav	No-take MNP (mid 1970s)
Watamu (lagoon, 2 m)	38.0	—"—	10.0	—"—	13.0	—"—	34.2	1.0	Mon, Glx	No-take MNP (mid 1970s)
Mombasa (lagoon, 2 m)	43.0	—"—	14.0	—"—	25.0	—"—	58.1	3.7	Por br, Pav, Mon, Glx	No-take MNP (1991)
Vipingo (lagoon, 2 m)	20.0	—"—	11.0	—"—	23.0	—"—	115.0	4.0	Por br	
Kanamai (lagoon, 2 m)	24.0	—"—	17.0	—"—	23.0	—"—	95.8	2.0	—"—	
Ras Iwatine (lagoon, 2 m)	18.0	—"—	3.0	—"—	5.0	—"—	27.8	0.7	—"—	
Lakshadweep Islands, India (1997/98)[4,5]	60-90	2000	9.0	2003	19.4	3	21-32	3.5		
Agatti west (5–12 m)	n.a.	—"—	13.0	—"—	34.0	—"—	n.a.	7.0	Acr	
Kadmat west (5–12 m)	—"—	—"—	5.0	—"—	19.0	—"—	—"—	4.7	—"—	
Kavaratti west (5–12 m)	—"—	—"—	18.0	—"—	26.0	—"—	—"—	2.7	—"—	
Agatti east (5–12 m)	—"—	—"—	5.0	—"—	11.0	—"—	—"—	2.0	Not mentioned	
Kadmat east (5–12 m)	—"—	—"—	4.0	—"—	7.0	—"—	—"—	1.0	—"—	
Maldives (1997/98)[4]	n.a.	1998	2.9	2002	12.2	4	n.a.	2.3		
Bandos (reef flat, 1–2 m)	—"—	—"—	1.9	—"—	6.9	—"—	—"—	1.3	Pcp	
Fesdoo (reef flat, 1–2 m)	—"—	—"—	3.3	—"—	22.1	—"—	—"—	4.7	—"—	

(continued on next page)

Table S6 (continued)

Location (bleaching event)	Pre-bleaching mean cover (%)	First record post-bleaching		Last record post-bleaching		No. recovery years	Recovery (%)[b]	Annual rate of change (%)	Dominant recovery taxa	Level of protection (year of designation)
		Year	Mean cover (%)	Year	Mean cover (%)					
Gan (reef flat, 1–2 m)	—"—	—"—	4.0	—"—	12.9	—"—	—"—	2.2	—"—	
Villingili (reef flat, 1–2 m)	—"—	—"—	4.3	—"—	13.2	—"—	—"—	2.2	—"—	
Kooddoo (reef flat, 1–2 m)	—"—	—"—	1.0	—"—	6.0	—"—	—"—	1.3	—"—	
Sri Lanka (1997/98)[4]	72.6	1999	12.0	2004	32.8	5	40.2	4.2		
Bar Reef (0–3 m)	78.5	—"—	1.0	—"—	17.7	—"—	22.5	3.3	Pcp, Acr	Marine Sanctuary (1992)
Hikkaduwa (0–3 m)	47.2	—"—	7.0	—"—	10.1	—"—	21.4	0.6	Mon	
Weligama (0–3 m)	92.0	—"—	28.0	—"—	70.6	—"—	76.7	8.5	Acr	
Thousand Islands, Indonesia (1982/83)[6]	24.0	1983	2.5	1988	12.5	5	52.1	2.0		
South Pari (reef flat)	22.0	—"—	3.0	—"—	14.0	—"—	63.6	2.2	Not mentioned	
South Tikus (reef flat)	26.0	—"—	2.0	—"—	11.0	—"—	42.3	1.8	Mon	
Palau (1997/98)[7,8]	34.4	2002	19.5	2010	36.1	8	105.0	2.1		
Outer reef west (3 m)	28.3	—"—	13.0	—"—	30.0	—"—	105.9	2.1	Mon, Por, Mer	
Outer reef west (10 m)	31.0	—"—	25.0	—"—	50.0	—"—	161.3	3.1	—"—	
Outer reef east (3 m)	n.a.	—"—	11.0	—"—	35.0	—"—	n.a.	3.0	—"—	
Outer reef east (10 m)	—"—	—"—	18.0	—"—	35.0	—"—	—"—	2.1	—"—	
Patch reef (3 m)	—"—	—"—	7.5	—"—	25.0	—"—	—"—	2.2	Acr, Por	
Patch reef (10 m)	—"—	—"—	2.6	—"—	15.0	—"—	—"—	1.6	Acr, Por, Aga	
Inner reef (3 m)	43.5	—"—	45.0	—"—	59.0	—"—	135.6	1.8	Por	
Inner reef (10 m)	34.8	—"—	34.0	—"—	40.0	—"—	115.1	0.8	Por, Mer	
Inner Islands, Seychelles (1997/98)[9]	26.2	2005	11.4	2014	27.4	9	126.4	1.8		
Mahe E Patch (reef slope)	19.0	—"—	6.0	—"—	7.0	—"—	36.8	0.1	Acr	
Mahe NW Carbonate (reef slope)	39.0	—"—	10.0	—"—	38.0	—"—	97.4	3.1	—"—	No-take MNP (1979)[10]
Mahe W Carbonate (reef slope)	34.0	—"—	16.0	—"—	38.0	—"—	111.8	2.4	—"—	
Praslin NE Patch (reef slope)	26.0	—"—	5.0	—"—	9.0	—"—	34.6	0.4	Acr, Pcp	No-take MNP (1979)[10]
Ste Anne Granite (reef slope)	40.0	—"—	14.0	—"—	14.0	—"—	35.0	0.0	—"—	No-take MNP (1973)[10]

(continued on next page)

Table S6 (continued)

Location (bleaching event)	Pre-bleaching mean cover (%)	First record post-bleaching		Last record post-bleaching		No recovery years	Recovery (%)[b]	Annual rate of change (%)	Dominant recovery taxa	Level of protection (year of designation)
		Year	Mean cover (%)	Year	Mean cover (%)					
Ste Anne Patch (reef slope)	55.0	—"—	8.0	—"—	43.0	—"—	78.2	3.9	Acr	No-take MNP (1973)[10]
Mahe NW Granite (reef slope)	11.0	—"—	10.0	—"—	36.0	—"—	327.3	2.9	Acr, Pcp	
Mahe NW Patch (reef slope)	18.0	—"—	15.0	—"—	25.0	—"—	138.9	1.1	—"—	
Mahe W Granite (reef slope)	19.0	—"—	16.0	—"—	35.0	—"—	184.2	2.1	—"—	
Mahe W Patch (reef slope)	19.0	—"—	29.0	—"—	31.0	—"—	163.2	0.2	—"—	
Praslin NE Granite (reef slope)	16.0	—"—	4.0	—"—	22.0	—"—	137.5	2.0	Not mentioned	No-take MNP (1979)[10]
Praslin SW Granite (reef slope)	18.0	—"—	4.0	—"—	31.0	—"—	172.2	3.0	Acr, Pcp	
Chagos Archipelago, BIOT (1997/98)[11]	39.8	2001	12.3	2012	40.8	11	102.5	2.6		No-take MPA (2010)[12]
Seaward slopes (5 m)	43.0	—"—	10.0	—"—	36.0	—"—	83.7	2.4	Iso, Acr	—"—
Seaward slopes (10 m)	44.0	—"—	11.0	—"—	50.0	—"—	113.6	3.5	Acr	—"—
Seaward slopes (15 m)	44.0	—"—	15.0	—"—	39.0	—"—	88.6	2.2	Not mentioned	—"—
Seaward slopes (25 m)	28.0	—"—	13.0	—"—	38.0	—"—	135.7	2.3	—"—	—"—
Cocos Islands, Costa Rica (1982/83)[13]	31.9	1987	3.2	2002	21.2	15	66.5	1.2		
Chatham (3-18 m)	29.1	—"—	2.9	—"—	16.7	—"—	57.4	0.9	Por	
Presidio (9-24 m)	34.7	—"—	3.5	—"—	25.7	—"—	74.1	1.5	Por, Pav	

[a] This study

[b] Percentage of ‘last record post-bleaching mean cover’ on ‘pre-bleaching mean cover’

Pcp = *Pocillopora*, Acp = *Acropora*, Por = *Porites*, Pav = *Pavona*, Mon = *Montipora*, Glx = *Galaxea*, Aga = Agaricidae, ms = massive, br = branching

n.a. = not available

BIOT = British Indian Ocean Territory

MNP = Marine National Park

MPA = Marine Protected Area

References to Table S6

1. Hagan, A. B. & Spencer, T. Reef resilience and change 1998-2007, Alphonse Atoll, Seychelles, *Proceedings of the 11th International Coral Reef Symposium* (eds. Riegl, B. & Dodge, R.) 388–392 (Nova Southeastern University National Coral Reef Institute, 2008).
2. McClanahan, T. R., Maina, J., Starger, C. J., Herron-Perez, P. & Dusek, E. Detriments to post-bleaching recovery of corals. *Coral Reefs* **24**, 230–246 (2005).
3. Baker, A. C., Glynn, P. W. & Riegl, B. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuar. Coast. Shelf Sci.* **80**, 435–471 (2008).
4. Rezai, H., Wilson, S. K., Claereboudt, M. & Riegl, B. Coral reef status of the ROPME sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea in *Status of Coral Reefs of the World: 2004* (ed. Wilkinson, C.) 155–170 (Global Coral Reef Monitoring Network and Australian Institute of Marine Science, 2004).
5. Arthur, R., Done, T. J., Marsh, H. & Harriott, V. Local processes strongly influence post-bleaching benthic recovery in the Lakshadweep Islands. *Coral Reefs* **25**, 427–440 (2006).
6. Brown, B. E. & Suharsono. Damage and recovery of coral reefs affected by El Niño related seawater warming in the Thousand Islands, Indonesia. *Coral Reefs* **8**, 163–170 (1990).
7. Gouezo, M. *et al.* Drivers of recovery and reassembly of coral reef communities. *Proc. R. Soc. B.* **286**, 20182908 (2019).
8. Bruno, J. F., Siddon, C., Witman, J., Colin, P. & Toscano, M. El Niño related coral bleaching in Palau, Western Caroline Islands. *Coral Reefs* **20**, 127–136 (2001).
9. Robinson, J. P. W., Wilson, S. K. & Graham, N. Abiotic and biotic controls on coral recovery 16 years after mass bleaching. *Coral Reefs* **38**, 1255–1265 (2019).
10. Jennings, S., Marshall, S. S., Cuet, P. & Naim, O. Chapter 13. The Seychelles in *Coral Reefs of the Indian Ocean. Their Ecology and Conservation* (eds. McClanahan, T. R., Sheppard, C. R. C. & Obura, D. O.) 383–410 (Oxford University Press, 2000).
11. Sheppard, C. & Sheppard, A. British Indian Ocean Territory (Chagos Archipelago) in *World Seas: An Environmental Evaluation. Volume II: The Indian Ocean to the Pacific* (ed. Sheppard, C.) 237–252 (Academic Press, 2018).
12. Sheppard, C. R. C. *et al.* Reefs and islands of the Chagos Archipelago, Indian Ocean: why it is the world's largest no-take marine protected area. *Aquat. Conserv.* **22**, 232–261 (2012).
13. Guzman, H. M. & Cortés, J. Reef recovery 20 years after the 1982-1983 El Niño massive mortality. *Mar. Biol.* **151**, 401–411 (2007).

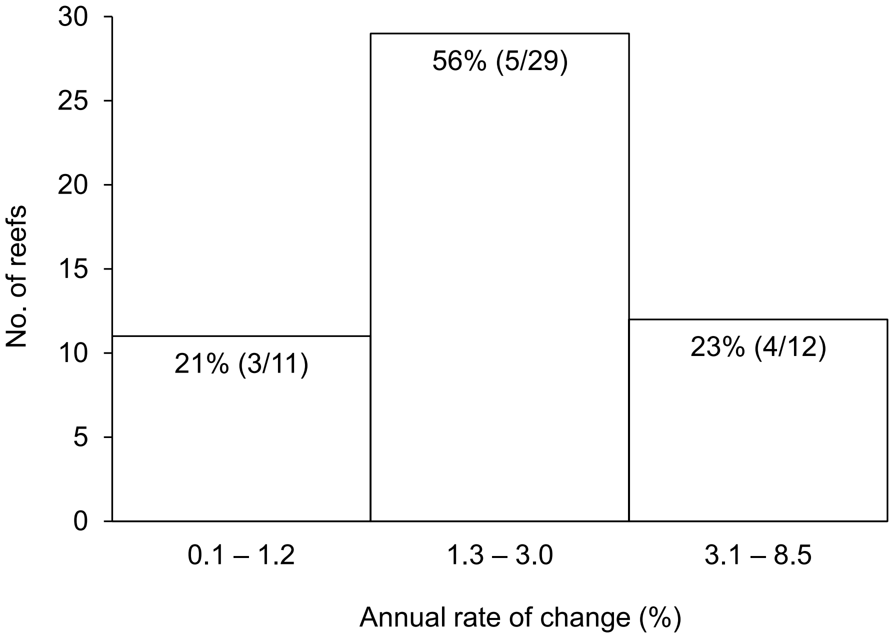


Figure S4: Histogram of the annual rates of change of the 52 reefs displayed in Table S6. Number of reefs (percentage on total shown in bins) with annual rates of change that fall within the same range as Aldabra's reefs (1.3–3.0%) as well as below and above. Values in brackets indicate the number of protected areas on the total number of reefs within the bin (reefs of the Chagos Archipelago not counted as protected area here as designation happened after the majority of recovery years).

Table S7: Cover of fleshy macroalgae between 2014 and 2019. Cover (mean ± SE) based on two (2014) and three (2016–2019) transect sections per site. At Site 5 (15 m) surveyed in December 2018, cover was entirely due to a *Caulerpa racemosa* bloom which had subsided by February 2019 (pers. obs. AK, February 2019).

Depth	Location	2014	2016	2017	2018	2019
2 m	**Lagoon**	**0.37 ± 0.19**	**0.06 ± 0.03**	**0.27 ± 0.12**	**0.46 ± 0.14**	**0.30 ± 0.11**
	Site 9	0.00 ± 0.00	0.12 ± 0.06	0.58 ± 0.27	0.32 ± 0.24	0.54 ± 0.20
	Site 10	0.51 ± 0.51	0.00 ± 0.00	0.22 ± 0.15	0.56 ± 0.21	0.30 ± 0.22
	Site 11	0.61 ± 0.23	0.06 ± 0.06	0.00 ± 0.00	0.50 ± 0.35	0.05 ± 0.05
5 m	**West**	**0.05 ± 0.02**	**0.02 ± 0.02**	**0.02 ± 0.02**	**0.18 ± 0.07**	**0.07 ± 0.03**
	Site 1	0.09 ± 0.09	0.06 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.17 ± 0.10
	Site 2	0.08 ± 0.08	0.00 ± 0.00	0.00 ± 0.00	0.05 ± 0.05	0.00 ± 0.00
	Site 6	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.31 ± 0.09	0.00 ± 0.00
	Site 7	0.08 ± 0.08	0.00 ± 0.00	0.11 ± 0.06	0.42 ± 0.27	0.11 ± 0.11
	Site 8	0.00 ± 0.00	0.06 ± 0.06	0.00 ± 0.00	0.11 ± 0.11	0.06 ± 0.06
	East	**0.01 ± 0.01**	**0.05 ± 0.05**	**0.00 ± 0.00**	**0.12 ± 0.12**	**0.13 ± 0.11**
	Site 3	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.06 ± 0.06
	Site 4	0.05 ± 0.05	0.19 ± 0.19	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
	Site 5	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.48 ± 0.48	0.45 ± 0.45
	Site 12	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00
15 m	**West**	**0.01 ± 0.01**	**0.55 ± 0.14**	**0.36 ± 0.10**	**0.40 ± 0.17**	**0.25 ± 0.05**
	Site 1	0.00 ± 0.00	0.61 ± 0.42	0.17 ± 0.08	0.06 ± 0.05	0.21 ± 0.12
	Site 2	0.00 ± 0.00	0.50 ± 0.27	0.17 ± 0.16	0.28 ± 0.11	0.01 ± 0.00
	Site 6	0.04 ± 0.04	0.66 ± 0.35	0.51 ± 0.29	1.30 ± 0.69	0.29 ± 0.11
	Site 7	0.00 ± 0.00	0.92 ± 0.42	0.71 ± 0.27	0.12 ± 0.05	0.41 ± 0.06
	Site 8	0.00 ± 0.00	0.08 ± 0.07	0.22 ± 0.14	0.22 ± 0.11	0.30 ± 0.16
	East	**0.00 ± 0.00**	**0.15 ± 0.06**	**1.53 ± 1.49**	**9.75 ± 5.70**	**0.02 ± 0.01**
	Site 3	0.00 ± 0.00	0.07 ± 0.06	0.01 ± 0.00	0.06 ± 0.05	0.07 ± 0.06
	Site 4	0.00 ± 0.00	0.25 ± 0.16	0.12 ± 0.06	0.01 ± 0.00	0.01 ± 0.00
	Site 5	0.00 ± 0.00	0.27 ± 0.18	5.97 ± 5.96	38.93 ± 12.11	0.01 ± 0.00
	Site 12	0.00 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00	0.01 ± 0.00

Equation 1 and 2

To further assess reef recovery, we calculated the annual rate of change in absolute hard coral cover increase (C_{RC}) following Coté et al[14]:

$$C_{RC} = \frac{C_{END} - C_{START}}{Y} \tag{1}$$

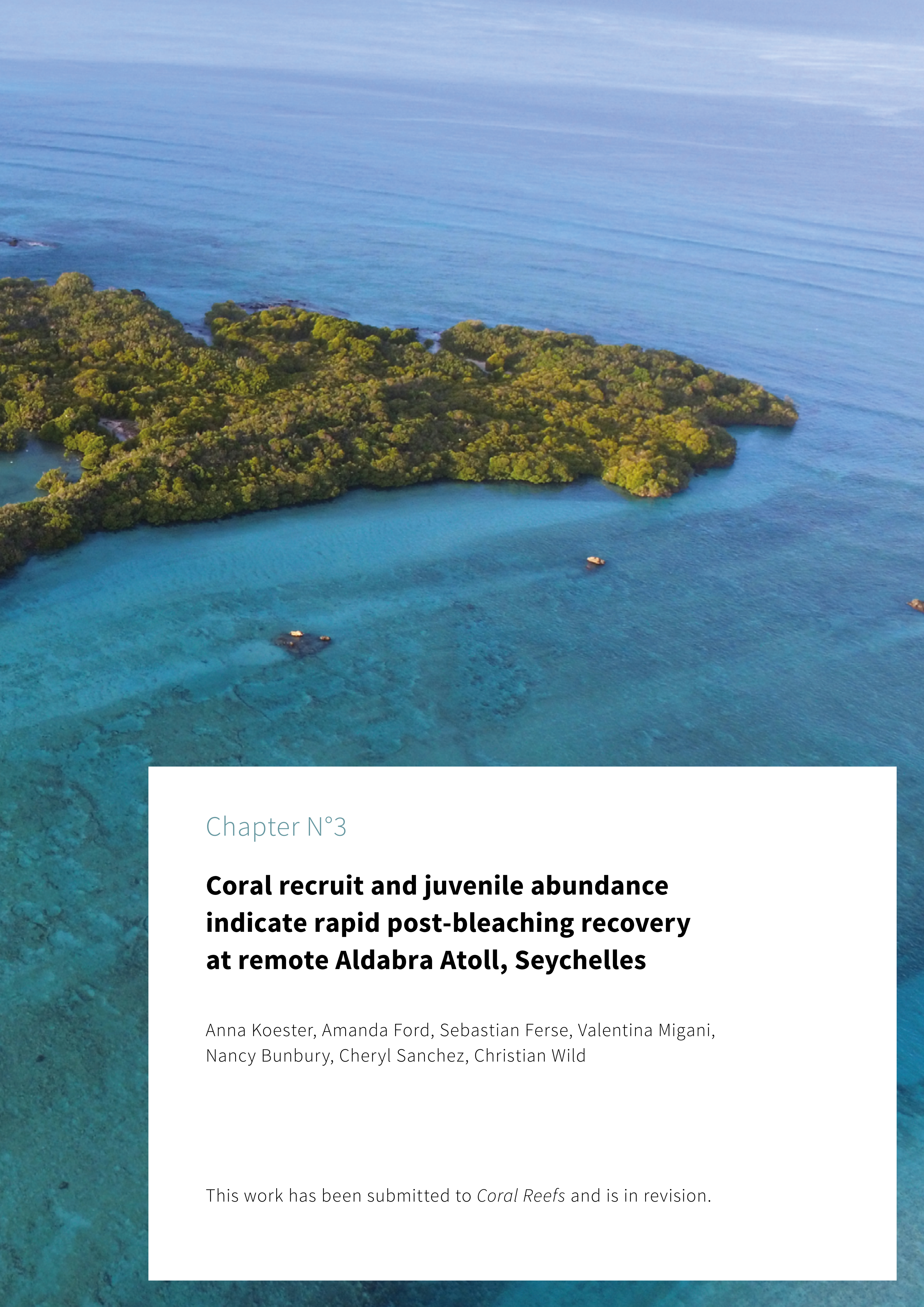
where C_{START} is the hard coral cover immediately post-bleaching (2016), C_{END} is the most recent record of hard coral cover (2019) and Y is the number of years between the two values. Based on the above, we obtained an estimate of years remaining (from 2019) until hard coral cover reaches pre-bleaching levels (Y_R):

$$Y_R = \frac{C_{PRE} - C_{END}}{C_{RC}} \tag{2}$$

where C_{PRE} is the pre-bleaching hard coral cover (2014).

Reference:

14. Coté, I. M., Gardner, T. A., Hutchinson, D. J. & Watkinson, A. R. New approaches to estimating recent ecological change on coral reefs in *Coral Reef Conservation* (eds. Coté, I. M. & Reynolds, J. R.) 293–313 (Cambridge University Press, 2006).



Chapter N°3

Coral recruit and juvenile abundance indicate rapid post-bleaching recovery at remote Aldabra Atoll, Seychelles

Anna Koester, Amanda Ford, Sebastian Ferse, Valentina Migani, Nancy Bunbury, Cheryl Sanchez, Christian Wild

This work has been submitted to *Coral Reefs* and is in revision.

Abstract

Coral recruitment is essential for post-bleaching reef recovery. As coral recruit and juvenile abundances vary across locations, their assessment at remote reefs improves our understanding of undisturbed reef recovery. We explored, first, changes in coral juvenile abundance across three locations (lagoon, seaward west and east) before (2015) and after (2016/2018/2019) the 2015/16 bleaching event at Aldabra Atoll, Seychelles, and, second, variation in coral recruit abundance on settlement tiles from two sites (lagoon, seaward reef) during August 2018–August 2019. Juvenile abundance decreased from 14.1 ± 1.2 to 7.4 ± 0.5 colonies m^{-2} (mean ± SE) during 2015–2016, and increased to 22.4 ± 1.2 colonies m^{-2} during 2016–2019, with all assessed taxa (except Merulinidae) reaching or exceeding pre-bleaching levels. Whilst juvenile abundance increased two- to three-fold at the lagoonal and seaward western sites during 2016–2018 (from 7.7–8.3 to 17.3–24.7 colonies m^{-2}), increases at the seaward eastern sites occurred later (2018–2019, from 5.8–6.9 to 16.6–24.1 colonies m^{-2}), indicating slower recovery. Post-bleaching recruit abundance on settlement tiles was highest in October–December 2018 (2164 ± 453 recruits m^{-2}) and lowest in June–August 2019 (240 ± 98 recruits m^{-2}), suggesting that broadcast spawning occurred during October–December, when water temperature increased from 26 to 29 °C. Recruit composition was dominated by Pocilloporidae (64–92% of all recruits), and recruit abundance was 7- to 47-fold higher inside than outside the lagoon, where larvae retention was likely enhanced, and coral juvenile abundance and coral cover was substantially higher. This study provides the first published record on coral recruitment in the Seychelles Outer Islands, indicates rapid (2–3 years) post-bleaching recovery of coral recruitment capacity and provides crucial baseline data for future research on reef resilience and connectivity within the region.

Introduction

Mass coral bleaching events have driven major losses of live coral worldwide, causing substantial changes to coral reef ecosystem structure and functioning. Coral reefs can recover from severe bleaching, and the reassembly of scleractinian coral communities, especially habitat-forming corals, is particularly important for the recovery of ecosystem functions (Connell et al. 1997; Gilmour et al. 2013; Graham et al. 2015). Post-bleaching reef recovery depends on the survival and growth of remnant coral colonies and on coral recruitment, (Connell et al. 1997; Graham et al. 2011; Doropoulos et al. 2015). Coral recruit and juvenile abundances are therefore important indicators of reef recovery (McClanahan et al. 2012; Graham et al. 2015) and can provide early insights into potential post-disturbance shifts in coral community composition.

Scleractinian corals, like most sessile marine invertebrates, have a bipartite life history. After a free-swimming pelagic larval phase and successful larvae settlement, the coral develops from recruit (< 1 cm diameter) to juvenile (< 5 cm diameter) to adult during its sessile benthic phase (Ritson-Williams et al. 2009; Penin et al. 2010). A prerequisite for recruitment is the sufficient supply of coral larvae, originating from within (self-recruitment) or outside the local coral community. Self-recruitment (see Swearer et al. 2002) is particularly important for geographically isolated reefs (Gilmour et al. 2013) and appears to be more common among brooding corals (Tioho et al. 2001; Doropoulos et al. 2015). Well-connected reefs benefit from the influx of external coral larvae, especially if the local adult coral population has been severely degraded (Elmhirst et al. 2009). In addition to larval supply, the availability of suitable benthic substrate for settlement and post-settlement survival plays a key role in coral recruitment (Doropoulos et al. 2016). For example, while crustose coralline algae (CCA) can promote recruitment by inducing larval settlement and by facilitating survival and growth of settlers (Arnold et al. 2010; Yadav et al. 2018), algal turfs (if not cropped short; Mumby et al. 2013) and macroalgae can inhibit coral larval settlement and are aggressive competitors for space (Johns et al. 2018). Unstable substrates (e.g. unconsolidated rubble) are also unsuitable, as their movement on the seafloor can cause major coral recruit and juvenile die-offs (Chong-Seng et al. 2014). Post-settlement mortality of corals is generally high until they have reached sizes of > 5 cm (Doropoulos et al. 2015), when they are more likely to withstand predation by corallivores or incidentally by herbivores (Cole et al. 2008; Doropoulos et al. 2012), and competition with other benthic organisms (e.g. turf and macroalgae; Hughes and Jackson 1985; Arnold et al. 2010).

Anthropogenic stressors, such as nutrient enrichment, coastal development, and overfishing, hamper coral recruitment through various processes, for example by altering the transmission of chemical signals involved in coral reproduction (Richmond 1997), reducing fertilisation of coral larvae due to high sedimentation (Erftemeijer et al. 2012; Perez et al. 2014), and facilitating the proliferation of algal turfs and macroalgae (Hughes 1994; Szmant 2002; Kuffner et al. 2006). However, even on relatively undisturbed reefs, mortality and varying coral growth rates influence the community structure of juvenile and adult corals and the trajectories of coral recovery following major disturbances (Edmunds 2000; Penin et al. 2010; Trapon et al. 2013).

Aldabra Atoll, in the Western Indian Ocean (WIO), provides an opportunity to study coral recruitment and coral reef recovery under conditions of minimal human disturbance. Aldabra was designated as a Special Reserve in 1981 (the highest level of national protection under Seychelles' legislation) and was inscribed as a UNESCO World Heritage Site in 1982. Its marine ecosystem has therefore been protected from commercial fishing pressure for almost 40 years, human-driven nutrient inputs are absent, and there is no coastal development. Nevertheless, coral bleaching events caused high coral mortality at Aldabra in 1998/1999 (38–66% mortality at 10–20 m water depth; Norström et al. 2009) and in 2015/2016 (34–62% mortality at 2–15 m water depth; Cerutti et al. 2020; Koester et al. 2020). However, while the reefs at 2–5 m water depth recovered 54–93% of their pre-bleaching (2015/2016) coral cover by 2019, no recovery was observed at 15 m water depth (Koester et al. 2020).

To better understand reef recovery dynamics under minimal anthropogenic disturbance, we measured changes in abundance of coral juveniles across three reef locations at Aldabra, spanning one survey period before, and three survey periods after the 2015/2016 coral bleaching event. With this data, we assess bleaching impact and post-bleaching recovery of Aldabra's reefs and ask, (1) how did the 2016 bleaching event affect the abundance and composition of coral juveniles?; and (2) how did this change in the post-bleaching years? Furthermore, to better understand these changes, we use coral recruitment data on settlement tiles from two reef sites and ask (3) how did abundance and composition of coral recruits vary in space and time following the bleaching event? The assessment of coral juvenile abundance primarily informs about the post-bleaching recovery of Aldabra's reefs, while the study on coral recruit abundance is the first of its kind in the Seychelles Outer Islands. We consider the implications of our results for coral reef monitoring and management in Seychelles and the broader region.

Study site

Aldabra (46°20’E, 9°24’S) is an elevated coral atoll in the south-west of the Seychelles archipelago (Fig. 3.1). Aldabra spans 34 × 14.5 km and consists of four main islands that encircle a large lagoon (196 km^2). During April–November, Aldabra is usually characterised by a drier and cooler climate, whilst the north-west monsoon during November/December–March creates wetter and warmer conditions.

There are 12 permanently marked marine survey sites around Aldabra (Cerutti et al. 2020). Of these, nine sites are located on the seaward reefs (five sites at seaward west – Sites 1, 2, 6, 7, 8; four at seaward east – Sites 3, 4, 5, 12; sites surveyed at 5 and 15 m water depth) and three sites are located at ca. 2 m water depth in the lagoon (Sites 9–11; Fig. 3.1). For the purposes of this study, the 2 m and 5 m depths are referred to as ‘shallow’ and the 15 m as ‘deep’. The division of the seaward reef sites into ‘west’ and ‘east’ is based on the different wind and wave exposure on either side of Aldabra and the differing benthic community compositions (Koester et al. 2020). The north-west and west of Aldabra are relatively sheltered throughout most of the year, while the north-east, east and south-east are more exposed to strong winds and high wave energy (Taylor 1971).

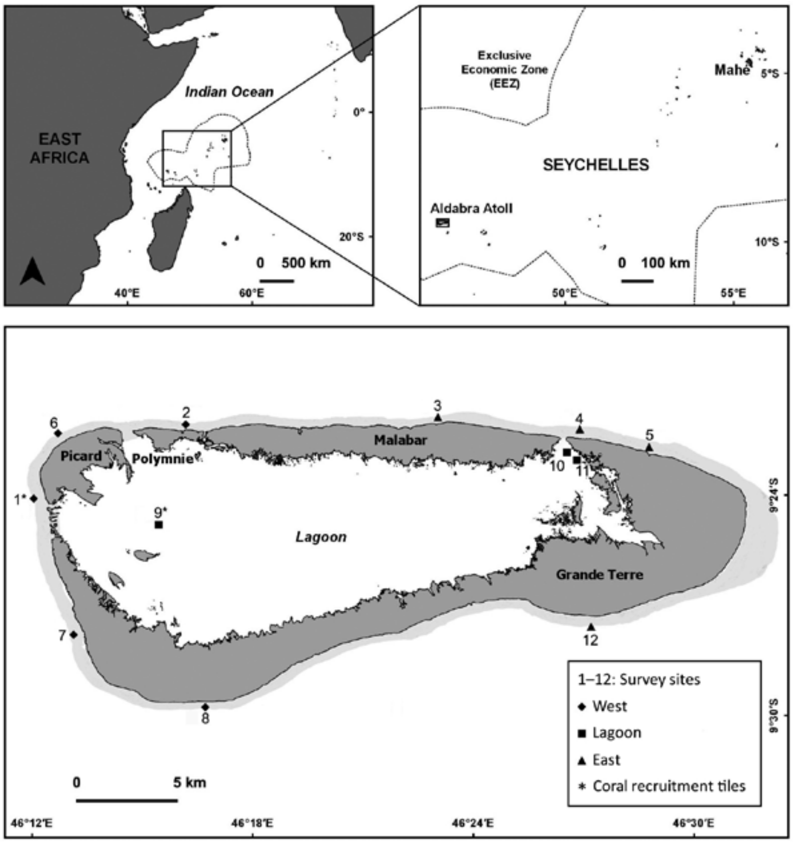


Figure 3.1: Location of Aldabra Atoll in the Indian Ocean and within the Seychelles (top) with its four main islands and 12 survey sites (represented by numbers) at the seaward western (‘West’, n = 5), seaward eastern (‘East’, n = 4) and lagoonal (‘Lagoon’, n = 3) reefs (bottom). The light grey shading around Aldabra indicates its seaward reefs.

Between December 2015 and June 2016, Aldabra's sea surface temperatures reached a maximum of 30.7 °C (March 2016), and the reefs experienced continuous bleaching risk as indicated by the degree heating week values which peaked at 3.4 °C-weeks (satellite derived temperature measured ca. 55 km north-east of Aldabra: 46°50'E, 9°00'S; Cerutti et al. 2020). By December 2016, hard coral cover had been reduced by 34% at 2 m water depth in the lagoon and by 51–62% on the seaward reefs at 5 m and 15 m water depth (Cerutti et al. 2020; Koester et al. 2020). By 2019, hard coral cover had not changed significantly at Aldabra's deep locations, but had increased significantly in the shallows and reached 54% (seaward east, 5 m depth), 68% (seaward west, 5 m depth) and 93% (lagoon) of the pre-bleaching hard coral cover (Koester et al. 2020).

Data collection

Coral juveniles

At each of the 12 survey sites, juvenile coral abundance (i.e. colonies < 5 cm diameter) was assessed along three 20-m transects separated by a 10-m gap (except in 2015, when only one or two transects were conducted at each deep site; Supplementary Table S1). Five 0.25-m^2 quadrats were randomly placed along each transect, within which the number of coral juveniles was recorded and identified to the lowest possible level, i.e. genus, or family where further identification was not possible. Surveys were conducted in December 2015 (immediately before the bleaching event), December 2016 (six months after the end of the bleaching event), December 2018–January 2019 (hereafter 2018) and November 2019–January 2020 (hereafter 2019), resulting in a total of 1085 quadrats assessed. Variable resources meant that survey effort varied across years and no data is available for the lagoonal reefs from 2015 (see Supplementary Table S1 for number of replicate transects and quadrats per site).

Coral recruits

The abundance of coral recruits (i.e. everything visible and identifiable as coral) was assessed on the unglazed side of ceramic tiles (15 × 15 × 1 cm). Tiles were attached to half concrete masonry blocks with stainless steel bolts and spacers (following Chong-Seng et al. 2014), with the unglazed side facing down. Between August 2018 and August 2019, tiles were placed at one lagoonal (Site 9) and one western seaward site (Site 1; 5 m depth; Fig. 3.1). These sites were selected because they are accessible for diving throughout the year. Tiles were replaced every two months and retrieved tiles were submerged in household bleach (10% solution) for 24 h, rinsed in freshwater, and dried before the unglazed underside was inspected under a stereo microscope. As coral recruits, particularly at shallow depths, settle predominantly on the sheltered side of recruitment tiles (Doropoulos et al. 2016; Ford et al. 2018), assessments were restricted to the underside of the tile. Coral recruits were counted and classified into three taxonomic categories (Acroporidae, Pocilloporidae, or 'other'; following Babcock et al. 2003). Between nine and 14 tiles were assessed per survey period for each site, as occasional storms damaged individual tiles at Site 1 (Supplementary Table S2).

Water temperature

Water temperature data (recorded every 30 min) was obtained from two Onset loggers (HOBO U22-001, accuracy: ± 0.2 °C; Onset Computer Corporation 2012) deployed at Site 9 (lagoon) between 10 February 2015 and 14 November 2018, and at Site 1 (seaward west, 5 m) between 16 December 2013 and 31 December 2019. Due to technical issues, there was a 3-week data gap at Site 9 (10 December 2016–1 January 2017), and two 1-week data gaps (2–9 April 2015; 23–30 December 2018) and one 5-month data gap (12 December 2016–5 May 2017) at Site 1.

Statistical analysis

Coral juveniles

We pooled coral juveniles into the families Acroporidae, Pocilloporidae, Poritidae, Merulinidae, and Agariciidae following the World Register of Marine Species (WoRMS Editorial Board 2020). *Leptastrea* was included as an individual genus due to its high abundance at Aldabra (9% of overall counts) and because it is not assigned to any family as it is considered as *Incertae sedis* at the family level (Budd et al. 2012). Combined, these taxa comprised 74% of overall counts; all other taxa were grouped into 'other'.

We used Generalised Linear Mixed Models (GLMM; R version 3.6.1, R Core Team 2019, lme4 package; Bates et al. 2015) with Poisson error distributions to test for differences in coral juvenile abundance across years (2015, 2016, 2018, 2019), locations (lagoon, east, west) and water depths (shallow, deep; Supplementary Table S3). Models with overall coral juvenile abundance and abundances of Acroporidae, Pocilloporidae, Merulinidae, Agariciidae and 'other' as response variables included survey year, location, depth and their interaction as fixed factors. Because models with Poritidae and *Leptastrea* as response variables had a poor fit when the interaction of fixed effects was included, only differences across years were tested, i.e. only 'survey year' was set as fixed factor. In all models, transect nested in site was set as a random factor to account for possible autocorrelation between quadrats. We validated the models by running a Generalised Linear Model (GLM; stats package, R Core Team 2019) and checking the residual distribution to see if the assumptions of homogeneity of variance, normality, and leverage were met; Pearson residual distributions were then checked for the GLMMs. We conducted a post-hoc analysis based on least square means with Bonferroni adjustment ('lsmean' function, lsmean package, Lenth 2016) to identify pairwise differences between the variables in significant models.

Coral recruits

We used GLMM with Poisson error distribution to test for differences in coral recruit abundance across survey period (August–October 2018, October–December 2018, December 2018–February 2019, February–April 2019, April–June 2019, June–August 2019) and location (Site 1: seaward site, Site 9: lagoonal site; Supplementary Table S4). Fixed factors included survey period, location, and their interaction with location set as a random factor. We validated the model in the same way as described for the coral juvenile analysis.

Coral juvenile and recruit abundance in relation to coral coverage

To evaluate patterns in coral juvenile and recruit abundance in relation to Aldabra's hard coral cover, percentage hard coral cover values were obtained from Koester et al. (2020) with coral categories re-assigned to match those described here (i.e. Acroporidae and Pocilloporidae for recruits and juveniles, and Poritidae, Merulinidae, Agariciidae and *Leptastrea* for juveniles).

Aldabra's coral juvenile abundance in a global context

We compiled a table of studies reporting coral juvenile abundances (Supplementary Table S5), including only research that employed a similar method as used here, i.e. where coral juveniles of < 5 cm diameter were assessed within quadrats, without further visual aid.

Effect of bleaching event on coral juvenile abundance and composition

Between 2015 and 2016, immediately before and after the bleaching, overall coral juvenile abundance at Aldabra's seaward reefs decreased by 48%, from 14.1 ± 1.2 to 7.4 ± 0.5 colonies m^{-2} (mean ± SE), but reductions differed across locations and water depths (Fig. 3.2; Supplementary Table S3). At western sites, abundances dropped by 60% in shallow and 46% in deep water, although the decline was not significant at the latter (Fig. 3.2a; Table 3.1). At the more exposed eastern sites, pre-bleaching abundances in shallow water were as low as post-bleaching abundances recorded at all other locations and abundances only dropped in deep water (52% loss; Fig. 3.2b, Table 3.1).

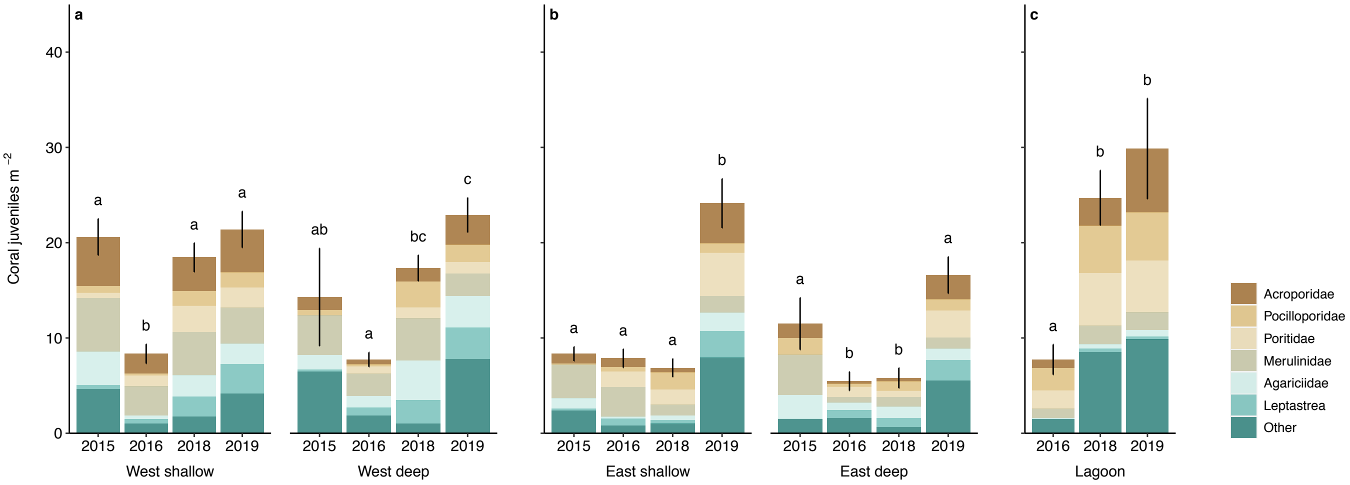


Figure 3.2: Coral juvenile abundance across locations and years. Values represent mean abundance per taxon and overall; standard error is displayed for overall mean abundance only. A: Seaward west (2015–2019); B: Seaward east (2015–2019); C: Lagoon (2016–2019). Letters indicate significant differences ($p < 0.05$) in overall abundances between years within locations and depths (see Supplementary Table S3).

Table 3.1: Information on coral juvenile abundances and percentage hard coral cover at Aldabra's lagoonal, seaward western and eastern sites between 2014 and 2019. Asterisks indicate significant differences between years (p < 0.05); n.a. = not available.

Measure	Location	Water depth	Pre-bleaching^{a} 2014/15		Post-bleaching 2016		Post-bleaching 2019		% Change 2014/15–2016	% Change 2016–2019	% Recovery^{b}
			Mean	SE	Mean	SE	Mean	SE			
Coral juveniles (no. m^{-2})	West	Shallow	20.6	1.9	8.3	1.0	21.4	1.9	-60 *	61 *	104
	West	Deep	14.3	5.1	7.7	0.8	22.9	1.8	-46	66 *	160
	East	Shallow	8.3	0.8	7.9	1.0	24.1	2.6	-6	67 *	290
	East	Deep	11.5	2.7	5.5	1.0	16.6	1.9	-52 *	67 *	144
	Lagoon	Shallow	n.a.	n.a.	7.7	1.6	29.9	5.3	—	74 *	—
Coral cover (%)^{c}	West	Shallow	34.1	2.9	15.9	1.8	23.7	2.0	-53 *	33 *	69
	West	Deep	20.8	1.9	8.6	1.0	13.6	1.2	-59 *	37	65
	East	Shallow	23.6	4.2	9.7	0.8	12.5	1.5	-59 *	22 *	53
	East	Deep	10.1	2.9	5.1	1.1	5.0	1.2	-49 *	-0.02	55
	Lagoon	Shallow	32.3	5.0	19.6	4.5	30.0	4.7	-39	35 *	93

[a] 2014: Coral cover; 2015: Coral juveniles;

[b] Percentage of pre-bleaching value reached in 2019;

[c] Significant changes based on Koester et al. (2020); note that mean coral cover values and percentage changes displayed here slightly deviate from back-transformed model estimates and percentage changes shown by Koester et al. (2020)

Overall, abundance of juvenile Acroporidae, Merulinidae, Agariciidae and 'other' corals declined significantly between 2015 and 2016 (mean abundances dropping by 66%, 54%, 73% and 63%, respectively; Fig. 3.3a–g; Supplementary Table S3), with reductions differing among taxa and locations (Fig 3h–u). At the western sites (Fig. 3.3h–n), declines in coral juvenile abundance were significant for Acroporidae (reduction of mean abundance: shallow: -60%, deep: -60), Merulinidae (shallow: -45%), Agariciidae (shallow: -88%) and 'other' (shallow: -79%, deep: -71%). At the eastern sites, only the abundance of Merulinidae juveniles declined significantly between 2015 and 2016 (deep: -86%; Fig. 3.3r).

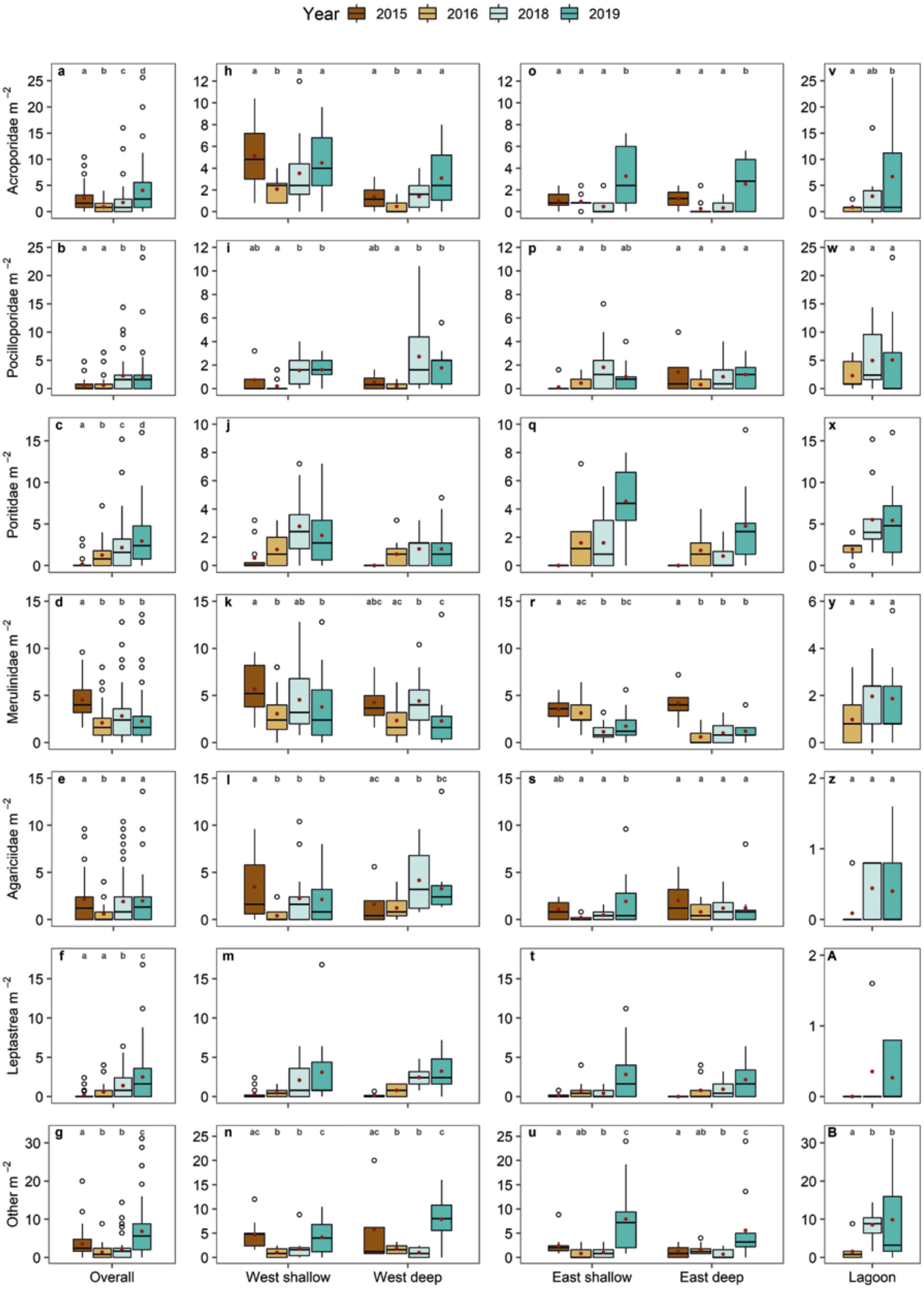


Figure 3.3: Coral juvenile abundance (median and interquartile range, outliers displayed as circles; means displayed as red dots) of the most abundant taxa overall (a–g) and at the seaward locations (h–u) during 2015–2019 and the lagoon (v–B) during 2016–2019. Note the different y-axis scaling. Small letters above boxplots indicate significant differences (p < 0.05) in abundances between years (see Supplementary Table S3). Note that only overall changes across years could be statistically tested for Poritidae and *Leptastrea* (see methods).

Change in coral juvenile abundance and composition during 2016–2019

Overall coral juvenile abundance tripled between 2016 and 2019, from 7.4 ± 0.5 to 22.4 ± 1.2 colonies m^{-2}, reaching or exceeding pre-bleaching levels at all seaward sites (Fig. 3.2; Table 3.1; Supplementary Table S3). Whilst mean coral juvenile abundance increased two- to three-fold at the lagoon and western sites between 2016 and 2018, a similar increase occurred later at the eastern sites, between 2018 and 2019 (Fig. 3.2).

Mean abundance of juveniles of all taxa (except Merulinidae) reached or exceeded pre-bleaching levels at all seaward sites during 2016–2019 (Fig 3.3h–u). Overall mean abundances were many times higher in 2019 than in 2015 for Poritidae (14-fold; Fig. 3.3c) and *Leptastrea* (nine-fold; Fig. 3.3f), while mean abundances of Merulinidae were lower in 2019 than 2015 at all seaward sites (Fig. 3.3k, r).

In the lagoon, abundances of Acroporidae and 'other' juveniles increased during 2016–2019 (Fig. 3.3v, B), with mean abundances of Acroporidae, Pocilloporidae, and Poritidae being relatively similar in 2019 (5.0–6.5 colonies m^{-2}; Fig. 3.3v–x). Abundances of 'other' juveniles were highest in 2019 (mean: 10.1 colonies m^{-2}; Fig. 3.3B), while few Merulinidae, Agariciidae, and *Leptastrea* juveniles were recorded in the lagoon in all years (mean: 0.3–2.0 colonies m^{-2}; Fig. 3.3y–A)

Post-bleaching coral recruit abundance and composition

Between August 2018 and August 2019, a total of 3591 coral recruits was counted on 142 tiles. Pocilloporidae comprised 72% of all counts, followed by Acroporidae (19%) and 'other' (9%). Of all recruits counted, 93% occurred on the tiles at the lagoonal site (3369 recruits on 72 tiles; 2080 ± 193 recruits m^{-2}; mean ± SE; Table 3.2), whilst 7% were recorded on the tiles of the seaward site (222 recruits on 70 tiles; 141 ± 26 recruits m^{-2}).

Overall coral recruit abundance ranged from 240 ± 98 recruits m^{-2} (mean ± SE) in June–August 2019 to 2164 ± 453 recruits m^{-2} in October–December 2018 (Fig. 3.4a). Recruit abundance was seven- to 47-fold higher at the lagoonal than the seaward site throughout the study period (Fig 4a; Supplementary Table S4). At the lagoonal site, mean abundance peaked in October–December 2018 (4080 ± 431 recruits m^{-2}) and was lowest in June–August 2019 (382 ± 164 recruits m^{-2}). At the seaward site, mean abundance was higher in October–December 2018 (244 ± 58 recruits m^{-2}) and December 2018–February 2019 (342 ± 98 recruits m^{-2}) than the remaining time periods (31–60 recruits m^{-2}).

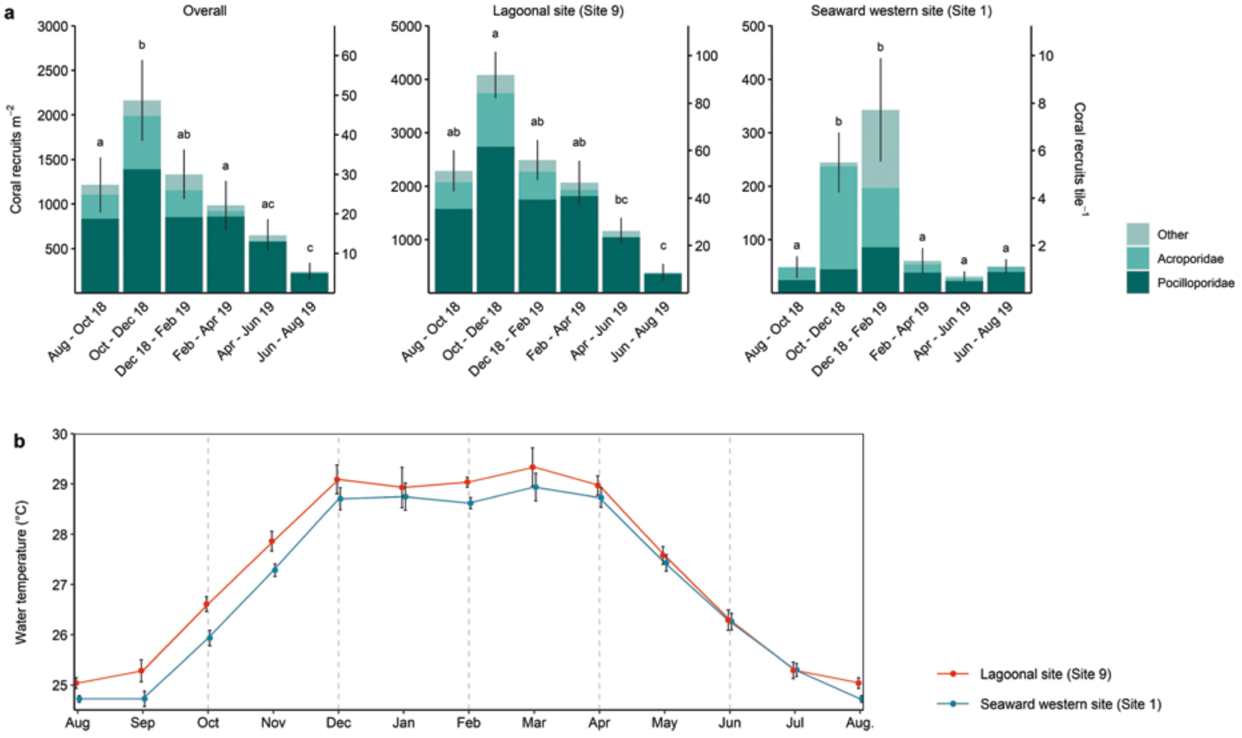


Figure 3.4: Coral recruitment study: (A) Coral recruit abundances overall and at each site. Values represent mean abundance for each taxon and in total, SE is displayed for total mean abundance only. Secondary y-axis indicates number of coral recruits per tile. Note the different y-axis scaling. Letters indicate significant differences ($p < 0.05$) between study periods (see Supplementary Table S4). (B) Mean (± SE) monthly water temperature during December 2013–Dec 2019 at the seaward western site and during February 2015–November 2018 at the lagoonal site where technical issues prevented the inclusion of data until December 2019. Horizontal dashed lines indicate month of recruitment tile change-over.

Table 3.2: Percentage coral cover, coral juvenile abundances and coral recruit abundances at the two study sites in Aldabra's lagoon and the seaward west.

Location	Taxa	Coral cover (%) 2019		Coral juveniles (no. m^{-2}) 2019		Coral recruits (no. m^{-2}) Aug 2018–Aug 2019	
		Mean	SE	Mean	SE	Mean	SE
Lagoon (ARM09)	Acroporidae	21.0	3.6	18.9	4.2	365.6	59.9
	Pocilloporidae	11.0	8.9	14.4	5.1	1545.7	138.9
	Other	10.4	3.2	34.7	8.3	171.1	21.1
	Total	42.4	4.8	68.0	9.8	2079.6	193.3
Seaward west (ARM01)	Acroporidae	7.2	3.5	2.1	0.9	64.1	15.6
	Pocilloporidae	0.6	0.2	1.9	0.7	44.4	7.5
	Other	6.6	1.9	13.3	2.9	32.4	15.3
	Total	14.4	5.4	17.3	3.2	141.0	26.4

Pocilloporidae comprised 74% of all recruits at the lagoonal site, which varied little throughout the study period (range: 67–93%). Acroporidae comprised 18% of the overall counts at the lagoonal site (21–25% in August 2018–February 2019; 1–6% in February–August 2019). At the seaward site, Pocilloporidae and Acroporidae comprised 32% and 45% of overall counts, respectively, but while the proportion of Pocilloporidae varied little throughout the study periods, Acroporidae abundance peaked in October–December (79% of overall count in this period) and was higher in December 2018–February 2019 (32%) than the remaining periods (14–26%). The contribution of 'other' recruits was lower at both sites (8% and 23% of overall counts at the lagoonal and seaward site, respectively), peaking at the seaward site in December 2018–February 2019 (43% of total counts).

The temporal variation in coral recruit abundances coincided with seasonal changes in water temperatures (Fig. 3.4b). At both sites, abundance of Acroporidae recruits was highest when water temperature increased during October–December. At the seaward site, abundances of 'other' recruits peaked when water temperatures remained around the maximum monthly mean for three months (December 2018–February 2019).

Discussion

How did the 2016 bleaching event affect the abundance and composition of coral juveniles?

Prolonged periods of elevated water temperatures during 2014–2017 caused widespread and severe bleaching of coral reefs worldwide (Eakin et al. 2019). Our study shows a substantial decrease in the abundance of coral juveniles following the 2016 bleaching event (48%), similar to reductions in overall hard coral cover (50%; Cerutti et al. 2020; Koester et al. 2020), which matches observations from the Inner Seychelles where the reduction of coral juveniles and coral cover was also similar (i.e. ca. 70% reduction of both; Dajka et al. 2019; Wilson et al. 2019).

Post-bleaching reductions in the abundance of coral juveniles showed high spatial variability at Aldabra; however, absolute abundances immediately after the bleaching (in 2016) were similar across locations. This suggests that spatial variation in juvenile coral losses reflects differences in pre-bleaching abundance and composition of juvenile corals, rather than differential impacts of the bleaching event. In contrast, reduction of hard coral cover in the lagoon was considerably lower, and post-bleaching cover considerably higher than on the seaward reefs (Table 3.1). Although taxon dependent (Álvarez-Noriega et al. 2018), small, flat coral colonies are generally less affected by bleaching than larger, branching ones due to faster mass-transfer of toxic by-products that occur during bleaching (Patterson 1992; Nakamura and Van Woesik 2001). Our results do not reflect this, potentially indicating that temperature stress at Aldabra was higher than expressed by the satellite derived degree-heating-weeks value of 3.4 °C (Cerutti et al. 2020) and possibly cancelling out colony-size benefits.

Taxonomic variations in bleaching susceptibility and mortality have been widely reported (Marshall and Baird 2000; Loya et al. 2001; McClanahan 2014). In the present study, Acroporidae, Agariciidae and Merulinidae juveniles exhibited the greatest decreases in abundance after the bleaching event, while Poritidae juvenile abundance slightly increased. These changes partially overlap with percentage cover changes of Aldabra's most abundant coral taxa: Acroporid (*Acropora* and *Montipora*) and Merulinidae cover decreased by 85% and 57%, respectively, following bleaching, while the reduction of massive *Porites* cover was lower (13%; Cerutti et al. 2020). Changes in percentage cover of Pocilloporidae, Agariciidae, and *Leptastrea* were not assessed previously at Aldabra, due to their low contribution to overall benthic cover (Supplementary Fig. S1), indicating limited correlation between juvenile and overall coral community composition at Aldabra.

How did abundance and composition of coral juveniles change in the post-bleaching years?

As hard coral recovery can speed up exponentially with ongoing coral recruitment (Gilmour et al. 2013), the abundance of coral juveniles is widely recognised as an important indicator of reef recovery, and several studies report coral juvenile abundance following disturbances (Supplementary Table S5). Overall abundance of coral juveniles tripled at Aldabra during 2016–2019, and absolute abundances in 2019 were high (16.6–29.9 coral juveniles m^{-2}), in comparison to both Aldabra's pre-bleaching abundances (8.3–20.6 coral juveniles m^{-2}), and other protected and unprotected locations: 83% of the sites in Supplementary Table S5 had abundances of ≤ 16 coral juveniles m^{-2}, whilst only 3% had abundances ≥ 30 coral juveniles m^{-2} (Supplementary Fig. S2). This increase has probably been facilitated by rapid recovery of the reproductive capacity of Aldabra's coral stock (and connected reefs; Crochelet et al. 2016), coupled with the availability of suitable settlement substrate and sufficient herbivory (Koester et al. 2020).

Post-disturbance reef recovery is often driven by branching hard corals of the families Acroporidae (e.g. *Acropora* in the Inner Seychelles: Wilson et al. 2019; Scott Reef, Australia: Gilmour et al. 2013) and Pocilloporidae (e.g. *Pocillopora* in Kenya: McClanahan 2014; Moorea, French Polynesia: Adjeroud et al. 2018) displaying life history traits characteristic of competitive and 'weedy' species, such as rapid growth (Darling et al. 2012; Adjeroud et al. 2018; Wilson et al. 2019). Previous work at Aldabra identified branching *Porites* (lagoon) and encrusting *Montipora* (seaward reefs) as key drivers of early hard coral cover increase during 2016–2019, likely driven by re-growth of remnant colonies (Koester et al. 2020). In contrast, juvenile coral communities at Aldabra were not dominated by individual coral taxa in any of the years studied (unlike e.g. reefs in the Maldives where *Acropora* juveniles dominated; Perry and Morgan 2017; or the Inner Seychelles with *Acropora*, *Porites*, and *Pocillopora* dominating; Chong-Seng et al. 2014), and juvenile abundances of all taxa (except Merulinidae) reached, or even exceeded, pre-bleaching levels at all locations by 2019. The increase of Pocilloporidae and *Leptastrea* juveniles at Aldabra, however, is conspicuous, as their percentage coverage in 2014–2019 was low (Supplementary Fig. S1). Pocilloporidae (i.e. the genera *Pocillopora*, *Stylophora*, *Seriatopora*), some *Leptastrea* species and also branching members of Poritidae (*Porites* species) follow a competitive or 'weedy' life history strategy (Darling et al. 2012). Weedy corals are generally characterised by small colony sizes, fast growth, and low resistance to perturbations, and can opportunistically colonise recently disturbed habitats (Darling et al. 2012). They often reproduce by brooding larvae, with some having the ability to produce larvae asexually by parthenogenesis (Ayre and Miller 2004; Combosch and Vollmer 2013), allowing successful reproduction even if the population of corals at reproductive age is small (Darling et al. 2012). The increased abundance of Pocilloporidae, *Lepastrea* and Poritidae juveniles observed at Aldabra between 2016 and 2019 thus likely arose from weedy species of these taxa.

Although coral juvenile abundances increased across all locations and water depths, increases at the lagoonal and western sites occurred earlier than at the more exposed eastern site. Spatial variation was also recorded for the recovery of hard coral cover (Koester et al. 2020), with significant increases only at the shallow reefs and by a substantially lower magnitude at the eastern sites compared with the other locations (Table 3.1). This slow recovery at the eastern sites was attributed to high *Halimeda* cover at the east (45–61 % in 2016–2019; Koester et al. 2020), which was already noted in the 1970s and attributed to the high hydrodynamic energy the eastern reefs are exposed to (Drew 1977; Stobart et al. 2002). High *Halimeda* cover may have increased post-settlement mortality of coral recruits (Nugues and Szmant 2006), thereby suppressing juvenile abundances until 2018. However, as *Halimeda* cover was also high in 2019, it is possible that *Halimeda* was not the only cause of low coral juvenile abundance, and that a change in environmental conditions may have favoured coral recruitment and growth of juvenile corals by 2019.

How did abundance and composition of coral recruits vary in space and time following the bleaching event?

Spatial variation was also pronounced for the abundance of coral recruits on settlement tiles, which is in line with several other studies (e.g. Dunstan and Johnson 1998; Adjeroud et al. 2007; Mangubhai et al. 2007a). Recruit abundances at Aldabra's lagoonal site was seven- to 47-fold higher than at the seaward site, where exposure to wind, swell, and currents may reduce larval settlement rates and/or increase post-settlement mortality (e.g. Adjeroud et al. 2007; Hata et al. 2017). Indeed, this western seaward site is located close to Aldabra's West Channels where water current velocities reach 1.5 m s^{-1} (Farrow and Brander 1971), and is possibly influenced by eddies forming on the north-western side of the atoll (Heywood et al. 1996). Coral gamete and larval dispersal may be enhanced on the seaward reefs compared to the lagoon, where residence times for complete water tidal exchange are 18 h and 53 h at spring and neap tides, respectively (Pugh and Rayner 1981). Most of the recruits counted in the lagoon are therefore likely of local (i.e. lagoonal) origin. This is supported by the strong stock-recruitment relationship of brooding Pocilloporidae found elsewhere (Doropoulos et al. 2015) and the dominance of Pocilloporidae recruits in the lagoon.

Overall recruit abundances in Aldabra's lagoon (2080 ± 193 recruits m^{-2}) were substantially higher than those reported at other lagoonal reefs (i.e. annual mean of 101–908 recruits m^{-2} post-1998 bleaching in Kenya, Mangubhai et al. 2007; means of 225–780 recruits m^{-2} pre-2016 bleaching in Fiji, Ford et al. 2018). However, the abundances at Aldabra's seaward site (141 ± 26 recruits m^{-2}) were low compared to those recorded at seaward reefs in the Inner Seychelles (means of 355–832 recruits m^{-2} pre-2016 bleaching, Chong-Seng et al. 2014), Vamizi Island, Mozambique (annual mean of 1135 recruits m^{-2} pre-2016 bleaching, Sola et al. 2015), the Spermonde Archipelago (annual mean of 286–686 recruits m^{-2}, Sawall et al. 2013) and French Polynesia (mean of 569 recruits m^{-2}, Penin and Adjeroud 2013), and more similar to values reported from the Mascarene Islands Réunion and Rodrigues (maximum 40–150 recruits m^{-2} post-2016 bleaching, Jouval et al. 2019). Comparisons, however, should be treated with caution due to different methods used (Glassom et al. 2004; Edmunds 2017) and high spatial variability of recruitment (Fisk and Harriott 1990; Dunstan and Johnson 1998).

Spatial discrepancies between the lagoonal and seaward site are also reflected in the sites' coral juvenile abundances and percentage coral cover, both of which were considerably higher at the lagoonal site than the seaward site. Noting that inferences drawn from the assessment of single sites include substantial speculation, taken together, the patterns in coral recruit abundance, juvenile abundance and coral coverage suggest that, compared to the seaward reefs, reefs in Aldabra's lagoon appeared not only less susceptible to the last coral bleaching event (Cerutti et al. 2020; Koester et al. 2020), but also seem to recover more rapidly by fast regrowth of remnant corals and high rates of coral recruitment (Table 3.1). Whether or not the lagoonal reefs may benefit Aldabra's entire reef system is currently not known, and research on Aldabra's reef connectivity is needed.

The results of the coral recruitment study provide important baseline data for further research. In common with tropical and sub-tropical reefs across the Indo-Pacific (Glassom et al. 2004; Glassom and Chadwick 2006; Adjeroud et al. 2007; Ferse et al. 2013; Chong-Seng et al. 2014; Ford et al. 2018; Jouval et al. 2019), Pocilloporidae recruits dominated at Aldabra and likely resulted predominantly from brooding corals (Fadlallah 1983; Harrison and Wallace 1990), which release planulae all year round (Foster and Gilmour 2018). Contrastingly, broadcast spawners (e.g. many members of the Acroporidae family) release gametes typically when environmental conditions are optimal for fertilisation, larval survival, and settlement (Foster et al. 2018), resulting in seasonal variation (Hughes et al. 1999). Coral recruitment at Aldabra (most notably of Acroporidae) was highest during October–December, suggesting that broadcast spawning at Aldabra (and potentially connected reefs; Crochelet et al. 2016) peaks at the beginning of the north-west monsoon, similar to observations from Kenya (Mangubhai and Harrison 2008). Although multi-annual recruitment studies and/or direct observations of coral reproduction are necessary to confirm the spawning patterns for a given location (e.g. Gouezo et al. 2020), the October–December time frame coincides with the period of most rapid seasonal increase in water temperature, serving as proximate cue for broadcast spawning (Babcock et al. 1986; Mangubhai et al. 2007b; Keith et al. 2016; Gouezo et al. 2020).

Our results are the first published record on coral recruitment in the Seychelles Outer Islands. The rapid recovery of reproductive capacity of Aldabra's reefs after bleaching, particularly in the lagoon, suggests that similar trajectories may occur at other remote reefs in the region and that managing local anthropogenic pressures, such as overfishing, coastal development and pollution, is critical to promote reef recovery following coral bleaching events. Continued monitoring of the recovery of reefs in this region as well as their connectivity will therefore be invaluable for the conservation of Aldabra's reefs and beyond.

References

Adjeroud M, Kayal M, Iborra-Cantonnet C, Vercelloni J, Bosserelle P, Liao V, Chancerelle Y, Claudet J, Penin L (2018) Recovery of coral assemblages despite acute and recurrent disturbances on a South Central Pacific reef. Sci Rep 8:9680

Adjeroud M, Penin L, Carroll A (2007) Spatio-temporal heterogeneity in coral recruitment around Moorea, French Polynesia: Implications for population maintenance. J Exp Mar Bio Ecol 341:204–218

Álvarez-Noriega M, Baird AH, Bridge TCL, Dornelas M, Fontoura L, Pizarro O, Precoda K, Torres-Pulliza D, Woods RM, Zawada K, Madin JS (2018) Contrasting patterns of changes in abundance following a bleaching event between juvenile and adult scleractinian corals. Coral Reefs 37:527–532

Arnold SN, Steneck RS, Mumby PJ (2010) Running the gauntlet: Inhibitory effects of algal turfs on the processes of coral recruitment. Mar Ecol Prog Ser 414:91–105

Ayre DJ, Miller KJ (2004) Where do clonal coral larvae go? Adult genotypic diversity conflicts with reproductive effort in the brooding coral Pocillopora damicornis. Mar Ecol Prog Ser 277:95–105

Babcock R, Baird AH, Piromvaragorn S, Thomson DP, Willis BL (2003) Identification of scleractinian coral recruits from Indo-Pacific reefs. Zool Stud 42:211–226

Babcock RC, Bull GD, Harrison PL, Heyward AJ, Oliver JK, Wallace CC, Willis BL (1986) Synchronous spawnings of 105 scleractinian coral species on the Great Barrier Reef. Mar Biol 90:379–394

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1–48

Budd AF, Fukami H, Smith ND, Knowlton N (2012) Taxonomic classification of the reef coral family Mussidae (Cnidaria: Anthozoa: Scleractinia). Zool J Linn Soc 166:465–529

Cerutti J, Burt AJ, Haupt P, Bunbury N, Mumby P, Schaepman-Strub G (2020) Impacts of the 2014–2017 global bleaching event on a protected remote atoll in the Western Indian Ocean. Coral Reefs 39:15–26

Chong-Seng K, Graham N, Pratchett M (2014) Bottlenecks to coral recovery in the Seychelles. Coral Reefs 33:449–461

Cole AJ, Pratchett M, Jones GP (2008) Diversity and functional importance of coral-feeding fishes on tropical coral reefs. Fish Fish 9:286–307

Combosch DJ, Vollmer S V. (2013) Mixed asexual and sexual reproduction in the Indo-Pacific reef coral Pocillopora damicornis. Ecol Evol 3:3379–3387

Connell JH, Hughes TP, Wallace CC (1997) A 30-year study of coral abundance, recruitment, and disturbance at several scales in space and time. Ecol Monogr 67:461

Crochelet E, Roberts J, Lagabrielle E, Obura D, Petit M, Chabanet P (2016) A model-based assessment of reef larvae dispersal in the Western Indian Ocean reveals regional connectivity patterns — potential implications for conservation policies. Reg Stud Mar Sci 7:159–167

Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. Ecol Lett 15:1378–1386

Doropoulos C, Roff G, Bozec YM, Zupan M, Werminghausen J, Mumby P (2016) Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. Ecol Monogr 86:20–44

Doropoulos C, Ward S, Marshell A, Díaz-Pulido G, Mumby P (2012) Interactions among chronic and acute impacts on coral recruits: the importance of size-escape thresholds. Ecology 93:2131–2138

Doropoulos C, Ward S, Roff G, González-Rivero M, Mumby PJ (2015) Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. PLoS One 10:e0128535

Drew E (1977) A photographic survey down the seaward reef-front of Aldabra Atoll. Atoll Res Bull 193:1–17

Dunstan PK, Johnson CR (1998) Spatio-temporal variation in coral recruitment at different scales on Heron Reef, southern Great Barrier Reef. Coral Reefs 17:71–81

Eakin CM, Sweatman HPA, Brainard RE (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38:539–545

Edmunds PJ (2000) Patterns in the distribution of juvenile corals and coral reef community structure in St. John, US Virgin Islands. Mar Ecol Prog Ser 202:113–124

Edmunds PJ (2017) Unusually high coral recruitment during the 2016 El Niño in Mo'orea, French Polynesia. PLoS One 12:e0185167

Elmhirst T, Connolly SR, Hughes TP (2009) Connectivity, regime shifts and the resilience of coral reefs. Coral Reefs 28:949–957

Erftemeijer PLA, Riegl B, Hoeksema BW, Todd PA (2012) Environmental impacts of dredging and other sediment disturbances on corals: A review. Mar Pollut Bull 64:1737–1765

Fadlallah Y (1983) Sexual Reproduction, development and larval biology in scleractinian corals. Coral Reefs 2:129–150

Farrow GE, Brander KM (1971) Tidal studies on Aldabra. Philos Trans R Soc London B 260:93–121

Ferse SCA, Nugues MM, Romatzki SBC, Kunzmann A (2013) Examining the use of mass transplantation of brooding and spawning corals to support natural coral recruitment in Sulawesi/Indonesia. Restor Ecol 21:745–754

Fisk DA, Harriott VJ (1990) Spatial and temporal variation in coral recruitment on the Great Barrier Reef: Implications for dispersal hypotheses. Mar Biol 107:485–490

Ford AK, Eich A, McAndrews RS, Mangubhai S, Nugues MM, Bejarano S, Moore BR, Rico C, Wild C, Ferse SCA (2018) Evaluation of coral reef management effectiveness using conventional versus resilience-based metrics. Ecol Indic 85:308–317

Foster T, Gilmour J (2018) Reproduction of brooding corals at Scott Reef, Western Australia. Matters 1–9

Foster T, Heyward AJ, Gilmour JP (2018) Split spawning realigns coral reproduction with optimal environmental windows. Nat Commun 9:718

Gilmour J, Smith LD, Heyward AJ, Baird AH, Pratchett M (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71

Glassom D, Chadwick NE (2006) Recruitment, growth and mortality of juvenile corals at Eilat, northern Red Sea. Mar Ecol Prog Ser 318:111–122

Glassom D, Zakai D, Chadwick-Furman NE (2004) Coral recruitment: A spatio-temporal analysis along the coastline of Eilat, northern Red Sea. Mar Biol 144:641–651

Gouezo M, Doropoulos C, Fabricius K, Olsudong D, Nestor V, Kurihara H, Golbuu Y, Harrison P (2020) Multispecific coral spawning events and extended breeding periods on an equatorial reef. Coral Reefs 39:1107–1123

Graham N, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:94–97

Graham N, Nash KL, Kool JT (2011) Coral reef recovery dynamics in a changing world. Coral Reefs 30:283–294

Harrison PL, Wallace CC (1990) Reproduction, dispersal and recruitment of scleractinian corals. In: Dubinsky Z. (eds) Ecosystems of the world. Elsevier Science, Amsterdam, pp 133–207

Hata T, Madin JS, Cumbo VR, Denny M, Figueiredo J, Harii S, Thomas CJ, Baird AH (2017) Coral larvae are poor swimmers and require fine-scale reef structure to settle. Sci Rep 7:2249

Heywood KJ, Stevens DP, Bigg GR (1996) Eddy formation behind the tropical island of Aldabra. Deep Sea Res Part I Oceanogr Res Pap 43:555–578

Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. Science 265:1547–1551

Hughes TP, Baird AH, Dinsdale EA, Moltschaniwskyj NA, Pratchett M, Tanner JE, Willis BL (1999) Patterns of recruitment and abundance of corals along the Great Barrier Reef. Nature 397:59–63

Hughes TP, Jackson JBC (1985) Population dynamics and life histories of foliaceous corals. Ecol Monogr 55:141–166

Johns KA, Emslie MJ, Hoey A, Osborne K, Jonker MJ, Cheal AJ (2018) Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9:e02349

Jouval F, Latreille AC, Bureau S, Adjeroud M, Penin L (2019) Multiscale variability in coral recruitment in the Mascarene Islands: From centimetric to geographical scale. PLoS One 14:e0214163

Keith SA, Maynard J, Edwards AJ, Guest JR, Bauman AG, van Hooidonk R, Heron SF, Berumen ML, Bouwmeester J, Piromvaragorn S, Rahbek C, Baird AH (2016) Coral mass spawning predicted by rapid seasonal rise in ocean temperature. Proc R Soc B Biol Sci 283:20160011

Koester A, Migani V, Bunbury N, Ford AK, Sanchez C, Wild C (2020) Early trajectories of benthic coral reef communities following the 2015/16 coral bleaching event at remote Aldabra Atoll, Seychelles. Sci Rep 10:17034

Kuffner IB, Walters LJ, Becerro MA, Paul VJ, Ritson-Williams R, Beach KS (2006) Inhibition of coral recruitment by macroalgae and cyanobacteria. Mar Ecol Prog Ser 323:107–117

Lenth R V. (2016) Least-squares means: The R package lsmeans. J Stat Softw 69:1–33

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

Mangubhai S, Harrison PL (2008) Asynchronous coral spawning patterns on equatorial reefs in Kenya. Mar Ecol Prog Ser 360:85–96

Mangubhai S, Harrison PL, Obura DO (2007) Patterns of coral larval settlement on lagoon reefs in the Mombasa Marine National Park and Reserve, Kenya. Mar Ecol Prog Ser 348:149–159

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163

McClanahan TR (2014) Decadal coral community reassembly on an African fringing reef. Coral Reefs 33:939–950

McClanahan TR, Donner SD, Maynard J, MacNeil MA, Graham N, Maina J, Baker AC, Alemu I. JB, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E, Mumby P, Paddack MJ, Selig ER, van Woesik R (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. PLoS One 7:e42884

Mumby P, Bejarano S, Golbuu Y, Steneck R, Arnold SN, van Woesik R, Friedlander A (2013) Empirical relationships among resilience indicators on Micronesian reefs. Coral Reefs 32:213–226

Nakamura T, Van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301–304

Norström A V., Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral-macroalgal phase shifts. Mar Ecol Prog Ser 376:293–306

Nugues MM, Szmant AM (2006) Coral settlement onto Halimeda opuntia: A fatal attraction to an ephemeral substrate? Coral Reefs 25:585–591

Onset Computer Corporation (2012) HOBO Water Temp Pro v2 (U22-001) Manual.

Patterson MR (1992) A mass transfer explanation of metabolic scaling relations in some aquatic invertebrates and algae. Science 255:1421–1423

Penin L, Adjeroud M (2013) Relative importance of recruitment and post-settlement processes in the maintenance of coral assemblages in an insular, fragmented reef system. Mar Ecol Prog Ser 473:149–162

Penin L, Michonneau F, Baird AH, Connolly SR, Pratchett M, Kayal M, Adjeroud M (2010) Early post-settlement mortality and the structure of coral assemblages. Mar Ecol Prog Ser 408:55–64

Perez K, Rodgers KS, Jokiel PL, Lager C V., Lager DJ (2014) Effects of terrigenous sediment on settlement and survival of the reef coral Pocillopora damicornis. PeerJ 2:e387

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

Pugh DT, Rayner RF (1981) The tidal regimes of three Indian Ocean atolls and some ecological implications. Estuar Coast Shelf Sci 13:389–407

R Core Team (2019) R: A Language and Environment for Statistical Computing.

Richmond RH (1997) Reproduction and recruitment in corals: critical links in the persistence of reefs. In: Birkeland C. (eds) Life and death of coral reefs. Chapman and Hall, New York, pp 175–197

Ritson-Williams R, Arnold SN, Fogarty N, Steneck RS, Vermeij M, Paul VJ (2009) New perspectives on ecological mechanisms affecting coral recruitment on reefs. Smithson Contrib Mar Sci 437–457

Sawall Y, Jompa J, Litaay M, Maddusila A, Richter C (2013) Coral recruitment and potential recovery of eutrophied and blast fishing impacted reefs in Spermonde Archipelago, Indonesia. Mar Pollut Bull 74:374–382

Sola E, Marques da Silva I, Glassom D (2015) Spatio-temporal patterns of coral recruitment at Vamizi Island, Quirimbas Archipelago, Mozambique. African J Mar Sci 37:557–565

Stobart B, Buckley R, Downing N, Callow M, LeClair L, Teleki K (2002) Aldabra Marine Programme phase III: Extending the survey eastward. Cambridge Coastal Research Unit. Department of Geography, University of Cambridge.

Swearer SE, Shima JS, Hellberg ME, Thorrold SR, Jones GP, Robertson DR, Morgan SG, Selkoe KA, Ruiz GM, Warner RR (2002) Evidence of self-recruitment in demersal marine populations. Bull Mar Sci 70:251–271

Szmant AM (2002) Nutrient enrichment on coral reefs: is it a major cause of coral reef decline? Estuaries 25:743–766

Taylor JD (1971) Intertidal zonation at Aldabra Atoll. Philos Trans R Soc London B 260:173–213

Tioho H, Tokeshi M, Nojima S (2001) Experimental analysis of recruitment in a scleractinian coral at high latitude. Mar Ecol Prog Ser 213:79–86

Trapon ML, Pratchett M, Adjeroud M, Hoey AS, Baird AH (2013) Post-settlement growth and mortality rates of juvenile scleractinian corals in Moorea, French Polynesia versus Trunk Reef, Australia. Mar Ecol Prog Ser 488:157–170

Wilson SK, Robinson JPW, Chong-Seng K, Robinson J, Graham N (2019) Boom and bust of keystone structure on coral reefs. Coral Reefs 38:625–635

WoRMS Editorial Board (2020) World Register of Marine Species. http://www.marinespecies.org

Yadav S, Alcoverro T, Arthur R (2018) Coral reefs respond to repeated ENSO events with increasing resistance but reduced recovery capacities in the Lakshadweep archipelago. Coral Reefs 37:1245–1257

Table S1: Coral juvenile survey replicates. Number of transects and quadrats completed at each location and site during each survey year. Lower number of replicates obtained in 2015 due to limited resources.

Location (water depth)/	2015		2016		2018		2019	
Site	Trans.	Quad.	Trans.	Quad.	Trans.	Quad.	Trans.	Quad.
West (5 m)	**12**	**60**	**12**	**60**	**15**	**75**	**15**	**75**
1	3	15	3	15	3	15	3	15
2	3	15	3	15	3	15	3	15
6	3	15	3	15	3	15	3	15
7	0	0	0	0	3	15	3	15
8	3	15	3	15	3	15	3	15
West (15 m)	**4**	**20**	**15**	**75**	**15**	**75**	**15**	**75**
1	1	5	3	15	3	15	3	15
2	1	5	3	15	3	15	3	15
6	1	5	3	15	3	15	3	15
7	0	0	3	15	3	15	3	15
8	1	5	3	15	3	15	3	15
East (5 m)	**12**	**60**	**12**	**60**	**12**	**60**	**12**	**60**
3	3	15	3	15	3	15	3	15
4	3	15	3	15	3	15	3	15
5	3	15	3	15	3	15	3	15
12	3	15	3	15	3	15	3	15
East (15 m)	**4**	**15**	**12**	**60**	**12**	**60**	**12**	**60**
3	1	5	3	15	3	15	3	15
4	0	0	3	15	3	15	3	15
5	2	5	3	15	3	15	3	15
12	1	5	3	15	3	15	3	15
Lagoon (2 m)	**0**	**0**	**9**	**45**	**9**	**45**	**9**	**45**
9	0	0	3	15	3	15	3	15
10	0	0	3	15	3	15	3	15
11	0	0	3	15	3	15	3	15

Trans. = Transect, Quad. = Quadrat

Table S2: Coral recruit survey replicates. Number of coral recruitment tiles retrieved per site and survey period. Replicates at the seaward site vary as some tiles were lost due to rough weather.

Survey period	Lagoonal site (Site 9)	Seaward western site (Site 1)
Aug–Oct 18	12	11
Oct–Dec 18	12	12
Dec 18–Feb 19	12	14
Feb–Apr 19	12	14
Apr–Jun 19	12	10
Jun–Aug 19	12	9

Table S3: Change in coral juvenile abundances. Effect of year (2015, 2016, 2018, 2019), location (lagoon, western seaward, eastern seaward) and depth (2 m, 5 m, 15 m) on coral juvenile abundances at Aldabra. Chi-square-value (χ^2), degrees of freedom (dF) and p-value obtained from GLMM model comparisons with ANOVA (type I). Significance level: *** $p < 0.001$; ** $p < 0.01$; ** $p < 0.05$; ns = not significant: $p > 0.05$.

	Overall			Acroporidae			Pocilloporidae			Merulinidae			Agariciidae			Other			Poritidae[a]			Leptastrea[a]		
Fixed factor	χ^2	dF	p	χ^2	dF	p	χ^2	dF	p	χ^2	dF	p	χ^2	dF	p	χ^2	dF	p	χ^2	dF	p	χ^2	dF	p
Year	247.2	3	***	88.0	3	***	43.5	3	***	33.0	3	***	40.4	3	***	134.3	3	***	94.8	3	***	73.1	3	*
Location	6.9	2	*	2.8	2	ns	4.0	2	ns	34.1	2	***	17.8	2	***	12.9	2	**	not tested			not tested		
Depth	4.9	1	*	19.5	1	***	0.6	1	ns	6.7	1	**	6.4	1	*	1.2	1	ns	–"–			–"–		
Year:Location	73.0	5	***	23.4	5	***	9.7	5	ns	14.7	5	*	7.4	5	ns	56.3	5	***	–"–			–"–		
Year:Depth	1.8	3	ns	7.3	3	ns	2.6	3	ns	7.9	3	*	10.0	3	*	13.6	3	**	–"–			–"–		
Location:Depth	1.5	1	ns	0.8	1	ns	0.3	1	ns	0.3	1	ns	0.0	1	ns	3.0	1	ns	–"–			–"–		
Year:Location:Depth	15.3	3	**	4.6	3	ns	11.4	3	***	9.4	3	*	13.3	3	**	5.9	3	ns	–"–			–"–		

[a] models including interacting fixed factors had poor model fit and only differences across years were test (see methods)

Table S4: Difference in coral recruit abundances. Effect of location (seaward western site: Site 1, lagoonal site: Site 9) and time period (Aug–Oct 2018, Oct–Dec 2018, Dec 2018–Feb 2019, Feb–Apr 2019, Apr–Jun 2019, Jun–Aug 2019) on coral recruit abundances on settlement tiles. Chi-square-value (χ^2), degrees of freedom (dF) and *p*-value obtained from GLMM model comparisons with ANOVA (type I). Results of the pairwise tests were derived from post-hoc analysis based on least square means with Bonferroni adjustment. Significance level: *** $p < 0.001$; ** $p < 0.01$.

	GLMM model comparison ANOVA (type I)			Pairwise test	
Fixed factor	χ^2	dF	*p*	z-ratio	*p*
Location	303.9	1	***		
Period	102.2	5	***		
Location:Period	21.4	5	***		
Aug – Oct, Site 1 vs 9				-8.8	***
Oct – Dec, Site 1 vs 9				-8.5	***
Dec – Feb, Site 1 vs 9				-6.7	***
Feb – Apr, Site 1 vs 9				-8.8	***
Apr – Jun, Site 1 vs 9				-7.0	***
Jun – Aug, Site 1 vs 9				-3.1	**

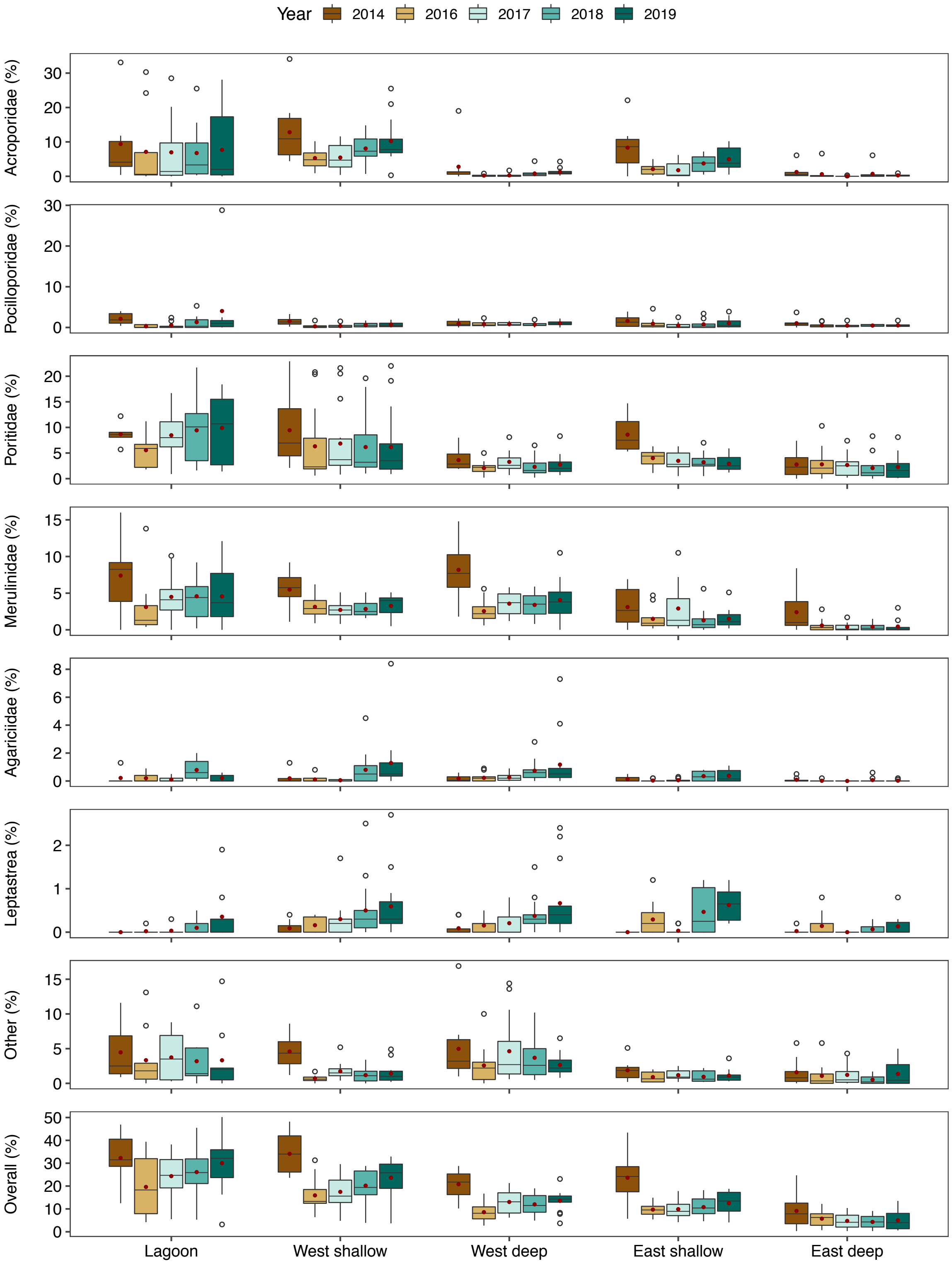


Figure S1: Percentage cover (median and interquartile range, outliers displayed as circles, means displayed as red dots) of different hard coral taxa and overall between 2014 and 2019 across Aldabra's locations. Note that no data is available from 2015 and the pre−bleaching reference is given by 2014 data.

Table S5: Coral juvenile abundances (per m^2) reported from 106 reefs at 11 locations worldwide. A: Studies reporting coral juvenile abundances before and/or after a bleaching event. B: Studies reporting coral juvenile abundance without referring to a bleaching event. Values in blue are those included in Figure S2 (comparison of Aldabra's coral juvenile abundance in 2019 to pre-bleaching values at Aldabra and reefs worldwide)

a	Pre-bleaching			First record post-bleaching				Last record post-bleaching					
Location (bleaching event)	Year	Mean	SE	Year	Mean	SE	% change^a	Year	Mean	SE	% change^b	Level of protection	Source and further notes
Aldabra Atoll, Seychelles (2015/16)	2015	14.1	1.2	2016	7.4	0.5	-48	2019	22.4	1.2	67	Special Reserve (1981)	This study
Lagoon	—"—	n.a.	n.a.	—"—	7.7	1.6	n.a.	—"—	29.9	5.3	74	—"—	
West (5 m)	—"—	20.6	1.9	—"—	8.3	1.0	-60	—"—	21.4	1.9	61	—"—	
East (5 m)	—"—	8.3	0.8	—"—	7.9	1.0	-5	—"—	24.1	2.6	67	—"—	
West (15 m)	—"—	14.2	5.1	—"—	7.7	0.8	-46	—"—	22.3	1.8	65	—"—	
East (15 m)	—"—	11.5	2.7	—"—	5.5	1.0	-52	—"—	16.6	1.9	67	—"—	
Aldabra Atoll, Seychelles (1998/99)				2001	6.0	0.8	n.a.	2005	5.9	0.9	-2	Special Reserve (1981)	Stobart et al. (2002) Values obtained by averaging site level data given in reference
Lagoon				—"—	7.4	1.9	—"—.	—"—	—"—	—"—	n.a.	—"—	
West (6 m)				—"—	4.5	0.8	—"—	—"—	—"—	—"—	—"—	—"—	
East (6 m)				—"—	8.2	0.4	—"—	—"—	—"—	—"—	—"—	—"—	
West (10 m)				—"—	6.7	1.8	—"—	—"—	4.4	0.7	-54	—"—	
East (10 m)				—"—	7.6	1.0	—"—	—"—	7.4	1.0	-4	—"—	
West (20 m)				—"—	4.1	1.0	—"—	—"—	—"—	—"—	—"—	—"—	
East (20 m)				—"—	3.7	1.6	—"—	—"—	—"—	—"—	—"—	—"—	
Inner Islands, Seychelles (2016)	2011	11.9	2.0	2017	3.1	0.7	-74						Dajka et al. (2019) Reef level values obtained with approval from J. Dajka and K. Chong-Seng (pers. comm, July 2020) Protection: Jennings et al. (2020)
Mahe East Carbonate	—"—	4.3	1.2	—"—	1.2	0.6	-72						
Mahe East Granite	—"—	5.2	1.1	—"—	0.0	0.0	-100						
Mahe East Patch	—"—	15.0	1.7	—"—	6.2	2.0	-59						
Mahe North West Carbonate	—"—	12.3	3.5	—"—	0.9	0.4	-92					No-take MNP (1979)	
Mahe North West Granite	—"—	37.9	4.1	—"—	8.3	2.3	-78						
Mahe North West Patch	—"—	10.6	1.7	—"—	3.1	0.9	-71						
Mahe St. Anne Carbonate	—"—	15.1	2.8	—"—	1.0	0.7	-93					No-take MNP (1973)	
Mahe St. Anne Granite	—"—	8.2	1.4	—"—	6.2	1.8	-25					—"—	
Mahe St. Anne Patch	—"—	15.0	2.1	—"—	0.2	0.2	-98					—"—	
Mahe West Carbonate	—"—	9.2	1.4	—"—	1.2	0.6	-87						
Mahe West Granite	—"—	15.9	2.6	—"—	9.1	2.2	-43						

(continued on next page)

Table S5 (continued)

a	Pre-bleaching			First record post-bleaching				Last record post-bleaching					
Location (bleaching event)	Year	Mean	SE	Year	Mean	SE	% change[a]	Year	Mean	SE	% change[b]	Level of protection	Source
Mahe West Patch	—"—	13.0	2.8	—"—	0.5	0.3	-96						
Praslin North East Carbonate	—"—	1.9	0.7	—"—	0.3	0.2	-84						
Praslin North East Granite	—"—	16.9	2.7	—"—	4.0	0.8	-76					No-take MNP (1979)	
Praslin North East Patch	—"—	4.1	0.9	—"—	2.6	0.6	-38					—"—	
Praslin South West Carbonate	—"—	0.7	0.4	—"—	1.6	0.8	135						
Praslin South West Granite	—"—	9.5	1.3	—"—	6.0	1.9	-37						
Praslin South West Patch	—"—	18.7	3.3	—"—	3.8	1.1	-80						
Lizard Island, Australia (2016)	2015	6.0	1.2	2016	5.4	0.7	-10					National Park (1939)	Álvarez-Noriega et al. (2018) Values estimated from Fig. A1 in supplement Protection: Queensland Government https://parks.des.qld.gov.au/parks/lizard-island/about#management
North Reef 1	—"—	10.6	0.5	—"—	10.5	0.3	-1					—"—	
North Reef 2	—"—	3.2	1.0	—"—	5.4	0.6	69					—"—	
North Reef 3	—"—	15.0	1.0	—"—	8.9	0.6	-41					—"—	
Gnarly Tree	—"—	9.8	1.0	—"—	8.9	1.0	-9					—"—	
North of Paradise	—"—	8.4	2.1	—"—	7.6	1.3	-10					—"—	
No Man's Land	—"—	9.0	2.2	—"—	6.8	1.1	-24					—"—	
Easter Point	—"—	10.2	1.3	—"—	7.6	1.2	-25					—"—	
Lizard Head	—"—	8.6	2.0	—"—	8.1	0.6	-6					—"—	
Southeast 1	—"—	3.0	1.3	—"—	5.4	0.5	80					—"—	
South Island	—"—	8.4	1.3	—"—	5.7	0.6	-32					—"—	
Lagoon 1	—"—	3.0	0.5	—"—	4.1	0.5	37					—"—	
Trimodal 1	—"—	4.4	1.6	—"—	2.4	0.5	-45					—"—	
Lagoon 2	—"—	1.6	0.6	—"—	3.2	0.7	100					—"—	
Horseshoe	—"—	5.4	1.1	—"—	1.9	0.5	-65					—"—	
Vickis	—"—	2.2	0.5	—"—	3.8	1.0	73					—"—	
Corner Beach	—"—	3.4	1.0	—"—	2.7	0.7	-21					—"—	
Osprey	—"—	1.0	0.5	—"—	2.7	0.8	170					—"—	
Resort	—"—	5.0	1.5	—"—	5.4	0.6	8					—"—	
Cooks Path	—"—	4.4	2.1	—"—	3.0	0.7	-32					—"—	
Turtle	—"—	2.4	0.5	—"—	3.2	0.6	33					—"—	

(continued on next page)

Table S5 (continued)

a	Pre-bleaching			First record post-bleaching				Last record post-bleaching					
Location (bleaching event)	Year	Mean	SE	Year	Mean	SE	% change[a]	Year	Mean	SE	% change[b]	Level of protection	Source
Huvadhoo Atoll, Maldives (2016)				2017	4	6.4*	n.a.					None	Perry and Morgan (2017)
Mahutigala (< 5m depth)				—"—	5.9	12.0*	—"—						
Kandahalagala				—"—	3	3.5*	—"—						
Kodehutigalaa				—"—	3.5	3.7*	—"—						
Kadumaigala				—"—	2.7	4.6*	—"—						
Kafigahla				—"—	5	8.0*	—"—						
Palau (1998/99)				2001	4.9	1.1	n.a.	2004	3.8	0.8	-29	No-take MPAs (individual sites, 1976–2005)	Golbuu et al. (2005) Protection: Friedlander et al. (2017), Golbuu et al. (2005)
West Exposed (3 m)				—"—	7.5	1.0	—"—	—"—	4	0.5	-88		
East Exposed (3 m)				—"—	4.5	1.0	—"—	—"—	6	0.9	25		
Patch (3 m)				—"—	5.5	1.5	—"—	—"—	2.5	0.5	-120		
Bay (3 m)				—"—	4	1.0	—"—	—"—	1.5	0.5	-167		
West Exposed (10 m)				—"—	7.5	1.0	—"—	—"—	4	0.5	-88		
East Exposed (10 m)				—"—	4	0.9	—"—	—"—	4	1	0		
Patch (10 m)				—"—	3	1.0	—"—	—"—	4	1.1	25		
Bay (10 m)				—"—	3	1.0	—"—	—"—	4	1	25		

(continued on next page)

[a] Percentage difference in coral juvenile abundance between pre-bleaching value and first record post-bleaching

[b] Percentage difference in coral juvenile abundance between first and last record post-bleaching

* SD not SE

n.a. = not applicable

MPA = Marine Protected Area

Table S5 (continued)

b

Location	Year	Mean	SE	Level of protection	Source and further notes
Central atolls Maldives	2007	28.2	1.1	None	Cardini et al. (2012)
Lagoon (5-6 m)	—"—	23.1	1.2		
Lagoon (10-12 m)	—"—	23.0	1.0		
Lagoon (16-18 m)	—"—	20.8	1.0		
Ocean facing reef (5-6 m)	—"—	38.2	1.1		
Ocean facing reef (10-12 m)	—"—	34.3	1.5		
Ocean facing reef (16-18 m)	—"—	29.5	0.9		
Moorea, French Polynesia	2003	7.7	1.3	None (at that time)	Penin et al. (2007)
Vaipahu (6 m)	—"—	6.8	1.0		
Vaipahu (12 m)	—"—	7.3	0.5		
Vaipahu (18 m)	—"—	10.5	1.2		
Tiahura (6 m)	—"—	7.1	0.8		
Tiahura (12 m)	—"—	8.1	1.2		
Tiahura (18 m)	—"—	12.3	3.8		
Haapiti (6 m)	—"—	3.7	1.0		
Haapiti (12 m)	—"—	6.1	1.2		
Haapiti (18 m)	—"—	7.7	0.8		
Grande Terre, New Caledonia	2008	9.4	1.1	None (at that time)	Adjeroud et al. (2019)
SM1	—"—	6.5	2.5		
SM2	—"—	4.0	0.8		
RA1	—"—	9.5	2.5		
RA2	—"—	3.0	0.7		
MA1	—"—	5.5	0.5		
MA2	—"—	3.0	0.8		
MS1	—"—	4.8	0.9		
MS2	—"—	17.0	0.5		
BA1	—"—	20.0	0.8		
BA2	—"—	20.2	0.8		
Tongatapu, Tonga	2006	5.5	1.0	None (at that time)	Adjeroud et al (2013)
S1 (2 -3 m)	—"—	8.0	1.8		
S2	—"—	4.8	0.5		
S3	—"—	8.5	1.5		
S4	—"—	3.8	1.5		
S5	—"—	6.5	1.0		
S6	—"—	1.6	0.1		
S7	—"—	10.3	2.0		
S8	—"—	5.0	0.5		
S9	—"—	0.7	0.1		
S10	—"—	5.8	0.5		

(continued on next page)

Table S5 (continued)

b

Location	Year	Mean	SE	Level of protection	Source
Vamizi Island, Mozambique	2013	17.8	11.6*		Sola et al. (2015)
S1 (5 - 9 m)	—"—	17.3	12.2*	No-take MR (2006)	Protection: da Silva et al (2015)
S2 (5 - 9 m)	—"—	25.0	18.2*	—"—	
S3 (5 - 9 m)	—"—	11.0	4.4*		
United Arab Emirates	2012	3.8	0.4	None	Pratchett et al. (2017)
Delma	—"—	2.5	0.4		
Saadiyat	—"—	5	0.5		
Ra Ghanada	—"—	5.5	1		
Dibba Rock	—"—	2.3	0.3		
Al Aqua	—"—	3.9	0.6		

* SD not SE
MR = marine reserve

Literature cited in Table S5

Adjeroud M, Briand MJ, Kayal M, Dumas P (2013) Coral assemblages in Tonga: Spatial patterns, replenishment capacities, and implications for conservation strategies. Environ Monit Assess 185:5763–5773

Adjeroud M, Poisson E, Peignon C, Penin L, Kayal M (2019) Spatial Patterns and Short-term Changes of Coral Assemblages Along a Cross-shelf Gradient in the Southwestern Lagoon of New Caledonia. Diversity 11:21

Álvarez-Noriega M, Baird AH, Bridge TCL, Dornelas M, Fontoura L, Pizarro O, Precoda K, Torres-Pulliza D, Woods RM, Zawada K, Madin JS (2018) Contrasting patterns of changes in abundance following a bleaching event between juvenile and adult scleractinian corals. Coral Reefs 37:527–532

Cardini U, Chiantore M, Lasagna R, Morri C, Bianchi CN (2012) Size-structure patterns of juvenile hard corals in the Maldives. J Mar Biol Assoc U K 92:1335–1339

Dajka JC, Wilson SK, Robinson JPW, Chong-Seng K, Harris A, Graham N (2019) Uncovering drivers of juvenile coral abundance following mass bleaching. Coral Reefs 38: 637–649

Friedlander AM, Golbuu Y, Ballesteros E, Caselle JE, Gouezo M, Olsudong D, Sala E (2017) Size, age, and habitat determine effectiveness of Palau's Marine Protected Areas. PLoS One 12:1–18

Golbuu Y, Bauman A, Kuartei J, Victor S (2005) The State of Coral Reef Ecosystems of Palau. In: The State of Coral Reef Ecosystems of the United States and Pacific Freely Associated States: 2005. NOAA Technical Memorandum NOS NCCOS 11. Waddell JE (ed) NOAA/NCCOS, Silver Spring, p 488–505

Golbuu Y, Victor S, Penland L, Idip D, Emaurois C, Okaji K, Yukihira H, Iwase A, van Woesik R (2007) Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. Coral Reefs 26:319–332

Jennings S, Marshall SS, Cuet P, Naim O (2000) Chapter 13. The Seychelles. In: Coral Reefs of the Indian Ocean. Their Ecology and Conservation. McClanahan TR, Sheppard CRC, Obura DO (eds) Oxford University Press, New York, p 383–410

Penin L, Adjeroud M, Schrimm M, Lenihan HS (2007) High spatial variability in coral bleaching around Moorea (French Polynesia): patterns across locations and water depths. C R Biol 330:171–181

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

Pratchett M, Baird AH, Bauman AG, Burt J (2017) Abundance and composition of juvenile corals reveals divergent trajectories for coral assemblages across the United Arab Emirates. Mar Pollut Bull 114:1031–1035

Da Silva IM, Hill N, Shimadzu H, Soares AMVM, Dornelas M (2015) Spillover effects of a community-managed marine reserve. PLoS One 10:e0111774

Sola E, Marques da Silva I, Glassom D (2015) Spatio-temporal patterns of coral recruitment at Vamizi Island, Quirimbas Archipelago, Mozambique. African J Mar Sci 37:557–565

Stobart B, Buckley R, Downing N, Callow M, LeClair L, Teleki K (2002) Aldabra Marine Programme Phase III. Aldabra: Extending the Survey Eastward. Cambridge Coastal Research Unit. Department of Geography, University of Cambridge

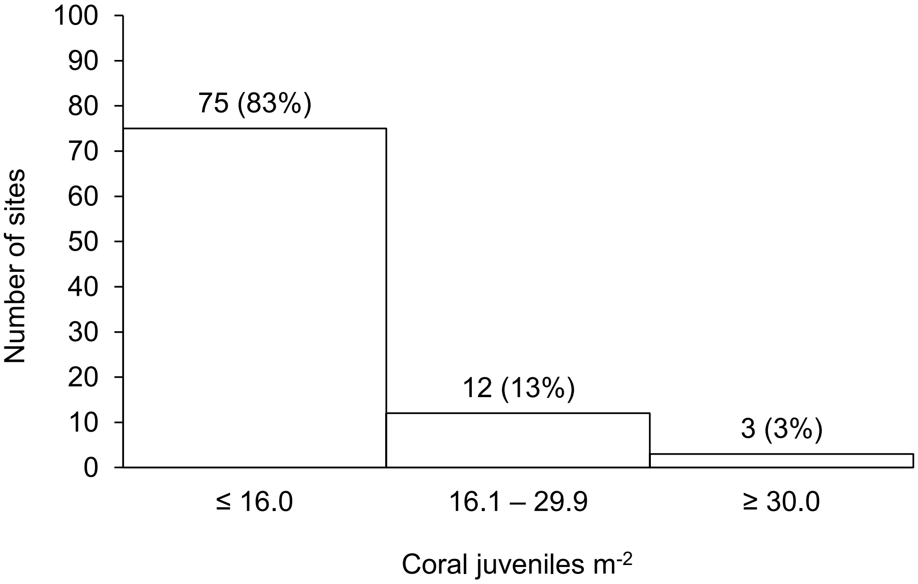
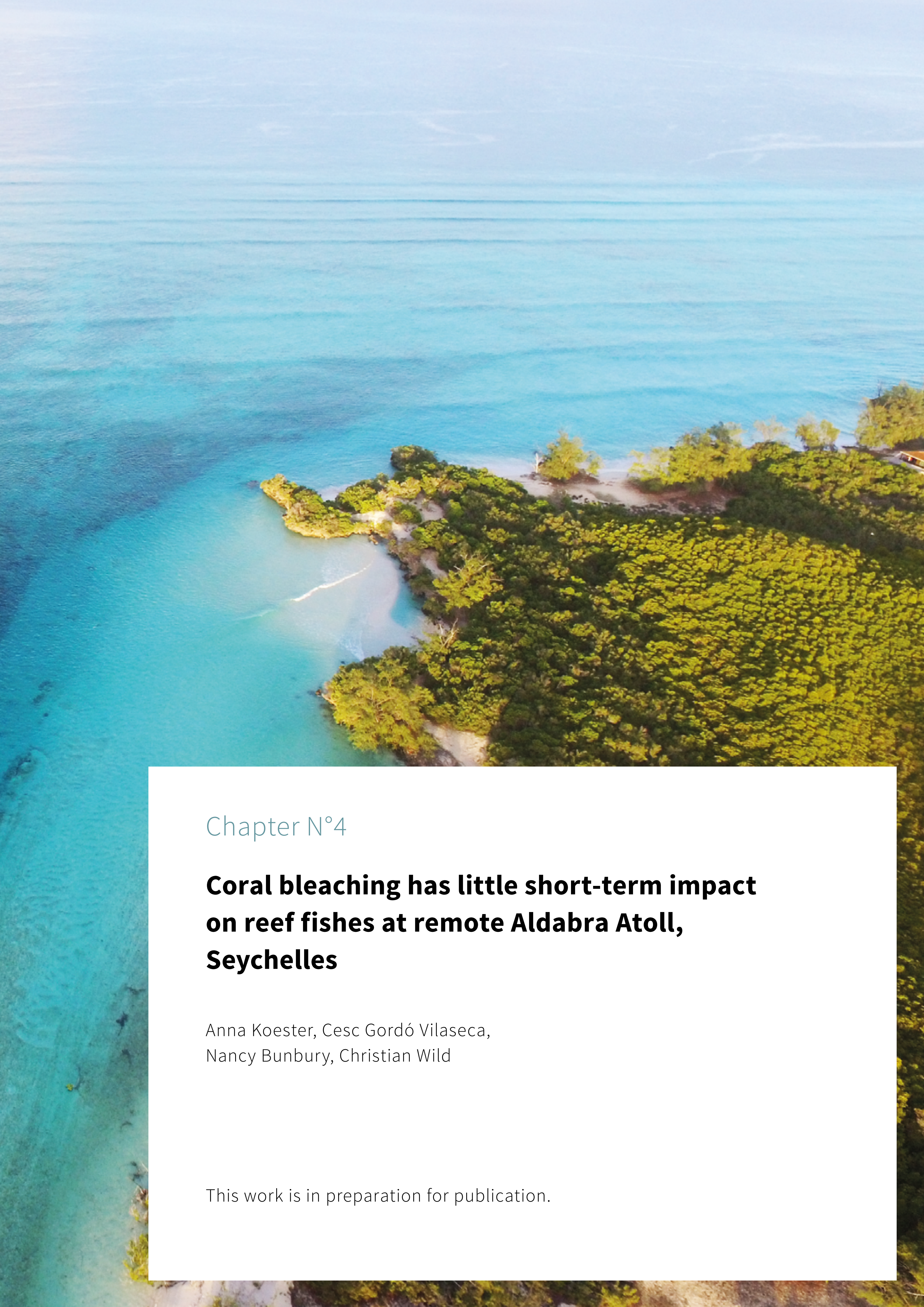


Figure S2: Comparison of Aldabra's coral juvenile abundance in 2019 with pre-bleaching values at Aldabra and reefs worldwide. Histogram shows the number (percentage) of sites (blue marked values in Table S5) with coral juvenile abundances that fall within the same range as Aldabra's reefs in 2019 (16.1–29.9 coral juveniles m^{-2}) as well as below or above.



Chapter N°4

Coral bleaching has little short-term impact on reef fishes at remote Aldabra Atoll, Seychelles

Anna Koester, Cesc Gordó Vilaseca,
Nancy Bunbury, Christian Wild

This work is in preparation for publication.

Abstract

Coral bleaching immediately impacts the reef benthos, but effects on fish communities can be delayed and unpredictable. Local human impacts such as fishing create additional pressures that can obscure clear assessment of the impacts of coral bleaching events on fish communities. We assessed changes in fish abundance, biomass and assemblage structure before and after the 2015/16 coral bleaching event at Aldabra Atoll, Seychelles, where local human impacts are minimal but where reefs suffered 50% bleaching-induced coral mortality. We monitored 12 shallow (2–5 m water depth) and nine deep (15 m water depth) permanent survey sites before (2014, 2015) and after (2016–2019) the coral bleaching event. Mean fish abundance increased by > 120% during 2015–2016 (from 3531–4669 to 9743–10557 fish/hectare). This was mainly driven by increases in herbivores (from 1613–2435 to 3650–6604 fish/hectare), likely as a response to increased turf algae cover following coral mortality. Changes in overall fish biomass were not significant between 2014 and 2016 (2014: 823–961 kg/hectare, 2015: 960–2311 kg/hectare, 2016: 1334–1817 kg/hectare), but corallivore, invertivore, piscivore and omnivore biomass was 24–84% lower in 2016 than in 2015, although similar to 2014 values. While fish abundance and biomass of all functional groups fluctuated between 2016 and 2019, post-bleaching values were similar to pre-bleaching data, and fish species assemblages observed in 2015, 2016, 2018, 2019 were very similar. This suggests a low overall impact of the bleaching event on Aldabra's fish communities, which may be related to rapid reef recovery. Results indicate that under limited direct human impacts, at least in the short-term, reef fish communities are little affected by climate change induced reef degradation.

Introduction

Coral reefs are highly biodiverse and complex ecosystems that are subject to a range of local and global factors of natural and anthropogenic origins (Bellwood et al. 2004; Graham et al. 2015). Much research and management effort is dedicated to coral reef fishes because of their value for fisheries and tourism and their crucial functional roles in coral reef ecosystems (Graham et al. 2015; Christ et al. 2020).

Reef fish assemblages are vulnerable to changes in coral reef habitat, e.g. via climate change-induced coral bleaching and coral mortality (Lindahl et al. 2001). The loss of live coral and the subsequent erosion of the physical reef structure can cause declines in fish abundance and diversity (Anderson et al. 2012). Fish species specialised on live corals for food and habitat are usually affected immediately or in the short-term (i.e., within ca. 3 years post-disturbance; Wilson et al. 2006), while recruitment failure due to loss of reef structure can impact fish assemblages and biomass in the longer term (Graham et al. 2007). In contrast, the abundance of herbivorous and detritivorous fish may increase as declines in coral cover are often linked to increases in algae cover and associated detritus (Lindahl et al. 2001; Sheppard et al. 2002). Herbivorous fish are therefore one of the most important functional groups of coral reef fishes; by regulating the abundance of algae on coral reefs, thereby facilitating the availability of suitable substrate for recruitment of reef-forming corals, they promote coral reef resilience and are a major component of post-disturbance reef recovery (Bellwood et al. 2004).

Habitat degradation usually co-occurs with localised fishing pressure, which can lead to substantial declines of fish abundance and biomass, especially in heavily populated regions of the world (Wilson et al. 2008). Several studies have documented rapid depletion of fish biomass even at relatively low fishing pressure (Dulvy et al. 2004; Wilson et al. 2010), with large, slow-growing, late-maturing fish species being particularly vulnerable as these are the first to be targeted (Jennings and Polunin 1996). Consequently, heavily fished communities are often dominated by small-bodied individuals and species of lower trophic groups (Dulvy et al. 2004; Graham et al. 2005; McClanahan 2008). As a means to counteract declines and restore fish assemblages, marine protected areas (MPAs) – ranging from no-take to multi-use managed areas – have become a standard conservation and management tool (Halpern 2003). Indeed, research from well-enforced no-take MPAs shows that abundance, biomass and sometimes diversity of reef fish communities can be enhanced compared to adjacent areas open to fishing (Russ et al. 2005; McClanahan et al. 2007; Stockwell et al. 2009). Nevertheless, recent work suggests that the benefits of relatively small MPAs are declining and/or shifting in the face of climate change, benefitting altered fish assemblages dominated by lower trophic levels (Graham et al. 2020). It is therefore useful to understand how reef fish communities respond to the effects of climate change at remote and large MPAs where direct anthropogenic impacts are minimal.

Aldabra Atoll in the Republic of Seychelles is one such area. Aldabra is located 407 km north and 700 km east from the nearest inhabited land (Madagascar and Tanzania, respectively), and more than 1000 km from the Seychelles Inner Islands. It was designated as a Special Reserve in 1981 (i.e., the highest level of national protection under Seychelles' legislation) and inscribed as a UNESCO World Heritage Site in 1982, with its protective boundaries surrounding 2559 km^2 since 2018 (439 km^2 prior to that; Seychelles Islands Foundation 2016). Aldabra's marine ecosystem has therefore been protected from commercial fishing pressure for almost 40 years, and human-driven nutrient inputs are absent. Nevertheless, bleaching-induced coral mortality was high at Aldabra in 1998/1999 (38–66% coral loss at 10–20 m water depth; Norström et al. 2009) and in 2015/2016 (34–62% coral loss at 2–15 m water depth; (Cerutti et al. 2020; Koester et al. 2020), although substantial coral reef recovery was observed during 2016–2019 with reefs ≤ 5 m water depth reaching 54–93% of their pre-bleaching cover by 2019 (Koester et al. 2020).

With over a billion people worldwide depending on reef fish for nutrition (NOAA 2020), it is critical to understand fish community susceptibility and recovery potential in the face of climate change induced coral bleaching and reef degradation. Here, we utilise data collected two survey periods before and four survey periods after the 2015/16 coral bleaching event at Aldabra, and specifically ask: (1) How did the 2016 coral bleaching event affect fish abundance and biomass at Aldabra? (2) How did this change in the four years following the bleaching event? And (3) How did fish assemblage structure change during the entire study period? Remote and strictly protected locations like Aldabra serve as valuable reference sites for comparisons with other locations where local human impacts are substantial. Ecological and environmental research and monitoring at locations like Aldabra is therefore crucial for an enhanced understanding of the effects of climate change on coral reef ecosystems, and paramount for their continued protection.

Study Site

The Republic of Seychelles is situated in the Western Indian Ocean (WIO) between 4° and 10° south of the equator. The Seychelles consist of more than 150 islands and atolls that are scattered across its 1,400,000 km^2 exclusive economic zone (Kawaley 1998). More than 99% of the country's population reside on the granitic islands (Inner Islands) in the north of the archipelago (Seychelles National Bureau of Statistics 2020), whilst the coralline islands and atolls in the south and south-west (Outer Islands) are not, or only scarcely populated.

Aldabra (46°20'E, 9°24'S) in the far southwest of the Seychelles, is an elevated coral atoll with a large lagoon (196 km^2) encircled by four main islands, spanning 34 × 14.5 km (Fig. 4.1). A public trust, the Seychelles Islands Foundation (SIF; managing authority of Aldabra since 1979) maintains a small research station (10–20 persons), to facilitate research and monitoring of Aldabra's terrestrial and marine habitats and protection of the atoll. A small and strictly regulated subsistence fishery by staff is permitted (Seychelles Islands Foundation 2016).

Between December 2015 and June 2016, reefs at Aldabra experienced continued bleaching risk, with degree heating week values peaking at 3.4 °C-weeks (temperature measured by satellite ca. 55 km north-east of Aldabra: 46°50'E, 9°00'S; Cerutti et al. 2020). Between December 2015 and December 2016, hard coral cover reduced by 51–62% on the seaward reefs at 5 m and 15 m water depth and by 34% in the lagoon (Cerutti et al. 2020; Koester et al. 2020).

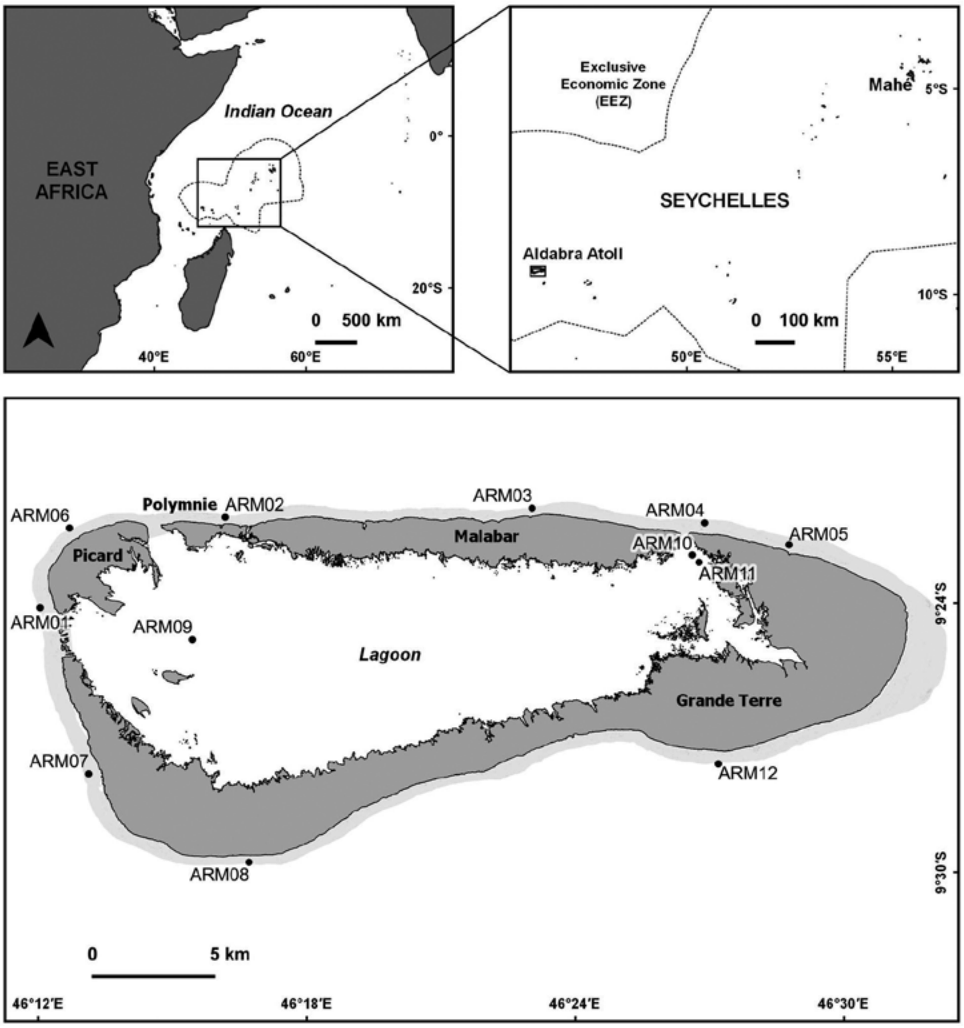


Figure 4.1: Location of Aldabra Atoll in the Indian Ocean and within the Seychelles, with its four main islands and 12 marine survey sites (Aldabra Reef Monitoring Sites: ARM01– ARM12, indicated by black dots). ARM01–08 & ARM12 are outside the lagoon on the seaward reefs (light grey shading around Aldabra), while ARM09–11 are in the lagoon.

Data collection

Twelve permanently marked marine survey sites are located around Aldabra (Fig. 4.1). Nine sites are located at both 5 m and 15 m water depth at the seaward reefs, while three sites are situated at 2 m water depth inside the lagoon (Fig. 4.1). Fish surveys were conducted in November 2014–January 2015 (hereafter 2014), December 2015 (immediately before the bleaching event), December 2016 (6 months following the end of the bleaching event), December 2018–January 2019 (hereafter 2018) and November 2019–January 2020 (hereafter 2019).

Due to variable availability of resources, the number of survey sites visited and number of transects completed varied during 2014–2019 (Supplementary Table S1) but the survey method remained constant (except for 2015, where all diurnally active, reef-associated fishes were identified to species level, counted and estimated to the nearest cm when larger than 5 cm): all fish of a pre-defined list (62 species and 10 genera of 19 families, Supplementary Table S2) were counted along 50 × 4 m belt transects (i.e., one transect = 200 m^2) and classified into one of six size class categories (i.e., < 5 cm, 5–9 cm, 10–19 cm, 20–29 cm, 30–39 cm, > 39 cm, based on total length). Large, more mobile fish were surveyed on the first pass of the transect, while smaller fish were surveyed on the return.

Data processing

Fish taxa were pooled into six functional groups based on broad feeding habits: piscivores, omnivores, invertivores, corallivores, planktivores, herbivores (Samoilys et al. 2018; Froese and Pauli 2019; Supplementary Table S2).

Fish biomass was estimated using the length-weight equation $W = a\ x\ L^b$ (Le Cren 1951), where W is weight, L is length for which the midpoint of each size class was used, and a and b are published species-specific constants (Froese and Pauli 2019). To obtain these constants for genera and families, constants from species present at Aldabra (Friedlander et al. 2015) were averaged. To approximate the length of fishes within the largest size class (i.e., > 39 cm), the median size within that size class was calculated of all available size estimates to the nearest cm (i.e., 55 cm based on 237 and 59 entries from 2015 and 2018, respectively).

Statistical analysis

Although benthic communities differed spatially across Aldabra (Koester et al. 2020), preliminary analysis of the fish assemblages did not identify spatial clustering in any of the study years (Supplementary Fig. S1) and spatial differences in fish abundance and biomass were only assessed across water depths. Due to the lower number of transects surveyed in the lagoon, data from the lagoonal sites were pooled with the 5 m survey sites of the seaward reefs (i.e., shallow water depth).

Generalised Linear Mixed Models (GLMM; R version 3.6.1, R Core Team 2019, *lme4* package; Bates et al. 2015) with Negative Binomial error distributions were used to test for differences in fish abundance across years (2014–2019) and water depths (shallow, deep). Fixed factors included 'survey year', 'water depth' and their interaction (except for omnivores for which only 'survey year' was set as a fixed factor due to poor model fit when the interaction term was included); 'site' was set as random factor to account for possible autocorrelation between transects. The same model structure was used to assess differences in biomass using GLMMs with Gamma error distributions with logarithmic link function. To validate the models, residual distributions of Generalised Linear Models (GLM, stats package, R Core Team 2019 and MASS package; Venables & Ripley 2002) were checked to see if the assumptions of homogeneity of variance, normality, and leverage were met; individual values that were found to drive the analysis were excluded. Pearson residual distributions were then checked for the GLMMs. To identify pairwise differences in significant models, a post-hoc analysis based on least square means with Bonferroni adjustment was run (lsmean package; Lenth 2016). As the data set is very heterogeneous due to the high amount of very large schools of fish encountered throughout all years, data is displayed as box and whisker plots.

To visualise changes is fish assemblage structure, square root-transformed fish biomass data (on lowest taxonomic level) per site, depth and year was converted into a Bray-Curtis similarity matrix to perform canonical analysis of principal coordinates (CAP) following non-metric multidimensional scaling (nMDS). CAP is a flexible method for constrained ordination that can uncover patterns that are not visible in an unconstrained ordination such as nMDS (Anderson and Willis 2014). PRIMER 6 with the PERMANOVA+ add-on (Primer-E, Plymouth, UK) was used for this analysis.

How did the 2016 coral bleaching event affect fish abundance and biomass at Aldabra?

Mean fish abundance increased by > 120% between 2015 and 2016 (shallow: from 4669 to 10557 fish/hectare; deep: from 3531 to 9742 fish/hectare), but abundances in 2016 did not differ from those in 2014 (shallow: 5945 fish/hectare; deep: 5144 fish/hectare; Fig. 4.2a; Table 4.1). Overall mean biomass did not change during 2014–2016 at the deep reefs (960–1334 fish/hectare; Fig. 4.2b, Table 4.1), but fluctuated at the shallow reefs and differed significantly between 2014 and 2015 (2014: 823 fish/hectare, 2015: 2311 fish/hectare); mean biomass in 2016 (1816 fish/hectare) did not differ from 2014 and 2015 values (Fig. 4.2b, Table 4.1).

Table 4.1: Changes in fish abundance and biomass. Effect of year (2014–2019) and water depth (shallow: 2–5 m; deep: 15 m) on fish abundance and biomass at Aldabra. Chi-square-value (χ^2), degrees of freedom (dF) and p-value obtained from GLMM model comparisons with ANOVA (type I). Significance level: *** $p < 0.001$; ** $p < 0.01$; ** $p < 0.05$; ns = not significant: $p > 0.05$.

Group	Fixed factor	Abundance			Biomass		
		χ^2	dF	p	χ^2	dF	p
Overall	Year	65.6	5	***	20.3	5	**
	Depth	15.6	1	***	9.1	1	**
	Year:Depth	16.2	5	**	21.1	5	***
Corallivores	Year	12.4	5	*[a]	39.3	5	***
	Depth	1.3	1	ns	0.2	1	ns
	Year:Depth	3.5	5	ns	7.8	5	ns
Herbivores	Year	102.1	5	***	38.5	5	***
	Depth	17.4	1	***	22.6	1	***
	Year:Depth	3.5	5	ns	3.5	5	ns
Invertivores	Year	10.3	5	ns	48.7	5	***
	Depth	16.1	1	***	2.0	1	ns
	Year:Depth	2.2	5	ns	4.8	5	ns
Piscivores	Year	56.4	5	***	43.0	5	***
	Depth	0.8	1	ns	11.3	1	***
	Year:Depth	5.5	5	ns	10.4	5	ns
Planktivores	Year	11.9	5	*	22.6	5	***
	Depth	39.8	1	***	18.2	1	***
	Year:Depth	10.3	5	ns	11.1	5	ns
Omnivores	Year	22.8	5	***	19.3	5	**
	Depth	not tested[b]			22.8	1	***
	Year:Depth	not tested[b]			16.7	5	**

[a] although the GLMM indicated a significant effect of 'year', the post-hoc analysis did not indicate significant differences between years

[b] model including interacting fixed factors had poor fit and only differences across years was test (see methods)

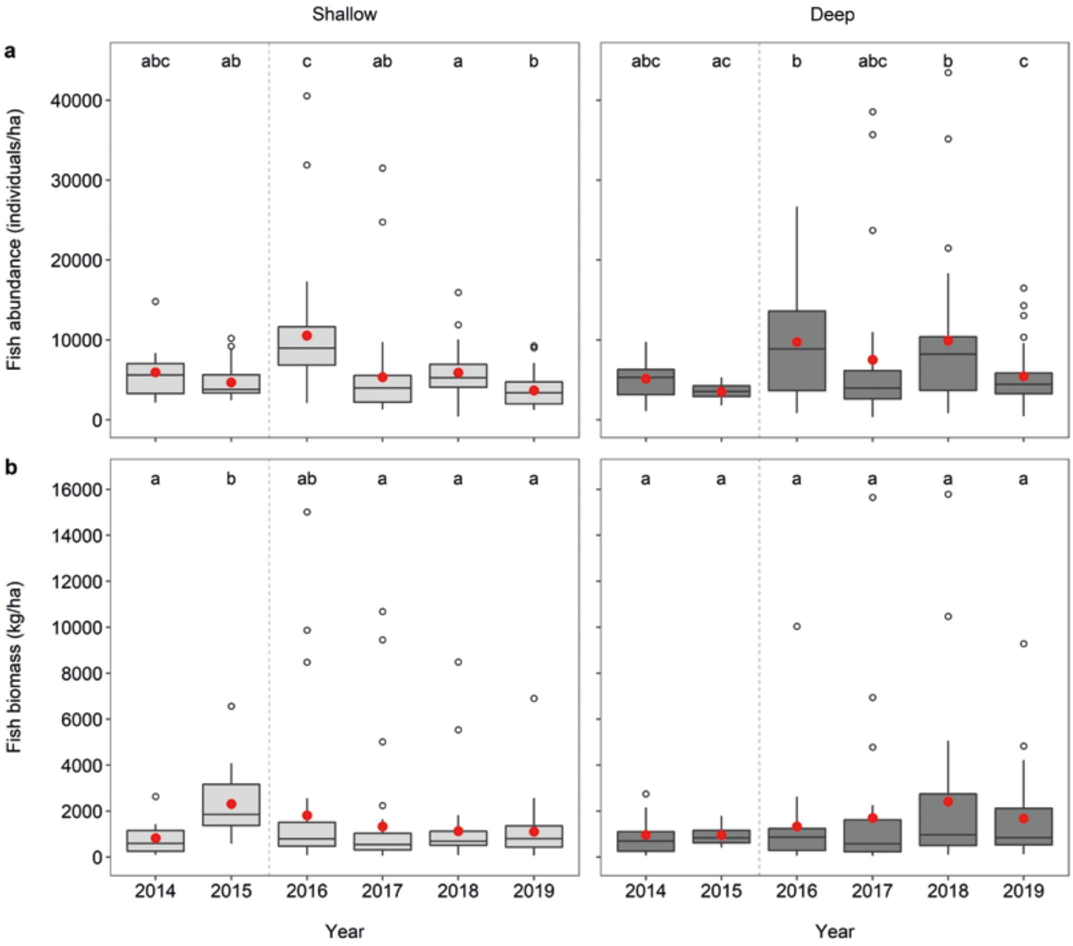


Figure 4.1: Overall fish abundance (a) and biomass in kg (b) per hectare displayed as median and interquartile range (outliers [sightings of very large schools of fish] are displayed as circles; means shown as red dots) during 2014–2019 at shallow (2–5 m depth; light grey) and deep (15 m depth; dark grey) water depths at Aldabra. Small letters above boxplots indicate significant differences ($p < 0.05$) between years (see also Table 4.1). Dashed line indicates the bleaching event.

Increases in overall fish abundance appeared to be driven primarily by herbivores; mean herbivore abundance more than doubled during 2015–2016 (shallow: 2435–6604 fish/hectare; deep: 1612–3650 fish/hectare), with abundances in 2016 being higher than in 2014 (shallow: 3855 fish/hectare; deep: 2094 fish/hectare; Fig. 4.3b; Table 4.1). Planktivores was the only other functional group that changed in abundance after the bleaching event (Fig. 4.3e; Table 4.1). Compared to all other years, mean planktivore abundance was low in 2015 (shallow: 181 fish/hectare; deep: 167 fish/hectare) and the increased abundance in 2016 (shallow: 504 fish/hectare; deep: 2415 fish/hectare) depicted levels more similar to those in 2014 (shallow: 790 fish/hectare; deep: 1242 fish/hectare).

Although overall biomass did not change between 2015 and 2016 (Fig. 4.2b), reductions in mean biomass were recorded for corallivores (shallow: -84%, 26 to 4 kg/hectare, deep: -49%, 14 to 7 kg/hectare), invertivores (shallow: -70%, 132 to 39 kg/hectare, deep: -54%, 68 to 32 kg/hectare), piscivores (shallow: -71%, 567 to 164 kg/hectare, deep: -26%, 364 to 196 kg/hectare) and omnivores (shallow: -24%, 484 to 366 kg/hectare; Fig. 4.4a, c, d, f; Table 4.1).

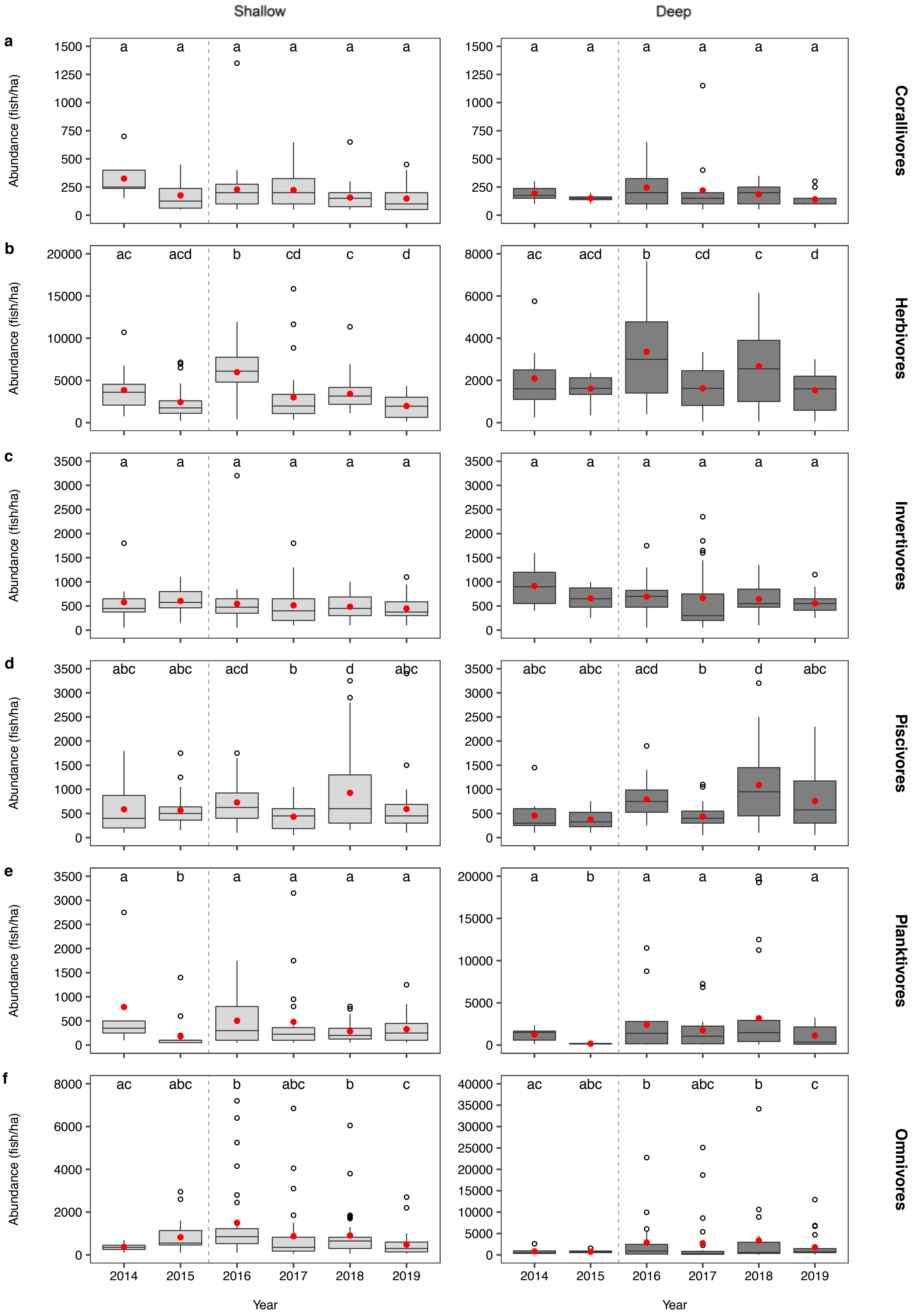


Figure 4.3: Fish abundance of functional groups per hectare (median and interquartile range, outliers [sightings of very large schools of fish] are displayed as circles; means displayed as red dots) during 2014–2019 at shallow (2–5 m depth; light grey) and deep (15 m depth; dark grey) water depths at Aldabra. Small letters above boxplots indicate significant differences ($p < 0.05$) between years (see also Table 4.1). Dashed line indicates the bleaching event.

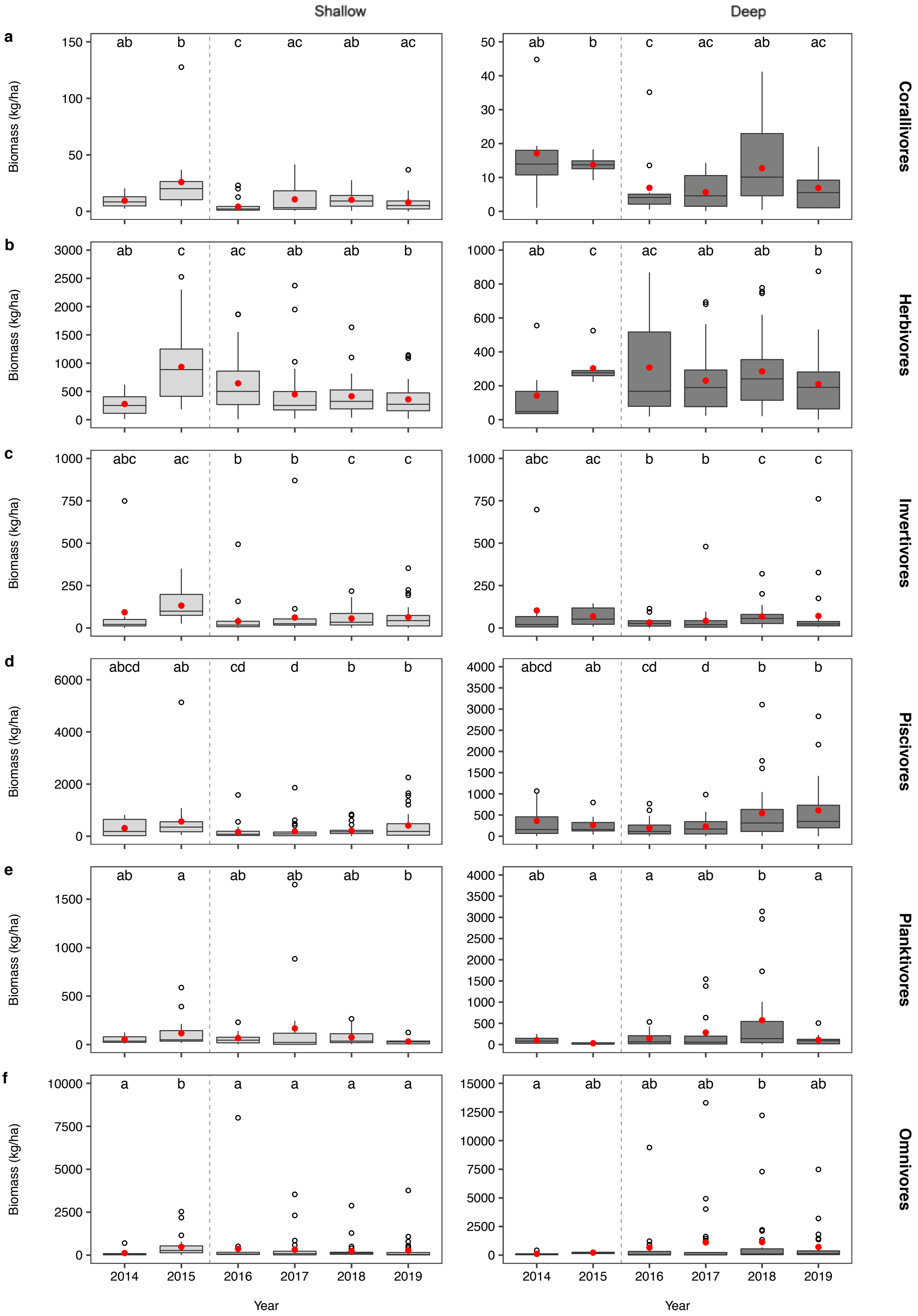


Figure 4.4: Fish biomass (kg) of functional groups per hectare (median and interquartile range, outliers [sightings of very large schools of fish] are displayed as circles; means displayed as red dots) during 2014–2019 at shallow (2–5 m depth; light grey) and deep (15 m depth; dark grey) water depths at Aldabra. Small letters above boxplots indicate significant differences ($p < 0.05$) between years (see also Table 4.1). Dashed line indicates the bleaching event.

How did fish abundance and biomass change in the four years following the bleaching event?

Overall mean fish abundance fluctuated during 2016–2019, and abundances in 2019 (shallow: 3678 fish/hectare; deep: 5440 fish/hectare) were lower than in 2016 (shallow: 10557 fish/hectare; deep: 9742 fish/hectare) but did not differ from pre-bleaching levels in 2014 and 2015 (Fig. 4.2a; Table 4.1). Overall mean fish biomass did not change significantly during 2016–2019 (2016 – shallow: 1817 kg/hectare; deep: 1334 kg/hectare; 2019 – shallow: 1104 kg/hectare; deep: 1674 kg/hectare), although biomass in the shallows was lower during 2017–2019 compared to the pre-bleaching values in 2015 (Fig. 4.2b, Table 4.1).

Mean abundances of herbivores, piscivores and omnivores fluctuated between 2016 and 2019 but abundances never dropped below pre-bleaching levels (2014 and 2015; apart from abundances of herbivores in 2019, which were similar in 2015, but higher in 2014; Fig. 4.3b, d, f; Table 4.1). Mean abundances of corallivores, invertivores and planktivores did not change during 2016–2019 (Fig. 4.3a, c, e).

Mean biomass of all functional groups also fluctuated between 2016 and 2019, but the 2019 values did not differ from the pre-bleaching values in 2014 for any of the groups (Fig 4, Table 4.1). However, mean biomass was higher in 2015 than 2019 for all functional groups except invertivores and piscivores (Fig 4, Table 4.1).

How did fish assemblage structure change during the study period?

Changes in fish assemblage structure during 2014–2019 were not detected by nMDS which poorly represented the data (Supplementary Fig. S2). Constrained ordination unravelled temporal differences in fish assemblages across years, with assemblages in 2014 and 2017 (which showed large differences among sites) deviating from all other years, but this appeared not to be driven by the bleaching event (Fig. 4.5).

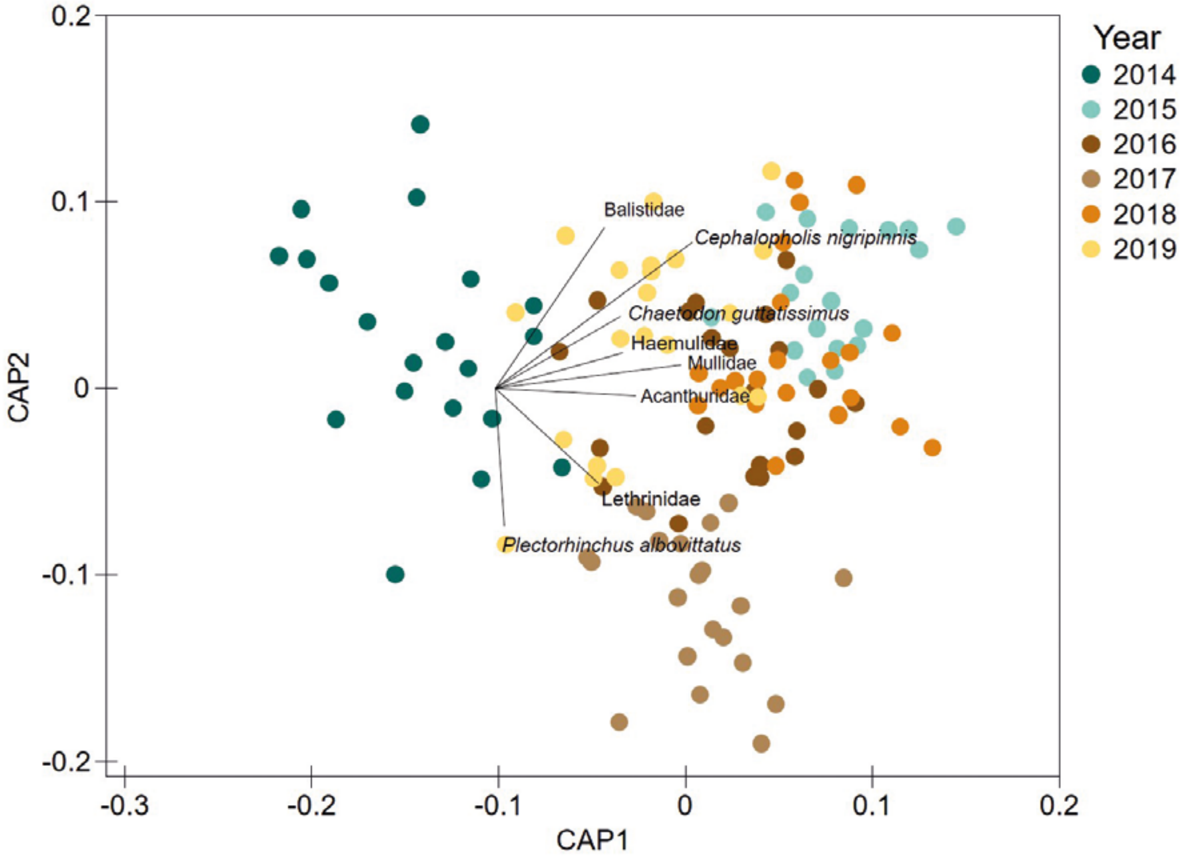


Figure 4.5: Plot of the canonical analysis of principal (CAP) coordinates of Aldabra's fish communities (biomass) at each survey site and depth across years. Fish taxa that contribute most to the temporal differences are displayed as vectors (spearman rank correlation values > 0.4; taxa in clockwise order: Balistidae, *Cephalophoris nigripinnis*, *Chaetodon guttatissimus*, Haemulidae, Mullidae, Acanthuridae, Lethrinidae, *Plectorhinchus albovitattus*).

How did the 2016 coral bleaching event affect fish abundance and biomass?

Prolonged periods of elevated water temperatures during 2014–2017 caused unprecedented thermal stress to reefs worldwide (Lough et al. 2018). This lead to widespread and severe coral bleaching and mortality (Eakin et al. 2019) and caused a 50% reduction of overall hard coral cover at Aldabra (Cerutti et al. 2020; Koester et al. 2020). In the present study, we show that Aldabra's fish community responded with an overall increase in abundance, fuelled mainly by increases in herbivorous fish. This is similar to studies elsewhere (Lindahl et al. 2001; Sheppard et al. 2002; Robinson et al. 2019) and likely due to the elevated turf algae cover at Aldabra's reefs following the bleaching event (Supplementary Fig. S3). Abundances of other functional groups, most notably of corallivores, which rely on live corals for food, were not affected. Corallivores are typically heavily affected by the loss of live corals (Wilson et al. 2006; Graham et al. 2007), but responses can vary substantially within and among species and locations, indicating that the abundance of corallivores is not always determined by live coral cover (Wilson et al. 2006).

The reduction in biomass of corallivores, invertivores, piscivores and omnivores, despite similar abundances, indicates that individuals recorded were smaller in 2016 compared to 2015. In contrast, previous work following coral bleaching documented increases in large fish and declines in small fish abundance (Graham et al. 2007). Body size is usually a key determinant of fish vulnerability to habitat degradation, as smaller size classes show the greatest declines once the reef structure needed for habitat, shelter and recruitment is lost (Graham et al. 2006, 2007; Wilson et al. 2008, 2010). This however can be delayed by several years as the physical reef structure typically remains intact for some time post-bleaching (Sheppard et al. 2002; Graham et al. 2007). The reduction of larger fishes at Aldabra during 2015–2016, most notably piscivores, omnivores and invertivores is therefore conspicuous. Habitat degradation affects interactions between predator and prey populations (Graham et al. 2006; Wilson et al. 2006) and some fish migrate to nearby and relatively unaffected areas (Wilson et al. 2006), which at Aldabra may be reefs below the depths surveyed (~20–25 m; A.K. pers. obs., 2016).

How did fish abundance and biomass change in the four years following the bleaching event?

Previous work reported substantial hard coral cover increase at Aldabra's shallow reefs during 2016–2019 (reefs reaching up to 93% of their pre-bleaching cover by 2019; Koester et al. 2020) and a tripling of coral juvenile densities at all water depths during this time (Koester et al. in review [Chapter 3]). Sufficient herbivory that mediated turf algae height, thereby reducing the potential negative effects of algae on adult and juvenile corals, was assumed to be an important driver for this rapid recovery (Koester et al. 2020, Koester et al. in review [Chapter 3], see also Gilmour et al. 2013). The present study supports this assumption as both, herbivorous fish abundance and turf algae cover (Supplementary Fig. S3) increased in 2016 (to the highest levels recorded within the study period) and had returned to pre-bleaching levels by 2017. Such rapid increase and reduction of herbivores is likely caused by fish migrating to areas of increased food availability, rather than actual population growth and decline (Wilson et al. 2006).

Herbivory is a key process for reef recovery, and herbivore biomass serves as a good proxy for this process (Lokrantz et al. 2008; Graham et al. 2015). A minimum threshold of 177 kg/hectare herbivore biomass reduced the risk of reefs in the Inner Seychelles to transition to fleshy algae-dominated states following the 1998 bleaching event (Graham et al. 2015), a value below those at Aldabra during 2014–2019 (means: 209–934 kg/hectare). More recent work from the Inner Seychelles, however, showed that herbivore biomass was relatively high (ca. 200–380 kg/hectare) on both recovered and regime-shifted reefs within the 15 years following the 1998 bleaching event, but herbivorous fish assemblages differed at these reefs as species responses varied (i.e. browsing herbivores associated with regime shifted reefs, scraping herbivores with recovering reefs; Robinson et al. 2019). The crude classification of several genera into the single group 'herbivores' (as done here) therefore carries the risk of missing important information on species diversity and the distinct functions of herbivores (e.g. scraping, browsing, grazing; Green and Bellwood 2009). However, as well as the rapid reduction of turf algae cover during 2016–2017, fleshy macroalgae cover at Aldabra was low throughout all study years (Supplementary Fig. S3), possibly a result of low (anthropogenically induced) nutrient levels and high herbivorous pressure, suggesting the functional diversity within Aldabra's herbivorous fish community is well represented. Nevertheless, further studies are needed to confirm this, especially in light of the increasing frequency of coral bleaching events (Van Hooidonk et al. 2014).

All functional groups at Aldabra fluctuated during 2016–2019 in abundance, biomass or both, but levels never dropped below pre-bleaching values of 2014 and/or 2015. The high variability in absolute abundance and biomass of Aldabra's fish functional groups during the entire study period may thus suggest that only herbivores responded to the bleaching event. However, even changes in herbivore biomass at Aldabra during 2016–2019 did not correspond to other studies that identified continuing increases in herbivore abundance and biomass following bleaching (Hempson et al. 2018; Robinson et al. 2019; Graham et al. 2020). In the Inner Seychelles, the response of reef fish communities to coral bleaching is well documented and showed substantial lag-effects (Graham et al. 2007) that persisted for 15 years following the 1998 bleaching event, even at reefs where coral cover returned to pre-bleaching levels (Hempson et al. 2018; Robinson et al. 2019; Graham et al. 2020). Most of the reef structure provided by dead corals will be retained for several years post-bleaching, but once this habitat structure deteriorates, a wide range of fish species is affected (Wilson 2006). Evidently, the post-bleaching period covered by this study is too short to detect such long-term effects, underlining the importance of continuing reef fish monitoring at Aldabra.

How did fish assemblage structure change during the study period?

Temporal changes in fish assemblage structure did not appear to be driven by the effects of the bleaching event as assemblages in 2015, 2016, 2018 and 2019 were very similar. Fish assemblages in 2014 and 2017 were different, with high among-site variability in both years. Spatial and temporal variation in estimates of reef fish abundance and biomass are ubiquitous and arise on scales of hours to years, with effects varying across taxa (Thompson and Mapstone 2002). Sources of this variation may be actual changes of population size and structure, temporal migration or sampling error (Thompson and Mapstone 2002). Although some bias is inevitable (e.g. in 2017, sea conditions were unusually rough, A.K., pers. obs.), efforts to reduce sampling error include e.g. the standardised training of observers and conducting surveys at similar times of the day or tidal cycle (Thompson and Mapstone 2002), both of which were done in this study.

As a location with low direct anthropogenic impact, fish communities at Aldabra may indeed be less affected by mass bleaching than at locations where fishing pressure is high (e.g. Inner Seychelles, Hempson et al. 2018; Robinson et al. 2019; Graham et al. 2020). Intact fish communities with high biomass (3200 kg/hectare) were observed at Farqhuar Atoll (Outer Islands, Seychelles), where local anthropogenic stressors are low, but where a combination of coral bleaching and cyclones have caused substantial reef degradation (Friedlander et al. 2014). Trophic structure at lightly fished, high fish biomass locations (i.e. > 650 kg/hectare) tends to be dominated by upper (piscivores) and lower (primary consumers) trophic levels, whereas fished locations typically have a pyramid-shaped trophic structure (i.e. dominated by lower trophic levels; Graham et al. 2017a). Differing predator-prey interactions may operate at low and high fish biomass locations, which may also influence the fish communities' response to mass coral mortality. Total fish biomass recorded at Aldabra fluctuated substantially between years (885–2253 kg/hectare) and are dwarfed by the biomass values recorded at the strictly protected northern atolls of the remote Chagos Archipelago (7260 kg/hectare), but appear indicative for a well-protected site compared to other protected locations in the Indian Ocean (438–4900 kg/hectare) where substantially more fish species were considered for biomass estimations (Table 4.2). Nevertheless, as the fish survey protocol at Aldabra is confined to a list of 19 families of which only 62 taxa are surveyed to species level, patterns in assemblage structure may be masked by the higher taxonomic classes included (genera, family). In comparison, reef fish assessments in other locations considered 134 fish species (Inner Seychelles: Hempson et al. 2018, Robinson et al. 2019, Graham et al. 2020), all species of 13 selected families (Chagos Archipelago: Samoilys et al. 2018) or all fish species encountered (e.g., 372 taxa of 56 families at Farquhar Atoll, Seychelles: Friedlander et al. 2014, 163 species at the Great Barrier Reef: Triki & Bshary 2019), allowing the detection of more subtle changes in fish assemblage structure, functional groups (e.g. the diverse functions of herbivores, Green and Bellwood 2009) and trophic levels (Hempson et al. 2018).

Table 4.2: Mean reef fish biomass (kg/hectare) across locations in the Indian Ocean.

Location	Fishing status	Year	Mean biomass (kg/hectare)	No of fish taxa surveyed	Source
Aldabra	protected[a]	2014	885	72 taxa (10 genera, 62 species) of 19 families	This study
		2015	1993		
		2016	1638		
		2017	1490		
		2018	2253		
		2019	1351		
Cosmodelo		2015	4900	332 species of 46 families	Friedlander et al. (2015), biomass values estimated from Figure 10
Aldabra	protected[a]	2015	4800		
Astove		2015	3900		
Assumption		2015	2800		
Farquhar		2015	3200	372 taxa of 56 families	Friedlander et al. (2014)
Chagos (Northern Atolls)	protected	2010	7260	All diurnally active, non-cryptic, reef-associated fish	Graham et al. (2013), biomass values estimated from Figure 19.8 Graham and McClanahan (2013), survey information from supplementary material
Mayotte	protected	2009-2010	1178		
Kenya	protected	2004-2010	1151		
Mozambique	protected	2008-2010	1123		
Tanzania	protected	2005-2010	959		
Inner Seychelles	protected	2008	685		
Madagascar	protected	2007-2009	548		
Mauritius	protected	2004	438		
Chagos (Diego Garcia)	[b]	2010	1288		
Maldives		2005	1507		
Mayotte		2009-2010	1096		
Mauritius		2004	932		
Mozambique		2008-2010	849		
Tanzania		2005-2010	575		
Madagascar		2007-2009	575		
Inner Seychelles		2008	521		
Kenya		2004-2010	438		

[a] subsistence fishing permitted (10-20 people)

[b] recreational fishing associated with US Navy base (Graham et al. 2013)

Our results indicate that overall, Aldabra's fish communities showed little response to the 2016 coral bleaching event during the first four post-bleaching years, with only herbivores appearing to have responded to the effects of coral mortality. The high heterogeneity within the data set and the relatively low taxonomic resolution surveyed may mask patterns of change. However, coral recovery within the first four post-bleaching years was substantial at Aldabra, particularly in the lagoon and shallow seaward reefs at the western side of the atoll, where coral cover reached 93% and 68% of pre-bleaching (2014) levels, respectively (vs. 54% of pre-bleaching levels at the seaward reefs at the eastern side; Koester et al. 2020). This rapid, but spatially variable recovery possible buffered some of the negative effects of initial hard coral loss on fish communities. As changes in fish communities following mass coral mortality can occur with substantial delay (Graham et al. 2007), continued fish monitoring at Aldabra is needed. Agencies responsible for monitoring and managing coral reefs are often resource-limited and ecological survey procedures need to be cost-effective and robust to be conducted regularly. At sites where local anthropogenic impacts are low, the cost-benefit relation of reef fish assessments may be improved by increasing the data accuracy (e.g. surveying more taxa to species level), whilst reducing the survey frequency. It is thus recommended that future studies at Aldabra assess fish communities to higher taxonomic resolution, allowing to identify not only longer-term changes, but also spatial differences and subtler variations in taxonomic and functional composition.

References

Anderson K, Pratchett M, Baird AH (2012) Summer growth rates of corals at Lord Howe Island, Australia. Proc 11th Int Coral Reef Symp 9–13

Anderson MJ, Willis TJ (2014) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. 84:511–525

Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. J Stat Softw 67:1–48

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

Cerutti J, Burt AJ, Haupt P, Bunbury N, Mumby P, Schaepman-Strub G (2020) Impacts of the 2014–2017 global bleaching event on a protected remote atoll in the Western Indian Ocean. Coral Reefs 39:15–26

Christ HJ, White R, Hood L, Vianna GMS, Zeller D (2020) A Baseline for the Blue Economy: Catch and Effort History in the Republic of Seychelles' Domestic Fisheries. Front Mar Sci 7:1–13

Le Cren ED (1951) The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (Perca fluviatilis). J Anim Ecol 20:201–219

Dulvy NK, Polunin NVC, Mill AC, Graham N (2004) Size structural change in lightly exploited coral reef fish communities: Evidence for weak indirect effects. Can J Fish Aquat Sci 61:466–475

Eakin CM, Sweatman HPA, Brainard RE (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38:539–545

Friedlander A, Ballesteros E, Beets J, Brown BE, Fay JM, Haupt P, Henning B, Rose P, Sala E (2015) Biodiversity and ecosystem health of the Aldabra Group, southern Seychelles: Scientific report to the government of Seychelles.

Friedlander A, Obura D, Aumeeruddy R, Ballesteros E, Chruch J, Cebrian E, Sala E (2014) Coexistence of low coral cover and high fish biomass at Farquhar Atoll, Seychelles. PLoS One 9:e87359

Froese R, Pauli D (2019) FishBase. www.fishbase.org

Gilmour J, Smith LD, Heyward AJ, Baird AH, Pratchett M (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71

Graham N, Dulvy NK, Jennings S, Polunin NVC (2005) Size-spectra as indicators of the effects of fishing on coral reef fish assemblages. Coral Reefs 24:118–124

Graham N, Jennings S, MacNeil MA, Mouillot D, Wilson S (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:1–17

Graham N, McClanahan TR (2013) The Last Call for Marine Wilderness? Bioscience 63:397–402

Graham N, McClanahan TR, MacNeil MA, Wilson SK, Cinner JE, Huchery C, Holmes TH (2017) Human Disruption of Coral Reef Trophic Structure. Curr Biol 27:231–236

Graham N, Pratchett M, McClanahan TR, Wilson SK (2013) The status of coral reef fish assemblages in the Chagos Archipelago, with implications for protected area management and climate change. In: Sheppard C.R.C. (eds) Coral Reefs of the United Kingdom Overseas Territories. Coral Reefs of the World, vol 4. Springer Netherlands, Dordrecht, pp 253–270

Graham N, Robinson JPW, Smith SE, Govinden R, Gendron G, Wilson SK (2020) Changing role of coral reef marine reserves in a warming climate. Nat Commun 11:1–8

Graham N, Wilson SK, Jennings S, Polunin NVC, Bijoux J, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. PNAS 103:8425–8429

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

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. IUCN working group on Climate Change and Coral Reefs. IUCN, Gland, Switzerland, pp 70

Halpern BS (2003) The impact of marine reserves: Do reserves work and does reserve size matter? Ecol Appl 13:117–137

Hempson TN, Graham N, Macneil MA, Hoey A, Wilson SK (2018) Ecosystem regime shifts disrupt trophic structure. Ecol Appl 28:191–200

Van Hooidonk R, Maynard JA, Manzello D, Planes S (2014) Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. Glob Chang Biol 20:103–112

Jennings S, Polunin NVC (1996) Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. J Appl Ecol 33:400–412

Kawaley I (1998) Implications of the Exclusive Economic Zone and EEZ management for Seychelles, a small midocean Island commonwealth territory. Ocean Dev Int Law 29:225–264

Koester A, Migani V, Bunbury N, Ford AK, Sanchez C, Wild C (2020) Early trajectories of benthic coral reef communities following the 2015/16 coral bleaching event at remote Aldabra Atoll, Seychelles. Sci Rep 10:17034

Lenth R V. (2016) Least-squares means: The R package lsmeans. J Stat Softw 69:1–33

Lindahl U, Öhman MC, Schelten CK (2001) The 1997/1998 mass mortality of corals: Effects on fish communities on a Tanzanian coral reef. Mar Pollut Bull 42:127–131

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

Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs: 1871-2017. Sci Rep 8:1–8

McClanahan TR (2008) Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. Oecologia 155:169–177

McClanahan TR, Graham N, Calnan JM, MacNeil MA (2007) Toward pristine biomass: Reef fish recovery in coral reef marine protected areas in Kenya. Ecol Appl 17:1055–1067

NOAA (2020) How does overfishing threaten coral reefs? https://oceanservice.noaa.gov/facts/coral-overfishing.html

Norström A V., Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: beyond coral-macroalgal phase shifts. Mar Ecol Prog Ser 376:293–306

R Core Team (2019) R: A Language and Environment for Statistical Computing.

Robinson JPW, Wilson SK, Jennings S, Graham N (2019) Thermal stress induces persistently altered coral reef fish assemblages. Glob Chang Biol 25:2739–2750

Russ GR, Stockwell B, Alcala AC (2005) Inferring versus measuring rates of recovery in no-take marine reserves. Mar Ecol Prog Ser 292:1–12

Samoilys M, Roche R, Koldewey H, Turner J (2018) Patterns in reef fish assemblages: Insights from the Chagos Archipelago. PLoS One 13:e0191448

Seychelles Islands Foundation (2016) Aldabra Atoll Management Plan 2016.

Seychelles National Bureau of Statistics (2020) Seychelles National Bureau of Statistics. https://www.nbs.gov.sc/

Sheppard C, Spalding M, Bradshaw C, Wilson S (2002) Erosion vs. recovery of coral reefs after 1998 El Niño: Chagos reefs, Indian Ocean. AMBIO A J Hum Environ 31:40–48

Stockwell B, Jadloc CRL, Abesamis RA, Alcala AC, Russ GR (2009) Trophic and benthic responses to no-take marine reserve protection in the Philippines. Mar Ecol Prog Ser 389:1–15

Thompson AA, Mapstone BD (2002) Intra- versus inter-annual variation in counts of reef fishes and interpretations of long-term monitoring studies. Mar Ecol Prog Ser 232:247–257

Triki Z, Bshary R (2019) Fluctuations in coral reef fish densities after environmental disturbances on the northern Great Barrier Reef. PeerJ 7:e6720

Venables WN, Ripley BD (2002) Modern Applied Statistics with S. Fourth edition. Springer, New York

Wilson SK, Fisher R, Pratchett M, Graham N, Dulvy NK, Turner RA, Cakacaka A, Polunin NVC (2010) Habitat degradation and fishing effects on the size structure of coral reef fish communities. Ecol Appl 20:442–451

Wilson SK, Fisher R, Pratchett MS, Graham N, Dulvy NK, Turner RA, 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 SK, Graham N, Pratchett M, 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

Table S1: Number of transects (1 transect = 200 m^2) completed during fish surveys at each site and year.

Location	Site	2014		2015		2016		2017		2018		2019	
		5m	15m	5m	15m	5m	15m	5m	15m	5m	15m	5m	15m
Seaward reef	ARM01	1	1	3	1	3	2	3	3	3	3	3	2
Seaward reef	ARM02	1	1	3	1	3	2	3	3	3	3	3	3
Seaward reef	ARM03	1	1	3	1	3	2	3	3	3	3	3	3
Seaward reef	ARM04	1	1	3	1	3	2	3	3	3	3	3	3
Seaward reef	ARM05	1	1	3	1	3	3	3	3	3	3	3	3
Seaward reef	ARM06	1	1	3	1	3	2	3	2	3	3	3	3
Seaward reef	ARM07	1	1	0	0	3	3	3	3	3	3	3	3
Seaward reef	ARM08	1	1	3	1	3	2	3	3	3	3	3	3
Lagoon[a]	ARM09	1	—	1	—	3	—	3	—	3	—	3	—
Lagoon[a]	ARM10	1	—	1	—	3	—	2	—	2	—	2	—
Lagoon[a]	ARM11	1	—	1	—	1	—	2	—	3	—	2	—
Seaward reef	ARM12	1	1	3	1	3	3	3	3	3	3	3	3
Total		**12**	**9**	**27**	**8**	**34**	**21**	**34**	**26**	**35**	**27**	**34**	**26**

[a] survey sites are located at 2–3 m water depth

Table S2: Surveyed fish taxa and their classification into functional groups based on broad feeding habits following Samoilys et al. (2018) and Froese and Pauli (2019).

Functional group	Family/group	Species	Common name
Piscivores	Carangidae	*Caranx ignobilis*	Giant trevally
		Caranx melampygus	Bluefin trevally
		Caranx sexfasciatus	Big-eye trevally
		Gnathanodon speciousus	Golden trevally
		other	Trevally
	Lutjanidae	*Aprion viriscens*	Green jobfish
		Lutjanus bohar	Twinspot snapper
	Scombridae	*Gymnosarda unicolor*	Dogtooth tuna
		other	Tuna, mackerel, bonito
	Serranidae	*Aethaloperca rogaa*	Redmouth grouper
		Cephalopholis nigripinnis	Blackfin rock cod
		Dermatolepsis striolata	Smooth grouper
		Epinephelus fuscoguttatus	Brown marbled grouper
		Epinephelus lanceolatus	Giant grouper
		Epinephelus polyphekadion	Camouflage grouper
		Epinephelus tukula	Potato grouper
		Gracila albomarginata	Masked grouper
		Plectropomus laevis	Blacksaddle grouper
		Plectropomus pessuliferus	Roving coral grouper
		Plectropomus punctatus	Marbled coral grouper
		Variola louti	Yellow-edged lyretail grouper
		other	Grouper
	Sphyraenidae	*Sphyraena barracuda*	Great barracuda
Omnivores	Balistidae	various	Triggerfish
	Haemulidae	*Plectorhinchus albovittatus*	Giant sweetlips
		Plectorhinchus gaterinus	Black-spotted sweetlips
		Plectorhinchus piccus	Spotted sweetlips
		Plectorhinchus plagiodesmus	Yellow rubberlip sweetlips
		Plectorhinchus vittatus	Oriental sweetlips
		other	Sweetlips
	Lethrinidae	*Lethrinus nebulosis*	Spangled emperor
		Lethrinus olivaceous	Longface emperor
		Monotaxis grandoculis	Humpnose big-eye bream
		other	Emperor
	Lutjanidae	*Lutjanus argentimaculatus*	Mangrove snapper
		Lutjanus gibbus	Humpback snapper
		Lutjanus rivulatus	Speckled snapper
		other	Snapper
	Mullidae	various	Goatfish
	Tetraodontidae	various	Pufferfish
	Zanclidae	*Zanclus cornutus*	Moorish idol

(continued on next page)

Table S2 (continued)

Functional group	Family/group	Species	Common name
Invertivores	Acanthuridae	*Naso* spp. (> 20 cm TL)	Unicornfish
	Balistidae	*Balistodes viridescens*	Titan triggerfish
		Pseudobalistes flavimarginatus	Yellow-margin triggerfish
		Sufflamen chrysopterum	Flagtail triggerfish
	Chaetodontidae	*Chaetodon auriga*	Threadfin butterflyfish
		Chaetodon citrinellus	Speckled butterflyfish
		Chaetodon falcula	Saddleback butterflyfish
		Chaetodon guttatissimus	Spotted butterflyfish
		Chaetodon interruptus	Indian Ocean teardrop butterflyfish
		Chaetodon kleinii	Klein's butterflyfish
		Chaetodon lunula	Racoon butterflyfish
		Chaetodon madagaskariensis	Seychelles butterflyfish
		Chaetodon mertensii	Mertens butterflyfish
		Chaetodon vagabundus	Vagabond butterflyfish
		Chaetodon xanthocephalus	Yellow-headed butterflyfish
		Forcipiger flavissimus	Longnose butterflyfish
		Heniochus monoceros	Masked bannerfish
	Diodontidae	other	Porcupinefish
	Labridae	*Cheilinus fasciatus*	Red-breasted wrasse
		Cheilinus trilobatus	Tripletail wrasse
		Cheilinus undulatus	Humphead wrasse
		Oxycheilinus digramma	Cheeklined splendour wrasse
	Pomacanthidae	various	Angelfish
Corallivores	Chaetodontidae	*Chaetodon benetti*	Bennet's butterflyfish
		Chaetodon lineolatus	Lined butterflyfish
		Chaetodon melannotus	Blackbacked butterflyfish
		Chaetodon meyeri	Meyer's butterflyfish
		Chaetodon trifascialis	Chevroned butterflyfish
		Chaetodon trifasciatus	Indian Redfin butterflyfish
		Chaetodon zanzibarensis	Zanzibar butterflyfish
Planktivores	Chaetodontidae	*Hemitaurichthys zoster*	Black pyramid butterflyfish
		Heniochus acuminatus	Longfin bannerfish
	Holocentridae	*Holocentrus* spp.	Squirrelfish
		Neoniphon spp.	Squirrelfish
		Sargocentron spp.	Squirrelfish
Herbivores/ detritivores*	Acanthuridae	*Acanthurus* spp.	Surgeonfish
		Ctenochaetus spp.	Bristletooth
		Zebrasoma spp.	Tang
		Naso spp. (< 21 cm)	Unicornfish
	Ephipidae	*Platax* spp.	Batfish
	Scarinae	*Bolbometopon muricatum*	Bumphead parrotfish
		other	Parrotfish
	Siganidae	*Siganus* spp.	Rabbitfish

* for simplicity called ‘herbivores’ throughout the article

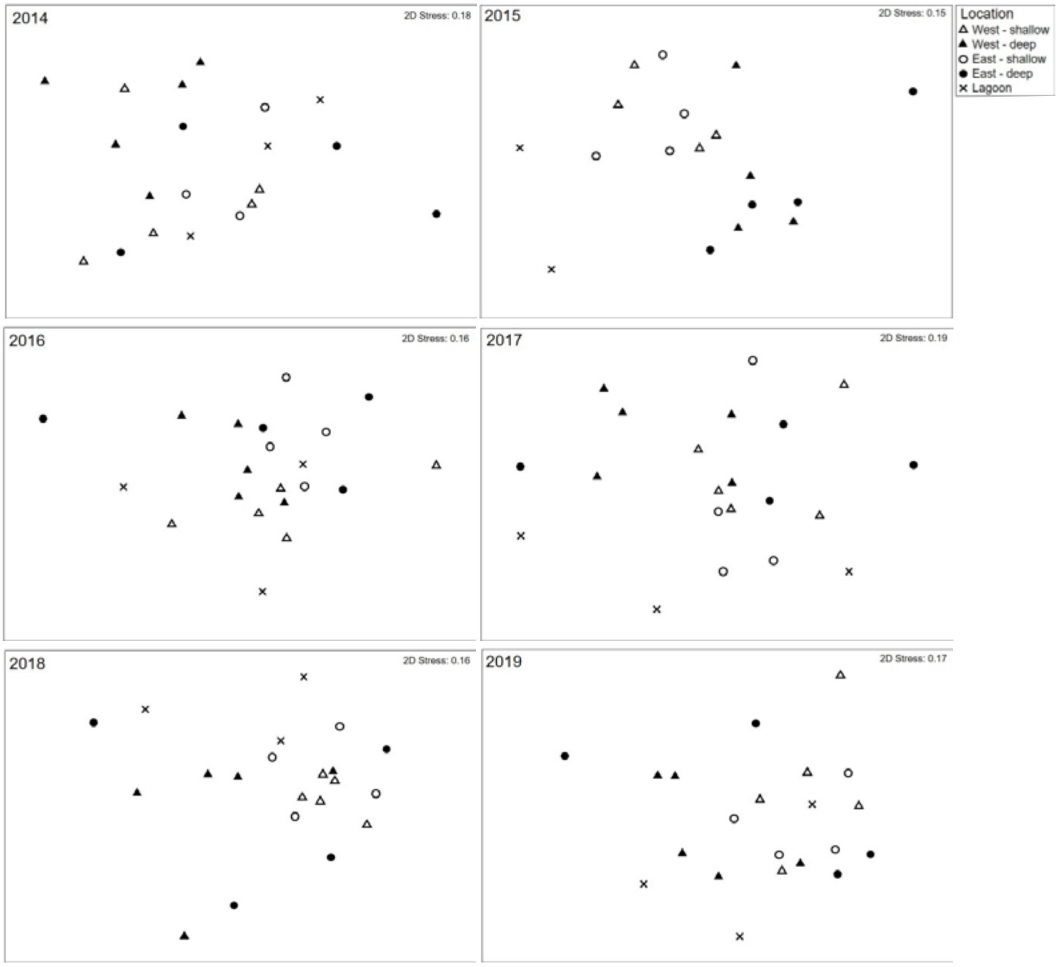


Figure S1: Non-metric multidimensional scaling plots of Aldabra's fish assemblages each year during 2014–2019 based on square-root transformed mean biomass per site and depth for the lowest taxonomic level possible (i.e. species or genus and family were species level was not surveyed). Labels demark the site locations for which spatial differenced were found for Aldabra's benthic assemblages (Koester et al. 2020; western sites = ARM01, ARM02, ARM06–ARM08; eastern sites = ARM03–ARM05, ARM12; Lagoon = ARM09–ARM11; Fig. 4.1). Analysis done with PRIMER 6 (Primer-E, Plymouth, UK).

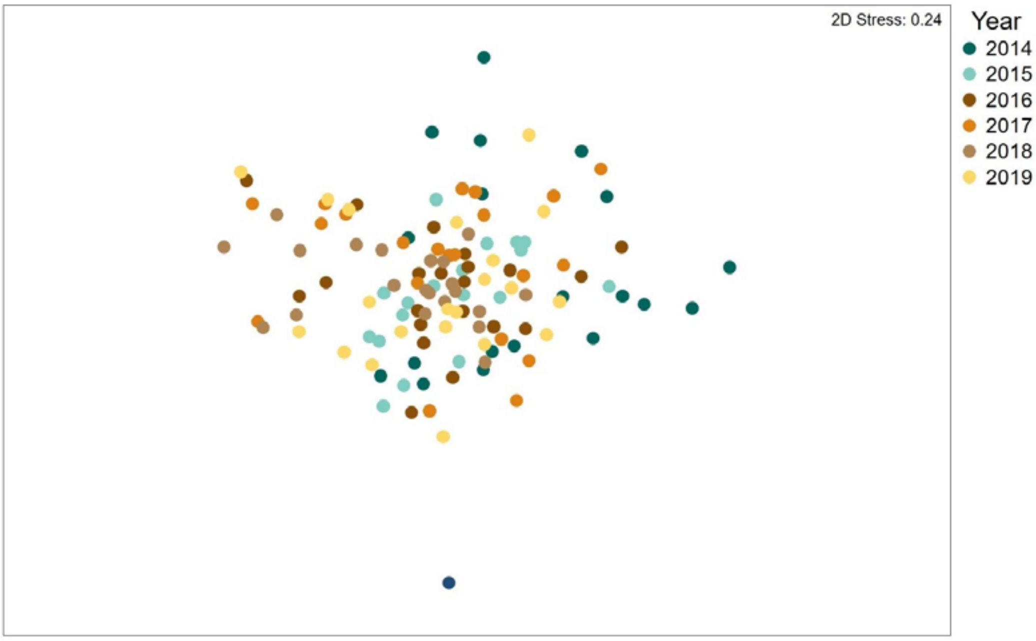


Figure S2: Non-metric multidimensional scaling (nMDS) plot of of Aldabra's fish communities (biomass) at each survey site and depth across years. A stress value > 0.2 indicates poor representation of the data (Clarke 1993).

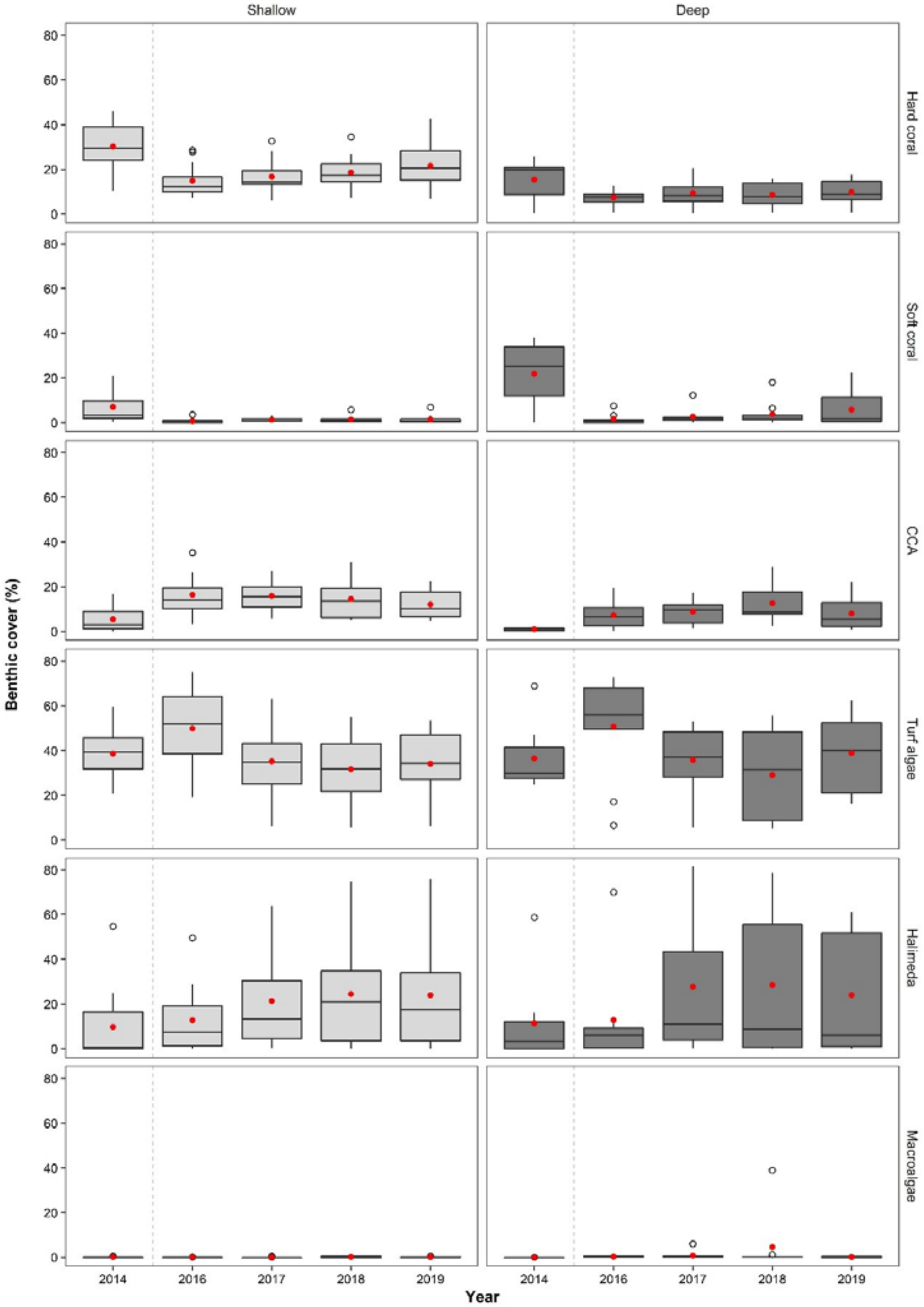


Figure S3: Percentage cover (median and interquartile range, outliers displayed as circles, means displayed as red dots) of different benthic taxa between 2014 and 2019 across Aldabra's locations. Note that no data is available from 2015 and the pre-bleaching reference is given by 2014 data.

References

Clarke KR (1993) Non-parametric multivariate analyses of changes in community structure. Aust J Ecol 18:117–143

Froese R, Pauli D (2019) FishBase. www.fishbase.org

Koester A, Migani V, Bunbury N, Ford AK, Sanchez C, Wild C (2020) Early trajectories of benthic coral reef communities following the 2015/16 coral bleaching event at remote Aldabra Atoll, Seychelles. Sci Rep 10:17034

Samoilys M, Roche R, Koldewey H, Turner J (2018) Patterns in reef fish assemblages: Insights from the Chagos Archipelago. PLoS One 13:e0191448

Chapter N°5

General Discussion

Overview

The degradation of coral reefs worldwide warrants more informed management approaches to increase conservation effectiveness during the climate crisis (McClanahan et al. 2012; Flower et al. 2017). Paramount to this is gaining a better understanding of coral reef resilience to inform reef management on local or regional scales. Remote, effectively protected coral reef systems provide critical baselines with which the influence of direct anthropogenic impacts on reef resilience can be better understood (Sandin et al. 2008). Using the remote and well protected atoll of Aldabra in the Seychelles, the overall aim of this thesis was to assess how coral reef ecosystems respond to and recover from mass coral bleaching events in the absence of direct anthropogenic stressors.

Key findings

The research in this thesis has resulted in several key findings:

- Coral bleaching susceptibility was substantially lower in Aldabra's lagoon than at the seaward reefs, probably driven by high water temperature variability in the lagoon that acclimatises hard corals to thermal stress (Chapter 2).
- The reefs of Aldabra's lagoon almost completely recovered to pre-bleaching hard coral cover and community composition within four years after the bleaching event. While seaward reefs also recovered, their recovery was slower and appeared to depend on the level of wave exposure and water depth. Overall, early recovery was mainly driven by growth of remnant hard corals (Chapter 2).
- While coral juvenile abundance was similar across Aldabra's reefs immediately after the bleaching event in 2016, abundances in the lagoon and the western seaward reefs had more than doubled two years after (2018). The same magnitude of increase was recorded at the eastern seaward reefs, but later, i.e. three years post-bleaching (2019), indicating slower recovery, likely due to higher wave exposure (Chapter 3).
- Post-bleaching coral recruitment in Aldabra's lagoon was an order of magnitude higher than on the seaward reefs and indicates strong self-recruitment of the lagoonal reefs. Furthermore, broadcast spawning at Aldabra, and likely the wider region, occurs during the north-west monsoon, when water temperature rapidly increases (Chapter 3).
- Assemblage structure of indicator fish species did not differ spatially across Aldabra and did not change in response to the bleaching event during the study period. Fish abundance and biomass fluctuated throughout the entire study period, but herbivorous fish abundance increased substantially following the bleaching event, and likely facilitated post-bleaching recovery (Chapter 4).

Patterns of reef resilience at Aldabra and beyond

Exposure to heat stress and mass coral bleaching events have increased in frequency and severity since the 1980s (Hughes et al. 2018a) and severe bleaching events are expected to occur on 90% of the world's coral reefs by 2055 (Van Hooidonk et al. 2014). The third and most recent global coral bleaching event, in 2014–2017 started in June 2014 in Guam and the Northern Mariana Islands, affected reefs in Hawai'i, the Marshall Islands and Florida throughout 2014 and continued into 2015, encompassing the South Pacific, Indian Ocean and the central and eastern tropical Pacific (Couch et al. 2017). With the 2015–2016 El Niño reaching its peak towards the end of 2015, coral bleaching continued in 2016 and 2017 in the Pacific and Indian Ocean (Couch et al. 2017). Many reefs experienced multiple, back-to-back bleaching events during this time (Hughes et al. 2017b; Manzello et al. 2018; Harrison et al. 2019; Head et al. 2019; Ritson-Williams and Gates 2020). Despite the geographic extent and the occurrence of three global coral bleaching events within the past three decades (Hughes et al. 2017a; Eakin et al. 2019), detailed, multi-annual in situ studies of coral community response to bleaching are relatively rare (e.g. Kayanne et al. 2002; van Woesik et al. 2011; Edmunds et al. 2014; Couch et al. 2017; Fox et al. 2019). In addition, while remote and well protected coral reef systems are widely considered benchmark locations where the influence of anthropogenic impacts on reef resilience can be better understood (Sandin et al. 2008; Graham et al. 2013; Fox et al. 2019), lack of access and logistical difficulties mean that many studies at such locations cover only a single point in time (e.g. Friedlander et al. 2014, 2015 or Pristine Seas Expeditions). This thesis therefore expands the limited amount of multi-year research programmes at such locations.

Spatial variability in bleaching susceptibility within a reef system is commonly reported and can be primarily attributed to prevailing environmental conditions. Coral loss in Aldabra's shallow lagoon was substantially lower than on its seaward reefs, likely due to high daily temperature variability that possibly confers higher temperature stress tolerance to lagoonal corals (Safaie et al. 2018). Similar observations were made in the Pacific on the lagoonal reef flats at Palmyra Atoll (Fox et al. 2019), and within sheltered bays at Palau (Golbuu et al. 2007). Furthermore, with the tide rising and receding twice a day, water flows in and out of Aldabra's lagoon at speeds of up to 3 m s^{-1} (Farrow and Brander 1971; Haupt 2019). Water flow can be an important determinant for bleaching prevalence and the survival of bleached corals. High water flow increases the mass transfer of toxic by-products produced by endosymbionts during heat stress and can lower bleaching prevalence (Nakamura and van Woesik 2001) and can also speed up recovery of bleached tissue (Nakamura et al. 2003). This, however, appears to be context dependent, as previous work found higher bleaching mortality at current exposed areas, which was attributed to reduced acclimatisation to temperature stress in these areas (McClanahan et al. 2005) and may also apply to Aldabra's seaward reefs. Water depth can also influence bleaching susceptibility; corals in deeper water are often buffered by lower temperatures and solar irradiance (Marshall and

Baird 2000; Couch et al. 2017). In Aldabra's case, seaward reefs at both 5 m and 15 m water depth showed similar levels of coral loss following bleaching, indicating that water depth did not confer protection at depths shallower than 15m. Extensive stands of live *Acropora* observed > 20 m water depth after the bleaching event (A.K. pers. obs. December 2017), however, suggest that at Aldabra, the benefits of depth may be restricted to areas deeper than 15 m. In addition, water depth and wave exposure appeared to influence recovery processes. Recovery of hard coral cover was not observed at Aldabra's deep reefs between 2016 and 2019, while the magnitude of recovery at shallow reefs reduced with increasing wave exposure. This is likely due to slower coral growth rates in deeper and more turbid waters, because of lower solar irradiance and/or differing coral community compositions (Robinson et al. 2019).

Overall, important features of reef resilience observed at Aldabra and at resilient reefs elsewhere (Table 5.1), are the rapid reduction of turf algae cover, very low fleshy macroalgae cover and stable or increasing cover of crustose coralline algae (CCA) in the years following bleaching events. Together, this is often attributed to high biomass of herbivorous fish (Sandin et al. 2008; Smith et al. 2010; Johns et al. 2018; Fox et al. 2019). Such developments are crucial for reef recovery, as they promote the growth of remnant coral colonies and the settlement of coral larvae and survival of juvenile corals that replenish the coral community (Gilmour et al. 2013; Graham et al. 2015; Yadav et al. 2016). Furthermore, recent work in the Chagos Archipelago showed that seabird guano has a positive influence on herbivorous fish and the cover of CCA (Benkwitt et al. 2019), which highlights an indirect and overlooked role of seabird colonies in reef resilience. As Aldabra harbours several large seabird colonies (Šúr et al. 2013), this is also likely to be a considerable factor for its reef resilience.

Table 5.1: Reef resilience at different minimally disturbed (e.g. absence of local anthropogenic stressors, storms, *Acanthaster* outbreaks) locations globally, as inferred from observations of several indicators during and after mass coral bleaching. Based on the primary literature, blue symbols indicate observations attributed to high resilience, and red symbols indicate observations attributed to low resilience. Observations are considered to be high (**H** or **H**) or low (**L**), stable (→), increasing (↗), decreasing (↘) or had a positive effect on resilience (**+**). Indicators not assessed or not specifically discussed in the reference are denoted with a dash (—). CCA = crustose coralline algae.

Indicators & further info	Aldabra Atoll [1] Seychelles	Chagos Archip. [2] UK	Scott Reef [3] Australia	Palmyra Atoll [4] USA
Bleaching prevalence	H	H	H	H
Bleaching-induced mortality	H [a]	H	H	L
Turf algae cover	↘	↘	↘	↘
CCA cover	↗ →	↗	↗	↗
Macroalgae cover	L	L	L	L
Remnant hard coral growth	↗	—	—	↗
Hard coral recruitment	↗	↗	↗	—
Herbivory	H	H	H	H
Seabird guano	— [b]	+	—	— [b]
Bleaching event assessed	2015/2016	1998, 2015, 2016	1998	2015
Status	protected	protected [c]	protected	protected
Fishing	subsistence	recreational [c]	artisanal	recreational

[1] This study; Chong-Seng 2016; [2] Sheppard et al. 2012; Benkwitt et al. 2019; Head et al. 2019; [3] Gilmour et al. 2013; Commonwealth of Australia 2020; [4] Fox et al. 2019; U.S. Fish & Wildlife Service 2020

[a] bleaching mortality considered high overall, although it was substantially lower in lagoon; [b] not measured but likely has an effect due to high abundance of seabirds (Aldabra: Šúr et al. 2013; Palmyra: U.S. Fish & Wildlife Service 2020b); [c] northern atolls protected, military base on Diego Garcia where recreational fishing is permitted (Graham et al. 2013)

The majority of remote or strictly protected coral reef systems, including Aldabra, were not spared extensive bleaching-induced coral mortality in the past (Gilmour et al. 2013; Sheppard et al. 2017; Hughes et al. 2018b; Cerutti et al. 2020), but there are exceptions (Table 5.1). Thermal stress is often measured as accumulated heat stress given in degree heating weeks (DHW), with a DHW value above 4 °C-weeks indicating 'significant coral bleaching likely', and above 8 °C-weeks indicating 'severe bleaching and mortality likely' (Liu et al. 2013). Corals at remote and highly protected Palmyra Atoll, in the Pacific, experienced accumulated thermal stress of 11.9 °C-weeks during 2015–2016 bleaching event (compared to 3.5 °C-weeks at Aldabra), but suffered no or relatively low mortality (< 9% coral loss), while e.g. corals at the Great Barrier Reef exhibited substantially higher mortality at similar stress levels (27% decline at > 8 °C-weeks; Hughes et al. 2018b; Fox et al. 2019). Similarly, reefs at several locations in Australia's protected Coral Sea Marine Park bleached less extensively in 2017 than 2016 despite higher exposure to heat stress in 2017, and overall coral mortality was low (Harrison et al. 2019). Frequent exposure to thermal stress and bleaching may lower bleaching susceptibility through adaptive processes, e.g. by symbiont shuffling or by changing protein expressions (Guest et al. 2012; Logan et al. 2014; Palumbi et al. 2014; Boulotte et al. 2016; McClanahan 2017). At Aldabra, the maximum of 3.5 °C-weeks during the 2015/2016 coral bleaching event (Cerutti et al. 2020) suggests that Aldabra's corals are highly susceptible to relatively low temperature stress compared with other locations. However, the NOAA satellite station for Aldabra is located ca. 55 km north east of the atoll (Cerutti et al. 2020), making these satellite measurements questionable for Aldabra. This represents a significant knowledge gap for the assessment of Aldabra's reef resilience, which can best be addressed by ongoing monitoring of in-situ water temperature.

Research and management recommendations

Aside from the urgent need to assess the local thermal stress threshold of Aldabra's reefs, this thesis reveals several other research and management recommendations that have global, regional and local relevance (Table 5.2). The recommendations address protection (Recommendation 1), research (Recommendations 2 and 5), monitoring (Recommendations 3, 4 and 6), and mapping (Recommendation 7) and are assigned a prioritisation level to assist implementation.

Table 5.2: Recommendations for management and future research highlighted by this thesis. 'Regional' relevance refers to Aldabra and other islands and atolls of the Seychelles. 'Local' relevance refers to recommendations only relevant for Aldabra.

Relevance	Recommendation	Explanation	Priority
Global	1. Protect shallow reefs	Identify and protect shallow reef locations where high temperature variability combined with high water flow may confer increased bleaching resistance and survival.	High
	2. Assess influence of seabird nutrients on coral reef functioning	Following initial findings by Benkwitt et al. (2019), further research at Aldabra and similar locations is needed to elucidate the role of seabird nutrients in coral reef functioning. Such an inter-ecosystem and inter-disciplinary approach can boost both coral reef and seabird conservation. At Aldabra, such research will be specifically pertinent before and after cat and rat-eradication efforts.	High
Regional	3. Quantify coral bleaching threshold	The NOAA satellite temperature measurement is taken 55 km from Aldabra and only a short time-series of in-situ temperature data is currently available. Reliable quantification of the local bleaching threshold is therefore crucial to better understand local resilience patterns. Continuous monitoring of in-situ water temperature is thus needed and should be followed by developing models on local bleaching threshold levels.	High
	4. Quantify sub-lethal bleaching events	Sub-lethal coral bleaching is observed annually at Aldabra (in March/April, pers. comm. A. Burt, C. Sanchez). Quantifying sub-lethal bleaching can provide valuable information on spatial and taxonomic variability in thermal sensitivity when combined with in-situ temperature measurements. This may help to broaden the applicability of NOAA bleaching watch tool for Aldabra and the region and subsequent response to potential lethal bleaching event (i.e. when extensive surveys should commence).	Medium
	5. Assess coral reef connectivity	Important to understand if (a) Aldabra's lagoon may boost recovery of its seaward reefs through supply of coral larvae and (b) which coral reefs in the region may be 'sources' and 'sinks' of coral larvae and hence important for protection. This knowledge gap is currently being addressed (pers. comm. A. Burt, N. Vogt-Vincent).	Medium
Local	6. Monitor full suite of reef fishes	To evaluate subtler changes in fish communities and improve comparisons to other locations, fish surveys should be done to species level at least every three years (standard monitoring considers 72 taxa, while similar work considers > 300 taxa).	High
	7. Assess coral species distribution	It would assist management if coral species distribution was mapped around Aldabra, to better understand reef resilience patterns and the role of the lagoon as potential source of coral larvae that may boost recovery of the seaward reefs.	Low

Concluding remarks

The increasing intensity and frequency in which heat stress is affecting coral reefs has emerged as the biggest challenge for reef conservation. This is drastically demonstrated by the Australian Great Barrier Reef, which has experienced three mass bleaching events between 2016 and 2020 (ScienceDaily 2020); a return time that was expected only mid-century (van Hooidonk et al. 2016). Nevertheless, although coral bleaching events have increased in intensity and frequency, their onset in the last decade has occurred at sea surface temperatures ~0.5 °C higher than in the previous decade (Sully et al. 2019). Predictions of climate related stressors and their impacts on coral reefs are largely based on thermal exposure models on large spatial scales, but recent work highlights the geographic variability in the response of coral communities to heat stress (Sully et al. 2019; McClanahan et al. 2020). Equatorial areas and areas exposed to high short-term fluctuations of sea surface temperatures are predicted to be most resilient to high temperature stress (Sully et al. 2019; McClanahan et al. 2020). *In-situ* observations of coral reef resilience, particularly at remote, strictly protected locations like Aldabra, thus remain critical to unravel local and regional variations, which can in turn inform local and regional management (Edmunds et al. 2019). The research presented in this thesis shows that, despite severe bleaching-induced coral mortality, post-bleaching reef recovery can be rapid in the absence of direct anthropogenic stressors. In addition, reef areas exposed to high temperature variability and water flow may be priority areas for conservation efforts to boost the recovery of connected, less resilient reefs. The thesis highlights that managing direct anthropogenic stressors is paramount to support post-bleaching reef recovery, alongside the continued protection of remote locations like Aldabra Atoll.

Needless to say, tackling the root cause of the problem – the climate crisis – is indispensable to avoid further declines of coral reefs and requires immediate global action, but conservation efforts will be more fruitful when not perceived as 'being too late'. Understanding and publicising the fate of iconic sites like Aldabra represents a powerful tool to raise awareness and draw attention to the critical situation of coral reefs.

References

Benkwitt CE, Wilson SK, Graham N (2019) Seabird nutrient subsidies alter patterns of algal abundance and fish biomass on coral reefs following a bleaching event. Glob Chang Biol 25:2619–2632

Boulotte NM, Dalton SJ, Carroll AG, Harrison PL, Putnam HM, Peplow LM, Van Oppen MJH (2016) Exploring the Symbiodinium rare biosphere provides evidence for symbiont switching in reef-building corals. ISME J 10:2693–2701

Cerutti J, Burt AJ, Haupt P, Bunbury N, Mumby P, Schaepman-Strub G (2020) Impacts of the 2014–2017 global bleaching event on a protected remote atoll in the Western Indian Ocean. Coral Reefs 39:15–26

Chong-Seng K (2016) Aldabra Marine Monitoring Programme. Unpublished report. Seychelles Islands Foundation.

Commonwealth of Australia (2020) Species Profile and Threats Database: Seringapatam Reef and Commonwealth waters in the Scott Reef complex. https://www.environment.gov.au/sprat-public/action/kef/view/6;jsessionid=01AD87551D0DE1B0248C8722BE137004

Couch CS, Burns JHR, Liu G, Steward K, Gutlay TN, Kenyon J, Eakin CM, Kosaki RK (2017) Mass coral bleaching due to unprecedented marine heatwave in Papahānaumokuākea Marine National Monument (Northwestern Hawaiian Islands). PLoS One 12:e0185121

Eakin CM, Sweatman HPA, Brainard RE (2019) The 2014–2017 global-scale coral bleaching event: insights and impacts. Coral Reefs 38:539–545

Edmunds P, Adam T, Baker A, Doo S, Glynn P, Manzello D, Silbiger N, Smith T, Fong P (2019) Why more comparative approaches are required in time-series analyses of coral reef ecosystems. Mar Ecol Prog Ser 608:297–306

Edmunds PJ, Adjeroud M, Baskett ML, Baums IB, Budd AF, Carpenter RC, Fabina NS, Fan T-Y, Franklin EC, Gross K, Han X, Jacobson L, Klaus JS, McClanahan TR, O'Leary JK, van Oppen MJH, Pochon X, Putnam HM, Smith TB, Stat M, Sweatman H, van Woesik R, Gates RD (2014) Persistence and Change in Community Composition of Reef Corals through Present, Past, and Future Climates. PLoS One 9:e107525

Farrow GE, Brander KM (1971) Tidal studies on Aldabra. Philos Trans R Soc London B 260:93–121

Flower J, Ortiz JC, Chollett I, Abelson A, Castro-Sanguino C, Hock K, Lam V, Mumby P (2017) Interpreting coral reef monitoring data: A guide for improved management decisions. Ecol Indic 72:848–869

Fox MD, Carter AL, Edwards C, Takeshita Y, Johnson MD, Petrovic V, Amir CG, Sala E, Sandin S, Smith J (2019) Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. Coral Reefs 38:701–712

Friedlander A, Ballesteros E, Beets J, Brown BE, Fay JM, Haupt P, Henning B, Rose P, Sala E (2015) Biodiversity and ecosystem health of the Aldabra Group, southern Seychelles: Scientific report to the government of Seychelles.

Friedlander A, Obura D, Aumeeruddy R, Ballesteros E, Chruch J, Cebrian E, Sala E (2014) Coexistence of low coral cover and high fish biomass at Farquhar Atoll, Seychelles. PLoS One 9:e87359

Gilmour J, Smith LD, Heyward AJ, Baird AH, Pratchett M (2013) Recovery of an isolated coral reef system following severe disturbance. Science 340:69–71

Golbuu Y, Victor S, Penland L, Idip D, Emaurois C, Okaji K, Yukihira H, Iwase A, van Woesik R (2007) Palau's coral reefs show differential habitat recovery following the 1998-bleaching event. Coral Reefs 26:319–332

Graham N, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. Nature 518:1–17

Graham N, Pratchett M, McClanahan TR, Wilson SK (2013) The status of coral reef fish assemblages in the Chagos Archipelago, with implications for protected area management and climate change. In: Sheppard C.R.C. (eds) Coral Reefs of the United Kingdom Overseas Territories. Coral Reefs of the World, Vol 4. Springer Netherlands, Dordrecht, pp 253–270

Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall K, Affendi YA, Chou LM (2012) Contrasting Patterns of Coral Bleaching Susceptibility in 2010 Suggest an Adaptive Response to Thermal Stress. PLoS One 7:e33353

Harrison HB, Álvarez-Noriega M, Baird AH, Heron SF, MacDonald C, Hughes TP (2019) Back-to-back coral bleaching events on isolated atolls in the Coral Sea. Coral Reefs 38:713–719

Haupt P (2019) Reef fish associations with benthic habitats at a remote protected coral reef ecosystem in the Western Indian Ocean ~ Aldabra Atoll, Seychelles. PhD Thesis. Rhodes University

Head C, Bayley DT., Rowlands G., Roche R, Tickler D., Roger A., Koldewey H, Turner J, Andradi-Brown DA (2019) Coral bleaching impacts from back-to-back 2015–2016 thermal anomalies in the remote central Indian Ocean. Coral Reefs 38:605–618

van Hooidonk R, Maynard J, Tamelander J, Gove J, Ahmadia G, Raymundo L, Williams G, Heron SF, Planes S (2016) Local-scale projections of coral reef futures and implications of the Paris Agreement. Sci Rep 6:39666

Van Hooidonk R, Maynard JA, Manzello D, Planes S (2014) Opposite latitudinal gradients in projected ocean acidification and bleaching impacts on coral reefs. Glob Chang Biol 20:103–112

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 J, Graham N, Harrison H, Hobbs JPA, Hoey A, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359:80–83

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

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

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey A, Hoogenboom M, Liu G, McWilliam MJ, Pears RJ, Pratchett M, Skirving WJ, Stella JS, Torda G (2018b) Global warming transforms coral reef assemblages. Nature 556:492–496

Johns KA, Emslie MJ, Hoey A, Osborne K, Jonker MJ, Cheal AJ (2018) Macroalgal feedbacks and substrate properties maintain a coral reef regime shift. Ecosphere 9:e02349

Kayanne H, Harii S, Ide Y, Akimoto F (2002) Recovery of coral populations after the 1998 bleaching on Shiraho Reef, in the southern Ryukyus, NW Pacific. Mar Ecol Prog Ser 239:93–103

Liu G, Rauenzahn J, Heron SF, Eakin C, Skirving W, Christensen T, Strong A, Li J (2013) NOAA Technical Report NESDIS 143. NOAA Coral Reef Watch 50 km satellite sea surface temperature-based decision support system for coral bleaching management.

Logan CA, Dunne JP, Eakin CM, Donner SD (2014) Incorporating adaptive responses into future projections of coral bleaching. Glob Chang Biol 20:125–139

Manzello DP, Enochs IC, Kolodziej G, Carlton R, Valentino L (2018) Resilience in carbonate production despite three coral bleaching events in 5 years on an inshore patch reef in the Florida Keys. Mar Biol 165:1–11

Marshall PA, Baird AH (2000) Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs 19:155–163

McClanahan TR (2017) Changes in coral sensitivity to thermal anomalies. Mar Ecol Prog Ser 570:71–85

McClanahan TR, Donner SD, Maynard J, MacNeil MA, Graham N, Maina J, Baker AC, Alemu I. JB, Beger M, Campbell SJ, Darling ES, Eakin CM, Heron SF, Jupiter SD, Lundquist CJ, McLeod E, Mumby P, Paddack MJ, Selig ER, van Woesik R (2012) Prioritizing key resilience indicators to support coral reef management in a changing climate. PLoS One 7:e42884

McClanahan TR, Maina J, Moothien-Pillay R, Baker AC (2005) Effects of geography, taxa, water flow, and temperature variation on coral bleaching intensity in Mauritius. Mar Ecol Prog Ser 298:131–142

McClanahan TR, Maina JM, Darling ES, Guillaume MMM, Muthiga NA, D'agata S, Leblond J, Arthur R, Jupiter SD, Wilson SK, Mangubhai S, Ussi AM, Humphries AT, Patankar V, Shedrawi G, Julius P, Ndagala J, Grimsditch G (2020) Large geographic variability in the resistance of corals to thermal stress. Glob Ecol Biogeogr 1–19

Nakamura T, van Woesik R (2001) Water-flow rates and passive diffusion partially explain differential survival of corals during the 1998 bleaching event. Mar Ecol Prog Ser 212:301–304

Nakamura T, Yamasaki H, Van Woesik R (2003) Water flow facilitates recovery from bleaching in the coral Stylophora pistillata. Mar Ecol Prog Ser 256:287–291

Palumbi S, Barshis DJ, Bay R a (2014) Mechanisms of reef coral resistance to Future Climate Change. 344:895–898

Ritson-Williams R, Gates RD (2020) Coral community resilience to successive years of bleaching in Kāneʻohe Bay, Hawaiʻi. Coral Reefs 39:757–769

Robinson JPW, Wilson SK, Graham N (2019) Abiotic and biotic controls on coral recovery 16 years after mass bleaching. Coral Reefs 38:1255–1265

Safaie A, Silbiger NJ, McClanahan TR, Pawlak G, Barshis DJ, Hench JL, Rogers JS, Williams G, Davis KA (2018) High frequency temperature variability reduces the risk of coral bleaching. Nat Commun 9:1671

Sandin SA, Smith JE, DeMartini EE, Dinsdale EA, Donner SD, Friedlander AM, Konotchick T, Malay M, Maragos JE, Obura D, Pantos O, Paulay G, Richie M, Rohwer F, Schroeder RE, Walsh S, Jackson JBC, Knowlton N, Sala E (2008) Baselines and Degradation of Coral Reefs in the Northern Line Islands. PLoS One 3:e1548

ScienceDaily (2020) ARC Centre of Excellence for Coral Reef Studies. “Climate change triggers Great Barrier Reef bleaching.” 7 April 2020. www.sciencedaily.com/releases/2020/04/200407101801.htm

Sheppard C, Ateweberhan M, Bowen BW, Carr P, Chen CA, Clubbe C, Craig MT, Ebinghaus R, Eble J, Fitzsimmons N, Gaither MR, Gan CH, Gollock M, Guzman N, Graham N, Harris A, Jones R, Keshavmurthy S, Koldewey H, Lundin CG, Mortimer JA, Obura D, Pfeiffer M, Price ARG, Purkis SJ, Raines P, Readman JW, Riegl B, Rogers A, Schleyer M, Seaward MRD, Tamelander J, Turner JR, Visram S, Vogler C, Vogt S, Wolschke H, Yang JMC, Yang SY, Yesson C (2012) Reefs and islands of the Chagos Archipelago, Indian Ocean: Why it is the world’s largest no-take marine protected area. Aquat Conserv Mar Freshw Ecosyst 22:232–261

Sheppard C, Sheppard A, Mogg A, Bayley D, Dempsey AC, Roche R, Turner J, Purkis S (2017) Coral bleaching and mortality in the Chagos Archipelago. Atoll Res Bull 613:1–26

Smith J, Hunter CL, Smith CM (2010) The effects of top-down versus bottom-up control on benthic coral reef community structure. Oecologia 163:497–507

Sully S, Burkepile DE, Donovan MK, Hodgson G, van Woesik R (2019) A global analysis of coral bleaching over the past two decades. Nat Commun 10:1–5

Šúr M, Bunbury N, Van De Crommenacker J (2013) Frigatebirds on Aldabra Atoll: population census, recommended monitoring protocol and sustainable tourism guidelines. Bird Conserv Int 23:214–220

U.S. Fish & Wildlife Service (2020a) Palmyra Atoll. https://www.fws.gov/refuge/Palmyra_Atoll/visit/visitor_activities.html

U.S. Fish & Wildlife Service (2020b) Birds of Palmyra Atoll. https://www.fws.gov/nwrs/threecolumn.aspx?id=2147513087

van Woesik R, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and the losers a decade after coral bleaching. Mar Ecol Prog Ser 434:67–76

Yadav S, Rathod P, Alcoverro T, Arthur R (2016) “Choice” and destiny: the substrate composition and mechanical stability of settlement structures can mediate coral recruit fate in post-bleached reefs. Coral Reefs 35:211–222

Versicherung an Eides Statt

Ich, Anna Koester, ____

versichere an Eides Statt durch meine Unterschrift, dass ich die vorstehende Arbeit selbstständig und ohne fremde Hilfe angefertigt und alle Stellen, die ich wörtlich dem Sinne nach aus Veröffentlichungen entnommen habe, als solche kenntlich gemacht habe, mich auch keiner anderen als der angegebenen Literatur oder sonstiger Hilfsmittel bedient habe. Ich versichere an Eides Statt, dass ich die vorgenannten Angaben nach bestem Wissen und Gewissen gemacht habe und dass die Angaben der Wahrheit entsprechen und ich nichts verschwiegen habe. Die Strafbarkeit einer falschen eidesstattlichen Versicherung ist mir bekannt, namentlich die Strafandrohung gemäß § 156 StGB bis zu drei Jahren Freiheitsstrafe oder Geldstrafe bei vorsätzlicher Begehung der Tat bzw. gemäß § 161 Abs. 1 StGB bis zu einem Jahr Freiheitsstrafe oder Geldstrafe bei fahrlässiger Begehung.

____

Ort, Datum, Unterschrift

Impressum

Author: Anna Koester

Co-Authors: Nancy Bunbury, Amanda Ford, Valentina Migani, Sebastian Ferse, Cheryl Sanchez, Cesc Gordó Vilaseca, Christian Wild

Design: Judith Bürger | Instagram: judithbuergerdesign

Print: Druckerei Wellmann | www.druckerei-wellmann.de

Photography: Jude Brice

Published in 2020