

**REEF CARBONATE BUDGETS &  
SYMBIODINIACEAE DIVERSITY IN THE  
ARABIAN GULF, WESTERN INDIAN OCEAN &  
CENTRAL INDO-PACIFIC**



**REEM ALMEALLA**

A thesis submitted for the degree of Doctor of Philosophy

School of Life Sciences

University of Essex

October 2020

This page was left intentionally blank

## **DEDICATION**

This work is dedicated towards my late mother, Seddiqa Mohammed Abdulwahab, who taught me that we are all born with unimaginable strength, and so to achieve what we dream off, we just have to tap into it, work hard and believe that it can be done. Everything that I am and everything I have achieved is a product of her loving upbringing, caring nurturing and life long sacrifices.

Mum, I know that you are watching, listening and I sincerely hope from the bottom of my heart that you are proud at this moment in time of what I have become and achieved. There are no words to express how I feel but for now all I can say is - Thank you.

This page was left intentionally blank

## **ABSTRACT**

Coral reefs are the result of long-term net calcium carbonate ( $\text{CaCO}_3$ ) accretion and the balance between carbonate production and erosion, referred to as the carbonate budget. Coral calcification is influenced by environmental conditions (e.g. temperature, depth and ocean acidification) and depends on a symbiotic partnership between the coral and its dinoflagellate algae in the family Symbiodiniaceae. When a coral encounters stress, the symbiosis breaks down resulting in coral bleaching which impacts reef calcification. To effectively monitor reef health, it is essential to determine the current status of reef environments and whether reef frameworks are actively accreting  $\text{CaCO}_3$  or being eroded away. This study aims to determine reef accretional health in three bioregions: Bahrain (located in the hottest sea on the planet – the Arabian Gulf), the Seychelles (with an environment susceptible to regular El Nino disturbances - Western Indian Ocean) and Indonesia (located within the epicenter of marine biodiversity, the Coral Triangle - Central Indo-Pacific). In addition, genetic diversity of selected coral symbionts is investigated. In light of predicted warming trends, which present a threat to the structural integrity of reefs worldwide, questions arise whether reefs will be able to maintain a positive carbonate budgetary state to keep pace with future sea level rise and maintain the stability of island-nations such as Bahrain, the Seychelles and Indonesia. This thesis explores the past and present trajectories of reefs within these bioregions whilst providing important insights for consideration to model future trajectories of these reefs.

## ACKNOWLEDGEMENTS

Firstly I would like to thank my parents, who are my biggest source of strength and without their blessings, this work would not have been achieved. In this PhD journey, I have found my primary supervisor, Dr. Leanne Hepburn to be an inspiration and a role model. Her unwavering support and guidance throughout the past 3.5 years has left me feeling very lucky to have had her not only as my supervisor and mentor but also as a friend and sister. I would also like to thank my secondary supervisor, Prof. Dave Smith, in particular for his help and advise throughout my field expeditions. Further gratitude goes to my collaborators, Dr. Michelle Taylor and Dr. Boyd McKew, for their endless support, encouragement and guidance in the lab as I navigated my way through learning molecular techniques. Deep gratitude goes to the Taylor lab and colleagues who gave me a sense of belonging especially that I was one of those PhD students who didn't belong to a particular lab. Much thanks goes to the best lab technician, Tania Cresswell-Maynard, whom without I could not have made it through my nine months of constant failure in the lab until one-day things magically worked. Deep gratitude goes to Emma Revill whom without, every PhD student at Essex would have an even rougher road to walk. Special thanks goes to Brisneve Edullantes for all his support with coding, data visualization and his endless patience with all my questions as I began my baby steps into the world of coding in R. Gratitude is extended to my friend Ines Hirata for help in learning and creating illustrations. Further thanks goes to my lab mates especially Alice, Declan, Jamie and Jess who made working in the lab fun and ensured I smiled despite the challenges! Much gratitude goes to Dr. Benjamin Hume for all his help and guidance with the SymPortal framework and answering my queries. This research could not have happened without the funding and support of the Gulf Petrochemical Industries Co. (BSC), Mitsubishi Corporation and Operation Wallacea that enabled me to work in Bahrain, Seychelles and Indonesia respectively. I would like to thank in

particular Maggie Hoareau from the Seychelles National Park Authority, Staff at EarthWatch and Pippa Mansell from Operation Wallacea for their incredible management of the research station and their support with my research whether it was through acquiring permits or ordering equipment. Deep gratitude goes to all the Seychellois and Indonesian staff whom took care of me, kept me fed, safe in the water and made sure I always was greeted with a warm smile after a long day on the field. Further gratitude is extended towards all the research assistants at my three research sites whom without I would have not been able to collect all my data especially Dr. Laura Blamey. Thank you to the people of my home country Bahrain who overwhelmed me with kindness especially Nouf Al Wasmi, Ali Mansour, Hani Bader, Tamera Al Husseini, Hanan Hasan, Jafar Juma and Hannah Lunt-Bell all of whom supported me voluntarily on the ground to execute my field work despite the challenges. I take pride in acknowledging the support of the University of Bahrain especially Dr. Humood Naser and Dr. Afnan Freije for providing me with lab access whilst working on the field. Further gratitude goes to Dr. Abdulrahman Jawahery for being one of the strongest supporters of my work on the island. Last but not least, a big thank you is due to my friends and family without whose continuing support I could never have achieved any of this. Thank you for your unconditional love despite all my tantrums, negativity, up's and down's throughout one of the craziest chapters in this exciting journey called life.

## TABLE OF CONTENT

<b>1. INTRODUCTION</b>	19
1.1. CORAL REEFS – DIVERSITY, STRUCTURE & IMPORTANCE	21
1.2. REEF CARBONATE BUDGETS	22
1.3. CARBONATE BUDGET ASSESSMENTS	30
1.4. THREATS TO CORAL REEF FRAMEWORKS	31
1.5. THE CORAL HOLOBIONT	33
1.6. CORAL BLEACHING	35
1.7. CONNECTING BIOREGIONS THROUGH EVOLUTIONARY HISTORY	38
1.8. THESIS AIM	44
<b>2. THERMAL HISTORY OF REEFS IN THE ARABIAN GULF, WESTERN INDIAN AND CENTRAL INDO-PACIFIC OCEAN</b>	47
2.1. INTRODUCTION	49
2.2. METHODOLOGY	52
2.2.1. SITE DESCRIPTION	52
2.2.2. SATELLITE DATA ACQUISITION AND PROCESSING	56
2.2.3. DEFINITIONS AND CALCULATION METHODS OF THERMAL HISTORY METRICS	56
2.2.4. DATA ANALYSIS	57
2.3. RESULTS	58
2.3.1. SPATIAL TRENDS IN REGIONAL SEA SURFACE TEMPERATURES	58
2.3.2. THERMAL HISTORY METRICS	59
2.4. DISCUSSION	64
<b>3. STATUS &amp; CHANGE IN CORAL COVER: HISTORY OF 35 YEARS THROUGH A SYSTEMATIC REVIEW OF THREE BIOREGIONS</b>	69
3.1. INTRODUCTION	72
3.2. METHODOLOGY	74
3.2.1. LITERATURE SEARCH AND DATA EXTRACTION	74
3.2.2. STUDY SITES	78
3.2.3. DATA ANALYSIS	79
3.3. RESULTS	80
3.3.1. TRENDS IN CORAL COVER WITHIN BIOREGIONS	80
3.3.2. RATE OF CHANGE IN CORAL COVER WITHIN BIOREGIONS	88
3.3.3. CHANGE IN CORAL COVER WITHIN REEF-SPECIFIC SITES	91
3.4. DISCUSSION	95
3.4.1. TRENDS IN CORAL COVER WITHIN BIOREGIONS	95
3.4.2. RATE OF CHANGE IN CORAL COVER ACROSS BIOREGIONS	100
3.4.3. CHANGE IN CORAL COVER FOR THESIS STUDY SITES	101
3.4.4. LIMITATIONS	103
<b>4. REEF CARBONATE BUDGETS IN THE ARABIAN GULF, WESTERN INDIAN OCEAN &amp; INDO-PACIFIC</b>	105
4.1. CHAPTER INTRODUCTION	107
<b>4.2. BLEACHING THREATENS POSITIVE CARBONATE BUDGETS AND REEF GROWTH POTENTIAL ON BAHRAIN REEFS</b>	108
4.2.1. INTRODUCTION	108
4.2.2. MATERIALS & METHODS	111
4.2.2.1. SITE DESCRIPTIONS	111
4.2.2.2. QUANTIFYING THE CARBONATE BUDGETARY STATE ON THE FIELD	114
4.2.2.3. REEF CARBONATE BUDGET CALCULATIONS	118
4.2.2.4. DATA ANALYSIS	121
4.2.3. RESULTS	122
4.2.3.1. SITE CHARACTERIZATION & CARBONATE BUDGETARY STATE	122
4.2.3.2. CARBONATE BUDGETARY STATE – PRE- AND POST BLEACHING (2017-2018)	126
4.2.4. DISCUSSION	128



4.2.4.1. SITE CHARACTERISATION & CARBONATE BUDGETARY STATE	128
4.2.4.2. CARBONATE BUDGETARY STATE – PRE- AND POST BLEACHING (2017-2018)	130
<b>4.3. STATUS &amp; TREND OF REEF CARBONATE BUDGETS IN THE PROTECTED AREA OF CURIEUSE ISLAND, SEYCHELLES</b>	132
4.3.1. INTRODUCTION	132
4.3.2. MATERIALS & METHODS	135
4.3.2.1. SITE DESCRIPTIONS	135
4.3.2.2. QUANTIFYING THE CARBONATE BUDGETARY STATE	138
4.3.2.3. DATA ANALYSIS	138
4.3.3. RESULTS	139
4.3.3.1. SITE CHARACTERIZATION & CARBONATE BUDGETARY STATE	139
4.3.3.2. CARBONATE BUDGETS	143
4.3.3.3. CHANGE IN GEOMORPHIC STATE OF REEFS	145
4.3.3.4. CHANGE IN REEF CARBONATE BUDGET (2014-2018) PRE AND POST – 2016 BLEACHING	147
4.3.4. DISCUSSION	147
4.3.4.1. CARBONATE BUDGETARY STATE	147
4.3.4.2. CHANGE IN GEOMORPHIC STATE	149
4.3.4.3. CHANGE IN REEF CARBONATE BUDGETS OVER TIME	150
<b>4.4. INTERANNUAL VARIABILITY OF REEF CARBONATE BUDGETS IN THE WAKATOBI MARINE NATIONAL PARK (WMNP), INDONESIA</b>	151
4.4.1. INTRODUCTION	152
4.4.2. MATERIALS & METHODS	154
4.4.2.1. SITE DESCRIPTIONS	154
4.4.2.2. QUANTIFYING THE CARBONATE BUDGETARY STATE	158
4.4.2.3. DATA ANALYSIS	158
4.4.3. RESULTS	159
4.4.3.1. CARBONATE PRODUCTION	159
4.4.3.2. CARBONATE EROSION	162
4.4.3.3. CARBONATE BUDGETARY STATE	166
4.4.4. DISCUSSION	167
<b>4.5. CONCLUSION: REEF CARBONATE BUDGETS ACROSS BIOREGIONS</b>	171
<b>5. SYMBIODINIACEAE DIVERSITY ACROSS THERMAL REGIMES AND LATITUDINAL GRADIENTS</b>	173
5.1. INTRODUCTION	176
5.2. METHODOLOGY	181
5.2.1. SITE SELECTION & DESCRIPTION	181
5.2.2. SAMPLE COLLECTION	185
5.2.3. MOLECULAR ANALYSIS	186
5.2.4. BIOINFORMATICS ANALYSIS	187
5.2.5. DATA AND STATISTICAL ANALYSIS	188
5.3. RESULTS	189
5.3.1. SYMBIODINIACEAE DIVERSITY & ABUNDANCE ACROSS BIOREGIONS	189
5.3.2. COMMUNITY COMPOSITION AND BIOGEOGRAPHICAL PATTERNS OF SYMBIODINIACEAE	194
5.4. DISCUSSION	199
5.4.1. SYMBIODINIACEAE DIVERSITY & ABUNDANCE ACROSS BIOREGIONS	199
5.4.2. COMMUNITY COMPOSITION AND BIOGEOGRAPHICAL PATTERNS OF SYMBIODINIACEAE	202
5.5. CONCLUSION	204
<b>6. GENERAL DISCUSSION</b>	207
6.1. SUMMARY OF KEY FINDINGS	209
6.2. LIMITATIONS	215
6.3. KEY MESSAGES & FUTURE DIRECTION OF RESEARCH	216
6.4. CONCLUDING REMARKS	219
<b>SUPPLEMENTARY MATERIAL</b>	221
S1. EXPLORING THERMAL HISTORY OF A CORAL REEF WITH THE PACKAGE IN R	223
S2. LIST OF STUDIES USED IN THE SYSTEMATIC REVIEW	224
S2.1. LIST OF STUDIS CORRESPONDING TO THE ARABIAN GULF DATA	224

S2.2. LIST OF STUDIS CORRESPONDING TO THE SEYCHELLES DATA	225
S2.3. LIST OF STUDIS CORRESPONDING TO THE WAKATOBI, INDONESIA DATA	227
S3. REEF CARBONATE BUDGETS	228
S3.1. SEYCHELLES - QUANTIFYING METHODOLOGY FORTH THE CARBONATE BUDGET	228
S3.2. INDONESIA - QUANTIFYING METHODOLOGY FORTH THE CARBONATE BUDGET	231
S3.3. RESULTS OF SECONDARY CARBONATE PRODUCTION RATES	235
S4. SYMBIODINIACEAE DNA EXTRACTION PROTOCOL & RELATIVE ABUNDANCE OF ASSOCIATED ITS2 TYPES	238
S4.1. QIAGEN DNEASY BLOOD & TISSUE KIT – PROTOCOL METHOD MODIFICATION	238
S4.2. RELATIVE ABUNDANCE OF ITS2 TYPE PROFILES IN EACH CORAL HOST SPECIES AND BIOREGION	239
<b>REFERENCES</b>	<b>243</b>

## LIST OF FIGURES

FIGURE 1.1	OVERVIEW OF THE CORAL REEF FRAMEWORK NET CARBONATE PRODUCTION & EROSION (ADAPTED FROM GLYNN, 1997; PHOTO CREDIT OF ORGANISMS: DR. LEANNE HEPBURN)	23
FIGURE 1.2	MEOOW BIOGEOGRAPHIC FRAMEWORK: (A) BIOGEOGRAPHIC REALMS WITH ECOREGIONS BOUNDARIES OUTLINED (B) PROVINCES WITH ECOREGIONS OUTLINED WHEREBY PROVINCES ARE NUMBERED AND LISTED IN THE ORIGINAL PAPER. SOURCE: SPALDING ET AL., 2007	40
FIGURE 1.3	LOCATION OF SELECTED STUDY BIOREGIONS: ARABIAN GULF (AG), THE WESTERN INDIAN OCEAN (WIO) AND CENTRAL INDO-PACIFIC (CIP).	44
FIGURE 2.1	LOCATION OF STUDY SITES – (A) LOCATION OF BAHRAIN (ARABIAN GULF), THE SEYCHELLES (WESTERN INDIAN OCEAN) AND INDONESIA (CENTRAL INDO-PACIFIC); (B) LOCATION OF STUDY SITES WITHIN BAHRAIN; (C) LOCATION OF STUDY SITES WITHIN CURIEUSE MARINE NATIONAL PARK, SEYCHELLES; (D) LOCATION OF STUDY SITES WITHIN THE WAKATOBI MARINE NATIONAL PARK, INDONESIA. DARK GREY AREAS INDICATE LAND WHILST LIGHT GREY INDICATES SHALLOW REEF AREAS	54
FIGURE 2.2	SPATIAL DISTRIBUTION OF THE OVERALL MINIMUM, MAXIMUM, MEAN AND STANDARD ERROR (SE) OF SST ACROSS THE THREE SELECTED BIOREGIONS FOR THE PERIOD (1982-2017). DATA DERIVED FROM CoRTAD VERSION 6, 4x4KM RESOLUTION - AVAILABLE ONLINE	61
FIGURE 2.3	TRENDS IN WEEKLY SST MEAN FOR THE PERIOD (1982-2017; N=1878) ILLUSTRATING THE CHANGE IN SST ACROSS THE THREE SELECTED STUDY SITES. THE BLUE AND RED DOTTED LINES INDICATE THE MINIMUM AND MAXIMUM CLIMATOLOGY, RESPECTIVELY, WHILST THE RED SOLID LINE INDICATES THE BLEACHING THRESHOLD. THE BLUE SOLID LINE INDICATES THE LINEAR FIT WITH STANDARD ERROR OF THE REGRESSION IN DARK GREY SHADING. DATA DERIVED FROM CoRTAD VERSION 6 DATABASE, 4x4KM RESOLUTION - AVAILABLE ONLINE	62
FIGURE 2.4	TRENDS IN DEGREE HEATING WEEKS (DHW; IN RED SOLID LINES) ACROSS THE THREE SELECTED STUDY SITES FOR THE PERIOD (1982-2017). DHW IS DEFINED AS OF ACCUMULATED DAILY HOTSPOTS OVER 12 CONSECUTIVE WEEKS WHEN THE THERMAL STRESS ANOMALY (TSA; IN BLACK SOLID LINES) IS $\geq 1^{\circ}\text{C}$ . THE GREY DOTTED LINES INDICATE THE DHW VALUES OF $\geq 4^{\circ}\text{C}$ AND $< 8^{\circ}\text{C}$ -WEEKS, WHICH CORRESPONDS TO DELINEATION BETWEEN CORAL BLEACHING AND MORTALITY LEVELS. YEARS THAT CORRESPOND TO CORAL BLEACHING AND MORTALITY WERE HIGHLIGHTED IN BLUE AND RED FONTS, RESPECTIVELY. DATA WERE DERIVED FROM CoRTAD VERSION 6 DATABASE, 4x4KM RESOLUTION - AVAILABLE ONLINE	63
FIGURE 3.1	FLOW DIAGRAM OF PRISMA (PREFERRED REPORTING ITEMS FOR SYSTEMATIC REVIEWS AND META-ANALYSIS) ILLUSTRATING THE STEPS TAKEN STARTING FROM STUDIES RETURNED FROM THE SEARCH FOR LITERATURE THROUGH THE WEB OF SCIENCE, GOOGLE SCHOLAR, ICRS PROCEEDINGS (REEFBASE DATABASE), REEF CHECK AND PERSONAL COMMUNICATIONS. INCLUSION CRITERIA STATES THAT STUDIES MUST INCLUDE: (1) PERCENTAGE COVER (%) OF	77

	HARD CORAL AT A GIVEN SITE; (2) SOME MEASURE OF VARIANCE I.E. STANDARD ERROR (SE) OR STANDARD DEVIATION (SD); (3) SAMPLE SIZE; (4) YEAR OF DATA COLLECTION AND (5) METHODS USED FOR DATA COLLECTION.	
	BIOREGIONS OF INTEREST: ARABIAN GULF (AG); SEYCHELLES, WESTERN INDIAN OCEAN (WIO); WAKATOBI, INDONESIA, CENTRAL INDO-PACIFIC (CIP)	
FIGURE 3.2	ESTIMATED LOCATION OF REEF SITES (RED POINTS) REPRESENTED THROUGH THE DATA POINTS EXTRACTED FOR THIS STUDY: (A) LOCATION OF THE SELECTED BIOREGIONS; (B) ARABIAN GULF; (C) SEYCHELLES (WESTERN INDIAN OCEAN) AND (D) WAKATOBI, INDONESIA (CENTRAL INDO-PACIFIC).	78
FIGURE 3.3	MEAN LIVE CORAL COVER ( $\pm$ SE) OF REEFS REPORTED FOR THE PERIOD 1986-2018 IN EACH IDENTIFIED STUDY IN THE ARABIAN GULF. DOTTED LINE REPRESENTS OVERALL REGIONAL MEAN PERCENTAGE COVER. METHODOLOGY CODES: LIP = LINE INTERCEPT POINT TRANSECT; PIT = POINT INTERCEPT TRANSECT. THE FULL LIST OF PAPERS USED IN THIS STUDY IS AVAILABLE IN SUPPLEMENTARY MATERIAL (S2).	82
FIGURE 3.4	MEAN CORAL COVER ( $\pm$ SE) OF REEFS REPORTED FOR THE PERIOD 1994-2018 IN EACH IDENTIFIED STUDY IN THE SEYCHELLES. DOTTED LINE REPRESENTS OVERALL REGIONAL MEAN PERCENTAGE COVER. METHODOLOGY CODES: LIP = LINE INTERCEPT POINT TRANSECT; PIT = POINT INTERCEPT TRANSECT. THE FULL LIST OF PAPERS USED IN THIS STUDY IS AVAILABLE IN SUPPLEMENTARY MATERIAL (S2).	85
FIGURE 3.5	MEAN CORAL COVER ( $\pm$ SE) OF REEFS REPORTED FOR THE PERIOD 2001-2018 IN EACH IDENTIFIED STUDY IN THE WAKATOBI MARINE NATIONAL PARK, INDONESIA. DOTTED LINE REPRESENTS OVERALL REGIONAL MEAN PERCENTAGE COVER. METHODOLOGY CODES: LIP = LINE INTERCEPT POINT TRANSECT; PIT = POINT INTERCEPT TRANSECT. THE FULL LIST OF PAPERS USED IN THIS STUDY IS AVAILABLE IN SUPPLEMENTARY MATERIAL (S2).	87
FIGURE 3.6	RATE OF CHANGE IN MEAN CORAL COVER OF REEFS OVER THREE TIME PERIODS (I.E. 1998-2003; 2003-2013; 2013-2018) IN THE THREE BIOREGIONS: (A) ARABIAN GULF; (B) SEYCHELLES; (C) WAKATOBI MARINE NATIONAL PARK, INDONESIA. BLACK CIRCLES REPRESENT INDIVIDUAL DATA POINTS WHILE COLOURED CIRCLES (RED, BLUE AND GREY) REPRESENT MEAN OF CORAL COVER ( $\pm$ SE) PER YEAR; LINES INDICATE TRENDS BASED ON THE SIMPLE LINEAR REGRESSION	90
FIGURE 3.7	CHANGE IN MEAN CORAL COVER OF REEFS OVER TIME WITHIN THE THREE BIOREGION: (A) ARABIAN GULF; (B) SEYCHELLES; (C) WAKATOBI MARINE NATIONAL PARK, INDONESIA. GREY DOTS REPRESENT INDIVIDUAL DATA POINTS EXTRACTED FOR THIS SYSTEMATIC REVIEW; IF MORE THAN TWO DATA POINTS OF THE SAME SITE/REEF IS DETECTED, A TREND IS PRESENTED; COLOURED LINES REPRESENT THE INTEREST SITES OF THIS STUDY/THESIS	93
FIGURE 3.8	DISTRIBUTION OF THE RATE OF CHANGE IN REEFS ACROSS THE THREE BIOREGIONS (ARABIAN GULF = 1986-2018; SEYCHELLES = 1994-2018; WAKATOBI, INDONESIA = 2001-2018). MEAN CORAL COVER ( $\pm$ SE) OF REEFS IS REPRESENTED BY THE CIRCLE IN THE MIDDLE OF EACH SHAPE; MEAN AT 0 = NO CHANGE, >0 = POSITIVE CHANGE/RECOVERY, <0 NEGATIVE CHANGE/DECLINE	94
FIGURE 4.2.1	LOCATION OF STUDY SITES – (A) LOCATION OF ARABIAN GULF (AG); (B) LOCATION OF BAHRAIN WITHIN THE AG; (C) LOCATION OF SELECTED STUDY SITES WITHIN BAHRAIN [SITE CODES: FASHT AL ADHM (BH-TB) AND REEF BUL THAMAH (BH-OP)]	112

FIGURE 4.2.2	CACO <sub>3</sub> PRODUCTION BY SECONDARY CARBONATE PRODUCERS OVER A ONE-YEAR PERIOD ON PVC PIPES DEPLOYED AT BH-TB (FASHT AL ADHM)	116
FIGURE 4.2.3	SHIFTS IN REEF STRUCTURAL DYNAMICS (2017-2018) PRE AND POST THE 2017 BLEACHING (A) FASHT AL ADHM (BH-TB) AND (B) REEF BUL THAMAH (BH-OP)	123
FIGURE 4.2.4	MEAN PERCENTAGE COVER OF CARBONATE PRODUCERS IN 2017 AND 2018: (A) HARD CORALS (N=6) AND (B) CCA = CRUSTOSE CORALLINE ALGAE (N=6); MEAN DENSITY (COUNT PER UNIT M <sup>2</sup> ) OF CARBONATE ERODERS: (C) ECHINOIDS (N=6; AREA=20M <sup>2</sup> PER TRANSECT; BH-TB) AND (D) PARROTFISH (N=3; AREA=120M <sup>2</sup> PER TRANSECT) AT BOTH STUDY SITES IN BAHRAIN	124
FIGURE 4.2.5	MEAN PERCENTAGE COVER (%) OF THE REEF BENTHIC COMMUNITY STRUCTURE PRE (2017) AND POST BLEACHING (2018) AT BOTH STUDY SITES (N=6)	125
FIGURE 4.2.6	TOTAL ABUNDANCE OF ECHINOIDS RECORDED BASED ON SIZE CLASS PRE AND POST BLEACHING AT BOTH STUDY SITES (N=6)	125
FIGURE 4.2.7	TOTAL ABUNDANCE OF SCARIDAE RECORDED IN 2017 AND 2018 BASED ON SIZE CLASS (IP = INITIAL PHASE / JUVENILES; TP = TERMINAL PHASE / ADULTS) PRE AND POST BLEACHING AT BOTH STUDY SITES (N=6)	126
FIGURE 4.2.8	REEF CARBONATE BUDGET RATES (KG CACO <sub>3</sub> M <sup>-2</sup> Y <sup>-1</sup> EXPRESSED AS G; 2017-2018) ACROSS STUDY SITES PRE- AND POST- THE 2017 BLEACHING ILLUSTRATING (A) GROSS CARBONATE PRODUCTION; (B) GROSS CARBONATE EROSION; (C) REEF GROWTH IN THE FORM OF NET CARBONATE PRODUCTION	128
FIGURE 4.3.1	LOCATION OF STUDY SITES – (A) LOCATION OF SEYCHELLES; (B) MAP OF THE MAIN ISLANDS OF THE SEYCHELLES AND; (C) LOCATION OF SELECTED STUDY SITES WITHIN THE SEYCHELLES [SITE CODES: EAST BAY (SY-OP) AND PRASLIN (SY-TB)]	136
FIGURE 4.3.2	MEAN PERCENTAGE COVER OF CARBONATE PRODUCERS BETWEEN 2017-2018 (A) HARD CORAL COVER (N=6) AND (B) CCA = CRUSTOSE CORALLINE ALGAE (N=6)	139
FIGURE 4.3.3	MEAN DENSITY (COUNT PER UNIT M <sup>2</sup> ) OF CARBONATE ERODERS (2018): (A) ECHINOIDS (N=6; AREA=20M <sup>2</sup> PER TRANSECT) AND (B) SCARIDAE (N=6; AREA=120M <sup>2</sup> PER TRANSECT) AT BOTH STUDY SITES	141
FIGURE 4.3.4	TOTAL ABUNDANCE OF ECHINOIDS (2017-2018) RECORDED BASED ON SIZE CLASS AT BOTH STUDY SITES (N=6)	142
FIGURE 4.3.5	TOTAL ABUNDANCE OF SCARIDAE (2017-2018) RECORDED BASED ON SIZE CLASS (IP = INITIAL PHASE / JUVENILES; TP = TERMINAL PHASE / ADULTS) PRE AND POST BLEACHING AT BOTH STUDY SITES (N=6)	142
FIGURE 4.3.6	REEF CARBONATE BUDGET RATES (KG CACO <sub>3</sub> M <sup>-2</sup> Y <sup>-1</sup> EXPRESSED AS G; 2017-2018) ACROSS STUDY SITES ILLUSTRATING GROSS CARBONATE PRODUCTION; GROSS CARBONATE EROSION AND REEF GROWTH IN THE FORM OF NET CARBONATE PRODUCTION	144
FIGURE 4.3.7	MEAN PERCENTAGE COVER OF PRIMARY CARBONATE PRODUCERS (2017-2018) GROWTH FORMS AT THE STUDY SITES (N=6)	146
FIGURE 4.3.8	CARBONATE PRODUCTION RATES (KG CACO <sub>3</sub> M <sup>-2</sup> Y <sup>-1</sup> EXPRESSED AS G; 2017-2018) BY THE DIFFERENT CORAL MORPHOLOGICAL GROUPS AT THE STUDY SITES (N=6)	146
FIGURE 4.4.1	LOCATION OF STUDY SITES – (A) LOCATION OF INDONESIA; (B) MAP OF THE	157

WAKATOBI MARINE NATIONAL PARK (WAKATOBI), SOUTH SULAWESI AND; (C)  
LOCATION OF SELECTED STUDY SITES AROUND HOGA ISLAND, WAKATOBI

FIGURE 4.4.2	COMPARISON OF GROSS CARBONATE PRODUCTION RATES (KG $\text{CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) ACROSS THE FOUR STUDY SITES BETWEEN THE PERIOD 2012-2018 (N=6; $G \pm \text{SE}$ ); $B3 = F_{(1,7)} = 14.2, p < 0.05$ ; $PK = F_{(1,7)} = 205.1, p < 0.05$ ; $R1 = F_{(1,6)} = 150.0, p < 0.05$ ; $S1 = F_{(1,7)} = 9.6, p < 0.05$	160
FIGURE 4.4.3	MEAN PERCENTAGE COVER OF PRIMARY CARBONATE PRODUCERS IN 2018 BASED ON THEIR MORPHOLOGICAL GROUPS ACROSS THE STUDY SITES (N=6)	161
FIGURE 4.4.4	CARBONATE PRODUCTION RATES (KG $\text{CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) IN 2018 BY THE DIFFERENT CORAL MORPHOLOGICAL GROUPS AT THE STUDY SITES (N=6)	161
FIGURE 4.4.5	TOTAL ABUNDANCE OF ECHINOIDS RECORDED IN 2018 BASED ON SIZE CLASS ACROSS STUDY SITES (N=6; AREA=20M <sup>2</sup> PER TRANSECT)	164
FIGURE 4.4.6	TOTAL ABUNDANCE OF SCARIDAE IN 2018 BASED ON SIZE CLASS (IP = INITIAL PHASE / JUVENILES; TP = TERMINAL PHASE / ADULTS) ACROSS STUDY SITES (N=6; AREA=120M <sup>2</sup> PER TRANSECT)	164
FIGURE 4.4.7	COMPARISON OF GROSS CARBONATE EROSION RATES (KG $\text{CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) ACROSS THE FOUR STUDY SITES BETWEEN THE PERIOD 2012-2018 (N=6; $G \pm \text{SE}$ )	165
FIGURE 4.4.8	REEF CARBONATE BUDGET RATES (KG $\text{CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) ACROSS STUDY SITES ILLUSTRATING GROSS CARBONATE PRODUCTION; GROSS CARBONATE EROSION AND REEF GROWTH IN THE FORM OF NET CARBONATE PRODUCTION FOR THE PERIOD 2012-2018 (N=6; $G \pm \text{SE}$ )	166
FIGURE 4.5.1	OVERALL CARBONATE BUDGET RATES (KG $\text{CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) OF REEFS IN 2018 ACROSS SITES: (A) BAHRAIN, (B) SEYCHELLES AND; (C) INDONESIA	172
FIGURE 5.1	LOCATION OF STUDY SITES – (A) LOCATION OF BAHRAIN (ARABIAN GULF), THE SEYCHELLES (WESTERN INDIAN OCEAN) AND INDONESIA (CENTRAL INDO-PACIFIC); (B) LOCATION OF STUDY SITES WITHIN BAHRAIN; (C) LOCATION OF STUDY SITES WITHIN CURIEUSE MARINE NATIONAL PARK, SEYCHELLES; (D) LOCATION OF STUDY SITES WITHIN THE WAKATOBI MARINE NATIONAL PARK, INDONESIA.	182
FIGURE 5.2	THE RELATIVE ABUNDANCE (>0.1% OF TOTAL COMMUNITY) OF ITS2 TYPES OF SYMBIODINIACEAE GENERA (CLADES) WITHIN EACH CORAL GENUS (HOST) AT SITES WITHIN BAHRAIN (ARABIAN GULF), SEYCHELLES (WESTERN INDIAN OCEAN) AND INDONESIA (CENTRAL INDO-PACIFIC). INDIVIDUAL COLONIES WERE SAMPLED IN BOTH 2017 AND 2018 FOR BAHRAIN AND THE SEYCHELLES WHILST INDONESIAN COLONIES WERE SAMPLED IN 2017 ONLY	191
FIGURE 5.3	(A) RICHNESS OF CORAL ASSOCIATED-SYMBIODINIACEAE ITS2 TYPES ACROSS ALL SITES IN BAHRAIN, SEYCHELLES AND INDONESIA. (B) SHANNON'S DIVERSITY INDEX ( $H'$ ) OF CORAL ASSOCIATED-SYMBIODINIACEAE ITS2 TYPES ACROSS ALL SITES (NA = NO SAMPLES ACQUIRED FROM RESPECTIVE SITES).	193
FIGURE 5.4	INDIVIDUAL COLONIES WERE SAMPLED IN BOTH 2017 AND 2018 FOR BAHRAIN AND THE SEYCHELLES WHILST INDONESIAN CORAL COLONIES WERE SAMPLED IN 2017 ONLY	
	THE RELATIVE ABUNDANCE OF ITS2 TYPES WITHIN EACH CORAL GENUS (HOST)	196

FIGURE 5.5	<p>AT SITES WITHIN THE THREE BIOREGIONS. INDIVIDUAL COLONIES WERE SAMPLED IN BOTH 2017 AND 2018 FOR BAHRAIN AND THE SEYCHELLES WHILST INDONESIAN COLONIES WERE SAMPLED IN 2017 ONLY</p> <p>PRINCIPAL COORDINATE ANALYSIS (PCA) OF SYMBIODINIACEAE ITS2 PROFILES ACROSS BIOREGIONS: (A) CLADOCOPIUM (CLADE C); (B) DURUSDINIUM (CLADE D). PERCENTAGES ON EACH AXIS INDICATE THE AMOUNT OF VARIATION EXPLAINED BY EACH AXIS (UNIfrac DISTANCE MATRIX)</p>	197
FIGURE 5.6	<p>PRINCIPAL COORDINATE ANALYSIS (PCA) PLOTS OF SYMBIODINIACEAE COMMUNITY COMPOSITION HIGHLIGHTING CORAL HOST AND BIOREGIONS: BAHRAIN (ARABIAN GULF), SEYCHELLES (WESTERN INDIAN OCEAN), INDONESIA (CENTRAL INDO-PACIFIC); (A) CLADOCOPIUM (CLADE C); (B) DURUSDINIUM (CLADE D), UTILISING A UNIfrac DISTANCE MATRIX; ADONIS P VALUES INDICATE SIGNIFICANT RESULTS OF PERMANOVA TESTS OUTLINED IN TABLE 5.5</p>	197
FIGURE 6.1	<p>SUMMARY OF OVERALL FINDINGS</p>	214
FIGURE S3.1	<p>QUANTIFICATION EXPERIMENT OF CARBONATE PRODUCTION BY SECONDARY PRODUCERS: (A) ONE OF THE PVC PIPES DEPLOYED IN INDONESIA WITH SIGNS OF ALGAL GROWTH AND CCA FOLLOWING A ONE-MONTH PERIOD; (B) ONE OF THE TILES DEPLOYED IN INDONESIA WITH SIGNS OF TURF ALGAL GROWTH FOLLOWING A ONE-MONTH PERIOD; (C) CLOSE UP OF ONE OF THE PVC PIPES DEPLOYED IN INDONESIA WITH CCA ESTABLISHMENT FOLLOWING A ONE-MONTH PERIOD</p>	236

## LIST OF TABLES

TABLE 1.1	EXAMPLES OF NET CARBONATE PRODUCTION RATES ON REEFS WORLDWIDE (UNIT = $\text{KG CaCO}_3 \text{ M}^{-2} \text{ YEAR}^{-1}$ EXPRESSED AS G; *PRE AND POST VALUES REFER TO PRE AND POST BLEACHING EVENTS)	26
TABLE 1.2	EXAMPLES OF GROSS CARBONATE EROSION RATES WORLDWIDE (UNIT = $\text{KG CaCO}_3 \text{ M}^{-2} \text{ YEAR}^{-1}$ EXPRESSED AS G; *PRE AND POST VALUES REFER TO PRE AND POST BLEACHING EVENTS)	29
TABLE 2.1	COORDINATES OF THE LOCALIZED SITES IN THE THREE SELECTED BIOREGIONS	53
TABLE 2.2	ENVIRONMENTAL CHARACTERISTICS OF THE SELECTED STUDY SITES	55
TABLE 2.3	SUMMARY OF THERMAL SST HISTORY METRICS ( $^{\circ}\text{C}$ ) ACROSS THE SELECTED SITES BETWEEN 1982-2017 WHEREBY ANNUAL MEAN REFERS TO LONG-TERM MEAN OVER A 35-YEAR PERIOD (N= 1878; *UNIT= $^{\circ}\text{C}$ -WEEKS)	60
TABLE 4.2.1	SITE DESCRIPTION AND CHARACTERISATION OF STUDY SITES IN BAHRAIN, ARABIAN GULF	113
TABLE 4.2.2	DETAILS OF CARBONATE BUDGET COMPONENTS AND NUMBER OF REPLICATES AT EACH STUDY SITE IN BAHRAIN, ARABIAN GULF	115
TABLE 4.2.3	SKELETAL DENSITIES AND LINEAR EXTENSION RATES OF CORALS (REFERRED TO AS GROWTH RATES) USED IN THE BAHRAIN REEF BUDGET STUDY	119
TABLE 4.2.4	EROSION RATES ( $\text{KG CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) BY MAJOR BIO-ERODERS AT STUDY SITES (2017-2018)	127
TABLE 4.3.1	SITE DESCRIPTION AND CHARACTERISATION OF STUDY SITES WITHIN CURIEUSE MARINE NATIONAL PARK, SEYCHELLES	137
TABLE 4.3.2	CARBONATE PRODUCTION RATES ( $\text{KG CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) BY PRIMARY AND SECONDARY PRODUCERS IN 2017 AND 2018 AT THE STUDY SITES IN THE SEYCHELLES (N=6; G $\pm$ SE)	140
TABLE 4.3.3	EROSION RATES ( $\text{KG CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) BY MAJOR BIO-ERODERS AT STUDY SITES (N=6; G $\pm$ SE)	144
TABLE 4.4.1	ENVIRONMENTAL CHARACTERISTICS OF THE SELECTED STUDY SITES IN THE WAKATOBI MARINE NATIONAL PARK, INDONESIA	156
TABLE 4.4.2	EROSION RATES ( $\text{KG CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) BY MAJOR BIO-ERODERS AT STUDY SITES (N=6; G $\pm$ SE)	162
TABLE 5.1	SYMBIODINIACEAE GENERA, ASSIGNED CLADES AND SPECIES (*LACKS ITS ALPHANUMERIC DESIGNATION-COULD BE A DIFFERENT/NEW SPECIES)	179
TABLE 5.2	CHARACTERIZATION OF THERMAL REGIME IN EACH OF THE BIOREGIONS (REFER TO CHAPTER 2 FOR EQUATIONS USED TO DERIVE THE DATA DISPLAYED BELOW; BRIEF DEFINITIONS OF THE VARIABLES ARE OUTLINED BELOW THE TABLE). ALL VALUES ARE TEMPERATURE IN $^{\circ}\text{C}$ WITH THE EXCEPTION OF DHW WHICH IS IN $^{\circ}\text{C}$ -WEEKS	183
TABLE 5.3	ENVIRONMENTAL CHARACTERISTICS OF THE SELECTED STUDY SITES	184



TABLE 5.4.	LIST OF CORAL SPECIMENS ALONG WITH TOTAL NUMBER OF INDIVIDUAL REPLICATES (N)	185
TABLE 5.5	RESULTS OF PERMANOVA ON PCA OF SYMBIODINIACEAE COMMUNITIES BETWEEN CORAL SPECIES BY THERMAL REGIME, INDIVIDUAL SITE, AND LATITUDINAL TRANSECT. SIGNIFICANT P-VALUES ( $P < 0.05$ ) ARE MARKED IN (*), ( $P < 0.001$ ) ARE MARKED IN (**) AND ( $P < 0$ ) ARE MARKED IN (***)	198
TABLE S3.1	CARBONATE BUDGET COMPONENTS AND NUMBER OF REPLICATES AT EACH STUDY SITE IN THE SEYCHELLES	228
TABLE S3.2	SKELETAL DENSITIES AND GROWTH RATES / LINEAR EXTENSION RATE OF CORALS DERIVED FROM THE SUPPLEMENTARY MATERIAL OF JANUCHOWSKI-HARTLEY ET AL., (2017) ( $\pm 95\%$ CI).	230
TABLE S3.3	DETAILS OF CARBONATE BUDGET COMPONENTS AND NUMBER OF REPLICATES AT EACH STUDY SITE IN THE WAKATOBI, INDONESIA	233
TABLE S3.4	CARBONATE PRODUCTION RATES ( $\text{KG CaCO}_3 \text{ M}^{-2} \text{ Y}^{-1}$ EXPRESSED AS G) BY SECONDARY CARBONATE PRODUCERS BETWEEN 2017-2018 AT EACH OF THE STUDY SITES ACROSS THE THREE BIOREGIONS	237
TABLE S4.2	RELATIVE ABUNDANCE OF ITS2 TYPE PROFILES IN EACH CORAL HOST SPECIES AND BIOREGION. ROW IN RED HIGHLIGHTS THE NOVEL OBSERVATION OF C3-GULF IN THE SEYCHELLES	239

## CHAPTER & MANUSCRIPT CONTRIBUTION

All field surveys, lab work, analysis and writing of chapters were performed by Reem AlMealla under the guidance and supervision of Dr. Leanne J Hepburn. Prof. David J Smith provided guidance on the field and review of drafts. Dr Michelle Taylor and Dr. Boyd McKew provided supervision and guidance for the genetics work (including in the lab) related to Chapter 5. Brisneve Edullantes provided guidance and support in writing R code scripts. All chapters have been written into the following manuscripts:

**Chapter 2 & 3:** AlMealla RK, Edullantes & Hepburn LJ (2020) Status & Change in Coral Cover: History of 35 Years Through A Systematic Review of Three Bioregions. *In prep.*

**Chapter 2 & 4:** AlMealla RK, Edullantes & Hepburn LJ (2020) Bleaching threatens positive carbonate budgets and reef growth potential on Bahraini reefs. *In prep for Functional Ecology.*

**Chapter 5:** AlMealla RK, Edullantes E, McKew B, Hepburn LJ, Smith DJ & Taylor, ML (2020) Symbiodiniaceae diversity across thermal regimes and latitudinal gradients. *In prep.*

# **CHAPTER ONE: INTRODUCTION**

This page was left intentionally blank

## 1. INTRODUCTION

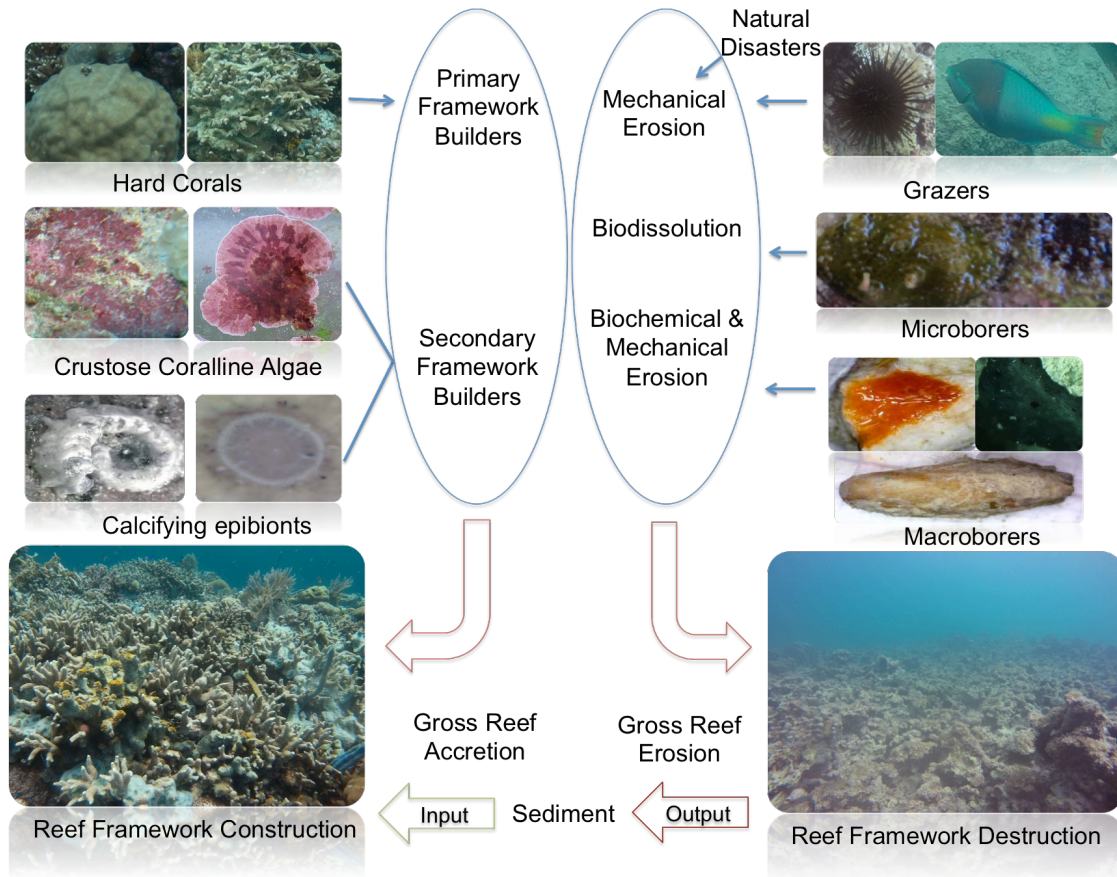
### 1.1 | CORAL REEFS – DIVERSITY, STRUCTURE & IMPORTANCE

Coral reefs are of high value, ecologically and economically, despite covering less than 0.1% of the ocean floor (Spalding & Grenfell, 1997). They harbour the highest concentration of marine biodiversity in the world's oceans (Carpenter *et al.*, 2008); amounting to one third of all recognized marine species (Bowen *et al.*, 2013) making them extremely important ecosystems that support biodiversity. They provide numerous ecological, social and economic benefits to communities worldwide through their ecosystem services (Smith, 1978; Moberg & Folke, 1999; Cinner *et al.*, 2013; Laurans *et al.*, 2013; Daw *et al.*, 2016). For example, some of these services include providing ~200 million people who live below 10 m elevation and within 50 km of reefs with coastal protection as reefs dissipate 97% of the energy that would otherwise hit shorelines (Ferrario *et al.*, 2014; Woodhead *et al.*, 2019). This service of shoreline protection contributes towards reducing annual expected damages from storms across reef coastlines, by more than \$4 billion (Woodhead *et al.*, 2019). In addition, reefs further contribute to economies through generating income via reef tourism which is estimated to be worth ca. US \$35.8 billion dollars per annum globally (Woodhead *et al.*, 2019). However, the extent to which coral reefs can deliver their services (e.g. coastal protection) and functions (e.g. biodiversity) is associated and dependent on the persistence of their reef framework structure (Perry *et al.*, 2008; Franco *et al.*, 2016). Coral reefs are geomorphic structures built from a calcium carbonate (CaCO<sub>3</sub>) skeleton produced by primary reef builders (e.g. hermatypic corals) thereby providing an important three-dimensional structure (Perry *et al.*, 2008). This structure gives rise to an array of different habitats for numerous associated species to use for foraging, shelter and interaction. The ability of coral reefs to sustain the integrity of their structural framework is based on the balance between the rate of carbonate production and erosion (removal)

or commonly known as the carbonate budget (Kleypas & Langdon, 2006; Perry & Hepburn, 2008; Perry *et al.*, 2008; Januchowski-Hartley *et al.*, 2017).

## 1.2 | REEF CARBONATE BUDGETS

Carbonate reef budgets rely on constructive (caused by reef-building organisms) and destructive (caused by bioeroders) influences, both of which, operate through a range of physical, chemical and biological processes over varying timescales and intensity (Tucker & Wright, 1990; Perry *et al.*, 2008) (Figure 1.1). Globally, ~50% of shallow water CaCO<sub>3</sub> produced is due to coral reef calcification (Milliman, 1993) with an estimated CaCO<sub>3</sub> production budget of 0.7-0.8 gigatonnes (Gt) year<sup>-1</sup> (Vecsei, 2004), most of which (>25%) is buried and preserved in marine sediment (Jones *et al.*, 2015). Therefore, unsurprisingly, calcification by coral reef communities is estimated to account for half of all carbonate produced in shallow water environments (Jones *et al.*, 2015). The carbonate budget is defined as the sum of gross carbonate production from both primary and secondary reef builders in addition to sediment produced within or imported into the reef, minus carbonate removed through destructive physical and/or biological processes or sediment export (Table 1.1; Mallela & Perry, 2007; Perry *et al.*, 2008, 2012; Leon & Woodroffe, 2013).



**Figure 1.1. Overview of the coral reef framework net carbonate production & erosion (adapted from Glynn, 1997; Photo credit of organisms: Dr. Leanne Hepburn).**

$\text{CaCO}_3$  production is mainly done by primary (hermatypic corals; Stearn & Scoffin, 1977; Perry & Hepburn, 2008) and secondary reef builders (calcareous encrusters; Goreau, 1963; Choi & Ginsburg, 1983), in addition to the reintroduction of carbonate sediment into the reef framework. Reef builders secrete, deposit and accumulate  $\text{CaCO}_3$  thereby, contributing towards the formation of the reef's structure through accretion. The extent of carbonate production is dependent on the distribution within a reef in addition to the disturbances (natural and anthropogenic; Eakin, 1996). The amount of  $\text{CaCO}_3$  produced by primary builders (corals) has been estimated to range between  $<1 \text{ kg m}^{-2} \text{ y}^{-1}$  on a degraded reef and  $14.3 \text{ kg m}^{-2} \text{ y}^{-1}$  on a healthy reef (Eakin, 1996; Edinger *et al.*,

2000; Mallela, 2013). Production by secondary carbonate producers (calcareous encrusters), most of which is based on limited data, is estimated as  $\sim 0.05 \text{ kg m}^{-2} \text{ y}^{-1}$  by all encrusters (Hubbard *et al.*, 1990; Mallela & Perry, 2007; Mallela, 2013; Hepburn *et al.*, 2015) with  $0.02 \text{ kg m}^{-2} \text{ y}^{-1}$  produced by crustose coralline algae (CCA; Hubbard *et al.*, 1990; Payri, 1997). Moreover, encrusting foraminifera (symbionts bearing ones and which are single-celled protists with shells) are estimated to produce a minimum of 130 million tons of  $\text{CaCO}_3$  per year thereby contributing approximately 5% of the annual world reefs carbonate production and 2.5% of  $\text{CaCO}_3$  of global oceans (Langer, 2008). The contribution of calcareous encrusters varies and is dependent on the reefs' microhabitat whereby cryptic microhabitats (such as cavities and overhangs) will usually harbour a higher abundance of heterotrophic encrusters (Mallela, 2013; Hepburn *et al.*, 2015) but these remain more difficult to quantify. In addition to being important producers of  $\text{CaCO}_3$  on reefs, encrusting organisms such as non-geniculate crustose coralline algae (CCA), bryozoans, foraminifera and serpulids, play an important role in binding the reef together through colonising reef substrate thereby contributing extensively towards its cementation and stability (Rasser & Riegl, 2002; Langer, 2008; Perry & Hepburn, 2008; Fujita *et al.*, 2009). This in turn, promotes accretion, enhances larval recruitment of various organisms and maintains wave resistance reef fronts (Rasser & Riegl, 2002; Mallela & Perry, 2007). Marine sediment also contributes to gross carbonate production rates on a reef, most of which is either imported from other areas (e.g. nearby shores through wave action), or present in-situ and form as a result of breakdown and/or degradation of calcareous organisms, which could be caused by grazers or disturbances on the reef (Hubbard *et al.*, 1990; Mallela & Perry, 2007). It is estimated that out of the 5 billion tons per year of  $\text{CaCO}_3$  produced in the world's oceans,  $\sim 3$  billion tons of it is accumulated in sediments (Milliman, 1993). Moreover,  $0.7 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  of carbonate sediment in a reef is estimated to be generated through



biological erosion whilst  $0.4 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  comes from sediment reincorporated into reef systems (Hubbard *et al.*, 1990).

**Table 1.1. Examples of net carbonate production rates on reefs worldwide (unit = kg CaCO<sub>3</sub> m<sup>-2</sup> year<sup>-1</sup> expressed as G; \*Pre and Post values refer to pre and post bleaching events).**

Location	Depth	Site	Net Carbonate Production Rate (G)	Source
Caribbean	Shallow reefs (<10 m)	Bellairs Reef, Barbados	4.5	(Scoffin <i>et al.</i> , 1980)
Caribbean	Depth range (0-60 m)	Discovery Bay, Jamaica	1.1	(Land, 1979)
Caribbean	5-10 m	Bonaire	Range: -0.9 to 9.5	(Perry <i>et al.</i> , 2012)
Caribbean	Shallow reefs	Bonaire	Range: 0.2 to 2.0	(de Bakker <i>et al.</i> , 2019)
Caribbean	-	Cane Bay, St Croix	0.9	(Hubbard <i>et al.</i> , 1990)
Eastern Pacific	Pre and Post-Bleaching*	Uva Island	Pre = 0.3; Post = -0.2	(Eakin, 1996)
Great Barrier Reef (North)	-	Reefs of Torres Strait	Range: 0.5 to 10	(Leon & Woodroffe, 2013)
West Indian Ocean	Shallow forereefs	Southern Maldivian atoll of Gaafu Dhaalu	Pre = 5.9; Post = -2.9	(Perry & Morgan, 2017)
West Indian Ocean	Reef crest and reef flat	Southern Maldives	2.5	(Ryan <i>et al.</i> , 2019)
West Indian Ocean	Pre and Post – Bleaching	Inner – reefs Seychelles	Pre = 4; Post = -1.5	(Januchowski-Hartley <i>et al.</i> , 2017)
West Indian Ocean	Pre and Post - Bleaching	Chagos Archipelago	Pre =13.1; Post = 3	(Lange & Perry, 2019)
West Indian Ocean	-	Chagos Archipelago	Range: -5 to 9.8	(Perry <i>et al.</i> , 2015a)
Indo-Pacific	Fringing reef	Kailua Bay, Oahu, Hawaii	0.9	(Harney & Fletcher, 2003)
Pacific	Fringing reef	Lizard Island, Australia	Range: 0.7 to 3.4	(Pescud, 2012)
Indo-Pacific	-	Java Sea and Ambon, Indonesia	Range: 7.6 to 11.7	(Edinger <i>et al.</i> , 2000)
Indo-Pacific	Fringing reefs (5-12 m)	Wakatobi National Biosphere Reserve, Indonesia	Range: 3.3 to 16.7	(Franco, 2014)
Red Sea	-	Gulf of Aqaba	Range: -1.5 to 2.4	(Roik <i>et al.</i> , 2017)

Bioerosion is the mechanical and/chemical dissolution of hard substrates by living agents and it generally occurs as a result of CaCO<sub>3</sub> removal from the reef framework. It is usually done by removing consolidated mineral matter either internally (within the calcareous reef skeleton) or

externally (on the reef surface) by organisms termed as bioeroders (Glynn, 1997). Bioeroders are key players in characterising a coral reef environment through sculpting its growth and in producing reef sediment (e.g. rubble and sand; Goreau & Hartman, 1963; Neumann, 1966; Hutchings & Bamber, 1985; Hubbard *et al.*, 1990). In addition, dominant bioeroders, such as bioeroding sponges, invertebrate grazers and excavating fish are known to be major players in removing  $\text{CaCO}_3$  from reefs (Scoffin *et al.*, 1980; Hutchings, 1986; Glynn, 1997; Schmidt & Richter, 2013), making bioerosion a key process in reef carbonate budgets. In addition, bioerosion rates are higher on dead substrate than live (Peyrot-Clausade *et al.*, 1992; Tribollet & Payri, 2001; Perry *et al.*, 2008). The net growth of coral reef frameworks is dependent on the balance between carbonate production and erosion, therefore, increased bioerosion could limit reef accretion – the overall net growth/ carbonate production - which may effectively lead to coral reef drowning (Holmes *et al.*, 2000; Perry *et al.*, 2018a). Bioerosion is dependent on various environmental variables such as light availability, depth and nutrient supply (Chazottes *et al.*, 1995). In addition, bioerosion is expected to increase with the weakening of existing carbonate structures driven by increasing ocean acidification and atmospheric carbon dioxide (Duckworth *et al.*, 2012; Fang *et al.*, 2013; Wisshak *et al.*, 2014).

Bioeroders can be separated into three main functional groups: macroborers (e.g. serpulids (polychaetes), bioeroding sponges, bivalves), microborers (e.g. cyanobacteria) and grazers (e.g. urchins). Macro- and micro- borers are known to usually infest dead carbonate substrate and live coral colonies beginning from the base through boring into the substrate utilising a chemical dissolution and/or mechanical abrasion mechanism (Glynn, 1997). Bioerosion rates of polychaetes are estimated to range between  $0.1 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  (Kiene & Hutchings, 1994) and  $0.2 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  (Peyrot-Clausade *et al.*, 1992). Excavating sponges compete for space with other sessile organisms through overgrowth by encrusting on the reef substratum (Marquez & Zea, 2012). Bioerosion rates for sponges vary greatly between species ranging from 0.1 (Rützler, 1975) to 12.5

kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> (Zundelevich *et al.*, 2007; De Bakker *et al.*, 2018). The variation in erosion rates is associated with a range of biotic and abiotic conditions such as substrate exposure time (Tribollet & Golubic, 2005), grazing pressure (Sammarco *et al.*, 1987), light availability (Magnusson *et al.*, 2007), sedimentation (Marlow *et al.*, 2018) and eutrophication (Chazottes *et al.*, 2002). Microborers bore holes in the reef substrate that are <100 µm diameter and include cyanobacteria, algae (e.g. chlorophytes, rhodophytes) and fungi (Enochs *et al.*, 2016). Their erosion rates are influenced by the mineralogy, porosity and structure of the carbonate substrate in addition to various environmental variables which influences their community composition on carbonate substrate (dead/alive; Chazottes *et al.*, 1995; Tribollet & Payri, 2001). Boring erosion rates of microborers documented include 0.03 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> in Jamaica (Mallela & Perry, 2007), 0.1 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> in French Polynesia (Chazottes *et al.*, 1995), 0.1 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> in La Reunion Islands (Chazottes *et al.*, 2002) and ranged between 0.1 and 1.3 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> in the Great Barrier Reef (Tribollet & Golubic, 2005). External CaCO<sub>3</sub> removed from hard reef substrata is a by-product of feeding by grazers (e.g. parrotfish and echinoids (urchins)). Parrotfish are well known for their important ecological role in controlling macroalgae on reefs, ensuring substrate availability for coral larval settlement and recruitment (Bellwood, 1995; Bellwood *et al.*, 2004; Hoey & Bellwood, 2008). Previous studies have shown that bioerosion rates of parrotfish depend on species-specific, size and life phase (Bruggemann *et al.*, 1994, 1996; Bellwood, 1995; Hoey & Bellwood, 2008). Parrotfish bioerosion in the Caribbean has been reported to be ~1 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> for *Scarus* spp. (Bruggemann *et al.*, 1996; Perry *et al.*, 2012) and 1.1 – 2.1 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> for *Sparisoma viride* (Bruggemann *et al.*, 1996; Perry *et al.*, 2012). In Australia, *Chlorurus microrhinos* was reported to remove 4.6 ± 3.1 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> while *C. gibbus* and *C. sordidus* removed 3.0 ± 2.0 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> (Bellwood, 1995; Hoey & Bellwood, 2008); while *Bolbometopon muricatum* was reported to remove an estimated 2.3 m<sup>3</sup> or 5.7 ± 0.5 t CaCO<sub>3</sub> y<sup>-1</sup> (Bellwood *et al.*, 2003). Echinoids bioerosion

rates also vary between species, size and abundance, with most belonging to the genera *Diadema*, *Echinometra*, *Echinostrephus* and *Eucidaris* (Scoffin *et al.*, 1980; Bak, 1990, 1994a). They are responsible for 80% of the total erosion of reefs (Scoffin *et al.*, 1980) as they can process  $\sim 9.7$  kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  (Hunter, 1977; Bak, 1990) In general, echinoids have been recorded to have an erosion rate between 0.4 (Appana & Vuki, 2004) and 14 kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  (Eakin, 1992). Lastly, physical disturbances associated with the periodic occurrence of severe storms, typhoons and cyclones, also contribute towards the destruction of the reef framework resulting in the production of coral rubble and removal of sediment (Eakin, 1996; Blanchon & Jones, 1997; Rasser & Riegl, 2002).

**Table 1.2. Examples of gross carbonate erosion rates worldwide (unit = kg  $\text{CaCO}_3 \text{ m}^{-2} \text{ year}^{-1}$  expressed as G; \*Pre and Post values refer to pre and post bleaching events).**

Location	Depth	Site	Gross Carbonate Erosion Rate (G)	Source
French Polynesia	Fringing reef	Moorea Island	2.6	(Chazottes <i>et al.</i> , 1995)
Caribbean	5-10 m	Bonaire	Range: 1.0 to 2.8	(Perry <i>et al.</i> , 2012)
West Indian Ocean	Pre and Post- El Nino	Inner – reefs Seychelles	Pre = 1.9; Post = 2.9	(Januchowski-Hartley <i>et al.</i> , 2017)
West Indian Ocean	Reef crest and reef flat	Southern Maldives	3.4	(Ryan <i>et al.</i> , 2019)
West Indian Ocean	-	Chagos Archipelago	Range: 1.4 to 7.4	(Perry <i>et al.</i> , 2015a)
Indo-Pacific	Fringing reef	Kailua Bay, Oahu, Hawaii	Range: 0.1 to 1.2	(Harney & Fletcher, 2003)
Indo-Pacific	-	Java Sea and Ambon, Indonesia	Range: 0.9 to 10.1	(Edinger <i>et al.</i> , 2000)
Indo-Pacific	Fringing reefs 5-12 m	Wakatobi National Biosphere Reserve, Indonesia	Range: 0.7 to 5.6	(Franco, 2014)
Red Sea	-	Gulf of Aqaba	Range: 0.4 to 1.0	(Roik <i>et al.</i> , 2017)

### 1.3 | CARBONATE BUDGET ASSESSMENTS

In recent years, reef carbonate budget measures have been recognised as a key metric in assessing coral reef health (Mace *et al.*, 2014; Perry & Morgan, 2017). Coral reef structural integrity is associated with carbonate budgets, which quantifies the overall  $\text{CaCO}_3$  input and output on a reef framework. Positive reef budgets occur when  $\text{CaCO}_3$  production exceeds erosion, representing reef accretion whilst negative reef budgets occur when physical abrasion, bioerosion and dissolution outweigh production (Leon & Woodroffe, 2013). In the last three decades, several attempts at quantifying and assessing coral reef gross production and calcification rates have been undertaken (Milliman, 1993; Eakin, 1996; Perry *et al.*, 2008, 2012; Leon & Woodroffe, 2013; Franco, 2014; Hepburn *et al.*, 2015; Vargas-Ángel *et al.*, 2015; Perry & Morgan, 2017). The carbonate budget approach enables linking ecological and morphological changes (within or between reefs) across different spatial scales whilst analysing various components of reef function and structure effectively over time (Perry *et al.*, 2008; Leon & Woodroffe, 2013; Januchowski-Hartley *et al.*, 2017). This allows us to understand the coping abilities of reefs to maintain themselves and enables detection of change in the budgetary trend as a result of reef functionality change or stressors (Perry *et al.*, 2014; Lange & Perry, 2019). Carbonate budgets have been used to investigate various processes that influence reef growth or degradation all of which are related to the dynamics amongst various physical, chemical and biological processes (Stearn & Scoffin, 1977; Kiene, 1988; Eakin, 1996; Edinger *et al.*, 2000; Appana & Vuki, 2004; Mallela & Perry, 2007; Perry *et al.*, 2012; Franco, 2014; Hepburn *et al.*, 2015; Vargas-Ángel *et al.*, 2015). The majority of previous studies adopted a census-based approach to quantify carbonate production on reefs in different locations, which can be translated into a mathematical equation (Mallela, 2004; Perry *et al.*, 2012; Franco, 2014) whereby each component is associated with the accretion or erosion aspect of the reef

framework. In order to calculate the production and erosion rate separately (in  $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  hereafter referred to as G), a rapid non-destructive census based protocol termed “*ReefBudget*” has been proposed as a standardized methodology to conduct carbonate budget assessments (Perry *et al.*, 2012, 2015b, 2018b). The protocol utilizes a series of equations to calculate production and erosion, derived from published work and empirical data. This standardized approach enables accurate global comparisons of carbonate budgets, even though designed originally for the Caribbean, it can be adapted to different regions through using algorithms for varying components e.g. bioerosion by parrotfish. Carbonate budget assessments play an important role in providing insights into coral reef health and status under various environmental conditions (Eakin, 1996; Mallela & Perry, 2007; Perry *et al.*, 2012). They can hence be utilised to aid in coral reef conservation management due to their ability to quantify functional and structural changes in reef ecosystems (Perry *et al.*, 2008) especially when integrated in models to predict future changes in reef systems (Franco, 2014).

#### **1.4 | THREATS TO CORAL REEF FRAMEWORKS**

Globally, coral reefs have suffered severe impacts due to various environmental and anthropogenic factors that have resulted in their degradation and destruction (Hoegh-Guldberg, 1999; Douglas, 2003; Hoegh-Guldberg *et al.*, 2007; Carpenter *et al.*, 2008; Hoegh-Guldberg, 2011; Seemann *et al.*, 2014). Anthropogenic pressures such as destructive fishing practices (Jones & Steven, 1997), overfishing activities (Bellwood *et al.*, 2004; Mallela & Perry, 2007) and pollution arising from urban and coastal developments (Lafferty *et al.*, 2004; Browne *et al.*, 2012a; Fan *et al.*, 2013) have resulted in altering coral reefs ecosystems worldwide, thus threatening their functionality. In addition, reef accretion and coral growth rates have been reported to be negatively impacted from anthropogenic pollution caused by sedimentation and eutrophication (Edinger *et al.*, 2000; Mallela

& Perry, 2007; Browne *et al.*, 2012b). Impacts of high sedimentation include declining calcification rates (Mallela, 2013), increase in coral mortality due to smothering and burial (Loya, 1976; Nugues & Roberts, 2003), increase in coral disease (Bruno *et al.*, 2003), reduced larval settlement (Fabricius *et al.*, 2005) and reduced light availability necessary for photosynthesis (Rogers, 1990; Wolanski & De'ath, 2005; Browne *et al.*, 2012a). In addition, sedimentation has been noted to negatively impact secondary reef builders, especially encrusters (Fabricius & De'ath, 2001; Mallela, 2007). Globally recognised as key threats to coral reefs, ocean warming and ocean acidification (both by-products of a changing climate) contribute immensely to altering ocean chemistry and temperature (Pandolfi *et al.*, 2011; IPCC, 2015). By the year 2100, climate change is expected to increase global ocean surface temperatures by  $>3^{\circ}\text{C}$  and decrease its pH by up to 0.32 units (IPCC, 2013; Prada *et al.*, 2017). Increasing atmospheric concentrations of  $\text{CO}_2$  are reducing ocean pH and carbonate ion concentrations ( $\text{CO}_3^{2-}$ ) resulting in more acidic water thereby reducing the calcification rate of reef framework builders due to lower levels of calcium carbonate ( $\text{CaCO}_3$ ; Gattuso *et al.*, 1998; Kleypas *et al.*, 1999; Orr *et al.*, 2005; Anthony *et al.*, 2008). As a result, it is predicted that within decades, erosion rates will exceed reef accretion rates due to lower  $\text{CaCO}_3$  production (Hoegh-Guldberg *et al.*, 2007; Fabry *et al.*, 2008; Pandolfi *et al.*, 2011). Moreover, increasing sea surface temperatures (SST) also impact corals and their symbiosis due to coral bleaching events, resulting in negative consequences for coral survival, growth and reproduction (Hoegh-Guldberg *et al.*, 2007; Anthony *et al.*, 2008). This is alarming especially with coral bleaching episodes predicted to increase in frequency and severity threatening reefs worldwide. The future of coral reefs look bleak with speculations of long-term degradation due to the rise in global mass coral bleaching incidences in recent decades attributed to rising temperatures (Hoegh-Guldberg, 1999; Wellington *et al.*, 2001; Sheppard, 2003; Donner *et al.*, 2005; Januchowski-Hartley *et al.*, 2017).



## 1.5 | THE CORAL HOLOBIONT

Hermatypic (reef-building) corals are typically composed of polyp colonies, however, solitary single polyp corals are also present (e.g. *Fungia*), whose tissues host a single-celled dinoflagellate microalgae (commonly known as zooxanthellae) in the family Symbiodiniaceae (LaJeunesse, 2001). The foundation of coral reefs is based on the symbiotic association between hermatypic corals and dinoflagellates in the family Symbiodiniaceae (Rouzé *et al.*, 2017). The Symbiodiniaceae species inhabits the vacuoles (known as symbiosome) which is present within the endodermic layer of the coral polyp tissue (Trench, 1979). Corals are supplied by photosynthetic products such as sugars, fatty and amino acids, carbohydrates and small peptides, thereby receiving 95% of its nutrition from the Symbiodiniaceae species (Trench, 1979; Papina *et al.*, 2003). This energy supply by the Symbiodiniaceae species is also related to the amount of energy available for calcification (Jones & Berkelmans, 2010). In return, the Symbiodiniaceae species receives crucial plant nutrients such as ammonia and phosphate from the coral's waste metabolism (Furla *et al.*, 2000; Al-Hammady, 2013). In addition, all corals host large populations of microorganisms including eukaryotic algae, bacteria, viruses, fungi and archaea in their mucus layer, skeleton and tissues whereby by the Symbiodiniaceae species is just one of them (Rosenberg *et al.*, 2007; Littman *et al.*, 2011). This collective diverse and dynamic group of microbial communities together with the Symbiodiniaceae species make up what is referred to as the coral holobiont (Rohwer *et al.*, 2002; Thompson *et al.*, 2015). These microorganisms provide their host with benefits by various mechanisms, including photosynthesis, nitrogen fixation, the provision of nutrients and infection prevention thereby contributing towards coral health (Trench, 1979; Rohwer *et al.*, 2002; Rosenberg *et al.*, 2007). The coral holobiont functions as a dynamic system whereby external environmental conditions determines its members (Shashar *et al.*, 1993; Tanner, 1996; Thompson *et al.*, 2015; Roik *et al.*,

2016). Therefore, any change in environmental conditions will change the relative abundance of microbial species in order to facilitate the coral holobiont to adapt to the new condition (Reshef *et al.*, 2006). In addition, these symbiont microbial populations may reach densities of several million or more per square centimeter of host tissue (LaJeunesse, 2002). With the advancement of molecular techniques in the last 20 years, evidence has been attained regarding the diversity in the Symbiodiniaceae species hosted within invertebrate populations (Rowan & Powers, 1991; LaJeunesse, 2001, 2002; Pochon *et al.*, 2001; Coffroth & Santos, 2005; Sampayo *et al.*, 2009; Hill *et al.*, 2011). Recent phylogenetic reconstructions have revealed nine widely recognized divergent phylogenetic lineages of Symbiodiniaceae species referred to as “clades” (A-I) which, based on the 18S rDNA and internal transcribed spacer regions (ITS) analyses (Rowan & Powers, 1991; LaJeunesse, 2001, 2002; Pochon *et al.*, 2006; Pochon & Gates, 2010; Hill *et al.*, 2011; Yang *et al.*, 2012; Rouzé *et al.*, 2017), are further divided into sub-clades or types (Rowan & Knowlton, 1995). Over the years, several new species of Symbiodiniaceae species have been formally described, classified and named amounting to 22 species at present (Trench & Blank, 1987; Jeong *et al.*, 2014; LaJeunesse *et al.*, 2014; Hume *et al.*, 2015; LaJeunesse *et al.*, 2015; Parkinson *et al.*, 2015; Ramsby *et al.*, 2017; LaJeunesse *et al.*, 2018). Studies have revealed that within various sub-clades Symbiodiniaceae species exhibit distinct genetic, physiological, and ecological variation associated with the multiple species concept (Lajeunesse *et al.*, 2012; LaJeunesse *et al.*, 2018). Symbiodiniaceae species clades and sub-clades vary in their levels of tolerance to heat and light (Stat *et al.*, 2006; Hennige *et al.*, 2011; Silverstein *et al.*, 2012). Coral-Symbiodiniaceae species associations have been seen to include mono or multi-clade associations (Fabina *et al.*, 2012; Silverstein *et al.*, 2012; Rouzé *et al.*, 2017). Regional and local environmental factors are known to influence their clade associations and ecological dominance (Baker, 2003; Ziegler *et al.*, 2017). Symbiodiniaceae species in clades A-D are commonly seen associated with corals (LaJeunesse,

2001), whilst those associated with clades F and G remain rare (Ramsby *et al.*, 2017). Favourable environmental conditions promote harmonious functions between the host and its associated symbiosis. However, when subjected to various stressors that induce environmental change caused by natural and/or anthropogenic sources, this symbiotic relationship is impacted and can breakdown. The degree of how this relationship is impacted is determined based on the degree of stress tolerance of either partner (Yang *et al.*, 2012; Rouzé *et al.*, 2017). Previous studies have suggested that accretion rates of corals are affected in hosts harbouring thermally tolerant symbionts when compared to those with the thermally sensitive type (Jones & Berkelmans, 2010; Pettay *et al.*, 2015). Reef carbonate budgets and associated coral-Symbiodiniaceae species in the bioregions selected for this study remain poorly explored, especially at this crucial time following the 2015-2016 named the “Godzilla El Nino” event that has generated significant coral bleaching and mortality worldwide (Ampou *et al.*, 2017).

## 1.6 | CORAL BLEACHING

Bleaching is a term used to address the partial or complete loss of the Symbiodiniaceae species from coral tissues which occurs when corals are under stress from elevated temperatures thereby exceeding their thermal tolerance levels (Hoegh-Guldberg, 1999; Donner *et al.*, 2005; Hoegh-Guldberg *et al.*, 2007). It can also be used to describe the discolouration due to the loss of pigmentation (from the Symbiodiniaceae species and coral cnidarian host tissue), in addition to, the loss of all the Symbiodiniaceae species cells from coral tissue (Suggett & Smith, 2010). An increase by one or two degrees Celsius is enough for corals to expel their associated Symbiodiniaceae species (Lesser, 2007; Desalvo *et al.*, 2008; Ricaurte *et al.*, 2016). The effects of coral bleaching may not have major consequences to the coral depending on the length of exposure and degree of elevation (Baker *et al.*, 2008). Suggett and Smith (2010) proposed that bleaching has three stages: (1) “non-

lethal” bleaching occurs as part of a natural phenomena that is driven by natural change in environmental conditions (e.g. temperature and light) and biological interactions (e.g. disease and microbial activities). (2) “sub-lethal” is when corals encounter stress due to an increase in the amplitude and frequency of environmental variability that is beyond normal thereby exceeding the coral’s tolerance. However, this kind of bleaching does not result in coral mortality and is reversible once conditions return to normal. (3) “lethal” bleaching is when corals exhibit an irreversible bleaching process due to rapid and extreme environmental change that results in coral mortality. The loss of Symbiodiniaceae species cells and/or host tissue leave the underlying CaCO<sub>3</sub> skeleton vulnerable with little hope of recovery when environmental conditions return to normal (Suggett & Smith, 2010). Lethal and sub-lethal bleaching, negatively impact accretion rates on reefs, as coral colonies are more prone to erosion during this vulnerable phase. Bleaching has been proposed to be a survival mechanism used by corals to overcome severe stress through dynamic modification of their Symbiodiniaceae species community composition which is a concept termed as “Adaptive Bleaching Hypothesis” (Buddemeier & Fautin, 1993). This is done by either switching their Symbiodiniaceae species clades with those more resistant in the present surrounding environment or through shuffling the pre-existing clades with those more resistant (Rowan & Powers, 1991; Baker *et al.*, 2004; Rouzé *et al.*, 2017). For example, in a study on a common Indo-Pacific branching coral species (*Acropora millepora*), it was found that switching to thermally tolerant Symbiodiniaceae species type D (*Durusdinium sp.*) increased the coral’s thermal tolerance between 1.0-1.5°C (Berkelmans & Van Oppen, 2006). Coral are known to be restricted to certain temperature thresholds (Webster *et al.*, 2011) and in light of rising SST levels, it is necessary to understand the various associations between the assemblages of Symbiodiniaceae species and coral host along with how this relationship will affect future accretion rates on reefs in the face of predicted global environmental change. Previous studies have stated that accretion rates of reef-building corals are

likely to be compromised significantly by two different processes: the effect of the actual bleaching stress and the other being the process of symbiont shuffling to more thermally tolerant types due to thermal stress before bleaching (Little *et al.*, 2004; Mieog *et al.*, 2009; Jones & Berkelmans, 2010). Moreover, it has been suggested that accretion rates of coral are affected in hosts harbouring thermally tolerant symbiont when compared to those with the thermally sensitive type (Jones & Berkelmans, 2010; Pettay *et al.*, 2015). Examining the cost-benefit trade-offs in hosting thermally tolerant Symbiodiniaceae species and its relation to accretion will aid in providing valuable insights as to the future of coral reefs. This is particularly pertinent given that one-third of the world's coral reefs are at risk of extinction (Carpenter *et al.*, 2008; Huang & Roy, 2015) due to climate change combined with other anthropogenic impacts such as overfishing and destructive fishing practices (Hoegh-Guldberg, 1999; Douglas, 2003; Hoegh-Guldberg *et al.*, 2007; Carpenter *et al.*, 2008; Hoegh-Guldberg, 2011; Seemann *et al.*, 2014). Therefore, this thesis aims to contribute towards filling the knowledge gap within the interlinked fields of reef carbonate budgets and coral-Symbiodiniaceae associations in three selected bioregions. These were chosen based on differences in their (1) thermal regimes (e.g. Arabian Gulf<sup>1</sup> (AG): 16-36°C; West-Indian Ocean (WIO)/Central Indo-Pacific (CIP): 24-33°C); (2) latitudinal position (reefs in AG are considered high latitude reefs whilst both WIO and CIP host low latitude reefs); and (3) range in species diversity (e.g. CIP = high biodiversity whereas AG = low biodiversity (see section 1.7 for more details). In addition, the selection of countries and local sites within each bioregion for this thesis was further determined based on local collaborations and the availability of reef sites that harbour different environmental characteristics (e.g. reefs in clear-water vs. turbid environments) to enable site comparisons.

---

<sup>1</sup> The Arabian Gulf is also referred to as the Persian Gulf (the difference in terminology is geopolitical), the UN refers to the region as the ROPME Sea Area. Since the selected site within this region for this thesis is located within an Arab nation, the terminology used will adhere to the official term referred to by the country i.e. the Arabian Gulf.

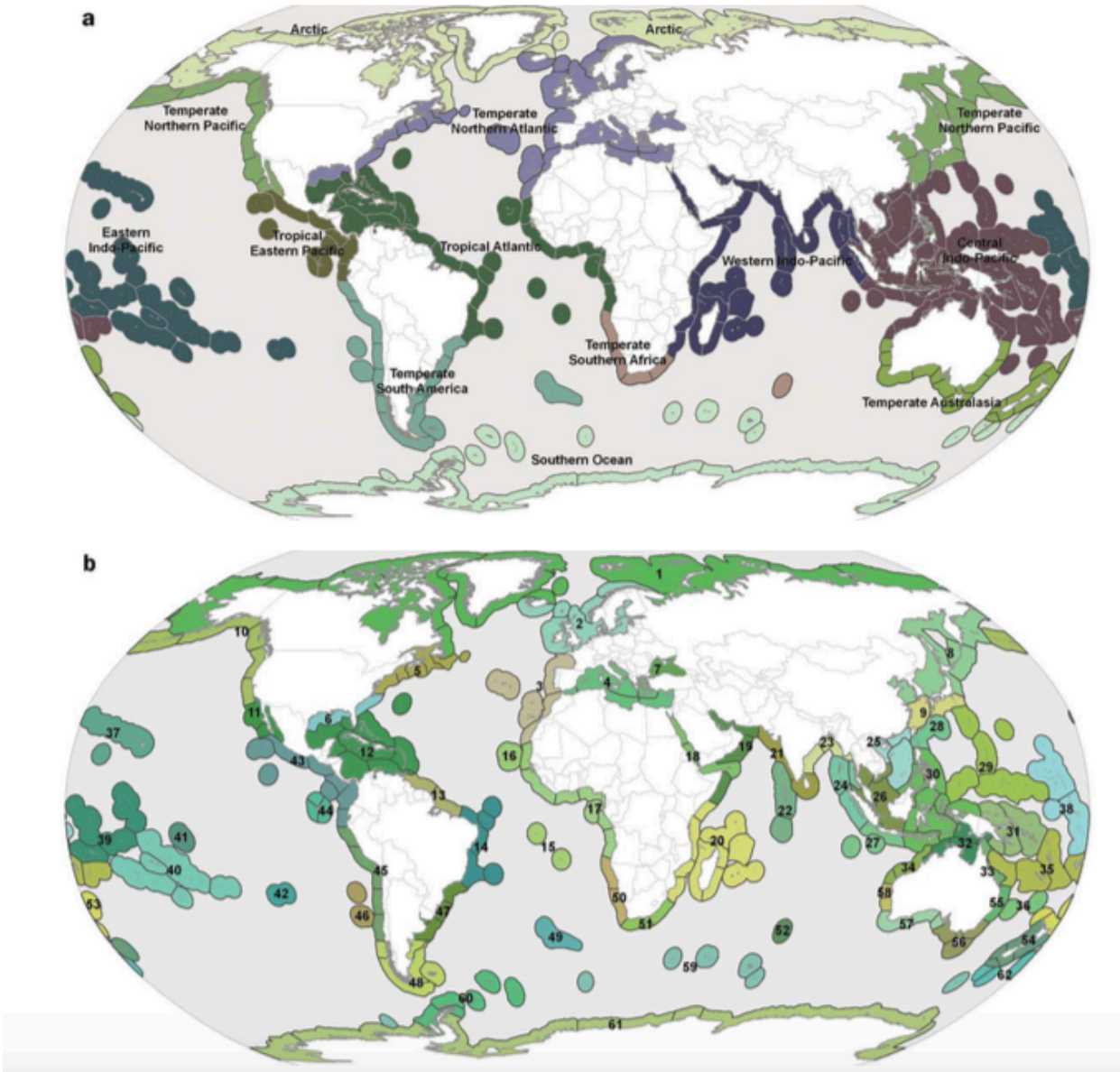
## 1.7 | CONNECTING BIOREGIONS THROUGH EVOLUTIONARY HISTORY

Ocean currents (past and present) determine biogeographic patterns which define connectivity among sites including historical patterns of speciation, extinction and immigration (Obura, 2012). Understanding biogeographic patterns and their mechanisms in addition to their classification is crucial for conserving ecologically representative systems which intends to protect genetic diversity, species, higher taxa including evolutionary patterns and ecological processes that sustain biodiversity (Spalding *et al.*, 2007). The Marine Ecoregions of the World (MEOW) provides a global hierarchy system which classifies the world's coastal and shelf waters into 12 realms, 26 provinces and a total of 232 ecoregions (Spalding *et al.*, 2007; Figure 1.2). The analysis of biogeographic datasets of scleractinian corals across all tropical MEOW provinces, showed significant segregation of provinces between the four Indo-Pacific realms (Obura, 2012). This thesis focuses on three of these provinces: (30) the Central Indo-Pacific (CIP; which includes the Coral Triangle) and the Western Indo-Pacific (Figure 1.2). Provinces within the Western Indo-Pacific realm cluster coral species strongly together with the exception of the Andaman Seas (Obura, 2012). The Western Indo-Pacific realm consists of 7 provinces namely: (18) the Red Sea and Gulf of Aden, (19) Somali/Arabian, (20) Western Indian Ocean, (21) West and South Indian Shelf, (22) Central Indian Ocean Islands, (23) Bay of Bengal and (24) Andaman (Figure 1.2; Spalding *et al.*, 2007). Of these seven provinces, two are of particular interest for this reef carbonate budget and Symbiodiniaceae species study: (19) Somali/Arabian (which includes the Arabian Gulf; AG) and (20) Western Indian Ocean (WIO; Figure 1.2). It is thought that sea level and climatic fluctuations during the Plio-Pleistocene period and their effect on dispersal–vicariance<sup>2</sup> may have acted as a diversity centre, driving the phylogenesis of new species in these ecoregions (Obura, 2016). In

---

<sup>2</sup>The geographical separation of a population, typically by a physical barrier such as a mountain range or river, resulting in a pair of closely related species [Source: Oxford Dictionary]

addition, species accumulation in the WIO is predicted to be a result of species immigration or gene flow from the Central Indo-Pacific Realm (Veron, 2000; Obura, 2012). Moreover, the fluctuating isolation and connectivity of the Red Sea and Arabian Gulf due to their shallow and restricted openings to the northern Indian Ocean may have impacted the speciation processes (Sheppard *et al.*, 1992; Dibattista *et al.*, 2016; Obura, 2016), thus contributing to their dispersal to the broader species pool shared across the Western and Northern Indian Ocean (Obura, 2012, 2016; Bowen *et al.*, 2013). Despite hosting unique coral reef ecosystems, the seas surrounding the Arabian Peninsula, including AG remains understudied (Ziegler *et al.*, 2017). In terms of coral communities (genera and species diversity), the Coral Triangle is considered the epicenter of marine diversity (Sanciangco *et al.*, 2013) as it hosts the highest diversity of hermatypic (reef building) corals (92%) on the planet (Veron, 2000). This pattern of maximum number of genera and species is seen to decrease once outside this zone whereby genera reach <30 in AG and the Gulf of Oman (Coles, 2003). Previous studies have quantified reef carbonate budgets in CIP to range between 0.9 and 16.7 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> (Edinger *et al.*, 2000; Harney & Fletcher, 2003; Franco, 2014) covering accretion of reefs that harbour different environmental gradients and are exposed to various anthropogenic pressures. Regional studies have also reported that Symbiodiniaceae species clades C (*Cladocopium sp.*) & D (*Durusdinium sp.*) are dominant in coral species hosting a mixture of thermo-tolerant and thermo-sensitive lineages (Lajeunesse *et al.*, 2004a; Lajeunesse, 2005; Hennige *et al.*, 2010).



**Figure 1.2. MEOW Biogeographic Framework: (a) Biogeographic realms with ecoregion boundaries outlined (b) Provinces with ecoregions outlined whereby provinces are numbered and listed in the original paper. Source: Spalding *et al.*, 2007.**

On the contrary, coral communities in AG are considered a subset of the extremely diverse Indo-Pacific which disperses across the Pacific and Indian Oceans from the west coast of Central and South America to the east coast of Africa (Coles, 2003). AG is reported to host only 10% of the



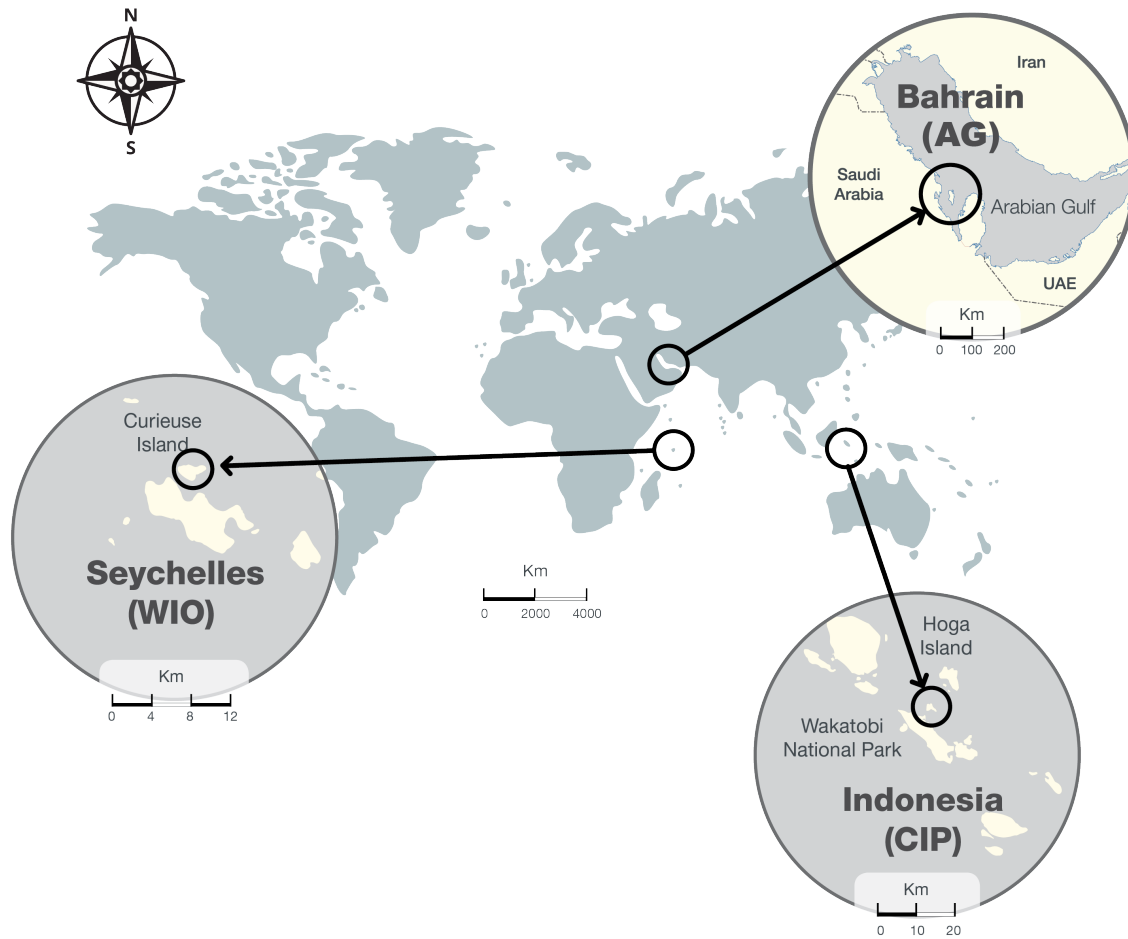
species that occur in the Indo-Pacific (Coles, 2003) which could be attributed towards the region's geographic isolation and its extreme and stressful environmental conditions defining it as the hottest sea on the planet which in turn limits the diversity of species it hosts (Coles, 2003; Coles & Riegl, 2013; Hume *et al.*, 2013). Coral reefs in this region exist in harsh environments enduring high (up to 36°C; Coles & Riegl, 2013; Hume *et al.*, 2013) and low (<18°C) temperatures (Coles & Fadlallah, 1991; Ziegler *et al.*, 2017), high salinity (42-44) and extreme low tides (Sheppard *et al.*, 2010; Hume *et al.*, 2013); all of which may contribute towards limiting coral genera diversity in the region. Due to its geographically isolated nature it is thought that corals have developed their thermal resistance over the period of the region's isolation (~6 kilo-annum years) during which reefs have been subjected to a warmer climate in comparison to corals from other regions (Purkis *et al.*, 2010; Hume *et al.*, 2013). It is thus unsurprising that coral communities in AG are seen to harbour the highest bleaching threshold globally (D'Angelo *et al.*, 2015), however, despite their high threshold, they are still susceptible to bleaching (Burt *et al.*, 2019). It is said that 70% of original AG reef cover may be considered lost and a further 27% threatened or at critical stages of degradation (van Lavieren *et al.*, 2011) with strong declines linked to major bleaching events (Sheppard & Loughland, 2002; Riegl *et al.*, 2011; Burt, 2013; Coles & Riegl, 2013). To date, no studies have been conducted to investigate accretional health of reefs in AG and to our knowledge this study is the first attempt to quantify reef carbonate budgets in this region. Nevertheless, in recent years, a rise in research has taken place in the region, most of which is focused on the reefs of the United Arab Emirates (UAE) and Oman (Burt, 2013) to understand the mechanisms behind the ability of these reefs to survive in their harsh environments particularly in relation to high temperatures (Sheppard *et al.*, 1992; Hume *et al.*, 2013; D'Angelo *et al.*, 2015; Bento *et al.*, 2016; Ziegler *et al.*, 2017). The presence of Symbiodiniaceae species type D (*Durusdinium sp.*; known to increase thermal tolerance in coral hosts) has been reported in northwest (off Saudi Arabia) and northeast (off Iran) of AG (Baker *et al.*, 2004; Ghavam

Mostafavi *et al.*, 2007; LaJeunesse *et al.*, 2014) and was inferred to as the reason behind their tolerance. However, recent studies reported that in areas where Symbiodiniaceae species (*Durusdinium sp.*) is said to be absent, sub-clade C3 (*Cladocopium sp.*) was prevalent instead all year-round in the south of AG (Abu Dhabi) (Hume *et al.*, 2013; D'Angelo *et al.*, 2015). This was surprising considering that sub-clade C3 members are considered cosmopolitan thermally sensitive generalists (Lajeunesse, 2005; Hume *et al.*, 2015). Following the recognition of this contradictory findings, the discovery of a new species (C3-Gulf) was announced which was found to be the predominant coral symbionts in the South of the AG and was named “*Cladocopium thermophilum*” (Hume *et al.*, 2015).

Whilst AG and CIP are considered as bioregions with characteristics that are on the opposite spectrum of each other both in terms of environmental conditions and diversity, WIO harbours a unique environmental gradient ranging from tropical to temperate due to complex currents that interact between the African coastline and nearby islands (e.g. La Reunion, Madagascar, the Maldives, Mauritius and the Seychelles; Mcclanahan *et al.*, 2011). Hence, acting as an ideal median bioregion in terms of environmental conditions for this study in between the two opposite bioregions. The WIO is known for its biodiverse rich marine life and hence is considered to be an important biogeographic region of tropical seas due to being a coherent subdivision of the Indo-Pacific (Sheppard, 2000; Ridgway & Sampayo, 2005). Reefs in the WIO are impacted by various anthropogenic activities (e.g. habitat destruction, overfishing and pollution) as a result of poverty and rapid population growth (Berg *et al.*, 2002). Similar to AG, the WIO was also severely impacted by the 1998 mass bleaching event which resulted in 75-99% mortality of corals in heavily impacted sites (Wilkinson *et al.*, 1999; Wilkinson, 2000; Graham *et al.*, 2006) while areas such as Mauritius and La Reunion reported lower levels of bleaching (Obura, 2005). Previous regional studies in WIO, have indicated that Symbiodiniaceae species clade C (*Cladocopium sp.*) is dominant across the

region with clade D (*Durusdinium sp.*) becoming more evident in areas (Burnett, 2002; Ridgway & Sampayo, 2005; Mcclanahan *et al.*, 2011). Reef carbonate budgets and Symbiodiniaceae diversity in this region remain understudied.

The ecological functions of reefs rely on their structural complexity, which depends on the ability of reef building corals to maintain their functional roles (net reef accretion) over the long term encompassing both chronic and acute shifts. Since maintaining their structural framework, measured by their carbonate budget, is linked to their survival in the face of rising sea levels (Perry *et al.*, 2015a, 2018a); carbonate budgets allow us to understand the coping abilities of reefs to maintain themselves in light of a changing climate that threatens their functionality. Understanding reef dynamics under extreme conditions such as AG, could present a possible window to the future of reefs worldwide since these reefs currently exist in a thermal environment that is similar to that predicted for future tropical reefs whereby climate scenarios predict a future in which reefs will face an increase in ocean temperatures by 1-3°C (Riegl *et al.*, 2011).



**Figure 1.3. Location of Selected Study Bioregions: Arabian Gulf (AG), the Western Indian Ocean (WIO) and Central Indo-Pacific (CIP).**

## 1.8 | THESIS AIM

The overall aim of this thesis is to assess reef accretional health and explore Symbiodiniaceae diversity of selected reef sites in Bahrain located in the Arabian Gulf (AG), the Seychelles located in the Western Indian Ocean (WIO) and Indonesia located in the Central Indo-Pacific (CIP; Figure 1.3).

***Chapter aims:***

- ***Chapter 2:*** To examine the thermal stress history on reefs in the three bioregions for a period of 35 years (1982-2017) in order to identify periods of vulnerability and mortality caused by bleaching events impacting reef carbonate budgets.
- ***Chapter 3:*** To determine the current status and trends of reefs in the three selected bioregions through conducting a systematic review.
- ***Chapter 4:*** To quantify reef carbonate budgets in the three selected bioregions.
- ***Chapter 5:*** To investigate the diversity of Symbiodiniaceae species for selected coral species across different thermal regimes in the three bioregions through ITS2 region sequence analysis.

This page was left intentionally blank

**CHAPTER TWO: THERMAL HISTORY OF REEFS IN THE  
ARABIAN GULF, WESTERN INDIAN AND CENTRAL INDO-  
PACIFIC OCEAN**

This page was left intentionally blank



## 2. THERMAL HISTORY OF REEFS IN THE ARABIAN GULF, WESTERN INDIAN AND CENTRAL INDO-PACIFIC OCEAN

### ABSTRACT

One of the main climatic shifts affecting tropical coral reefs is increased sea surface temperatures (SST), which is one of the main triggers of coral bleaching. However, the effects of temperature on many localized regions remain unexplored and it is important at this time, to determine refugia areas for reefs. Therefore, this study aimed to characterize the thermal history of three bioregions located in three latitudes. Sea surface temperature (SST) between the periods 1982-2017 (35 years) was derived from the CoRTAD satellite to quantify spatial and temporal characteristics of thermal history metrics in localized sites within the three bioregions. Results illustrated that the higher latitude bioregion was subject to warmer conditions. In addition, thermal stress anomalies were observed to significantly increase over time in all three bioregions, which could impact accretional health and framework production. High latitude reefs (e.g. Bahrain) experience high and intense temperature disturbance ( $>4^{\circ}\text{C-DHW}$ ) in comparison to those in the eastern lower latitudes (e.g. Indonesia), which experience low intensity, increase in temperatures ( $<4^{\circ}\text{C-DHW}$ ) but at a higher frequency. Reefs in the higher latitudes persist despite frequent disturbances caused by temperature changes, which may imply that corals in these regions exhibit resilience towards such climatic extremes. This offers a window of opportunity for exploration as to how reefs in other lower latitudes might cope in the future in light of predicted increased warming.

### 2.1 | INTRODUCTION

Sea surface temperatures (SST) have witnessed an increase globally with records documenting a rise by  $0.7^{\circ}\text{C}$ ,  $0.4^{\circ}\text{C}$  and  $0.3^{\circ}\text{C}$  in the Indian, Atlantic and Pacific oceans respectively between 1950-2009

(Hoegh-Guldberg *et al.*, 2014). Temperature anomalies, which are predicted to increase with climate change, have been well documented to cause coral bleaching and increase coral mortality (Berkelmans & Oliver, 1999; Baker *et al.*, 2004; Hughes *et al.*, 2017a). This in turn impacts reef capacity to sustain their three dimensional framework through accretion and keep pace with sea level rise (Januchowski-Hartley *et al.*, 2017; Perry & Morgan, 2017). Despite reefs being faced with multiple stressors (e.g. changes in light, salinity and nutrient availability), all of which may contribute towards triggering bleaching (Coles & Jokiel, 1978; Lesser *et al.*, 1990; Kleypas *et al.*, 1999b; Baker *et al.*, 2008; Wooldridge, 2009), SST anomalies are seen as the most influential trigger (Pramanik, 2014; Hoegh-Guldberg *et al.*, 2017; Claar *et al.*, 2018). In environments such as the Arabian Gulf (AG), corals are subjected to dramatic swings in environmental conditions with temperatures 5-6°C higher than any other reef system (Coles & Riegl, 2013; Hume *et al.*, 2013). In the last two decades, reefs in this region have been exposed to severe temperature anomalies at a rapid and high recurring rate (Riegl, 2002, 2003; Sheppard & Loughland, 2002; Burt *et al.*, 2012) similar to those projected to occur globally by 2100 (IPCC, 2014).

Thermal limits of corals are known to vary by region with high latitude sub-tropical reefs (e.g. AG) existing in more stressful environmental conditions than those in tropical waters (Riegl, 2003). This variation results in different thermal thresholds which range from as low as 25°C (e.g. South-Eastern Pacific Ocean; Wellington *et al.*, 2001) to 36°C (e.g. AG; Kleypas *et al.*, 1999; Coles & Riegl, 2013). Despite this range an increase in temperature anomaly by just a 1-2°C is sufficient to cause global mass bleaching (Hoegh-Guldberg, 1999; Kleypas *et al.*, 1999b; Purkis & Riegl, 2005; Heron *et al.*, 2016; Hoegh-Guldberg *et al.*, 2017; Lough *et al.*, 2018).

Due to their geographically isolated nature, it is thought that corals in the AG have developed their thermal resistance over the period of the region's isolation (~6000 years – Holocene) during which reefs have been subjected to a warmer climate in comparison to corals from other regions (Purkis *et*

*al.*, 2010; Hume *et al.*, 2013). It is thus unsurprising that coral communities in the AG are seen to harbour the highest bleaching threshold globally (D'Angelo *et al.*, 2015). However, despite their high threshold, they are still susceptible to bleaching with reports of bleaching between 1997-2017 (Rezai *et al.*, 2004; Riegl *et al.*, 2011; Kavousi *et al.*, 2014; Shuail *et al.*, 2016). Reefs in the lower latitude tropics region such as the Central Indo-Pacific (CIP) have also been impacted by bleaching (Wouthuyzen *et al.*, 2018), however, interestingly, the rate and magnitude of bleaching severity is observed to be lower in comparison to other regions (Goreau *et al.*, 2000). Despite this, contrary to CIP, reefs in the Western Indian Ocean (WIO; also considered in a low latitude area), reefs have experienced severe bleaching events that has resulted in fatal mortality on many reefs (Goreau *et al.*, 2000; Smith *et al.*, 2008; Zinke *et al.*, 2014; Januchowski-Hartley *et al.*, 2017). Severe bleaching events are associated with the El Niño Southern Oscillation (ENSO) events, which occur due to an atmospheric shift in circulation caused by SST rising above normal in the central and eastern tropical Pacific Ocean.

To date, efforts have been made to describe the thermal patterns that induce coral stress and mortality in a global and/or regional context (Purkis & Riegl, 2005; Selig *et al.*, 2010; Hoegh-Guldberg *et al.*, 2014; Pramanik, 2014; Claar *et al.*, 2018). However, only a few have focused on describing the patterns in a more localized context (Riegl, 2003; Purkis & Riegl, 2005; Kavousi *et al.*, 2014), which is crucial for locating and identifying future reef refugia areas. Understanding how these reefs cope may present a clue as to the survival mechanism future reefs experiencing historic temperature fluctuations may adopt to persist in the face of climate change. Therefore, the aim of this chapter is to investigate the thermal history of SST of three selected site-specific reefs in Bahrain, the Seychelles and Indonesia located in three bioregions (AG, WIO and CIP respectively). This will be achieved through the following objectives:

- To assess the temporal change in SST over a 35-year period (1982 -2017) across the study sites and identify anomalies associated with documented global mass bleaching events.
- To assess the extent (duration) of degree heating weeks (DHW) across the study sites as a mode of investigating the severity of bleaching.

## **2.2 | METHODOLOGY**

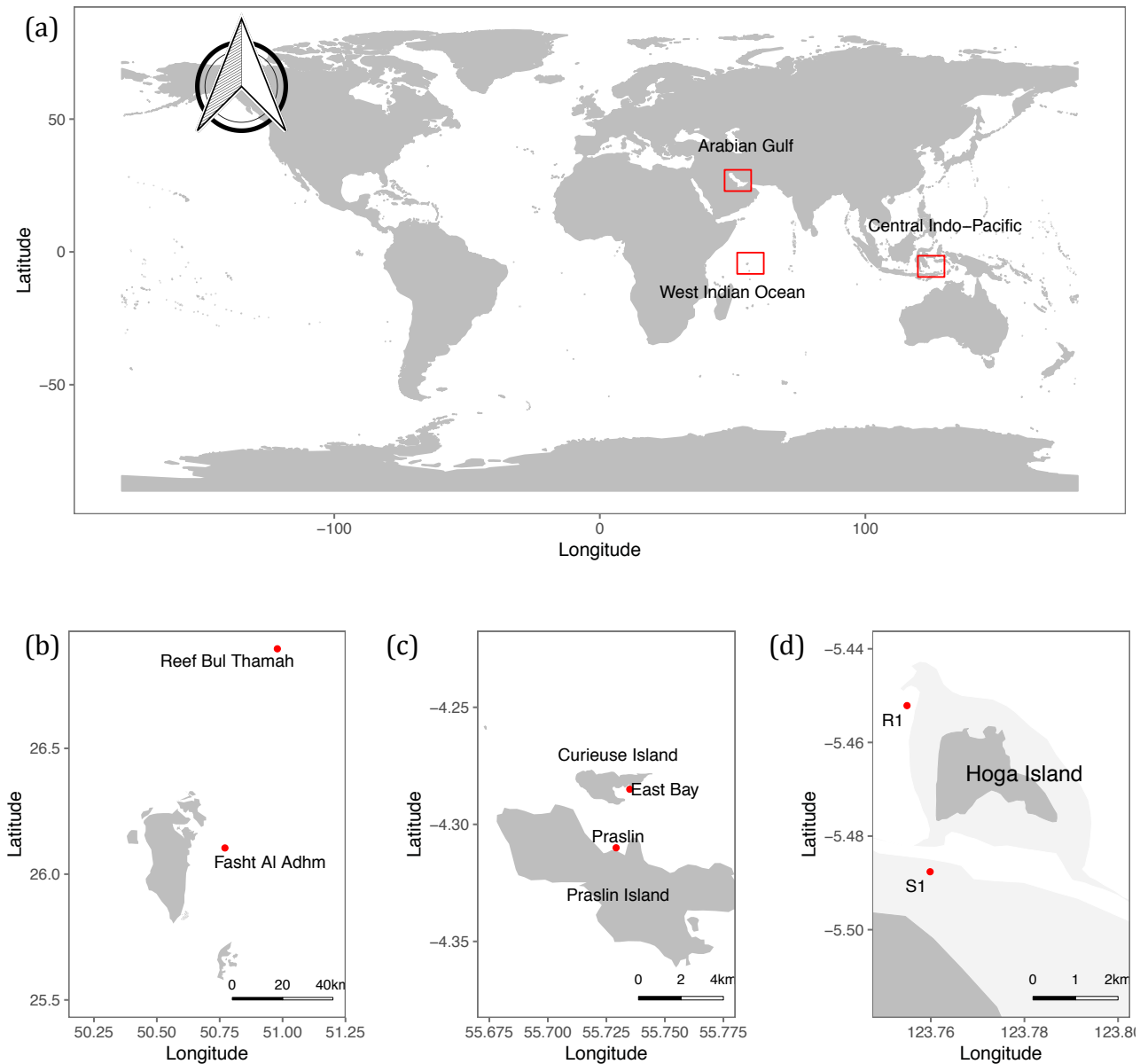
### **2.2.1 | Site description**

Three study locations (Figure 2.1) situated across three bioregions (AG, WIO and CIP), were targeted representing different latitudes (Table 2.1) using remote sensing tools over a period of 35 years (1982-2017). At each location, reefs from both turbid and clear-water (herein referred to as optimal) sites were chosen to represent different environmental characteristics (Table 2.2)

**Table 2.1. Coordinates of the localized sites in the three selected bioregions.**

Site	Site Code	Latitudinal Gradient*	Latitude	Longitude
<b>Bahrain (AG)</b>				
Fasht Al Adhm (Turbid)	BH-TB	High	26.104166	50.770828
Reef Bul Thamah (Optimal)	BH-OP		26.895834	50.97916
<b>Seychelles (WIO) - Curieuse Marine National Park</b>				
Praslin (Turbid)	SY-TB	Low	-4.3125	55.72916
East Bay (Optimal)	SY-OP		-4.270833	55.72916
<b>Indonesia (CIP) – Wakatobi Marine National Park, South East Sulawesi</b>				
Sampela (Turbid)	IN-TB	Low	-5.479167	123.729164
Ridge (Optimal)	IN-OP		-5.4375	123.770828

\* For the purpose of this study, study sites are assigned a latitudinal gradient category.



**Figure 2.1. Location of Study Sites – (a) Location of Bahrain (Arabian Gulf), the Seychelles (Western Indian Ocean) and Indonesia (Central Indo-Pacific); (b) Location of study sites within Bahrain; (c) Location of study sites within Curieuse Marine National Park, Seychelles; (d) Location of study sites within the Wakatobi Marine National Park, Indonesia. Dark grey areas indicate land whilst light grey indicates shallow reef areas.**

Table 2.2 Environmental characteristics of the selected study sites.

Site	Site Code	Depth (m)	Temp. (°C)	Salinity (ppt)	Sedimentation rates (g cm <sup>-2</sup> d <sup>-1</sup> )**	Light attenuation (K <sub>d</sub> PAR)***	Distance	Impacts
<b>Bahrain (AG)</b>								
<b>Fasht Al Adhm (Turbid)</b>	BH-TB	5-7	16-35	42-44	0.23±0.04	0.02	~11 km east of the main island.	Heavily impacted due to various anthropogenic activities mainly reclamation and dredging.
<b>Reef Bul Thamah (Optimal)*</b>	BH-OP	10-12			0.19±0.04	0.04	~80 km northeast of the main island.	Although located within a Marine Protected National Park (MPA), the site is subjected to illegal fishing and destructive fishing practices.
<b>Seychelles (WIO) - Curieuse National Park</b>								
<b>Praslin (Turbid)</b>	SY-TB	5-10	25-29	~35	0.03±0.01	0.2-0.4	~1.5 km southwest Curieuse Island	Site is subjected to large sediment load since it is located closer to Praline island, which has intensive tourist marine activities.
<b>East Bay (Optimal)*</b>	SY-OP	5-12			0.04±0.01	0.1-0.2	~1.5 km southeast Curieuse Island	One of the least impacted sites with minimum anthropogenic impacts. Carbonate fringing reefs with minimal tourist activity.
<b>Indonesia (CIP) – Wakatobi Marine National Park, South East Sulawesi</b>								
<b>Sampela (Turbid)</b>	IN-TB	3-10	26-30	32-34	6.3±2.7	0.01	~1.5 km southwest Hoga Island	Site is adjacent to the Bajo village of Sama Bahari and is subjected to large sediment load and various anthropogenic activities, thus heavily impacted.
<b>Ridge (Optimal)*</b>	IN-OP	5-20			2.6±1.0	0.02	~1 km northwest Hoga Island	One of the least impacted sites within the area with some artisanal line fishing occurring.

\* Optimal in this study is referred to as clear waters.

\*\* **Bahrain:** Due to time restrictions, sedimentation rates (g cm<sup>-2</sup> d<sup>-1</sup>) were measured at 10m depth using sediment traps (n=6). Traps were deployed for a period of three days at each of the study sites in May 2018; **Seychelles:** Sedimentation rates (g cm<sup>-2</sup> d<sup>-1</sup>) were measured at 10m depth using sediment traps, however, due to expedition time constraints the traps were only deployed for a total of 4 days in April 2018; **Indonesia:** Sedimentation rates (mg cm<sup>-2</sup> d<sup>-1</sup>) collected by Operation Wallacea between 2006-2011 (mean values are reported here along with ±SD and taken from Franco, 2014).

\*\*\* **Bahrain & Indonesia:** Light intensity was measured using hobo loggers deployed at two measurements 3 and 7m in Bahrain and 5 and 10m in Indonesia, then calibrated following the methods outlined in Long *et al.*, (2012) to calculate photosynthetically active radiation (PAR). **Seychelles:** Light attenuation coefficients (K<sub>d</sub> (PAR), m<sup>-1</sup>) for each site was obtained from Gardner *et al.*, (2018).

NB: Although the data collected from the hobologgers does not reflect a clear distinction between turbid and clear-water due to time restraints on the field, these sites were chosen and classified based on local knowledge acquired from local people and/or long term researchers who have worked in these sites for over 20 years e.g. Operation Wallacea & EarthWatch-Seychelles.

### 2.2.2 | Satellite Data Acquisition and Processing

To characterise the thermal history of the three selected bioregions, weekly SST data was acquired from the CoRTAD<sup>1</sup> version 6 database. Data was extracted and assessed for thermal history of SST during the period 1982-2017. Data was processed via the “University of Essex – School of Biological Sciences’ Genomic Cluster” due to large file datasets requiring high computational capacity. SST values derived from the CoRTAD database were converted from Kelvin (K) to Celsius (°C). Following the conversion, data was extracted for the specific sites through their coordinates and calculations were conducted to determine the change in SST metrics over time to examine the thermal history of the bioregions over the 35-year period.

### 2.2.3 | Definitions and Calculation Methods of Thermal History Metrics

**SST Trends:** Defined as the rate of change in SST over time.

**Climatology:** Defined as the long-term mean of SST conditions. Positive or negative values of SST that exceed long term mean SST (climatology) of a particular area, which indicates whether SST is warmer or cooler than usual (Heron *et al.*, 2016).

$$\text{Climatology} = \Sigma \text{ weekly SST over an extended period } / n \text{ (total no. of weeks)}$$

**SST Variability:** Seasonal variability in SST over time was calculated based on the difference between the maximum and minimum climatology.

$$\text{Seasonal Variability} = \text{Maximum Climatology} - \text{Minimum Climatology}$$

**Thermal Stress Anomaly (TSA):** Described as a positive SST anomaly above the maximum of the monthly mean SST climatology. TSA, also referred to as “Hotspots”, is calculated through

---

<sup>1</sup> **Coral Reef Temperature Anomaly Database (CoRTAD)** is a dataset of SST and related thermal stress metrics, which was developed by NOAA specifically for coral reef ecosystem applications. The CoRTAD Version 6 database used in this study contains global ~4km resolution SST data on a weekly time scale for the period 1982 – 2017. <<ftp://ftp.nodc.noaa.gov/pub/data.nodc/cortad/README.html>>



examining the difference between the weekly SST and maximum long term SST mean (climatology; Pineda *et al.*, 2013).

$$TSA = \text{Weekly SST} - \text{Maximum weekly Climatology}$$

**Degree Heating Weeks (DHW):** Defined as the accumulated thermal stress on corals whereby one DHW unit equals to when SST are 1°C above the expected mean summertime maximum for a period of one week (Wellington *et al.*, 2001; Heron *et al.*, 2016). Therefore, a DHW is calculated as the sum of accumulated daily hotspots over 12 consecutive weeks when the hotspot value (TSA) is  $\geq 1^\circ\text{C}$  (Couch *et al.*, 2017).

$$DHW = \sum TSA \geq 1^\circ\text{C for 12 consecutive weeks}$$

**Bleaching Threshold:** Described as the value where SST has exceeded maximum long-term mean by 1°C. It is calculated based on DHW combining magnitude and duration of temperature exceeding the long-term mean (climatology). DHW at  $\geq 4^\circ\text{C-weeks}$  is used as an indicator of thermal stress of bleaching level whilst  $\geq 8^\circ\text{C-weeks}$  is referred to as the threshold for thermal stress mortality-level (Liu *et al.*, 2006; Heron *et al.*, 2016; Couch *et al.*, 2017).

$$\text{Bleaching Threshold} = \text{Max. weekly Climatology} + 1^\circ\text{C}$$

#### 2.2.4 | Data analysis

Data was analysed using the “R” software (R, 2018) and “RStudio” version 1.1383 through which raster maps and plots were produced using the ggplot function in the “tidyverse” package in R (Wickham *et al.*, 2019). The R code written by Brisneve Edullates was used to calculate the thermal history metrics utilizing the equations outlined in Section 2.2.3, whilst the R package *THE* (see Supplementary Material - S1), was utilised to retrieve and curate for time series analysis and SST values for each study site. To determine significant differences in the thermal metrics across

bioregions, analysis of variance (ANOVA) was used. Through this test, each of the continuous dependent variables (i.e. mean, min and max SST; TSA values) was compared across the categorical independent variable, which are the bioregions (i.e. AG, WIO, and CIP). All observations were independent of each other. The data was tested for normality using histograms, which illustrated that in general, the data was normally distributed. In addition, Levene's test was conducted to test for homogeneity of variance, which showcased that the variance among groups (i.e. bioregions) was observed to be generally equal. A post hoc Tukey test was used to compare the means (i.e. mean, min and max SST; TSA values) between groups. Furthermore, a time series analysis was conducted to determine how SST changes over time in each of the bioregion. The time series was decomposed to examine the trend, seasonality, and random variation of SST. The time series data was further analysed using a linear regression to determine the direction and magnitude of the slope.

## 2.3 | RESULTS

### 2.3.1 | Spatial Trends in Regional Sea Surface Temperatures

Results from the CoRTAD dataset illustrate that, on a bioregional level, there is a difference across the three sites in the overall mean SST with the AG being 2°C higher than WIO and CIP (Figure 2.2 and Table 2.3). In addition, the variance in seasonal SST is greater in the AG when compared to the lower latitude sites, with the overall minimum SST recorded as 16.5°C for the AG, 23.3°C for WIO and 24.5°C for CIP whilst the overall maximum SST is recorded as 37.0°C for the AG, 32.2°C for WIO and 33.5 °C for CIP (Figure 2.2 and Table 2.3). Significant differences in maximum SST ( $F_{(2,5825.2)} = 1331.2, p < 0.05$ ) and minimum SST ( $F_{(2,28318)} = 1272.2, p < 0.05$ ) across sites was also noted across bioregions.

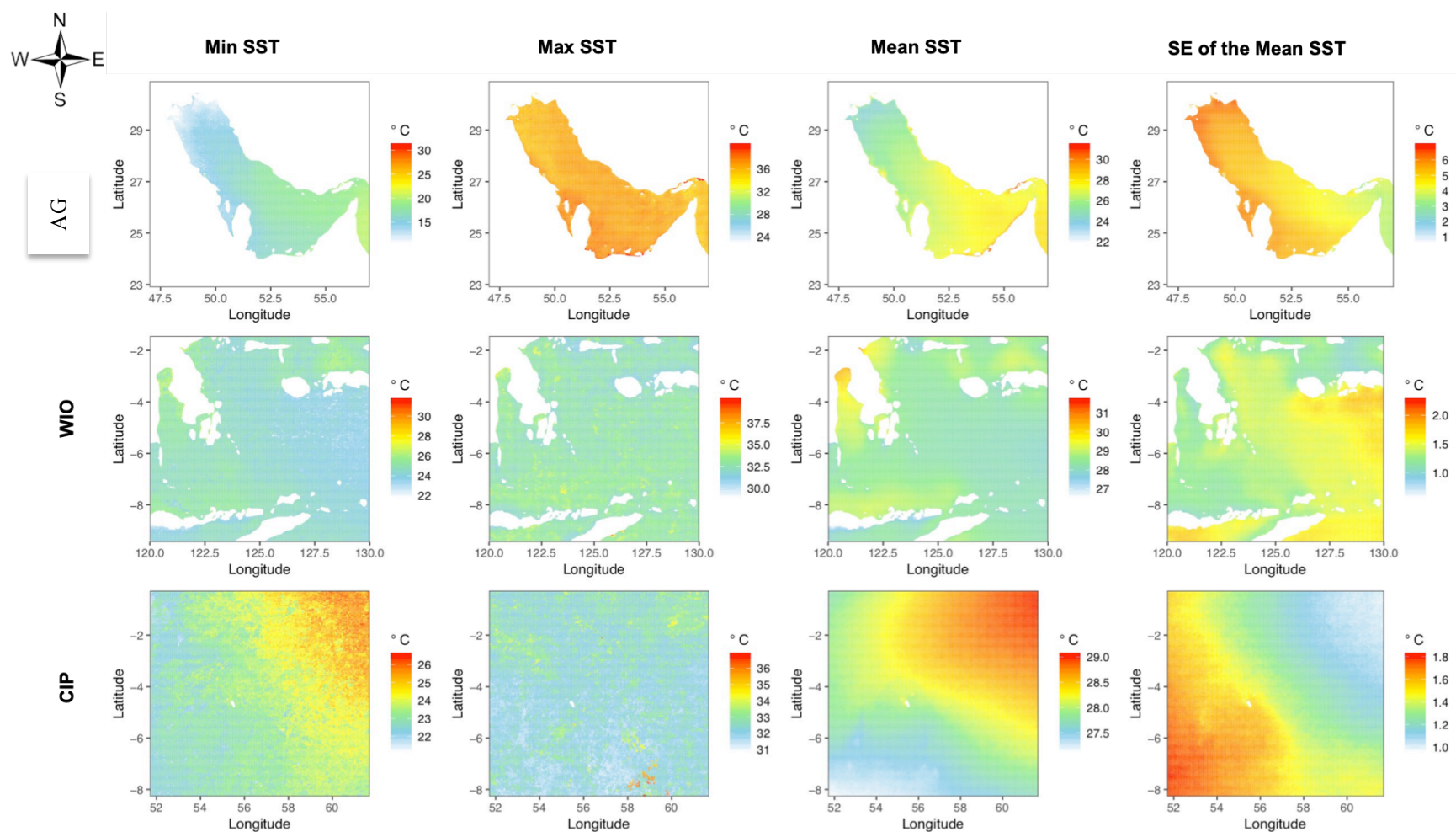
### 2.3.2 | Thermal History Metrics

Results of the localized sites showed that there were no differences observed in terms of all thermal metrics between optimal and turbid sites in both the Seychelles and Indonesia (Table 2.3) whereas, in Bahrain slight but not significant difference was observed between the two sites (Table 2.3). The turbid site in Bahrain had the highest bleaching threshold, maximum SST, climatology and DHW across all sites (Table 2.3). In addition, it is also the site with the lowest minimum climatology and with the highest variance in seasonality. Negligible differences were observed between Indonesian sites when compared to the Seychelles. In terms of the trends in weekly mean SST, remote sensing data showed a significant increase across sites over time across the three bioregions ( $F_{(2,2369)} = 115.4$ ,  $p < 0.05$ ; Figure 2.3). Sites in Bahrain had the highest rate of change (slope =  $1.6 \times 10^{-4}$ ,  $SE = 3.0 \times 10^{-5}$ ,  $p = 2.3 \times 10^{-7}$ ) followed by the Seychelles (slope:  $4.5 \times 10^{-5}$ ,  $SE = 8.7 \times 10^{-6}$ ,  $p = 2.0 \times 10^{-7}$ ) and Indonesia (slope:  $4.5 \times 10^{-5}$ ,  $SE = 7.6 \times 10^{-6}$ ,  $p = 4.7 \times 10^{-9}$ ; Figure 2.3). In addition, the Bahraini sites were observed to have more pronounced positive and negative temperature anomalies. Trends in TSA are in-line with the reported global mass bleaching events (e.g. 1998 and 2016), however, Bahrain had a delayed response whereby a severe bleaching event took place in 2017, following the 2016 elevated SST episode. The dataset shows a significant difference in TSA trends across sites ( $F_{(2,15493)} = 485.8$ ,  $p < 0.05$ ). TSA was highest in Bahrain ( $-6.9 \pm 0.1$ ) and lowest in the Seychelles ( $-10.4 \pm 0.1$ ; Figure 2.4). Trends in DHWs revealed that prior to the 1998 bleaching, all DHWs were constantly lower than  $4^\circ\text{C}$ -weeks across all bioregions (Figure 2.4). This remained the case in the Seychelles until 2016 where for the first time, DHWs was recorded to reach  $7^\circ\text{C}$ -weeks. However, for Bahrain, in the last 20 years, DHWs were recorded to reach  $\geq 8^\circ\text{C}$ -weeks, however, 1998 and 2017 were the only episodes whereby DHW reached  $\geq 15^\circ\text{C}$ -weeks, ironically these episodes are 20 years apart. In Indonesia, DHW remained  $\leq 8^\circ\text{C}$ -weeks for the last 35 years, though it is interesting to note that high DHW and TSA episodes are seen to be frequent and less intense than those in Bahrain, whereas in

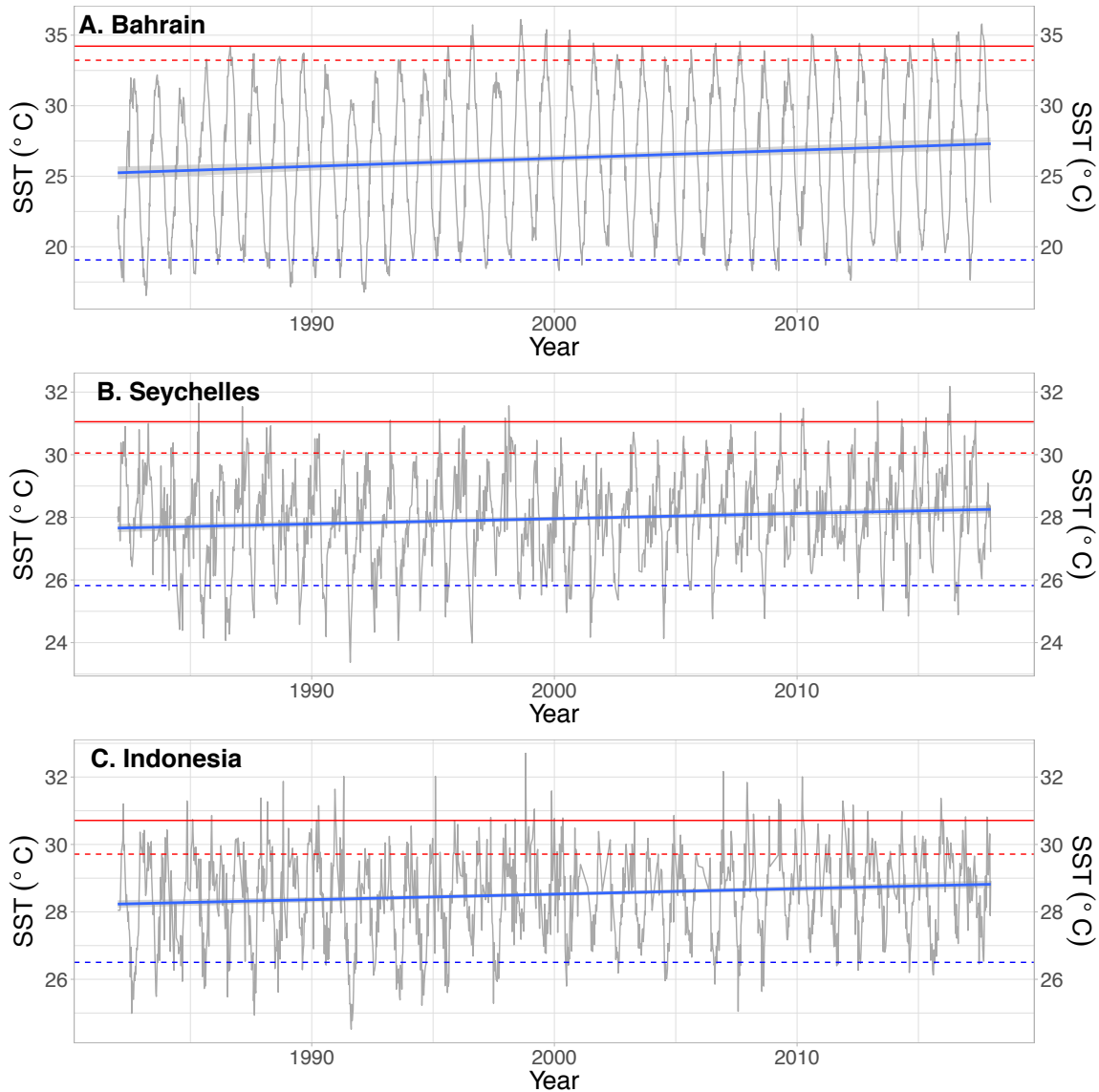
Bahrain the episodes are less frequent but higher in intensity (Figure 2.4). It can be concluded that thermal stress, measured by DHWs, that reach  $\geq 8^{\circ}\text{C}$ -weeks are more intense but less frequent in Bahrain whilst in Indonesia DHWs are more frequent but with lower intensity ( $< 4^{\circ}\text{C}$ -weeks).

**Table 2.3. Summary of thermal SST history metrics ( $^{\circ}\text{C}$ ) across the selected sites between 1982-2017 whereby annual mean refers to long-term mean over a 35-year period (n= 1878; \*unit= $^{\circ}\text{C}$ -weeks).**

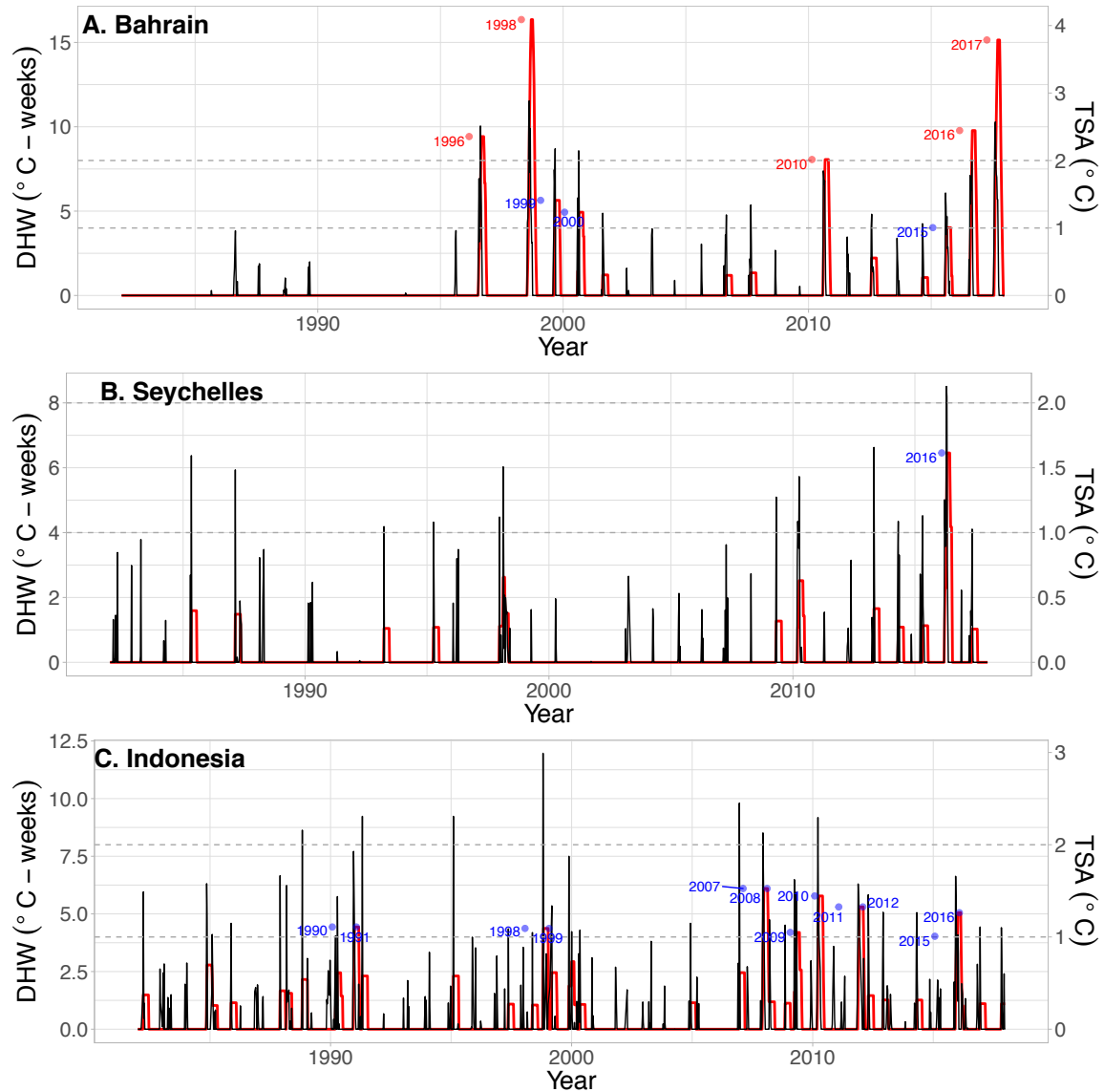
SST metrics ( $^{\circ}\text{C}$ )	BH-OP	BH-TB	SY-OP	SY-TB	IN-OP	IN-TB
Min. SST	16.5	15.5	23.4	23.3	24.5	24.6
Max. SST	36.2	37.0	32.2	31.9	32.7	33.5
Annual Mean	26.2 $\pm$ 0.1	26.0 $\pm$ 0.1	28.0 $\pm$ 0.1	28.0 $\pm$ 0.1	28.5 $\pm$ 0.1	28.4 $\pm$ 0.1
Min. Climatology	19.1	17.9	25.8	25.7	26.5	26.6
Max. Climatology	33.1	33.5	30.1	30.0	29.7	29.9
Seasonal Range	14.0	15.6	4.2	4.3	3.2	3.3
Bleaching Threshold	34.1	34.5	31.1	31.1	30.7	30.9
Max DHW*	18.2	20.8	6.5	5.6	6.1	14.7
Mean DHW*	4.8 $\pm$ 0.3	4.7 $\pm$ 0.3	1.7 $\pm$ 0.1	1.6 $\pm$ 0.1	2.2 $\pm$ 0.1	3.7 $\pm$ 0.2



**Figure 2.2. Spatial distribution of the overall minimum, maximum, mean and standard error (SE) of SST across the three selected bioregions for the period (1982-2017). Data derived from CoRTAD version 6, 4x4km resolution - available online.**



**Figure 2.3.** Trends in weekly SST mean for the period (1982-2017;  $n=1878$ ) illustrating the change in SST across the three selected study sites. The blue and red dotted lines indicate the minimum and maximum climatology, respectively, whilst the red solid line indicates the bleaching threshold. The blue solid line indicates the linear fit with standard error of the regression in dark grey shading. Data derived from CoRTAD version 6 database, 4x4km resolution - available online.



**Figure 2.4. Trends in Degree Heating Weeks (DHW; in red solid lines) across the three selected study sites for the period (1982-2017). DHW is defined as of accumulated daily hotspots over 12 consecutive weeks when the thermal stress anomaly (TSA; in black solid lines) is  $\geq 1^{\circ}\text{C}$ . The grey dotted lines indicate the DHW values of  $\geq 4^{\circ}\text{C}$  and  $< 8^{\circ}\text{C}$ -weeks, which corresponds to delineation between coral bleaching and mortality levels. Years that correspond to coral bleaching and mortality were highlighted in blue and red fonts, respectively. Data were derived from CoRTAD version 6 database, 4x4km resolution - available online.**

## 2.4 | DISCUSSION

Historically, as the hottest sea on the planet (Sheppard *et al.*, 2010; Riegl & Purkis, 2012; Burt, 2013), it is unsurprising that the AG was observed to have the highest maximum and lowest minimum mean SST in comparison to the other bioregions illustrating the ability of these reefs to exist in waters that are 5-6°C higher than other regions. In addition, due to their location in a higher latitude, reefs are expected to face harsher environmental conditions in comparison to low latitude tropical reefs (Beger *et al.*, 2014).

On a local scale, trends in Bahrain SST illustrated that the local sites were subjected to both positive and negative temperature anomalies. The negative anomalies are caused due to the extreme cold Shamal north winds that blow from the highlands of Iran into the low atmospheric pressure of the Arabian peninsula (Murty & El-Sabh, 1984; Riegl, 2003). Interestingly, the turbid site in Bahrain showed more pronounced thermal history metric conditions (e.g. higher max SST, bleaching threshold, DHW), which could be attributed to the shallow depth of the site (~ 5-6 m) making it warmer than the clear-water site, which is deeper (~10m; Wilkinson, 1998).

Furthermore, trends in SST showed significant increases overtime across sites in all three bioregions showcasing that high latitude reefs experience different temperature dynamics than those in lower-latitude tropical reefs with higher seasonal ranges and extreme temperatures. Similarly, trends in TSA were seen to be mostly in-line with the reported global mass bleaching events (e.g. 1998, 2002, 2016; Wilkinson, 2000; Berkelmans, 2002; Kavousi *et al.*, 2014; Hughes *et al.*, 2017; Perry & Morgan, 2017; Burt *et al.*, 2019) across all sites reflecting the different disturbance dynamics amongst reefs. This was also reflected in the results of the extent and duration of the DHWs and the impact this has had on coral mortality which has been reported in Bahrain (see Chapters 3 and 4) and the Seychelles (Januchowski-Hartley *et al.*, 2017). In regards to Indonesia, interestingly,



previous reports have stated that there was no evidence of bleaching in the area (in and around South-East Sulawesi) in 1998 (Wilkinson, 1998) and no reports were found in regards to the 2016 bleaching hence flagging this area as a possible refugia area for reefs. Despite some reports of bleaching in specific areas of Indonesia (e.g. Badi Island (Spermonde Islands) in 2010, DHW  $>8^{\circ}\text{C}$ -week (severe bleaching) and Mentawai Islands and Pagai Islands in 2016,  $>8^{\circ}\text{C}$ -week (mild to severe with bleaching cover: 37-89%) (Wouthuyzen *et al.*, 2018), interestingly, the rate and magnitude of bleaching severity is observed to be lower in comparison to other regions (Goreau *et al.*, 2000) which is also supported by the remote sensing data. DHWs that reach above  $4^{\circ}\text{C}$ -weeks are seen to be more intense in Bahrain however, Indonesia had more frequent DHW but with low intensity ( $<4^{\circ}\text{C}$ -weeks). Overall, it can be concluded that across the selected study sites high latitude reefs experienced high and intense temperature disturbances at a higher frequency in comparison to both the mid and low latitude tropical reefs of the Seychelles and Indonesia.

In light of the projected increase in global SST as a result of climate change, reefs in the future are expected to experience greater disturbances due to further warming and more frequent bleaching events lessening the time for reef recovery and regeneration (Sheppard & Loughland, 2002; Riegl, 2003; Sheppard, 2003). Therefore, higher latitude reefs such as in the AG offer a window of opportunity to study what reefs may face in the future and what the outcome might look like in tropical low latitude reefs. Previous studies have reported shifts in the diversity and abundance of coral symbionts (Symbiodiniaceae species – see Chapter 5 for more details) whereby diversity and richness is lower in higher latitude reefs in comparison to those in low latitude reefs (Chen *et al.*, 2019). This is in line with the pattern observed in terms of coral communities (genera and species diversity) where high latitude reefs, e.g. the AG, host low coral diversity ( $\sim 10\%$ ; Coles, 2003) when compared to low latitude reefs e.g. reefs in the coral triangle located in the Indo-Pacific host 92% of the world's reef building corals (Sanciangco *et al.*, 2013; Veron, 2000). Fluctuations in both climate

and sea level during the Plio-Pleistocene period could be attributed towards driving the phylogenesis and gene flow of these species thereby defining the diversity within these bioregions in relation to their thermal regime which is also influenced by their latitudinal position (Obura, 2016). Linking thermal regimes to shifts in coral symbionts communities, evidence suggests that shifts tend to occur in the composition of Symbiodiniaceae species from thermal sensitive species (e.g. common generalist *Cladocopium* also referred to as C3) to thermally tolerant types (e.g. *Durusdinium*) as a mechanism to adapt and acclimatise to long term exposure to elevated temperatures (Berkelmans & Van Oppen, 2006; Palumbi *et al.*, 2014; Wang *et al.*, 2019). In addition, previous studies have reported a dramatic shift in C3 prevalence depending on the reefs' latitudinal position whereby the usually common (on low latitude reefs) C3 was reported to be extremely rare or absent on high-latitude reefs (Lajeunesse *et al.*, 2004b).

Recent research has revealed that corals in the AG are associated with thermo-tolerant symbiont species based on the discovery of a new species (C3-Gulf) which was found to be the pre-dominant coral symbionts in the South of the AG and was named “*Cladocopium thermophilum*” which plays a role in their resilience (Riegl, 2003; Hume *et al.*, 2013; D'Angelo *et al.*, 2015; Hume *et al.*, 2015). This indicates that these corals have evolved with symbionts that may enable them to display resilience in these extreme conditions and thus to persist in a climate with frequent disturbances. In addition, representatives of the AG symbiont group have been detected adjacent to the AG within the Gulf of Oman providing a potential source of thermo-tolerant symbionts that may facilitate the adaptation of Indian Ocean coral holobionts to the predicted future warmer temperatures (D'Angelo *et al.*, 2015). Findings from the genetic study conducted for this thesis have detected the presence of C3-Gulf Symbiodiniaceae species in the Seychelles (WIO), which is a novel observation as no documentation or reports, has been found in regards to its presence at the time of writing this thesis. This suggests that perhaps as water temperatures continue to rise due to climate change, corals are

evolving towards hosting more specialized thermo-tolerant Symbiodiniaceae species. However, despite this exhibited resilience in the AG reefs, this comes at what might be described as a “trade off” where, resilience comes at a cost of a low ability of carbonate production resulting in low accretion rates and minimal reef framework structures (Riegl, 2003; Riegl & Purkis, 2012). In WIO, the recent bleaching events has highly impacted accretional health of reefs with their carbonate budgets tipping over from positive to negative budgets in reefs such as the Maldives (Perry & Morgan, 2017) and the Seychelles (Januchowski-Hartley *et al.*, 2017). To date, no long-term comparison of pre and post accretion rates have been reported for reefs in CIP and the AG. Future research must focus on understanding the degree or extent of the cost and benefit relationship of hosting specialised thermo-tolerant symbionts especially in the context of reef carbonate budgets. In order for reefs to cope with rising temperatures, it is crucial for corals to evolve through harbouring thermo-tolerant symbionts, however, for reefs to keep pace with sea level rise, this requires reefs to accrete at a rate that exceeds their erosive state. If one aspect hinders the other, how are reefs meant to cope? These are questions that reefs in the AG might offer insights into.

In conclusion, higher latitude reefs persist in areas faced with frequent disturbances caused by temperature changes, which may infer that corals in these regions exhibit resilience towards such climatic extremes. This offers a window of opportunity for exploration as to how reefs in lower latitudes might cope in the future of a changing climate.

This page was left intentionally blank

**CHAPTER THREE: STATUS & CHANGE IN CORAL COVER:  
HISTORY OF 35 YEARS THROUGH A SYSTEMATIC REVIEW  
OF THREE BIOREGIONS**

This page was left intentionally blank

### **3. STATUS & CHANGE IN CORAL COVER: HISTORY OF 35 YEARS THROUGH A SYSTEMATIC REVIEW OF THREE BIOREGIONS**

#### **ABSTRACT**

Coral reefs worldwide are experiencing continuous change due to amplified heat stress events that induce coral bleaching as a consequence of ocean warming. This impacts coral mortality and calcification rates which influences reef growth threatening reefs accretional health and structural integrity. This study aims to determine the current status of reefs (represented as percentage of live coral cover) and rate of change in coral cover over the past 35 years (1985-2020) in three bioregions: the Arabian Gulf (AG), Western Indian Ocean (WIO) and Central Indo-Pacific (CIP). In order to identify the temporal change of coral cover, a systematic review of the available literature on the topic was conducted using the ISI Web of Science and Google Scholar search engines in addition to other online databases. Results from the extracted data points illustrated non-linear fluctuations in the change of live coral cover over time with reefs experiencing an increasing trend at certain periods followed by declines across all bioregions. Overall recovery rates were estimated at 0.9, 1.2 and 2.0 % per year on reefs in the AG, the Seychelles (WIO) and Wakatobi, Indonesia (CIP) respectively. Disturbances that interrupted recovery rates on reefs in the AG and the Seychelles (WIO) were mainly attributed to bleaching events, while in the Wakatobi anthropogenic impacts were the main drivers of coral decline.

### 3.1 | INTRODUCTION

Coral reef ecosystems are in decline worldwide driven by global and local stressors such as rising ocean temperatures (Hughes *et al.*, 2017), ocean acidification (Anthony *et al.*, 2008), overfishing (Loh *et al.*, 2015), declining water quality associated with nutrient runoffs (Browne *et al.*, 2012) and excessive sedimentation (Nugues & Roberts, 2003). Coral mortality, reduced coral growth and reproduction rates are results of these stressors which combined result in overall reef degradation (Darling *et al.*, 2010). One of the most traditional methods to assess reef degradation and health is through measuring the change in live hermatypic (reef building) coral cover on reefs over time. Their ability to produce calcium carbonate ( $\text{CaCO}_3$ ) allows for coral reefs' geomorphic structure, thereby, providing structural complexity (Perry *et al.*, 2008). Therefore, hard corals are important reef builders and engineers (Zawada *et al.*, 2019) due to their calcification role as primary reef carbonate producers (Eakin, 1996; Edinger *et al.*, 2000) thereby influencing reef accretion rates. In addition, hermatypic corals are documented to have a significant influence on reef associated fish communities (Bell & Galzin, 1984).

In recent years, reef carbonate budget measures (the difference between carbonate production and erosion) have been used as a key metric in assessing coral reef health (Mace *et al.*, 2014; Perry & Morgan, 2017). Therefore, decline in coral cover ultimately implicates the 3-D framework of reefs through reduced accretion compromising structural integrity (Perry & Morgan, 2017) and the functionality of reef associated fish (Pratchett *et al.*, 2011). Many reefs worldwide are reported to have experienced shifts in coral and associated species community composition (Hoey *et al.*, 2016; Ryan *et al.*, 2019), as coral cover continues to decline worldwide (Wilkinson, 2000; Hughes *et al.*, 2003; Sheppard *et al.*, 2010; Burt *et al.*, 2013; Graham *et al.*, 2015; Perry & Morgan, 2017; Gouraguine *et al.*, 2019).



In order to track temporal and spatial change in accretional health of reefs, it is important to identify the current status and trajectories of reefs which could reveal the ability of reefs to recover from disturbances and the time frame required for recovery. This could provide insights as to reef resilience in the face of a warming ocean and increasing local pressures. Studies investigating the status and trajectories of reefs have increased, especially following global mass bleaching events (Smith *et al.*, 2008; Harris *et al.*, 2014; Januchowski-Hartley *et al.*, 2017; Perry & Morgan, 2017; Robinson *et al.*, 2019). Examining reefs that exist under naturally extreme (e.g. reefs in the Arabian Gulf), and marginal (e.g. turbid sites) conditions, which persist on the edge or outside the perceived thresholds of coral growth (Kleypas *et al.*, 1999), yet support corals that have acclimatized or adapted to these extreme conditions (Palumbi *et al.*, 2014), are important to aid predictions of future reef structure and function (Camp *et al.*, 2018). Understanding how reefs vary over a range of environmental conditions in different bioregions is key to understanding how coral reefs will adapt to changing environments worldwide. Therefore, this chapter presents a collective assessment of essential information on hard coral cover, their ability to recover and persist following major bleaching disturbances (e.g. 1998 and 2016). This is achieved by reviewing the current state of knowledge that exists on the status and change in coral cover over the past 35 years (1985-2020) in three different bioregions (the Arabian Gulf (AG), Western Indian Ocean (WIO) and Central Indo-Pacific (CIP)). This analysis will allow for the tracking of temporal change of primary carbonate producers in reefs inhabiting various environmental gradients in different geographic regions and latitudes of reef growth. Overall, this study aims to determine the current status of reefs (represented as percentage of live coral cover) through tracking change in coral cover over a 35 year period (1985-2020) in three bioregions: the Arabian Gulf (AG), Western Indian Ocean (WIO) and Central Indo-Pacific (CIP).

## 3.2 | METHODOLOGY

### 3.2.1 | Literature search and data extraction

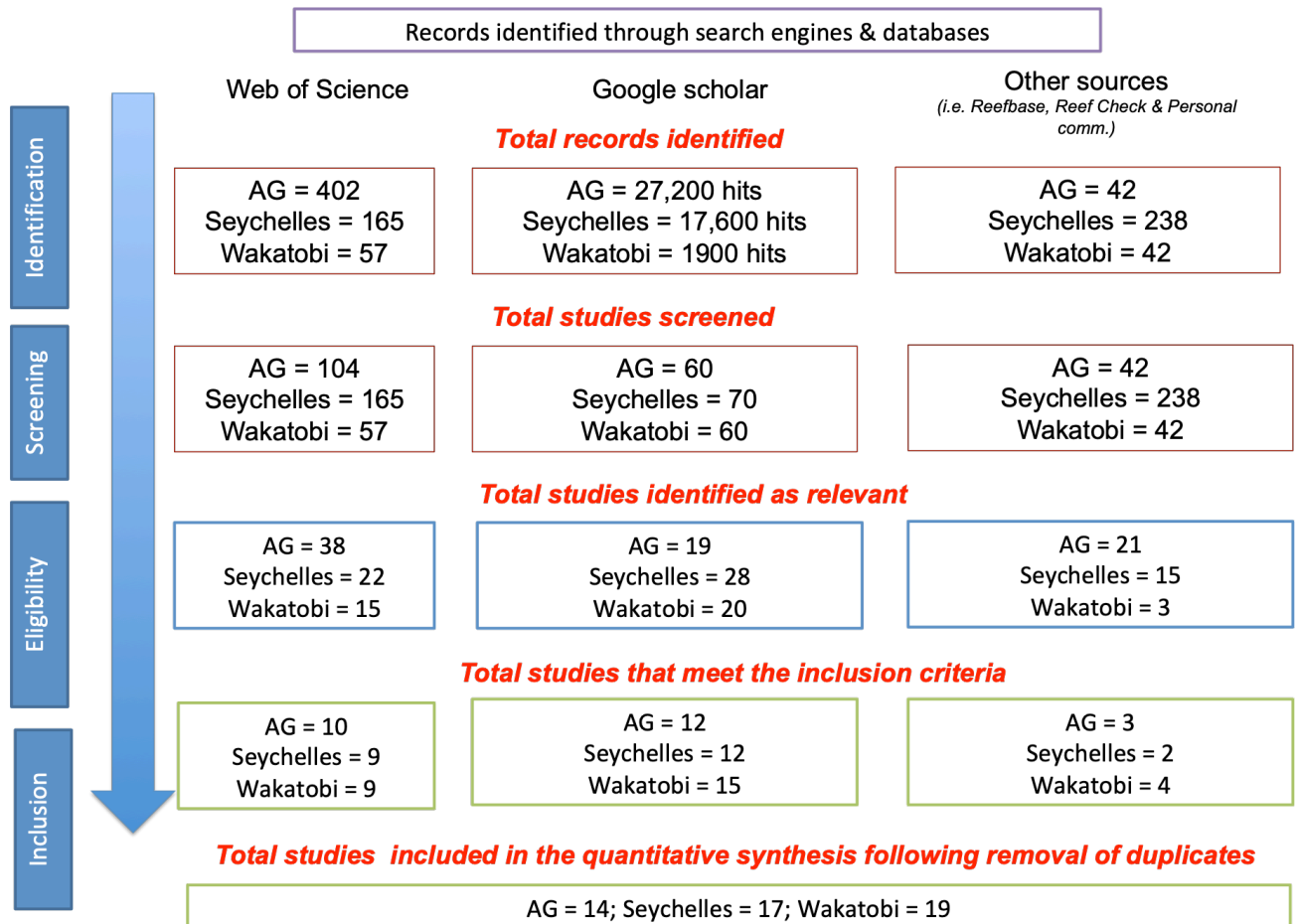
To identify primary literature associated with the reporting of coral cover on reefs in the selected bioregions, a systematic review of the available literature on the topic was conducted using the ISI Web of Science and Google Scholar search engines. The following search terms were therefore used: (coral\* OR reef\*) AND (coral\* OR cover\* OR health\* OR status) AND (Persian\* OR Arabian Gulf); (coral\* OR reef\*) AND (coral\* OR cover\* OR health\* OR status) AND (Seychelles); (coral\* OR reef\*) AND (coral\* OR cover\* OR health\* OR status) AND (Wakatobi). The systematic review literature search for each selected bioregion was conducted separately and was performed over the period between February and April 2020. Initially, the intention for this review was to target the specific selected local sites of interest in this thesis, this was possible with the Indonesian sites, however, due to the limited research done on the local sites in Bahrain and the Seychelles, a decision was made to focus efforts to track coral cover change on a country level. During the search, data revealed that although this was appropriate for the Seychelles, unfortunately, reefs in Bahrain remain understudied and available data was limited. Using the search terms: (coral\* OR reef\*) AND (coral\* OR cover\* OR health\* OR status) AND (Bahrain); in the Web of Science search yielded a total of only 9 hits of which only one hit was relevant to this study. Similarly, the same search terms were used in the Google Scholar engine, which yield a total of 690 hits of which 50 studies were examined and only 2 studies were relevant to this study. Therefore, a decision was made to conduct the search on a regional level in the AG.

In order to further access studies or reports that might not have been published in the primary literature, the online database of the International Coral Reef Symposium (ICRS) through Reefbase and Reef Check were both used. To determine relevance of a paper, abstracts were systematically

reviewed and evaluated, if the abstract was found relevant to the research question the full text was evaluated for the presence of the required data. If data was included in the paper, raw data were either extracted from the text if available or figures using WebPlot Digitizer (Rohatgi, 2019). In order for a publication or dataset to be included in the study, it had to provide: (1) the hard coral percentage cover (%) at a given site; (2) some measure of variance i.e. standard error (SE) or standard deviation (SD); (3) sample size; (4) year of data collection and (5) methods used for data collection. Methods were grouped in general based on the overall methodology i.e. studies that reported data collected via photo quadrats and underwater visual quadrats were assigned into the same group. Similarly, those that were collected via benthic transects, but did not specify whether it was through point intercept transect (PIT; measurements are made at specific points throughout the transect e.g. every 1m or 5m), or line intercept transect (LIP; measurements are taken at a higher resolution of 1 cm increments throughout the transect), were assigned to the LIP group (which for the purpose of this study, is considered any data collected via benthic transect). In general, if a published paper was relevant to the study but did not meet the inclusion criteria for this study (Figure 3.1), the authors were contacted and requested to share the missing information. If a response was received with the missing factors (e.g. sample size) thus enabling the dataset to meet the inclusion criteria, the data was used in this analysis, if not, then the paper was excluded. Due to the low number of studies that qualified for inclusion from the AG and the Seychelles, personal communications were made with regional researchers to identify datasets that were published and/or in the grey literature that could have not appeared through the database searches.

To avoid data duplication and pseudo-replication, data from papers with similar authors and/or co-authors were examined carefully. If relevant studies had similar authorships, the year of collection verses reef sites were used as a determiner of whether the dataset should be included. Furthermore,

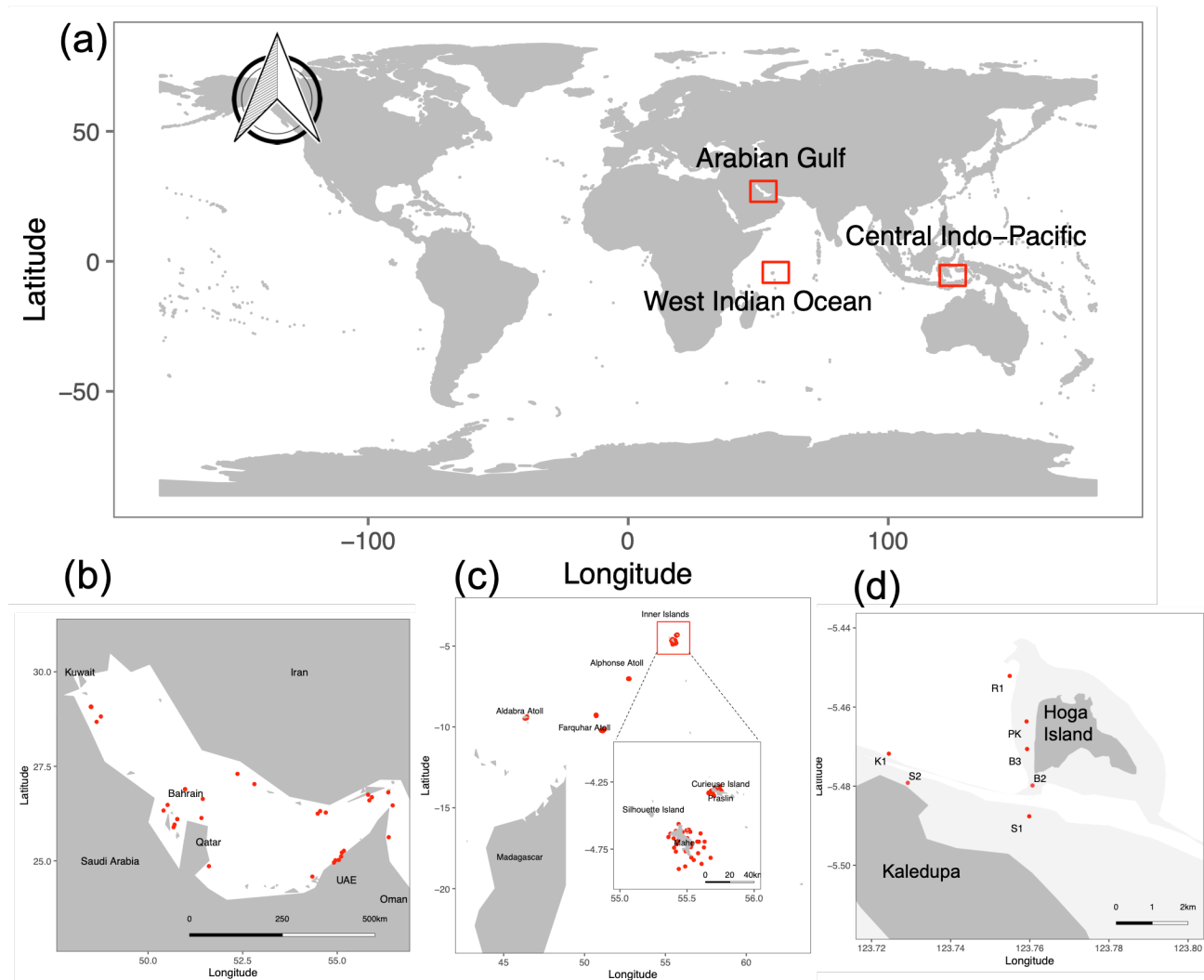
authors were contacted for confirmation and if no response was received, only one of the data points was included.



**Figure 3.1.** Flow diagram of PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-analysis) illustrating the steps taken starting from studies returned from the search for literature through the Web of Science, Google Scholar, ICRS Proceedings (Reefbase database), Reef Check and Personal communications. Inclusion criteria states that studies must include: (1) percentage cover (%) of hard coral at a given site; (2) some measure of variance i.e. standard error (SE) or standard deviation (SD); (3) sample size; (4) year of data collection and (5) methods used for data collection. Bioregions of interest: Arabian Gulf (AG); Seychelles, Western Indian Ocean (WIO); Wakatobi, Indonesia, Central Indo-Pacific (CIP).

### 3.2.2 | Study Sites

Overall, the data extracted and included in this study represent a total of 44 reef sites in the AG, 133 in the Seychelles (WIO) and 7 in the Wakatobi Marine National Park, Indonesia (CIP; hereafter referred to as Wakatobi) (Figure 3.2).



**Figure 3.2. Estimated location of reef sites (red points) represented through the data points extracted for this study: (a) Location of the selected bioregions; (b) Arabian Gulf; (c) Seychelles (Western Indian Ocean) and (d) Wakatobi, Indonesia (Central Indo-Pacific).**

### 3.2.3 | Data analysis

#### *Trends in coral cover over time within bioregions*

The R software (R Development Core Team, 2016) was used to conduct the data analysis. Initial plots were created using the ggplot function in the “tidyverse” R package (Wickham *et al.*, 2019) to estimate the mean percentage coral cover at each reef data point reported in the selected published literature across the three bioregions. Further plots exploring patterns in the variation of mean coral cover among studies on these reefs in relation to year of data collection, methodology, and sample size were created.

#### *Rate of change in coral cover over time within bioregions*

Temporal variation in coral cover was analysed in two stages for each of the following time periods: (a) 1993-2003, (b) 2003-2013, and (c) 2013-2018. These time periods were chosen to assess change in correspondence to major bleaching events identified in Chapter 2, e.g. the 1998 bleaching event occurred in the middle of the 1993-2003 allowing a 5 year observation period for reef change (i.e. recovery or decline). Firstly, coral cover was fitted against time (year collected) in a simple linear regression model to determine the rate of change in each time period ( $\text{lm}(\text{coral cover} \sim \text{year collected, data})$ ). Secondly, generalised linear mixed models (GLMM) were used, with the package lme4 (Bates *et al.*, 2015), to further examine the temporal variation in coral cover while taking into account the random effects of methodology used and the site of data collection. The mean estimates of coral cover were fitted against the year of collection in each of the three time periods to examine the temporal variation (fixed effect) whilst taking into account the random effects of site-specificity and methodology dependency, and were weighted by the sample sizes. This preferred model (GLMM 1) was compared against a model without the weights, and models with one random variable omitted from the equation (GLMM 2 – 4). This analysis was also used to infer the contribution of the random effects to the temporal variation of coral cover. The marginal  $R^2$  and

conditional  $R^2$  were also computed to examine how much variation was explained by the fixed and/or the random effects. The analysis of variance (ANOVA) was also used to compare this preferred model to the reduced model. The following outlines the structure of the GLMMs used for the analysis:

```
GLMM1 <- glmer(coral cover ~ year collected + (1|Methodology) + (1|Site), weights = sample size, data)
```

```
GLMM2 <- glmer(coral cover ~ year collected + (1|Methodology), weights = sample size, data)
```

```
GLMM3 <- glmer(coral cover ~ year collected + (1|Site), weights = sample size, data)
```

```
GLMM4 <- glmer(coral cover ~ year collected + (1|Methodology) + (1|Site), data)
```

Lastly, a likelihood ratio (LR) test was used to determine the significance of a single factor by comparing the fit for models with and without the factor. The Chi square statistic was used as a bases for determining the difference in the rate of change in coral cover between the full and reduced model. Akaike information criterion (AIC) was used to determine whether the preferred model would describe the relationship better than the reduced models.

### 3.3 | RESULTS

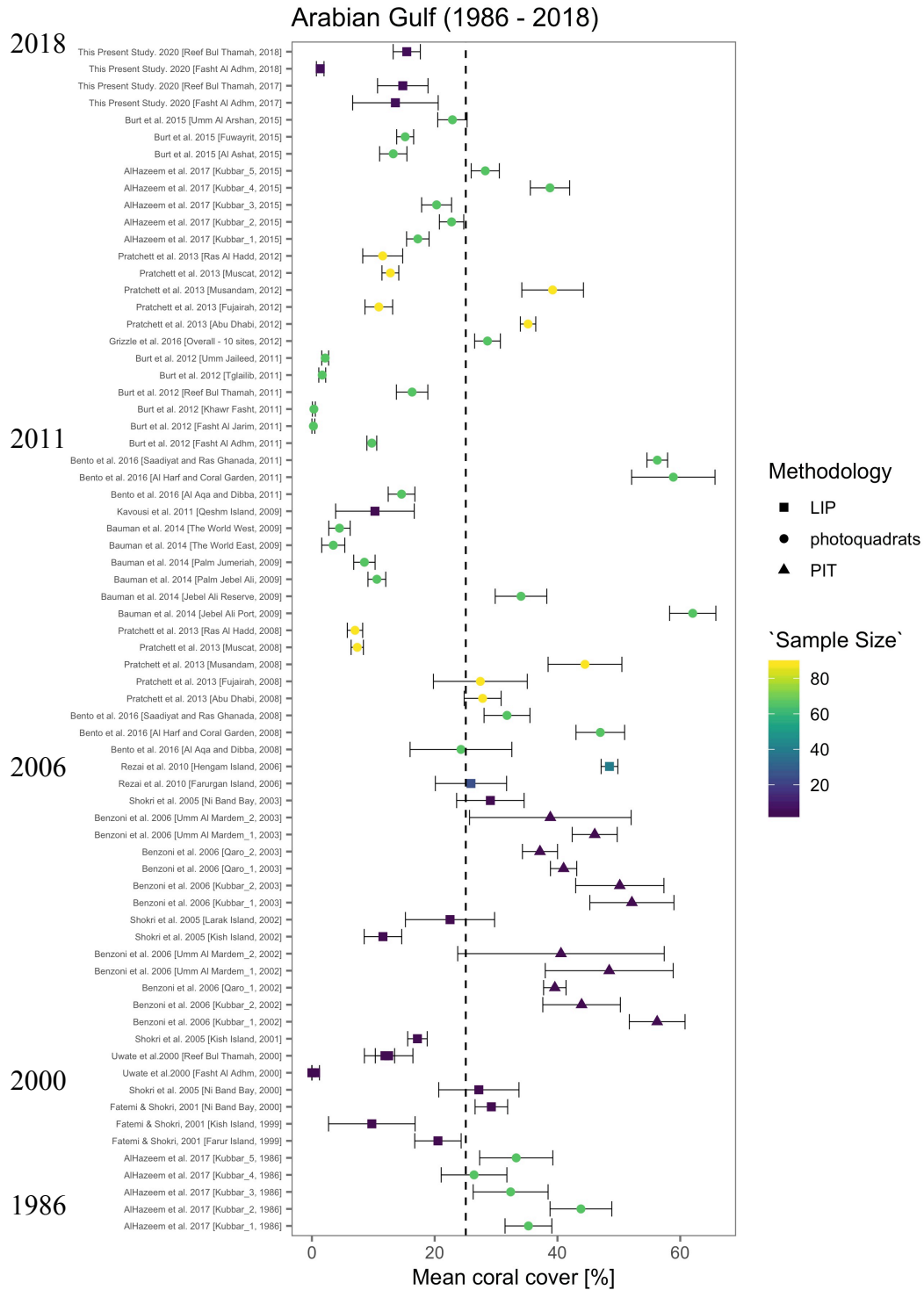
#### 3.3.1 | Trends in coral cover within bioregions

##### *Arabian Gulf*

Overall, estimates of mean coral cover varied across time in each of the three bioregions. In the AG, the extracted data have enabled the tracking of coral cover on reefs in this region over a 32-year period (1986-2018). The distribution of data points over time illustrates a non-linear change in the temporal trend of coral cover, which averaged at  $25.1 \pm 2.0\%$  between 1986-2018 regardless of methodology used for measurement by the studies (Figure 3.3). Data points reported in 1986 were collected via the use of quadrats following which a 12-year data gap is observed between 1987-1999



(Figure 3.3). Between 1999-2006, all data was collected using LIT/PIT following which photo quadrats were used over the next 10 years (2006-2015), with LIT/PIT used in the most recent years (2015-2018; Figure 3.3). Results (Figure 3.3) showcase coral cover on reefs in 1986 to be above average (i.e. >25%) with reports of reefs in Kuwait to range between  $26.4 \pm 5.4\%$  and  $43.8 \pm 5.0\%$ . Between 1999-2001, coral cover is observed to be on the lower spectrum (below and/or average) with reports ranging between  $0 \pm 0\%$  in Bahrain and  $29.2 \pm 2.7\%$  in Iran (Figure 3.3). In 2002-2008, the majority of the reefs are observed to shift towards higher (above average, i.e. >25%) coral cover reaching  $56.2 \pm 4.5\%$  in Kuwait (2002),  $48.5 \pm 1.4\%$  in Iran (2010),  $47.0 \pm 4.0\%$  in Oman (2008) and  $44.5 \pm 6.0\%$  in United Arab Emirates (UAE; 2008; Figure 3.3). Following those six years of positive shifts, the next three years (2009-2012) find the majority of reefs beginning to fall into the lower spectrum (below average, i.e. <25%) with reports of coral cover estimated between  $0.2 \pm 0.2\%$  and  $16.3 \pm 2.6\%$  in Bahrain (2011) whilst reefs in Iran reported  $10.3 \pm 6.4\%$  (2009; Figure 3.3). Nevertheless, during this period, some reefs (mainly in the South of AG) remained stable and maintained their high coral cover such as some reefs in the UAE ( $62.0 \pm 3.8\%$ ; 2009) and Oman ( $58.9 \pm 6.8\%$ ; 2011; Figure 3.3). This pattern of coral cover dipping into the lower spectrum on the majority of reefs is observed to continue throughout 2013-2018. During this period, the majority of coral cover on reefs is observed to be below average (<25%) such as reefs in Bahrain ( $1.4 \pm 0.6\%$ ; 2018) and Qatar ( $22.9 \pm 2.4\%$ ; 2015) whilst reefs in Kuwait maintained their position in the higher spectrum ( $38.8 \pm 3.2\%$  and  $28.2 \pm 2.3\%$ ; 2015; Figure 3.3).



**Figure 3.3. Mean live coral cover ( $\pm$ SE) of reefs reported for the period 1986-2018 in each identified study in the Arabian Gulf. Dotted line represents overall regional mean percentage cover. Methodology codes: LIP = Line intercept point transect; PIT = Point intercept transect. The full list of papers used in this study is available in Supplementary Material (S2).**

### *Seychelles*

The overall live coral cover in the Seychelles averages at  $14.4 \pm 0.8\%$  based on the data points extracted for the period 1994-2018. The distribution of the data points reveal an interesting trend regarding coral cover which indicates that the majority of reefs in this region have predominantly hosted low coral cover (i.e. below average  $<14\%$ ) over the course of this 24 year period (Figure 3.4). Coral cover in the Seychelles is observed to be above average (i.e.  $>14\%$ ) prior to 1998 following which a decline is noted which puts coral cover on reefs in the lower spectrum (i.e.  $<14\%$ ) for almost a decade (Figure 3.4). Between 2009-2016, a shift is noted with coral cover on many reefs exceeding the overall mean ( $14.4 \pm 0.8\%$ ) illustrating a rise in coral cover which is terminated in 2016, resulting in coral cover to decline again between 2016 and 2018 (Figure 3.4). The majority of the data extracted from studies are observed to be measured through LIT/PIT with only a few data points collected using random points (i.e. random quadrats placed on a reef; Figure 3.4).

In 1994, the reefs in the inner Seychelles (e.g. Mahe, Praslin and Cousine Island) were reported to have coral cover ranging between  $19.2 \pm 0.7\%$  and  $38.6 \pm 9.2\%$  across coral, granitic and rocky habitats. In 1998, the reefs in the outer Seychelles (e.g. Aldabra Atoll) were reported to host high coral cover ( $59.1 \pm 9.6\%$ ), however, this was documented to decrease a year later ( $15.8 \pm 3.6\%$ ; Figure 3.4). Similarly, reefs in the Southern Seychelles (e.g. Alphonse Atoll) also witnessed a decrease from coral cover that ranges between  $17.7 \pm 3.0\%$  and  $26.6 \pm 5.7\%$  in 1998 to  $10.3 \pm 0.3\%$  in 1999 (Figure 3.4).

Over the next five years (2001-2005), reefs in the inner Seychelles were seen to continue declining with coral cover ranging between  $0.9 \pm 0.3\%$  and  $31.3 \pm 5.1\%$  in Mahe,  $0 \pm 0\%$  and  $15.0 \pm 3.3\%$  in Praslin,  $0.5 \pm 0.1\%$  and  $1.8 \pm 0.7\%$  in Cousine Island (Figure 3.4). Both the outer (Aldabra Atoll) and southern reefs (Alphonse Atoll) were observed to maintain their coral cover ranges in this time period ( $0.3 \pm 0.8\%$  and  $15.3 \pm 3.5\%$ ;  $17.5 \pm 1.4\%$  and  $22.6 \pm 1.4\%$  respectively; Figure 3.4). Coral

cover remained low ( $3.3 \pm 1.8\%$ ) in the following five year period (2005-2010) for reefs in the outer Seychelles (Aldabra Atoll) while coral cover on reefs in the inner Seychelles varied widely with some harbouring higher than average coral cover ( $>14\%$ ) whilst others had low cover (Figure 3.4). For example, coral cover on reefs around Mahe ranged between  $0 \pm 0\%$  and  $45.7 \pm 5.2\%$ , similarly coral cover in Praslin ranged between  $0.1 \pm 0.4\%$  and  $30.0 \pm 2.0\%$  whilst reefs around Cousine Island had the lowest coral cover in the region ( $1.0 \pm 0.4\%$  and  $5.5 \pm 0.7\%$ ; Figure 2.4). The southern reefs such as Alphonse Atoll ( $21.2 \pm 1.7\%$ ) and Farquhar Atoll (range =  $3.4 \pm 0.9\%$  and  $33.0 \pm 6.3\%$ ) are seen to have maintained their coral cover.

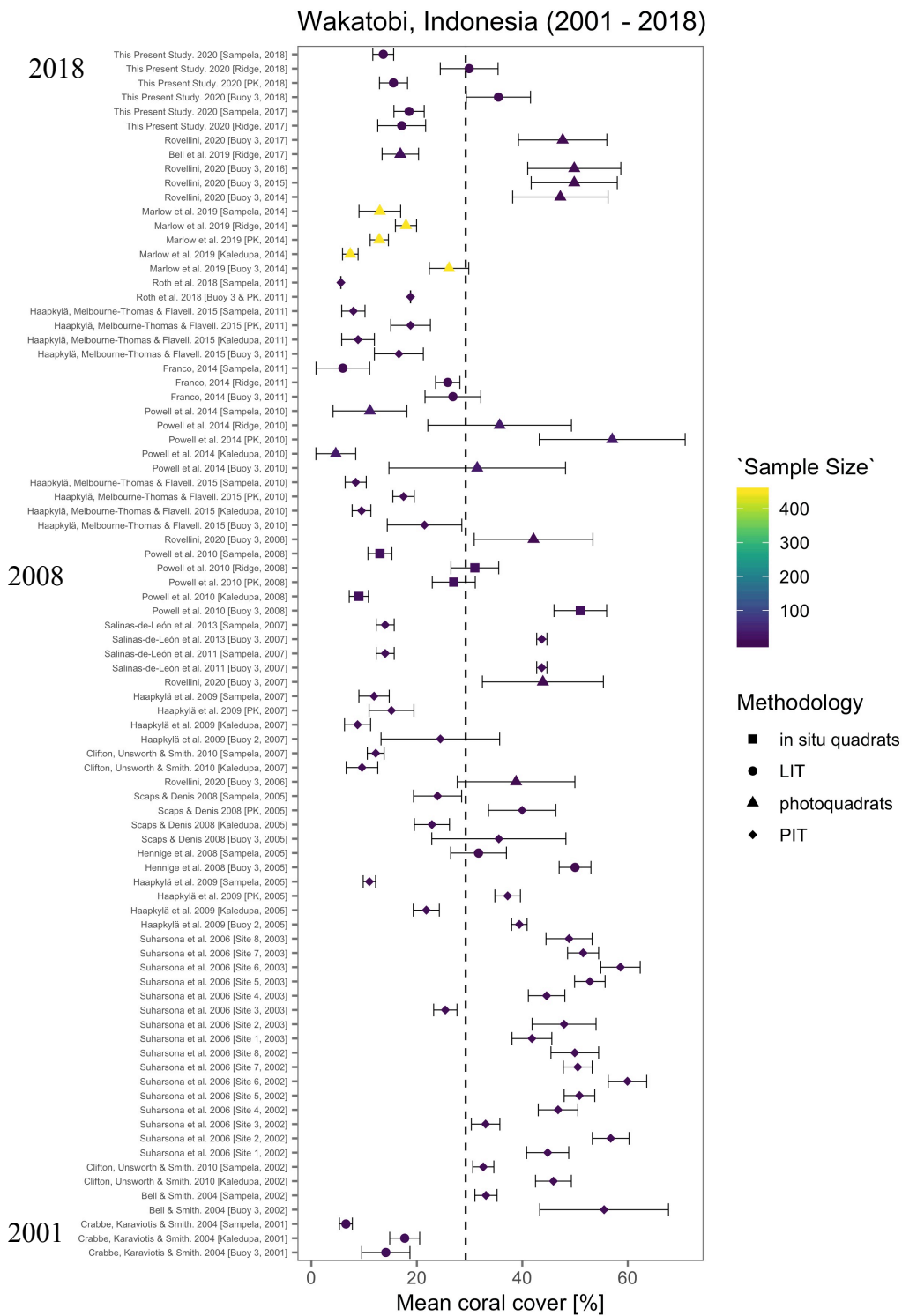
In the eight years between 2010 and 2018, no data points were found during the study search for reefs in both the outer and southern Seychelles whilst reefs in the inner Seychelles continued to harbour reefs with a large variation in coral cover some of which had higher than average coral cover ( $>14\%$ ) whilst others had low cover (Figure 2.4). This includes reefs around Mahe ( $3.0 \pm 1.6\%$  and  $38.3 \pm 7.1\%$ ), Praslin ( $0.1 \pm 0.1\%$  and  $42.0 \pm 7.0\%$ ) and Cousine Island ( $0.3 \pm 0.3\%$  and  $11.1 \pm 2.8\%$ ; Figure 2.4).



**Figure 3.4. Mean coral cover ( $\pm$ SE) of reefs reported for the period 1994-2018 in each identified study in the Seychelles. Dotted line represents overall regional mean percentage cover. Methodology codes: LIP = Line intercept point transect; PIT = Point intercept transect. The full list of papers used in this study is available in Supplementary Material (S2).**

***Wakatobi, Indonesia***

In the Wakatobi, distribution of the extracted data points over time illustrates that between 2001-2018 coral cover on reefs in this region averaged at  $29.3 \pm 1.8\%$  regardless of the method used for measurement by the studies (Figure 3.5). In 2001, coral cover was reported to range between  $6.6 \pm 1.2\%$  and  $17.7 \pm 2.8\%$ , these measurements were obtained through utilising LIT and PIT methods (Figure 3.5). No records of data prior to 2001 was found through all the search routes used in this study, thus, making this year the starting point for these reefs. Between the period 2002-2006, the Wakatobi was observed to maintain high coral cover (highest =  $59.9 \pm 3.7\%$ ) in relation to the average mean ( $29.3 \pm 1.8\%$ ) measured across extracted data points (Figure 3.5). Beginning 2006-2007, the majority of the data points illustrate low values of coral cover ( $<29\%$ ) with the lowest coral cover reported at  $4.6 \pm 3.8\%$  (Site Kaledupa, 2010; Figure 3.5). This trend of low cover is noted profoundly between 2010 and 2014 (Figure 3.5). However, high variation in coral cover is observed to return between 2014-2017 revealing that coral cover on reefs in the Wakatobi maintain the range between  $7.4 \pm 1.5\%$  and  $49.9 \pm 8.2\%$ , which is similar to the range reported a decade ago (Figure 3.5). In terms of methodology used to measure coral cover reported in the studies, LIT and PIT were used to collect data points reported on reefs for 2001- 2007 whereas, 2007 onwards a mixture between photo quadrats and LIT/PIT methods were used. Data reported for the period 2014-2017 was collected via photoquadrats whilst data collected for the period 2017-2018 using LIT revealed the final range of coral cover at this moment in time to be between  $13.6 \pm 2.0\%$  and  $35.5 \pm 6.1\%$  (Figure 3.5).



**Figure 3.5. Mean coral cover ( $\pm$ SE) of reefs reported for the period 2001-2018 in each identified study in the Wakatobi Marine National Park, Indonesia. Dotted line represents overall regional mean percentage cover. Methodology codes: LIP = Line intercept point transect; PIT = Point intercept transect. The full list of papers used in this study is available in Supplementary Material (S2).**

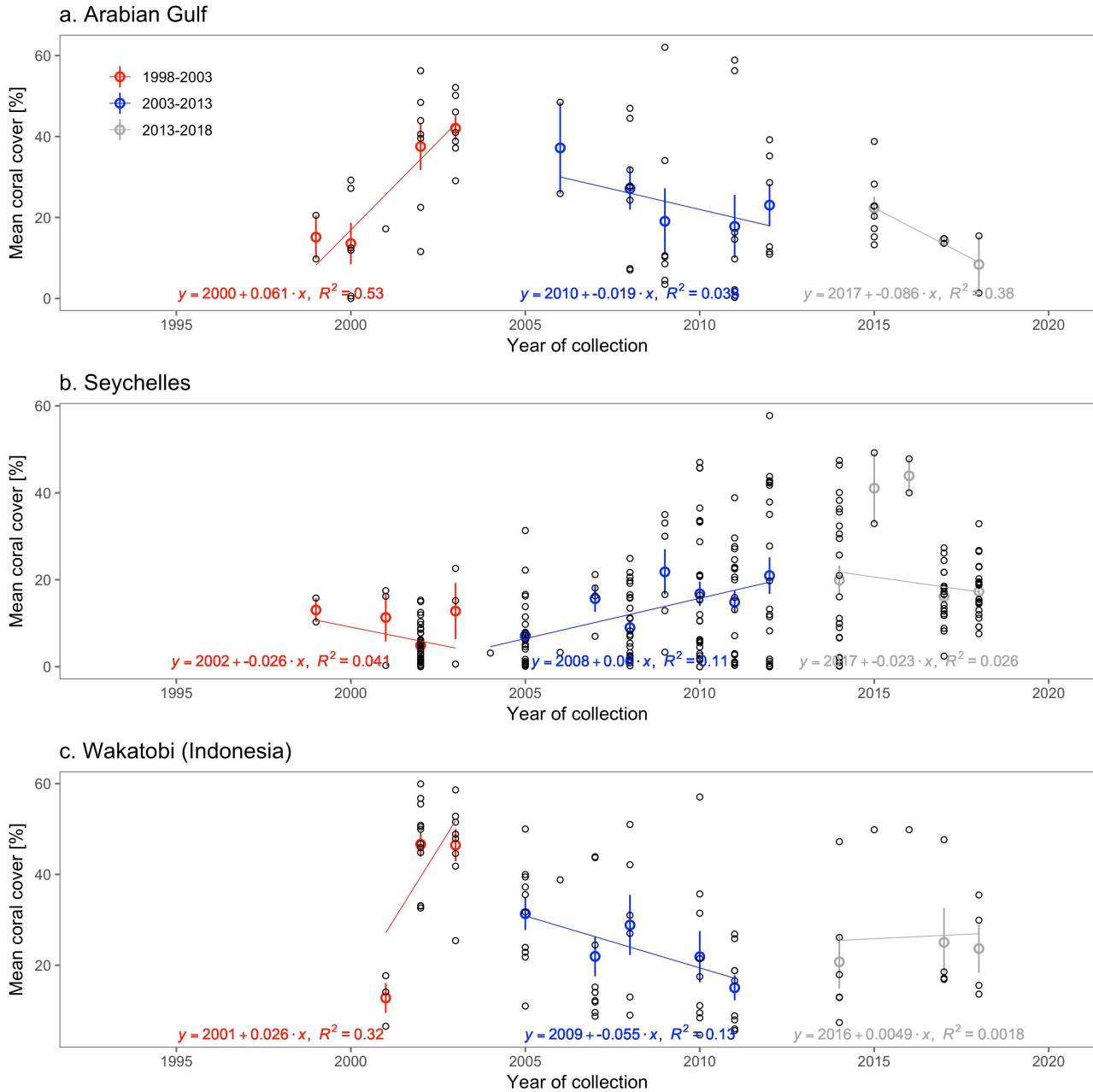
### 3.3.2. Rate of change in coral cover within bioregions

Despite the inconsistency encountered in terms of the reporting of mean coral cover on site specific reefs in the three bioregions, extracted data points allow a detection of the trends in coral cover over time. Through calculating the mean for each individual data point reported per year regardless of site, an increasing trend can be detected in coral cover on the AG reefs between 1998-2003 indicating slow recovery (Figure 3.6). However, the GLMM does not reflect this as it indicates a change of -0.6% per year during this period. The fixed effect of 'year' in the GLMM indicates a negligible percentage of the variation, however taking into account the random effect of methodology, sites and sample size used to measure coral cover, it suggests that the majority (94.4%) of variation in coral cover and trend is dependent on sites ( $x^2 = 20.7$ ,  $p < 0.01$ ), methodology ( $x^2 = 9.3$ ,  $p < 0.01$ ), and sample size ( $x^2 = 0$ ,  $p < 0.01$ ). Between 2003-2013, the decline continued in coral cover at a decreased rate of 0.3% per year (Figure 3.6). Only 4.3% of the coral cover variation was explained by the GLMM fixed model whilst the random effect model indicated that the trend is dependent on the site ( $x^2 = 7.3$ ,  $p < 0.01$ ) and sample size ( $x^2 = 0.8$ ,  $p < 0.01$ ) but not the methodology. The following five-years (2013-2018) witnessed an increase in the decline of coral cover by a rate of 4.7% per year on reefs across the AG (Figure 3.6) with the GLMM fixed effect explaining only 15% of the coral cover variation whilst the random model offered 40.9% suggesting that the trend is site dependent rather than methodology or sample size dependent.

In the Seychelles, reefs witnessed a decrease at a rate of 0.6% per year between 1998-2003 with GLMM indicating that sample size ( $x^2 = 29.1$ ,  $p < 0.01$ ) has an effect on coral cover variation (Figure 3.6). Through the following ten-year period (2003-2013), these reefs witnessed an increase in coral cover by 1.2% per year; with GLMMs indicating that the variation of coral cover is affected by sample size ( $x^2 = 64.1$ ,  $p < 0.01$ ; Figure 3.6). However this increasing trend began to decline by 1.0% throughout 2013-2018 with the GLMM suggesting that sample size ( $x^2 = 0.9$ ,  $p < 0.01$ ) has an effect



on coral cover variation (Figure 3.6). Reefs in the Wakatobi were observed to have an decreasing trend at a rate of 2.3% per year between 1998-2003 with GLMM indicating that sites ( $x^2 = 15.0$ ,  $p < 0.01$ ), methodology ( $x^2 = 20.9$ ,  $p < 0.01$ ) and sample size ( $x^2 = 0.4$ ,  $p < 0.01$ ) all have an effect on the variation in coral cover (Figure 3.6). Following which a further decline in coral cover was encountered at a rate of 2.6% throughout the period 2003-2013 with both site ( $x^2 = 31.7$ ,  $p < 0.01$ ) and sample size ( $x^2 = 3.9$ ,  $p < 0.01$ ) causing coral cover variation based on the GLMM (Figure 3.6). However, reefs illustrated an increase in their coral cover by a rate of 1.9% per year in the five years between 2013-2018 with the GLMM indicating that the only factor contributing to the variation in coral cover is site ( $x^2 = 18.0$ ,  $p < 0.01$ ).



**Figure 3.6. Rate of change in mean coral cover of reefs over three time periods (i.e. 1998-2003; 2003-2013; 2013-2018) in the three bioregions: (a) Arabian Gulf; (b) Seychelles; (c) Wakatobi Marine National Park, Indonesia. Black circles represent individual data points while coloured circles (red, blue and grey) represent mean of coral cover (%±SE) per year; lines indicate trends based on the simple linear regression.**

### 3.3.3. Change in coral cover within reef-specific sites

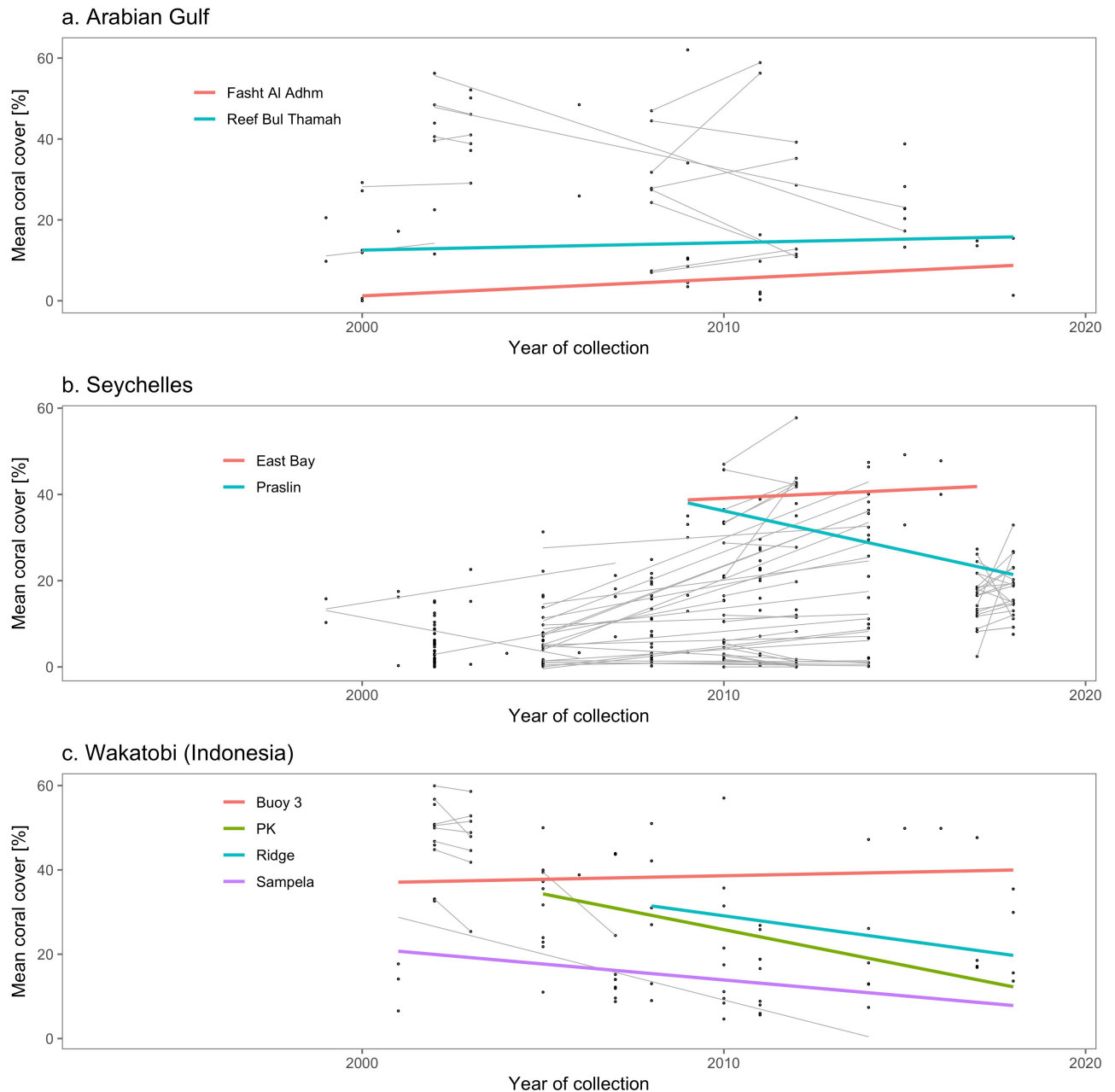
Despite the gaps between the data points available on reef specific sites, enough data was obtained to enable the tracking of coral cover change over time. Data revealed that in the AG some reefs experienced an increase in coral cover over time whilst others suffered a decrease (Figure 3.7). Both site specific reefs of interest in Bahrain showed opposite trends with Fasht Al Adhm (turbid reef) experiencing an increase in coral cover from  $0 \pm 0\%$  reported in 2000 to  $9.8 \pm 0.8\%$  in 2011 to a further  $13.6 \pm 7.0\%$  in 2017; however, this reef witnessed a drastic decline in 2018 with coral cover averaging at  $1.4 \pm 0.6\%$  (Figure 3.7). On the other hand, Reef Bul Thamah (clear water reef), experienced a continuous increase from  $12.5 \pm 4.0\%$  in 2000 to  $16.3 \pm 2.6\%$  in 2011 with a 0.8% decrease in 2018 ( $15.5 \pm 2.2\%$ ; Figure 3.7).

The majority of the reefs in the Seychelles appear to have an increasing trend on reef specific sites however, both of the interest sites around Curieuse Island are observed to experience the opposite with a decline in coral cover over time (Figure 3.7). In 2009, the East Bay reef (clear water) was reported to have  $34.9 \pm 5.1\%$  coral cover which increased to  $49.2 \pm 9.0\%$  by 2015, followed by a drastic decrease by 44.5% in 2017 ( $27.3 \pm 5.7\%$ ) and a further -43.3% by 2018 ( $15.5 \pm 1.6\%$ ; Figure 3.7). Similarly, coral cover on the Praslin (known locally as PS2; turbid) reef was documented as  $29.0 \pm 1.8\%$  in 2009 increasing to  $40.0 \pm 6.9\%$  in 2016, however, this rise drastically declined to  $18.2 \pm 7.5\%$  in 2017 and further to  $7.6 \pm 2.2\%$  by 2018 (Figure 3.7).

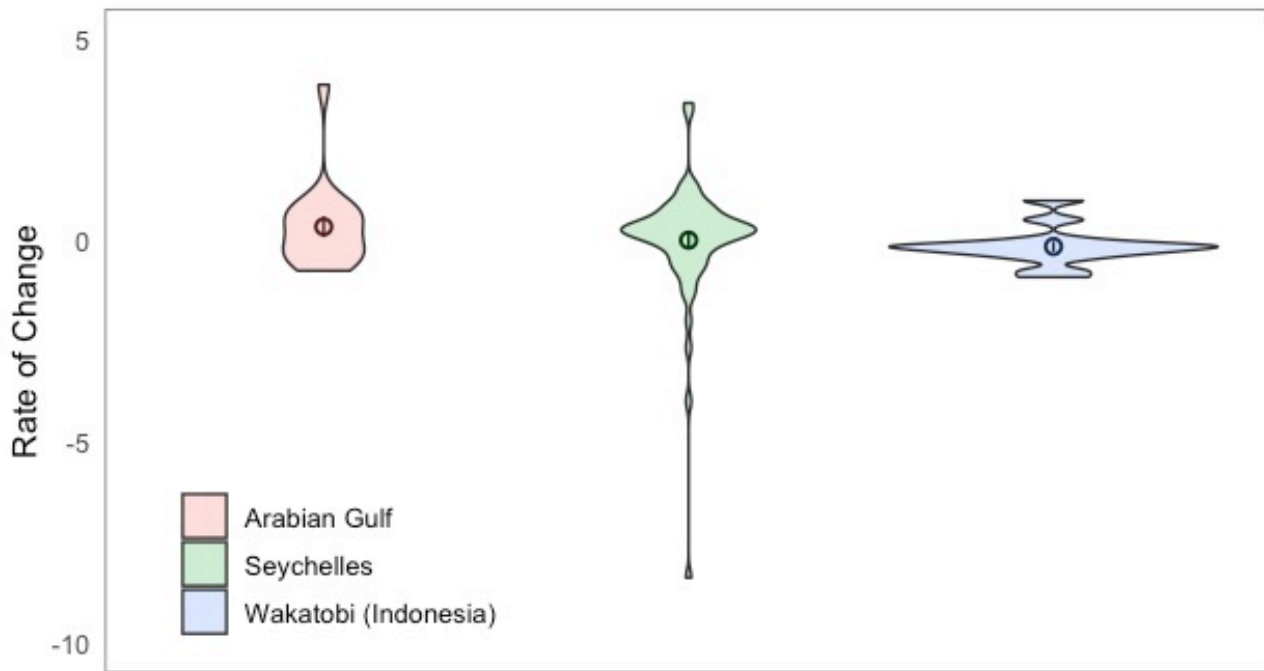
Unfortunately, the majority of the reefs in the Wakatobi experienced a declining trend (Figure 3.7). Over the course of ten-years, coral cover on the Ridge reef was noted to decline by approximately 3.5% (2008 =  $31.0 \pm 4.5\%$ ; 2018 =  $29.9 \pm 5.5\%$ ; Figure 3.7). Coral cover at the Buoy 3 reef decreased from  $55.5 \pm 12.2\%$  in 2002 to  $35.5 \pm 6.1\%$  in 2018 whilst the PK reef also experienced a drastic decrease of 61.3% over a period of 13 years (2005 =  $40.0 \pm 6.4\%$ ; 2018 =  $15.5 \pm 2.7\%$ ;

Figure 3.7). Lastly, the Sampela reef witnessed a heavy decrease in coral cover from  $33.1 \pm 2.2\%$  in 2002 to  $13.6 \pm 2.0\%$  in 2018 (Figure 3.7).

Overall, when evaluating the distribution of the rate of change in coral cover across bioregions, the average rate was higher in the AG by 0.3% per year compared to the estimated rates in the Seychelles and Indonesia despite its insignificance ( $F_{(2,91)} = 0.6$ ,  $p = 0.5$ ; Figure 3.8).



**Figure 3.7. Change in mean coral cover of reefs over time within the three bioregion: (a) Arabian Gulf; (b) Seychelles; (c) Wakatobi Marine National Park, Indonesia. Grey dots represent individual data points extracted for this systematic review; if more than two data points of the same site/reef is detected, a trend is presented; coloured lines represent the interest sites of this study/thesis.**



**Figure 3.8.** Distribution of the rate of change in reefs across the three bioregions (Arabian Gulf = 1986-2018; Seychelles = 1994-2018; Wakatobi, Indonesia = 2001-2018). Mean coral cover ( $\pm$ SE) of reefs is represented by the circle in the middle of each shape; mean at 0 = no change,  $>0$  = positive change/recovery,  $<0$  negative change/decline.

### 3.4 | DISCUSSION

Through conducting a systematic review this chapter aimed to establish the current status and trends of reefs in the three chosen bioregions through investigating the temporal change in the abundance (percentage cover) of the primary reef carbonate producers (hard corals).

#### 3.4.1 | Trends in coral cover within bioregions

Using the data points identified from the primary literature, coral cover change was tracked over a 32-year period in the AG (1986-2018), 24-year period in the Seychelles (1994-2018) and 19-year period in the Wakatobi, Indonesia (2001-2018). Change in coral cover trends were non-linear fluctuating between an increase indicating recovery and declines across all bioregions.

##### *Arabian Gulf*

Despite the 12-year gap (1987-1999) in the AG data points, a few data points were obtained from 1986 providing insights into what coral cover might potentially have been on reefs in this area (Figure 3.3). This large gap in data can be attributed to the limited research in the region with a study reporting that between 1950-2012 a total of 270 articles were published on reefs in the region, of which half (49.8%) were published between 2003-2012 (Burt, 2013). This lack of publications in the area coupled with literature not meeting the inclusion criteria when found through the systematic search has resulted in the gap observed. Nevertheless, although these studies were not included in the data analysis of this review, these publications reported an overview of the status of reefs during that period, which document reefs with high coral cover. In 1988, colonies of *Acropora pharaonis* were reported to cover 95% of the reef in Tarut Bay, Saudi Arabia (Coles & Fadlallah, 1991) with similar observations of dense *Acropora* spp. cover on reefs in Bahrain (50-90%; Vousden, 1995) and Qatar in the 1980s (Emara *et al.*, 1985). Reports of high coral cover (75%) on reefs in Oman were also documented (Salm, 1993), and dense coral cover in the early 1990s between Ras Ghantoot

and Jebel Ali off the Deira corniche in Dubai, UAE (Purkis & Riegl, 2005; Purkis *et al.*, 2005). These reports compliment the few data points identified in this study for the 1986 time point, filling in the gap whilst providing an overview covering the north, mid and south of the AG.

Sharp declining trends were detected in coral cover between 1999-2001, which can be attributed to the 1998 global mass bleaching event (Figure 3.3). Reefs in the AG were reported to suffer major losses, which reduced live coral cover in many shallow areas to less than 1% due to the 1996, 1998 and 2002 bleaching events (Sheppard & Loughland, 2002; Rezai *et al.*, 2004). On a more local scale, for example, reefs in Bahrain recorded an estimated loss of >90% of coral cover (Rezai *et al.*, 2004; Al-kuwari, 2006) linked to the mass bleaching events in 1996 and 1998 where temperatures reached 37.7°C and 38°C respectively, making Bahrain the worst affected Gulf country by these events (Wilkinson, 1998; Uwate & Shams, 1999; Lough, 2000). Shifts towards increasing coral cover was detected on reefs over the next six years (2002-2008) indicating possible reef recovery and new coral establishments (Figure 3.3; 3.6; 3.7). Benzoni *et al.*, (2006) documented an observation on reefs in Kuwait which experienced the 1992 bleaching episode that resulted in high (nearly 100% for *Acropora downingi*) coral mortality on shallow reefs. However, ten years later (2002), numerous *Acropora downingi* colonies (up to 4m in diameter) are reported to have recovered at all impacted reefs, suggesting that corals in this region can withstand extreme conditions and hence enable recovery following major disturbances (Benzoni *et al.*, 2006). A similar observation was also reported in Dubai where six species of *Acropora* sp. ‘disappeared’ following the 1996 bleaching episode, however, ten years later, these species were reported to have re-established themselves on the reef (Sheppard *et al.*, 2010). This in turn could help explain the trend observed between 2002-2008, nevertheless, this recovery phase was short lived with a reverse trend observed between 2009-2012, causing a decline in coral cover on the majority of reefs (Figure 3.6; 3.7). This can be attributed to the 2010 bleaching disturbance (Riegl & Purkis, 2015; Paparella *et al.*,



2019), with the exception of some reefs in the South of the AG that were observed to maintain their status. The following years (2013-2018), witnessed an overall decline in the AG coral cover which is well documented (Figure 3.6; Bento *et al.*, 2016; Grizzle *et al.*, 2016; Sheppard, 2016; UNEP, 2016; Riegl *et al.*, 2018). It should be noted that reef degradation in the AG is not only a consequence of bleaching episodes, although this is the primary reason based on the literature reports, the presence of many local pressures that threaten and impact reef sites throughout the region are also contributors. One of the major pressures include coastal development, which is said to have altered 40% of the AG coastline in the last 20 years through dredging and reclamation activities (van Lavieren *et al.*, 2011). For example, reefs in Dubai, UAE located between Ras Ghantoot and Jebel Ali off the Deira corniche which were reported to have dense coral cover in the early 1990s, have suffered severe losses, shortly following the intensive construction of the Jebel Ali Palm (Sheppard *et al.*, 2010). Other contributors towards reef degradation include overfishing and destructive fishing practices (van Lavieren *et al.*, 2011; Burt, 2014).

### ***Seychelles***

Data points identified for reefs in the Seychelles presented the temporal trends of reefs throughout a 24-year period (1994-2018) which revealed large variations in coral cover between the inner, outer and southern Seychelles reefs (Figure 3.4). This variation could be linked to the unique geomorphological substrata found on these reefs. These are commonly categorized into coral patch reef habitats (with sand, rubble or rock base), carbonate fringing reefs or granite habitats (reef growth occurs on granitic rock substrate) especially in the Inner Seychelles reefs (Collier & Humber, 2012; Harris *et al.*, 2014). Prior to the 1998 bleaching event, data points indicated that coral cover was higher than the average mean calculated for the Seychelles in this study (i.e. >14%) with reports of coral cover ranging between 19-39% in the inner reefs, 59% in the outer reefs and

17.7% in the southern reefs (Figure 3.4). This supports observations made by other studies that stated reefs in the Seychelles were characterised with high structural complexity and rich live branching and massive coral cover in 1994 (Graham *et al.*, 2006). However, this positive status endured severe impacts due to the 1998 mass bleaching event which reduced coral cover to 3-5% (Obura *et al.*, 2017). Due to this bleaching event, reefs in the inner Seychelles were reported to have suffered >90% coral cover loss (Goreau *et al.*, 2000; Sheppard, 2003). In addition, reefs in the outer and southern Seychelles also suffered major losses in coral cover (41% and 74% respectively; Spencer *et al.*, 2000), resulting in the collapse of their structural complexity with reports of slow recovery rates thereafter (Graham *et al.*, 2015). The trends detected through the data points in this study between 1998 and 2015 are in line with these observations and indicate that reefs in the years following 1998 experienced a slow shift into a positive state (despite multiple minor bleaching episodes during this period); with coral cover growth on some reefs regaining its pre-bleaching level by 2015 (Figure 3.4; 3.6; Obura *et al.*, 2017). Unfortunately, this positive recovery trend on reefs was abruptly cut short by another global mass bleaching event in 2016, resulting in devastating loss for reefs across the Seychelles (Figure 3.6; 3.7). On a more positive note, although the 2016 bleaching episode was severe on reefs in this region, impacting the inner reefs more than the outer reefs (60% and 17% respectively), it is reported to be less severe than the 1998 event (Gudka *et al.*, 2018). During the period 2016-2020, coral cover decline has been reported by various studies on reefs in the Seychelles, all of which are mainly attributed to the 2016 bleaching event (Obura *et al.*, 2017; Gardner *et al.*, 2018; Gudka *et al.*, 2018, 2020; GVI Seychelles, 2018).

### ***Wakatobi, Indonesia***

Located in the heart of the Coral Triangle, the Wakatobi is naturally expected to have the highest coral cover in comparison to reefs in the AG and the Seychelles. Unfortunately, data prior to 2001

could not be found making it impossible to examine change in coral cover that might have been an implication of the 1998 bleaching event. The earliest record of coral cover found for this region was 2001 following which the change in coral cover was documented to be non-linear. Coral cover increased with time and maintained a high range (i.e. above average = >29%, reaching 60%), this increase was interrupted around the period 2005-2006 which caused a clear decline in coral cover (Figure 3.5; 3.6). This observation is in line with other reports (Clifton *et al.*, 2010; Gouraguine *et al.*, 2019), although no clear reason is known for this decline, it has been suggested that this disturbance could be a result of anthropogenic activities. Evidence of destructive fishing techniques (blast fishing) has been reported to take place in the region between 2004-2005 which could be a reason behind the decline during the 2005-2006 period (Figure 3.5; 3.7; Pet-Soede & Erdmann, 2003; Clifton *et al.*, 2010). Despite the absence of bleaching reports in this region, data from remote sensing (see Chapter 2) indicates that these reefs experienced thermal anomaly temperatures in 2002, 2005 and 2006 which could have contributed to the observed decline in coral cover (Gouraguine *et al.*, 2019). Coral cover trends continued to remain lower (<29%) throughout the following ten years (2005-2015), which could be attributed to the increasing human population on the adjacent islands that rely on these reefs for their livelihoods and food. This reliance coupled with a history of poor resource management within the Wakatobi (Cullen-Unsworth, 2010), coral disease incidents (Haapkylä *et al.*, 2009) and regional/global pressures have resulted in declines in both coral cover and fish abundance (Curtis-Quick, 2013; Gouraguine *et al.*, 2019). During the last four years (2014-2018), increasing trends in coral cover have been observed through the extracted data points, however, the data also illustrates large variation in coral cover (7-50%) across reefs (Figure 3.7). This result corresponds to that reported by Marlow *et al.*, (2019) who observed a similar (7-48%) variation in coral cover within the Wakatobi. This variation could be caused by the difference in methodology used to measure coral cover on reefs and sample size since for example, the use of

photoquadrats results in higher sample size. However, other studies have demonstrated that data obtained using different methodologies to measure coral cover can be legitimately comparable with no significant difference in results (Franklin *et al.*, 2013; Jokiel *et al.*, 2015). Overall, despite the increase in coral cover over the last four years (2014-2018), the decline in coral cover in comparison to nearly twenty years ago is evident with supporting studies (Clifton *et al.*, 2010; Curtis-Quick, 2013; Gouraguine *et al.*, 2019; Marlow *et al.*, 2019).

### **3.4.2. Rate of change in coral cover across bioregions**

Following the major bleaching event documented in 1998, reefs in the AG experienced a decline at a rate of 0.6% per year in coral cover during the period 1998-2003 (Figure 3.6). Despite this, signs of recovery and/or stability were observed between 2003-2013 on different individual reefs (Benzoni *et al.*, 2006; Burt *et al.*, 2013). However, during the period 2013-2018, a higher decline in coral cover was detected at a rate of 4.7% per year, which can be attributed to the bleaching disturbance documented in 2017 resulting in mass mortality throughout the region (Figure 3.6; Burt *et al.*, 2019; Paparella *et al.*, 2019). Observations from previous studies (Benzoni *et al.*, 2006; Sheppard *et al.*, 2010) have indicated that reefs in the AG, required an estimated ten years to recover and establish their pre-bleaching coral cover state. With bleaching episodes on the rise in both frequency and intensity (Sully *et al.*, 2019), questions remain whether reefs can re-establish themselves enough to maintain their structural integrity and keep track of sea level rise. Similar to the AG, reefs in the Seychelles have also suffered extensive coral cover loss (>90%) as a result of the 1998 bleaching event (Obura *et al.*, 2017). Based on the results of this study, coral cover was estimated to decrease at a rate of 0.6% per year between 1998-2003. This was reversed by a recovery trend in coral cover observed between 2003-2013 and estimated at a rate of 1.2% per year which is in line with previous studies that reported coral cover recovery rate at 1% per year between 2005-2011 (Wilson *et al.*,

2012). Results from this study have also revealed that current trends reflect a decrease in coral cover at a rate of 1% per year since the 2016-bleaching event. Overall, it took reefs in the Seychelles a total of 17 years (1998-2015) to return to their pre-bleaching state which was severely interrupted by the 2016 bleaching event with observations suggesting that granitic reefs fared better than the carbonate in recovery (Obura *et al.*, 2017). On the other hand, reefs in the Wakatobi, Indonesia have not been documented or observed to have suffered losses as a result of bleaching events, instead most of the decline in coral cover in the region is attributed towards anthropogenic impacts (Clifton *et al.*, 2010). Prior to 2004, coral cover began to decline at a rate of 2.3% per year, which continued in the following years ten years, all of which could be linked to anthropogenic impacts and incidents of coral disease (Clifton *et al.*, 2010; Haapkylä *et al.*, 2015; Gouraguine *et al.*, 2019). Since 2014, an increase of 1.9% per year was noted indicating a slow initiative of re-establishment in coral cover across reefs in the Wakatobi (Figure 3.6).

### **3.4.3. Change in coral cover for thesis study sites**

#### ***Reefs of Bahrain, AG***

In Bahrain, the status of the reefs of interest are contrasting over time, with one reef fluctuating between positive signs of recovery and decline whilst the other suggests stability over time. Fasht Al Adhm represents a shallow (~5-7 m) reef in Bahrain that was majorly impacted by the 1998 bleaching resulting in 0% coral cover documented by the year 2000 (Uwate *et al.*, 2000). Ten years later, coral cover was observed to recover to  $9.8 \pm 0.8\%$  in 2011 (Burt *et al.*, 2013) indicating a recovery rate of 0.9% per year (Figure 3.3; 3.7). However, the 2017 bleaching episode resulted in severe mortality (Burt *et al.*, 2019; Paparella *et al.*, 2019) and coral cover declined to  $1.4 \pm 0.6\%$  in 2018 (Chapter 4). Contrastingly, at Reef Bul Thamah, coral cover increased between 2000 and 2011 from  $12.5 \pm 4.0\%$  to  $16.3 \pm 2.6\%$  (Uwate *et al.*, 2000; Burt *et al.*, 2013) with a minor decrease in

2018 bringing its coral cover to  $15.5 \pm 2.2\%$  (Chapter 4). The ability of this reef to maintain its coral cover despite the bleaching disturbances and other local pressures could be attributed to its depth ( $\sim 10$  m), which is an advantage (Bridge *et al.*, 2014; Baird *et al.*, 2018) and location ( $\sim 80$  km off-shore) in comparison to the Fasht Al Adhm reef (depth =  $\sim 5-7$  m; located  $\sim 11$  km off-shore). In addition, Hence, Reef Bul Thamah could be considered as a potential future refugia reef due to its high resilience to environmental change.

### ***Reefs of Curieuse Island, Seychelles – Western Indian Ocean***

Coral cover was observed to drastically decline at both interest sites around Curieuse Island (East Bay and Praslin). In 2016, prior to the bleaching event, it was reported that the live coral coverage at these sites were witnessing a steady increase between 2009 and 2016 from  $35 \pm 5\%$  to  $49 \pm 9\%$  in East Bay and  $30 \pm 2\%$  to  $42 \pm 7\%$  in Praslin (Gardner *et al.*, 2018). However, the 2016 bleaching event terminated this growth in coral cover causing it to decline from  $49 \pm 9\%$  (2016) to  $15.5 \pm 1.6\%$  (2018) in East Bay and  $42 \pm 7\%$  (2016) to  $7.6 \pm 2.1\%$  (2018) in Praslin (Figure 3.7; 2016 values = Gardner *et al.*, 2018; 2018 values = Chapter 4). Overall, the trajectories of the sites of interest are unfortunately negative placing these reefs in a very vulnerable position in the face of rising sea levels.

### ***Reefs of Hoga Island, Wakatobi, Indonesia – Central Indo-Pacific Ocean***

Overall, declining trends were detected at all of the interest sites within the Wakatobi (Figure 3.7). Sampela is a reef adjacent to the Bajo village of Sama Bahari and is subjected to large sediment load and various anthropogenic activities which heavily impact the site (Clifton *et al.*, 2010; Powell *et al.*, 2010). This is clearly reflected in the decline in coral cover from  $33.1 \pm 2.2\%$  in 2002 (Crabbe *et al.*, 2004) to  $13.6 \pm 2.0\%$  in 2018 (Chapter 4). Ridge reef is considered one of the “healthiest” reefs

in the Wakatobi due to its geographical position and very low anthropogenic impacts, however, at Ridge reef live coral cover declined by 3.5% over the course of 10 years (2008 =  $31.0 \pm 4.5\%$ ; 2018 =  $29.9 \pm 5.5\%$ ; Powell *et al.*, 2010; Chapter 4 respectively). On the Hoga Island fringing reefs, Buoy 3 exhibited a decline by 36% between 2002 and 2018 (2002 =  $55.5 \pm 12.2\%$ ; 2018 =  $35.5 \pm 6.1\%$ ; Haapkylä *et al.*, 2015; Chapter 4 respectively) whilst PK decreased by 61.3% over 13 years (2005 =  $40.0 \pm 6.4\%$ ; 2018 =  $15.5 \pm 2.7\%$ ; Scaps & Denis, 2008; Chapter 4 respectively). This decline in coral cover can be attributed towards synergistic disturbances, the majority of which are anthropogenic, whilst some may be biological such as coral disease occurrences and thermal anomalies detected through remote sensing data (Haapkylä *et al.*, 2009; Clifton *et al.*, 2010; Haapkylä *et al.*, 2015; Gouraguine *et al.*, 2019).

#### **3.4.4. Limitations**

Systematic reviews are considered evidence based to answer a scientific question, however, similar to every scientific process challenges and limitations are inherent. Some of the limitations encountered include the use of software to extract numerical values from published figures due to their absence in the text, which results in discrepancy in the extracted values. In addition, there might be data available at a governmental, NGO and/or private sector level that can contribute to filling the knowledge gap within the bioregions that might not be available online or is inaccessible hence contributing towards publication bias. This also results in some countries being under-represented (e.g. reefs in Saudi Arabia in the AG).

Nevertheless, despite these limitations, the results presented in this systematic assessment has revealed that despite the low rate of recovery on reefs within the three bioregions, disturbances caused mainly by bleaching events have impacted coral cover (primary carbonate producers) on reefs in the AG and the Seychelles whilst anthropogenic impacts were the main drivers of coral

decline in the Wakatobi. This decline across the bioregions influences long-term patterns in reef ecology and impacts accretional health especially that studies suggest that a threshold of 10% live coral cover is critical to enable reefs to keep pace with sea level rise through maintaining a positive carbonate production rates (Perry *et al.*, 2013; Herrán *et al.*, 2017).

In conclusion, the findings derived from this systematic review have enabled the tracking and establishment of the current status and trends of coral reefs in the interest sites within Bahrain (AG), Curieuse Island, (Seychelles) and the Wakatobi (Indonesia) as well as providing insights into the overall status and trends of reefs at regional levels.



**CHAPTER FOUR: REEFS CARBONATE BUDGETS IN THE  
ARABIAN GULF, WESTERN INDIAN AND CENTRAL INDO-  
PACIFIC OCEAN**

This page was left intentionally blank

## 4.1 | CHAPTER INTRODUCTION

In the last two decades, reef carbonate budgets have been recognised as a key metric to assess coral reef health thereby developing a greater understanding of reef state (Perry *et al.*, 2008; Mace *et al.*, 2014; Perry & Morgan, 2017). The geomorphic state of coral reefs and their structural integrity can be assessed by their carbonate budgets, which quantify the overall CaCO<sub>3</sub> input and output in a coral reef. Reef accretion occurs when CaCO<sub>3</sub> production exceeds erosion, thereby considering a reef in a positive budgetary state whilst the contrary implies that reefs are in a negative state represented by physical abrasion, bioerosion and dissolution (Leon & Woodroffe, 2013). Insights are gained when quantifying and assessing reef carbonate budgets under different environmental conditions and across bioregions with regards to current status of reefs, change in reef functionality and whether reefs are able to track sea level rise (SLR). This comes at a crucial time as reefs worldwide are presented with anthropogenic challenges both on a global and local scale. This chapter documents the status of reef carbonate budgets in the three selected bioregions and determines whether reefs are maintaining a positive budgetary state or are exhibiting an erosive state with consequences for their future survival. In the last two decades, reefs in these three bioregions have faced multiple bleaching events, with some extreme episodes (e.g. DHW=  $\geq 15^{\circ}\text{C}$ -weeks in Bahrain (2017);  $7^{\circ}\text{C}$ -weeks in Seychelles (2016); whilst Indonesia did not face extreme events ( $5^{\circ}\text{C}$ -weeks; 2016)) resulting in high mortality rates of primary carbonate producers (see Chapters 2 and 3). Therefore, this chapter describes the current accretional health of reefs in each bioregion. Findings are presented as individual papers representing each bioregion.

## 4.2 | BLEACHING THREATENS POSITIVE CARBONATE BUDGETS AND REEF GROWTH POTENTIAL ON BAHRAINI REEFS

### ABSTRACT

Coral reefs have been at the forefront of climate change threats, with rising sea surface temperatures (SST) contributing to intense and increasing episodes of global bleaching events. These episodes have impacted carbonate budget dynamics, which is reflected in reduced reef framework accretion of calcium carbonate ( $\text{CaCO}_3$ ), with future consequences on reef ability to keep pace with sea level rise (SLR) projections. Reefs in the Arabian Gulf (AG) exist in harsh environmental conditions with temperatures ranging between 16-36°C. Despite the high thermal thresholds ( $\sim 35^\circ\text{C}$ ; mean DHW =  $4.8 \pm 0.3^\circ\text{C-weeks}$ ) of corals in this region, extensive bleaching and high coral mortality has been reported regionally in 2017. This study quantifies reef carbonate budgets between 2017-2018 in Bahrain at shallow sites (5-10 m) and assesses the impact of the 2017 severe bleaching event on their budgetary state. Results indicate a decrease in hard coral cover from  $14.2 \pm 5.5\%$  to  $8.4 \pm 1.4\%$ . In addition, a decline in positive budgetary state from  $2.7 \pm 0.7$  to  $1.7 \pm 0.4 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  was recorded in the offshore Reef Bul Thamah, whilst the shallower nearer shore Fasht Al Adhm has shifted into a negative budgetary state. This shift is attributed to the severe bleaching, which took place between June – September 2017, resulting in high coral mortality rates and subsequent reduced framework accretion. Predicted warming trends present a threat to the structural integrity of Bahraini reefs, compromising their ability to keep pace with future SLR projections.

### 4.2.1 | INTRODUCTION

Coral reefs are known for their high diversity and productivity (Carpenter *et al.*, 2008; Bowen *et al.*, 2013) which makes them important ecosystems for both nature and mankind. They provide

numerous environmental (e.g. coastal protection; van Beukering *et al.*, 2010), social (e.g. fisheries; Laurans *et al.*, 2013) and economic (e.g. tourism; Cesar & Beukering, 2004) benefits to communities worldwide through their ecosystem services (Moberg & Folke, 1999; Cinner *et al.*, 2013; Daw *et al.*, 2016). The extent to which coral reefs can deliver their services (e.g. coastal protection) and functions (e.g. biodiversity) is associated and dependent on the persistence of their reef framework structure (Franco *et al.*, 2016; Perry, Spencer, & Kench, 2008). The ability of coral reefs to sustain their three dimensional structural integrity depends on the balance between the rate of carbonate production and erosion (Hubbard, Miller & Scaturro, 1990; Kleypas & Langdon, 2006; Perry *et al.*, 2008; Perry *et al.*, 2015; Stearn & Scoffin, 1977). Calcium carbonate ( $\text{CaCO}_3$ ) production is done by primary (hermatypic corals; Perry & Hepburn, 2008; Stearn & Scoffin, 1977) and secondary reef builders (calcareous encrusters; Goreau, 1963; Choi & Ginsburg, 1983) in addition to the reintroduction of carbonate sediment into the reef framework. Reef builders secrete, deposit and accumulate  $\text{CaCO}_3$  thereby contributing towards the formation of the reef's structure leading to accretion. Sea surface temperatures (SST) have increased globally with records documenting rises of  $0.7^\circ\text{C}$ ,  $0.4^\circ\text{C}$  and  $0.3^\circ\text{C}$  in the Indian, Atlantic and Pacific oceans respectively between 1950-2009 (IPCC, 2014a). Temperature anomalies, which are predicted to increase with global rising temperatures, have been proven to cause coral bleaching and coral mortality (Baker *et al.*, 2004; Berkelmans & Oliver, 1999; Hughes *et al.*, 2017). An increase in temperature anomaly by just  $1\text{-}2^\circ\text{C}$  is sufficient to cause bleaching (Heron *et al.*, 2016; Hoegh-Guldberg, 1999; Hoegh-Guldberg *et al.*, 2017; Kleypas, Mcmanus, & Menez, 1999; Lough, Anderson, & Hughes, 2018; Purkis & Riegl, 2005), impacting reef carbonate budgets and reef capacity to sustain their framework development (Januchowski-Hartley *et al.*, 2017; Perry & Morgan, 2017). Despite reefs being faced with multiple stressors (e.g. changes in light, salinity and nutrient availability), all of which may contribute towards triggering bleaching (Baker, Glynn, & Riegl, 2008; Coles & Jokiel,

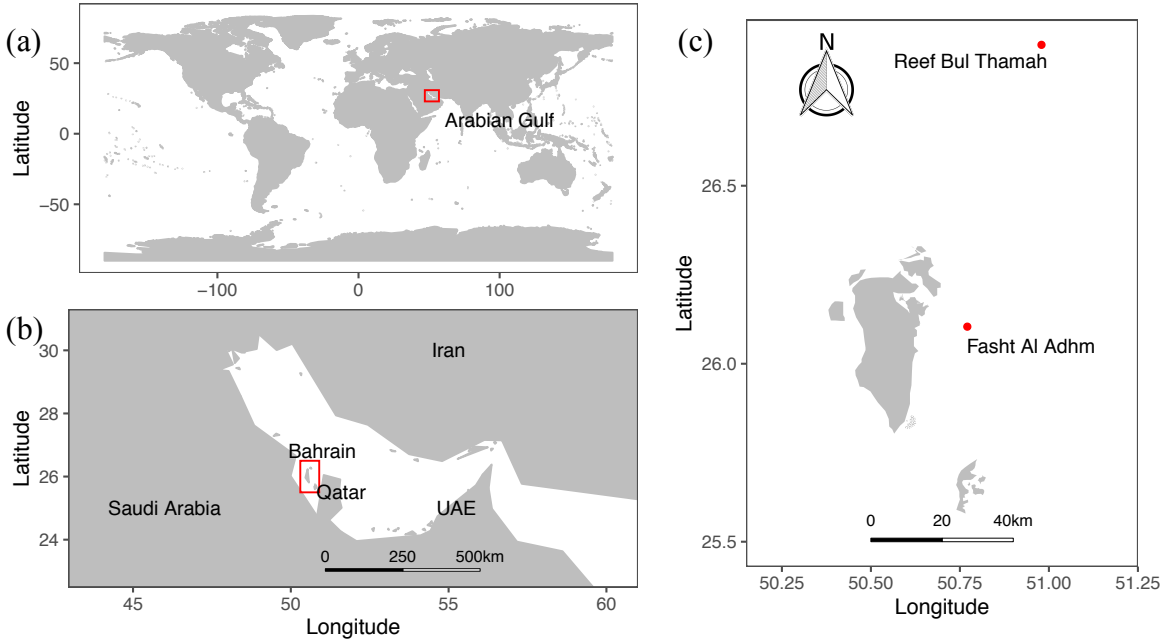
1978; Kleypas *et al.*, 1999; Lesser *et al.*, 1990; Wooldridge, 2009), SST anomalies are seen as the most influential trigger (Claar *et al.*, 2018; Hoegh-Guldberg *et al.*, 2017; Pramanik, 2014). In environments such as the Arabian Gulf (AG), corals are subjected to seasonal variations in temperatures (16-36°C; Coles & Riegl, 2013; Hume *et al.*, 2013). In the last two decades, reefs in this region have been exposed to severe temperature anomalies (~2°C above the average) at a rapid and high recurring rate (Burt, Bartholomew, & Feary, 2012; Riegl, 2002; Sheppard & Loughland, 2002), similar to those projected (1.5-2°C above pre-industrial levels) to occur globally by 2100 (IPCC, 2014b). It is thus unsurprising that coral communities in the AG have the highest bleaching threshold globally (Kavousi *et al.*, 2014; Rezai *et al.*, 2004; Riegl *et al.*, 2011; Shuail *et al.*, 2016). However, despite their high threshold, they are still susceptible to bleaching. It is documented that 70% of original the AG reef cover may be considered lost with declines linked to major bleaching events e.g.1998 (van Lavieren *et al.*, 2011; refer to Chapters 2 and 3). Regional studies, mostly focused on the reefs of the United Arab Emirates and Oman (Burt *et al.*, 2016; Howells *et al.*, 2014; Purkis & Riegl, 2005; Purkis *et al.*, 2010; Sheppard *et al.*, 2010; Sheppard, Price, & Roberts, 1992) have found that these reefs have the adaptive mechanisms to survive under harsh conditions, particularly in relation to high temperatures and large seasonal fluctuations (Burt, 2013). Over the past decades, efforts have been made to calculate reef carbonate budgets (Browne, 2011; Hepburn, 2006; Holmes *et al.*, 2000; Hutchings & Bamber, 1985) and assess the rate of change due to bleaching on reefs such as the Maldives and Seychelles (Januchowski-Hartley *et al.*, 2017; Perry & Morgan, 2017; Perry *et al.*, 2014). However, no previous attempt has been made to calculate and assess reef carbonate budgets in the AG. Therefore, the aim of this study was to: (1) characterise the benthic composition of reefs in Bahrain in order to quantify the rate of carbonate production and erosion and; (2) assess the change in carbonate budgets on these reefs between 2017-2018 post the

2017 bleaching which is considered as the most intense bleaching event in Bahrain following the documented event in 1998 (see Chapter 2).

## 4.2.2 | MATERIALS & METHODS

### 4.2.2.1 | Site descriptions

Two study sites in Bahrain located in the southwest of the AG were investigated in April 2017 & 2018 and September 2017 & 2018 (Figure 4.2.1). Reefs from both turbid and clear-water (herein referred to as optimal) sites were chosen to represent different environmental gradients with sampling occurring between 5-7 m in Fasht Al Adhm and 10-12 m in Reef Bul Thamah (see Table 4.2.1 for environmental characteristics of sites). Sampling depths differ due to the natural topography of the sites; site BH-TB is a near-shore gently sloping shallow reef, with a maximum depth of 7 m and minimal relief due to the site being relatively homogenous and lacking in structural complexity. Site BH-OP is an off shore reef, also relatively homogenous, with a gentle slope starting at 10 m and continuing to 12 m when Pleistocene bedrock continues to a depth of 18 m after which the substrate becomes more patchy with sand and bedrock formations as it slopes off into the deep (>50 m). Bahrain is an archipelago of 33 low lying islands (Figure 4.2.1) and historically, its coral reefs were among the most extensive in the southern basin of the AG (Kavousi *et al.*, 2014; Purkis & Riegl, 2005; Riegl, 2003). However, in the last four decades, these reefs have undergone significant decline due to intense bleaching events and large-scale coastal development in pursuit of socio-economic growth. This has added 12.8% to the Kingdom's total land area between 1961 (690 km<sup>2</sup>) and 2018 (778 km<sup>2</sup>) (World Bank, 2018). Coral reefs (locally known as “*fasht*”) occupy a total area larger than Bahrain (850 km<sup>2</sup>) with Fasht Al Adhm itself covering 200 km<sup>2</sup>, with most restricted to the east and north of the main island (Burt *et al.*, 2013).



**Figure 4.2.1. Location of Study Sites – (a) Location of Arabian Gulf (AG); (b) Location of Bahrain within the AG; (c) Location of selected study sites within Bahrain [Site codes: Fasht Al Adhm (BH-TB) and Reef Bul Thamah (BH-OP)].**



**Table 4.2.1. Site description and characterisation of study sites in Bahrain, Arabian Gulf.**

Site	Site Code	Depth (m)	Temp. (°C)	Salinity (ppt)	Sedimentation rates (mg cm <sup>-2</sup> d <sup>-1</sup> )*	Light attenuation (K <sub>d</sub> PAR)**	Distance	Impacts
<b>Fasht Al Adhm (Turbid)</b>	BH-TB	5-7			0.23±0.04	0.02 ± 0.04	~11 km east of the main island	Heavily impacted due to various anthropogenic activities mainly reclamation and dredging.
<b>Reef Bul Thamah (Optimal)</b>	BH-OP	10-12	20-36	42-44	0.19±0.04	0.04 ± 0.07	~80 km northeast of the main island	Although located within a Marine Protected National Park (MPA), the site is subjected to illegal fishing and destructive fishing practices.

\* Due to time restrictions, sediment traps (n=6) were deployed for a period of three days at each of the study sites in May 2018.

\*\* Data was logged using a hobologger at a one minute interval at two depths (BH-OP = 5m and 10m; BH-TB = 3m and 7m) over 5 days and were converted from Lux to  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$  (as per Long, Rheuban, Berg, & Zieman, 2012) to return light attenuation coefficients (K<sub>d</sub> (PAR), m<sup>-1</sup>) for each site.

#### 4.2.2.2 | Quantifying the Carbonate Budgetary State in the Field

Surveys were conducted in May and September 2017 & 2018 on both the near-shore (BH-TB) and off-shore reefs (BH-OP). Since the reef structure in Bahrain is almost flat but does have a gentle slope (<2 m), all transects were conducted on the bottom flat of the reef at a depth of ~6-7 m in BH-TB and ~10 m in BH-OP. At each site, six replicate transect lines were established running parallel where possible along the reef flat, with a spacing of 5 m between transects (Table 4.2.2). In order to quantify reef rugosity, substrate composition and gross carbonate production and erosion to collectively determine the net carbonate budgets ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  hereafter expressed as G), the international standardised census-based *ReefBudget* methodology was used (Perry *et al.*, 2012). The *ReefBudget* methodology was originally designed for the Caribbean region but a slightly modified version of the methodology described in Perry *et al.*, (2012) was used for this study. The modifications made are mainly using different growth rates for primary producers and the number of transects / replicates conducted which was mainly due to time constraints. Table 4.2.2 outlines the various carbonate budget components measured and the number of replicates at each study site. Benthic composition and cover was measured following the integrated method outlined in Perry *et al.*, (2012) whereby benthic cover and surface rugosity data were collected using a modified version of the standard linear intercept methodology where benthic cover was recorded along every 1 cm increment of the tape. Rugosity was calculated from the total surface distance for each linear 1m of reef.

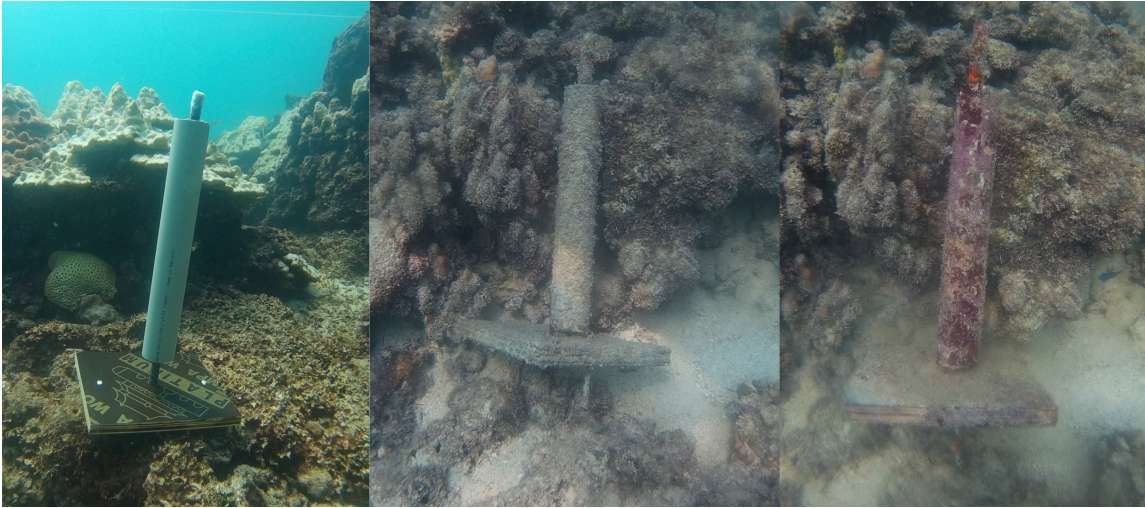
**Table 4.2.2. Details of carbonate budget components and number of replicates at each study site in Bahrain, Arabian Gulf.**

Carbonate Budget Component	Variable	Number of transects	Length of transect (m)
Carbonate production rate	Benthic composition assessment	6	10
	Rugosity	6	10
	Carbonate producers	6	10
Carbonate erosion rate	Echinoids (Urchins)	6	10
	Scaridae (Parrotfish)	3	30
	Bioeroding sponges (Clionidae)	6	10

### Carbonate Producers

- **Primary Carbonate Producers:** Scleractinian corals were identified to genus level e.g. *Porites spp.*
- **Secondary Carbonate Producers:** Crustose coralline algae (CCA) was recorded as CCA throughout the benthic cover measurement however, other secondary carbonate producers such as bryozoans, foraminifera and serpulids were recorded as other calcareous encrusters (OCE). In order to quantify secondary carbonate producers, six PVC pipes were deployed for a period of one-year at each study site measuring 35 cm x 16 cm (length x circumference of the pipe; Figure 4.2.2). Following the one-year period, pipes were photographed underwater, placed in a plastic bag secured with cable ties over the upper part of the pipe for removal. Once in the lab, pipes were examined and photographed in detail following which they were placed in 10% sodium hypochlorite (bleach) for 36 hours. Once removed from the bleach, the pipes were left to dry after which, they were weighed three times. The pipes were then soaked in 10% HCl for another 36 hours. Once all the calcium carbonate was dissolved, the

pipes were taken out and weighted for a second time (in replicates of three). This allowed for a weight per unit area to be derived.



September 2017

September 2018 (Exposed Side) September 2018 (Cryptic Side)

**Figure 4.2.2.  $\text{CaCO}_3$  production by secondary carbonate producers over a one-year period on PVC pipes deployed at BH-TB (Fasht Al Adhm).**

### Carbonate Eroders

- **Echinoids:** The area surveyed along each of the six transects was 1 m on either side of the 10 m transect line covering a total of 20 sq m per transect (10 m length x 2 m width). The number of individuals along each transect were counted, identified to species level and recorded in the following size class: 0-20 mm, 21-40 mm, 41-60 mm, 61-80 mm, 81-100 mm.
- **Scaridae:** The area surveyed along each of the three transects was 4 m in width of the 30 m transect line covering a total of 120 sq m per transect (30 m length x 4 m width). The number of individuals encountered along each transect were counted, identified to species level and recorded in the following size class: 5-10 cm, 15-24 cm, 25-34 cm 35-44 cm and >45 cm.
- **Bioeroding sponge:** The area surveyed along each of the six transects was 0.5 m width of the 10 m transect line covering a total of 10 sq m per transect (10 m length x 1 m width). The area of individual bioeroding sponge colonies with visual papillae were estimated using a transparent sheet with a printed 1x1 cm grid along the transect, however identification to species level was difficult as there is no bio-eroding sponge guide available for the AG. In order to confirm that the sponges recorded were bioeroding, a hammer and chisel were used to verify boring activity.

### 4.2.2.3 | Reef Carbonate Budget Calculations

#### *Carbonate Producers*

##### **- Primary Carbonate Producers:**

In order to calculate carbonate production rates (G), coral colonies were identified to genus level whilst both colony size (calculated based on linear coverage by the transect tape in this study) and morphology were noted. To date, there are no published growth rates or skeletal densities for corals in the AG with the exception of two species (Table 4.2.3), therefore, for the purpose of this study, general growth rates for coral genus from published literature were used (Table 4.2.3). The data was then inserted in open source datasheets that have been set up with standardized *Reefbudget* equations that automatically calculate the carbonate production rates for each transect. Datasheets can be downloaded for use through: <https://geography.exeter.ac.uk/reefbudget/caribbean/>. The primary carbonate production rates were calculated based on the following equation (Perry *et al.*, 2012):

$$\text{Carbonate production rate} = R_z * ((X_i / 100) \times ((D_i * G_i * 10,000)/1000))$$

where,  $X_i$  = mean percent cover of the  $i$ th species;

$D_i$  = density ( $\text{g cm}^{-3}$ ) of the  $i$ th species

$G_i$  = growth rate ( $\text{cm}\cdot\text{year}^{-1}$ ) of the  $i$ th species

$R_z$  = rugosity for the zone (or transect)

##### **- Secondary Carbonate Producers:**

To calculate secondary carbonate production, the weight per unit area previously derived through the one-year experiment was inserted in the *Reefbudget* calculation sheet in the growth rates column thereby automatically including it in the overall production budget calculation.

**Table 4.2.3. Skeletal densities and linear extension rates of corals (referred to as growth rates) used in the Bahrain reef budget study.**

<b>Coral Genera / Species</b>	<b>Morphology</b>	<b>Skeletal Density (g/cm<sup>3</sup>)</b>	<b>Growth rate (cm/yr)</b>	<b>Location</b>	<b>Source</b>
<i>Galaxea fascicularis</i>	columnar, encrusting, massive	1.9	0.9	China	(Shi <i>et al.</i> , 2009)
<i>Dipsastrea spp.</i> (formely <i>Favia spp.</i> )	encrusting, massive	1.4	0.6	Marshall Islands; China	(Highsmith, 1979; Harriott, 1999; Shi <i>et al.</i> , 2009)
<i>Favites spp.</i>	encrusting, massive	1.5	1.6	GBR	(Browne, 2012)
<i>Leptoseris gardineri</i>	encrusting	1.7	1.7	Cocos Island	(Plucer-Rosario & Randall, 1987)
<i>Millipora spp.</i>	encrusting, plating	2.3	1.5	Marshall Islands; Egypt	(Odum & Odum, 1955; Attalla <i>et al.</i> , 2011)
<i>Montipora spp.</i>	encrusting	1.2	1.6	Cocos Island	(Plucer-Rosario & Randall, 1987)
<i>Platygyra spp.</i>	encrusting, massive	2.3	0.5	UAE	(Howells <i>et al.</i> , 2018)
<i>Pocillopora spp.</i>	submassive	1.4	3.5	Lab based – Jamaica; Field based - Maldives; Marshall Islands	(Buddemeier <i>et al.</i> , 1974; Davies, 1989; Morgan & Kench, 2012)
<i>Porites spp.</i>	massive	1.4	1.3	Mexico	(Elizalde-Rendón <i>et al.</i> , 2010)
<i>Psammocora stellata</i>	encrusting, massive, plating	1.4	1.8	Marshall Islands; Costa Rica; Australia	(Buddemeier <i>et al.</i> , 1974; Guzmán & Cortés, 1989; Roberts & Harriott, 2003)

### ***Carbonate Eroders***

- **Echinoids:** Total area surveyed per transect was 20 sq m. The number of individuals were counted, identified to species level and recorded in the following size class: 0-20 mm, 21-40 mm, 41-60 mm, 61-80 mm, 81-100 mm. Data was then inputted into the open source datasheets downloaded from: <https://geography.exeter.ac.uk/reefbudget/caribbean/>.

Bioerosion rate for echinoids was calculated based on the following equation:

*Bioerosion rate for Echinometra urchins (g/urchin/day) = 0.0007 \* x<sup>1.7309</sup> (where x is the size class of the urchin in millimetres) (Perry et al., 2012)*

- **Scaridae:** Biomass of parrotfish was calculated using published species-specific length-weight relationships as per the rates outlined in the *Reefbudget* datasheets which can be downloaded from: <https://geography.exeter.ac.uk/reefbudget/caribbean/>.

Below outlines the basic equation used for the calculation of parrotfish bite rate. For more information on conversion into bioerosion rate and in depth detail of this method, please refer to Perry et al. (2012).

*Bite rate (h-1) of Scarus spp. = CSc ((3329 – (3.00 x FL) – O)*

where, FL = fork length (cm),

*Scarus* species offset = O

CSc = weighting factor for *Scarus* life phases; 0.85 for terminal phase (TP) and 1 for initial phase (IP) and juveniles.

- **Bioeroding Sponge:**

To determine bioerosion rates by macroborers, the area covered by individual eroding sponge colonies was quantified within a 1 m<sup>2</sup> covering an area of 10 m<sup>2</sup> per transect (n=6). The area



occupied by bio-eroding sponge with visible papillae was measured using a 1x1 cm grid printed on a transparent sheet.

*Percentage of bioeroding sponge surface area = a/b*

whereby: a = surface area of sponge tissue (cm<sup>2</sup>) and b = surface area of belt transect (cm<sup>2</sup>)

Data collected on bioeroding sponge surface size was entered directly into the open access *Reefbudget* datasheets accessible through: <https://geography.exeter.ac.uk/reefbudget/caribbean/>.

Bioeroding sponge bioerosion rates were derived from Perry *et al.* (2012). Globally not much work has been done on internal microbioerosion rates of coral substrate and hence for this study the rates were taken as outlined in Perry *et al.* (2012).

#### **4.2.2.4 | Data Analysis**

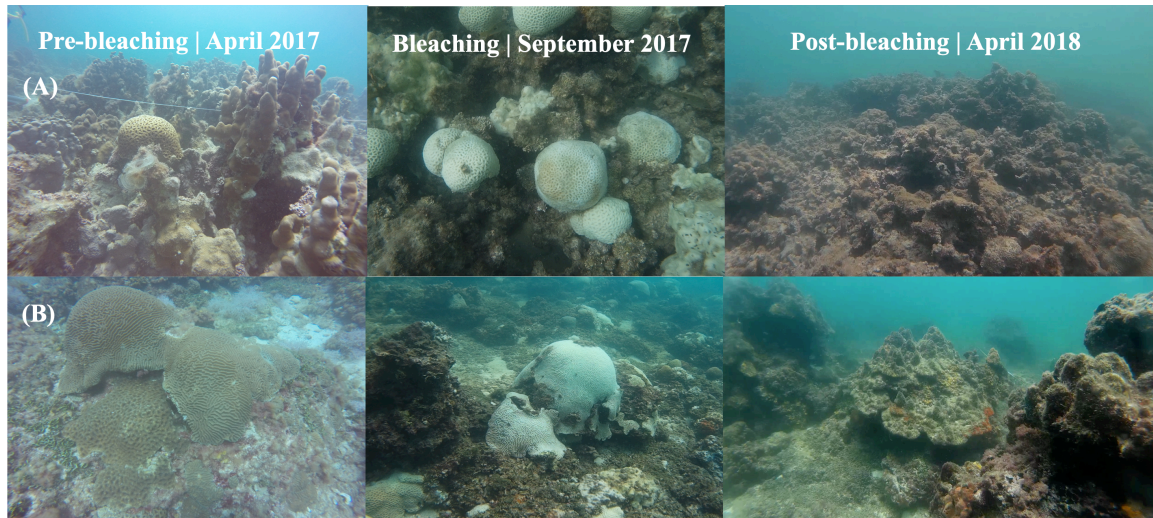
Data analysis was conducted using the software “R” and “RStudio” version 3.5.1 (R, 2018). R statistical packages such as ggplot (Hothorn *et al.*, 2008) and tidyverse (Wickham *et al.*, 2019) were used for plotting maps, processing data and statistical analysis. Generalised linear models (GLMs) were used to test the effects of pre- and post-bleaching events on the percent cover of carbonate producers (i.e. hard coral cover and CCA), rugosity, and density of eroders (i.e. Scaridae and echinoids) at both sites. Likelihood ratio tests (LRT) were conducted to analyse the deviance between null and alternative models to determine the effect of the interaction between bleaching events and sites on the observations using the ANOVA function. The interaction term was included in the model if LRT was found to be significant. Post hoc comparison tests were implemented using the glht functions. Similarly, GLMs were used to test for significant change in the gross carbonate production, gross carbonate erosion and net carbonate production. In addition, ±SE is stated throughout.

## 4.2.3 | RESULTS

### 4.2.3.1 | Site Characterization & Carbonate Budgetary State

#### *Carbonate Producers*

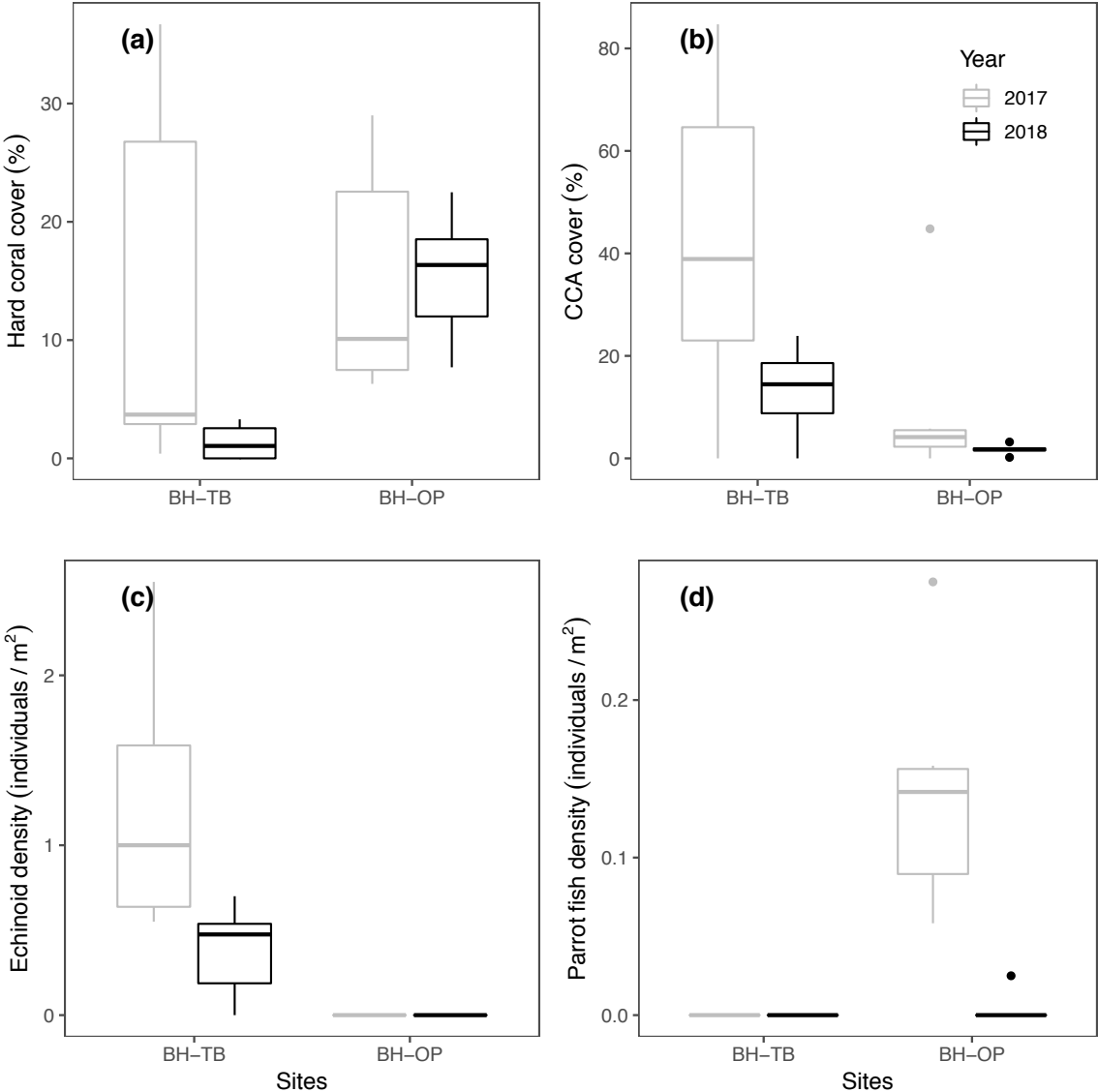
Hard coral cover declined from  $13.6 \pm 6.9\%$  pre-bleaching to  $1.4 \pm 0.6\%$  post-bleaching at BH-TB whilst BH-OP maintained its coral cover, however no significant difference was observed at either site (Figure 4.2.3 and 4.2.4a). Dominant hard corals recorded included *Galaxea sp.*, *Favia sp.*, *Montipora sp.*, *Porites sp.* and *Pocillipora sp.* all of which were either massive, sub-massive or encrusting with no branching corals observed at any of the study sites. CCA cover was extremely high in BH-TB pre-bleaching (mean =  $42.2 \pm 12.9\%$ ), however, this declined significantly to  $29.0 \pm 10.7\%$  (GLM,  $z = -2.7$ ,  $p < 0.05$ ) post-bleaching. CCA was also observed to decline in BH-OP post-bleaching by  $8.4 \pm 10.7\%$  (pre-bleaching mean =  $10.1 \pm 7.0\%$ ; post-bleaching mean =  $1.73 \pm 0.4\%$ ; Figure 4.2.4b). In addition, reef rugosity decreased by 5.4% ( $0.9 \pm 0.02$  to  $0.9 \pm 0.01$  post-bleaching) in BH-OP post-bleaching whereby in BH-TB a negligible decrease was recorded. Figure 4.2.5 illustrates the change in benthic community composition of the reefs both pre and post bleaching reflecting the change in structure following the 2017 bleaching event. It is important to note that in both cases, pre- and post-bleaching, the primary carbonate producers were noted to be massive and sub-massive coral colonies. No branching coral colonies were observed throughout the survey period at both study sites.



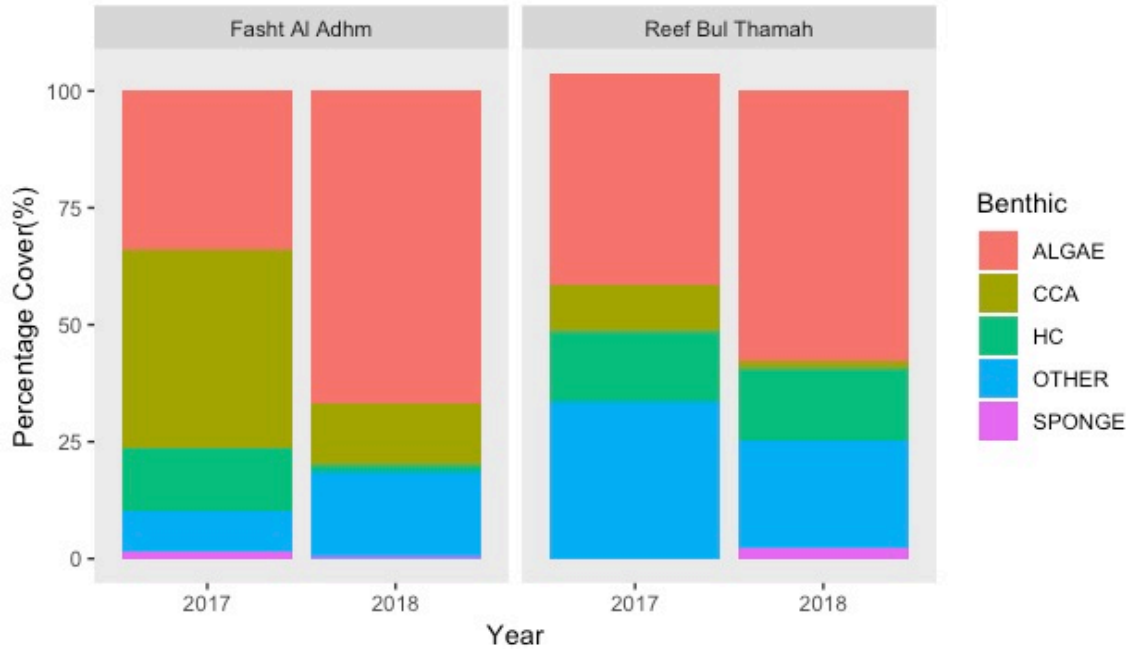
**Figure 4.2.3. Shifts in reef structural dynamics (2017-2018) pre and post the 2017 bleaching (a) Fasht Al Adhm (BH-TB) and (b) Reef Bul Thamah (BH-OP).**

### ***Carbonate Eroders***

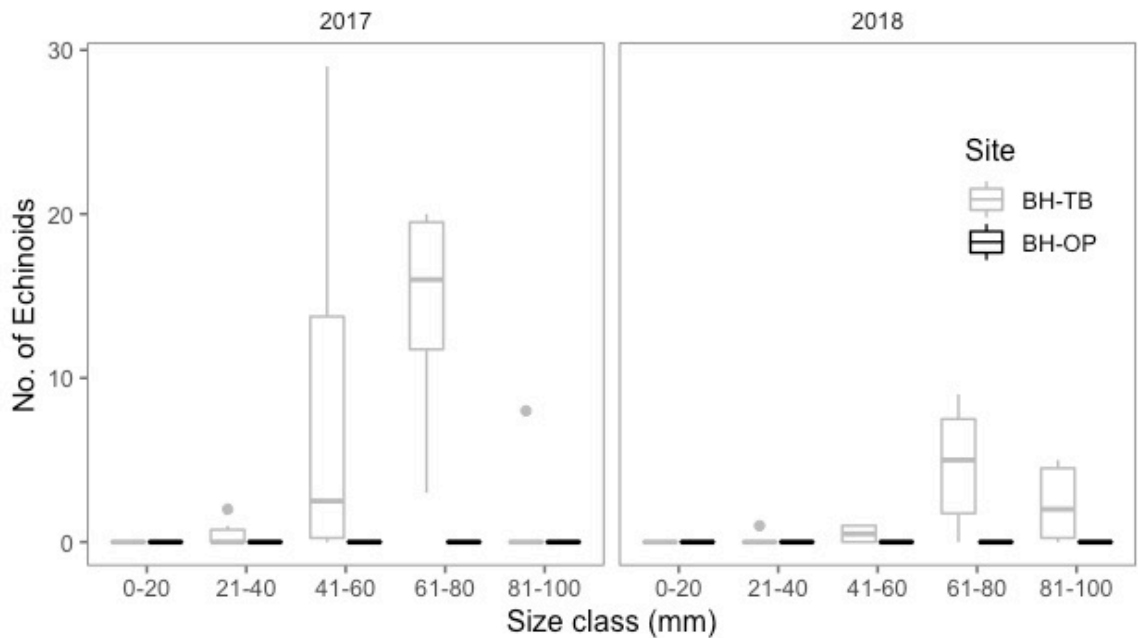
Echinoid densities were observed to be higher pre-bleaching ( $25.0 \pm 6.4$  individuals per  $20 \text{ m}^2$ ) with a significant reduction by  $63.5 \pm 14.9 \%$  post-bleaching at BH-TB (GLM,  $z = 3.6$ ,  $p < 0.05$ ) (Figure 4.2.4c), whilst no parrotfish were observed both pre- and post-bleaching (Figure 4.2.4d). On the contrary, no echinoids were recorded in BH-OP both pre- and post-bleaching; however, parrotfish were recorded ( $17.0 \pm 3.8$  individuals per  $120 \text{ m}^2$ ) in BH-OP pre-bleaching whilst none were recorded post-bleaching (Figure 4.2.4d). *Echinometra mathei* (short spined urchin) was the only species of echinoids recorded along the study transects at BH-TB throughout the study period whereas in BH-OP no echinoids were observed. Despite the decline recorded in the number of echinoids in 2018, the size classes of echinoids recorded post bleaching was seen to be higher (Figure 4.2.6).



**Figure 4.2.4. Mean percentage cover of carbonate producers in 2017 and 2018: (a) Hard corals (n=6) and (b) CCA = Crustose Coralline Algae (n=6); Mean density (count per unit m<sup>2</sup>) of carbonate eroders: (c) Echinoids (n=6; area=20m<sup>2</sup> per transect; BH-TB) and (d) Parrotfish (n=3; area=120m<sup>2</sup> per transect) at both study sites in Bahrain.**

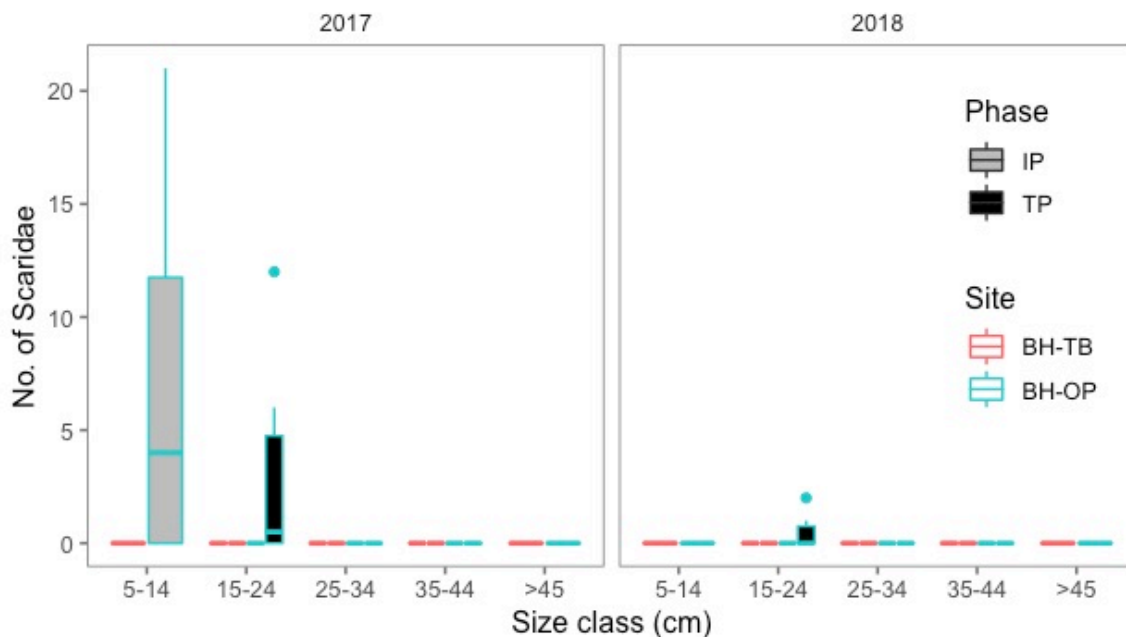


**Figure 4.2.5. Mean percentage cover (%) of the reef benthic community structure pre (2017) and post (2018) bleaching at both study sites (n=6).**



**Figure 4.2.6. Total abundance of echinoids recorded based on size class pre and post bleaching at both study sites (n=6).**

In 2017, 100% of the parrotfish recorded were scrapers, most of which were in their initial phase of life (Figure 4.2.7) whilst in 2018, despite the decline observed in parrotfish abundance, 66.7% were scrapers whilst the remaining 33.3% were excavators all of whom were in their terminal phase (Figure 4.2.7). Species observed were restricted to three species (*Chlorurus sordidus*, *Scarus ghobban* and *Scarus persicus*).



**Figure 4.2.7. Total abundance of Scaridae recorded in 2017 and 2018 based on size class (IP = initial phase / juveniles; TP = terminal phase / adults) pre and post bleaching at both study sites (n=6).**

#### 4.2.3.2 | Carbonate Budgetary State – Pre- and Post Bleaching (2017-2018)

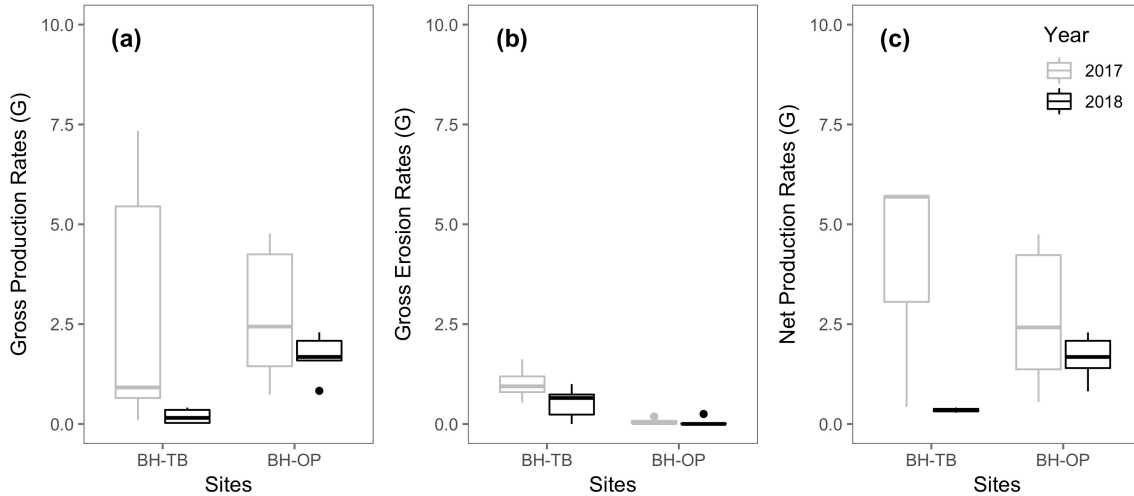
Gross carbonate production rates decreased in both study sites with BH-TB showing a decrease from  $2.8 \pm 1.4$  G pre-bleaching to  $0.2 \pm 0.1$  G post-bleaching (Figure 4.2.8a). Similarly, BH-OP experienced a decline in gross carbonate production from  $2.7 \pm 0.7$  G to  $1.7 \pm 0.2$  G pre to post-bleaching respectively (Figure 4.2.8a). In terms of gross carbonate erosion, BH-TB had a higher rate

of gross erosion amounting to  $1.0 \pm 0.4$  G pre-bleaching which was seen to significantly decrease by 50% ( $0.5 \pm 0.0001$  G) post bleaching (GLM,  $z = 0.03$ ,  $p < 0.05$ ) (Figure 4.2.8b). The majority of erosion at this site is dominated by echinoids followed by bioeroding sponges, whilst in BH-OP, although erosion was dominated by parrotfish with some contribution from bioeroding sponge, parrotfish erosion is observed to be minimal (Table 4.2.4). BH-OP witnessed a negligible decrease in gross carbonate erosion from  $0.1 \pm 0.03$  G pre-bleaching to  $0.04 \pm 0.04$  G post-bleaching (Figure 4.2.8b).

**Table 4.2.4. Erosion rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G) by major bio-eroders at study sites (2017-2018).**

	BH-TB		BH-OP	
	2017	2018	2017	2018
Echinoids	$1.0 \pm 0.2$	$0.5 \pm 0.2$	0	0
Parrotfish	0	0	$0.1 \pm 0.02$	$0.04 \pm 0.04$
Bio-eroding Sponge	$0.002 \pm 0.0004$	$0.003 \pm 0.0001$	0	$0.002 \pm 0.0001$

Overall, major decreases in the net carbonate production rates were recorded on Bahraini reefs. BH-TB showed a steep decline in net carbonate production rate following the 2017 bleaching (pre =  $1.8 \pm 1.8$ ; post =  $-0.3 \pm 0.2$  G) indicating a shift from a positive budget state to a negative budget state (Figure 4.2.8c). BH-OP also demonstrated a major decline in net carbonate production from  $2.7 \pm 0.7$  to  $1.7 \pm 0.4$  G but remains in a low positive budgetary state.



**Figure 4.2.8. Reef carbonate budget rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G; 2017-2018) across study sites pre- and post- the 2017 bleaching illustrating (a) Gross Carbonate Production; (b) Gross Carbonate Erosion; (c) Reef Growth in the form of Net Carbonate Production.**

#### 4.2.4 | DISCUSSION

This study aimed to characterise the benthic composition of reefs in Bahrain in order to quantify the rate of carbonate production and erosion whilst assessing the change in their budgetary state pre and post the 2017 severe bleaching. The following discussion presents the inference of the obtained results and the implication of bleaching on the reef structural integrity on Bahraini reefs.

##### 4.2.4.1 | Site Characterisation & Carbonate Budgetary State

Hard coral (primary reef producers) live cover was observed to drastically decline in BH-TB following the 2017 severe bleaching, heavily impacting the accretional health of this reef. In 2012, it was reported that the live coral coverage in this site averaged 9.8% (Burt *et al.*, 2013). Our results from 2017 indicated that this reef was recovering between 2010-2017, where coral cover had reached  $13.6 \pm 6.9\%$  despite facing two bleaching events in that duration. Unfortunately, following the 2017 bleaching event, coral cover decreased to  $1.4 \pm 0.6\%$  at this site. One of the factors that



could have contributed towards this steep decline could be the depth of the reef (<7 m). The recovery witnessed prior to the 2017-bleaching event creates a positive outlook for the post 2017 bleaching period as temporal data indicates the reef's ability for recovery despite encountering multiple bleaching events in previous years (e.g. 1998 and 2010; see Chapter 2 for further details). Therefore, monitoring is crucial for the carbonate budgets of these sites to detect the rate of recovery in the coming years. On the contrary, BH-OP which is an offshore and deeper site (>10 m) saw a 2% increase in coral cover reaching  $14.8 \pm 4.1\%$  in 2018, maintaining its coral cover, which was reported to be 16.3% in 2012 (Burt *et al.*, 2013). It is important to note that reefs in Bahrain are known to be impacted by various anthropogenic activities such as reclamation and dredging which has contributed significantly towards diminishing coral cover (Burt *et al.*, 2013; Naser, 2012). Interestingly, CCA (secondary reef producers) percentage cover was extremely high in BH-TB pre-bleaching (mean =  $42.2 \pm 12.9\%$ ), which could be due to the presence of high rubble cover caused by previous dredging activities in the area (Vousden, 1988). In addition to being an important carbonate producer, CCA plays an important role in binding the reef together through colonising reef substrate thereby contributing extensively towards its cementation and stability (Fujita *et al.*, 2009; Langer, 2008; Perry & Hepburn, 2008; Rasser & Riegl, 2002). This in turn, promotes accretion, enhances larval recruitment of various organisms and maintains wave resistance reef fronts (Rasser & Riegl, 2002; Mallela & Perry, 2007). During the field surveys in April 2017, extensive rubble binding was witnessed following what was suspected to be a dredging event (c. 10 years), this would also explain the rise in coral cover between the period 2010 and 2017.

### ***Carbonate Eroders & Bioerosion***

Erosion rates in Bahrain both pre and post bleaching (0.04-1.9 and 0.04-0.5 G respectively) are generally seen to be comparable with other regions (e.g. Caribbean = 1.0-2.8 G (Perry *et al.*, 2012)

and the Red Sea = 1.9-2.9 G (Roik *et al.*, 2017)). Erosion rates by echinoids quantified in this study for Bahrain fall below previous recorded rates (0.9-1.4 g urchin<sup>-1</sup> d<sup>-1</sup>) for the region (Bak, 1994b). This could be because erosion in general was observed to be on the lower scale. Lastly, although parrotfish were observed in BH-OP pre-bleaching, they were observed in low numbers, whilst none were found in BH-TB. This could be attributed to extensive overfishing activities at both sites (Morgan, 2006). Despite BH-OP being a marine national park, there is no law enforcement or patrol in the area. Erosion rates in Bahrain caused by bio-eroding sponges were noted to be almost negligible (0.002-0.003 G). Despite the low contribution, it is considered within the reported ranges when compared to other studies globally (Brazil = 0.2–3.0 G; Reis & Leão, 2000), Bonaire (Caribbean) = 0.01-0.1 G (Perry *et al.*, 2012) and Gulf of Aqaba (Red Sea) = 0.3 G (Zundeleovich *et al.*, 2007). Bioerosion was higher in BH-TB, this could possibly be attributed to turbidity at the site which is likely to affect erosion rates which is known to be influenced by various environmental parameters such as depth and turbidity (Mallela, 2007; Perry & Hepburn, 2008).

#### 4.2.4.2 | Carbonate Budgetary State – Pre- and Post Bleaching (2017-2018)

Thermal anomalies are known to reduce calcification rates in corals (De'ath *et al.*, 2009) and therefore reef accretion. This is witnessed in previous studies such as in the Seychelles, which utilised a 20 year dataset and reported a 62.5% difference in reef accretional rates post-bleaching (-1.5 G; erosive state) compared to pre-bleaching (~4 G; positive state; Januchowski-Hartley *et al.*, 2017). The results from this study show a similar trend, highlighting a decrease in the Bahraini reef budget by 114.5% at BH-TB (pre = 1.8 ± 1.8; post = -0.3 ± 0.2 G) and by 36.3 % at BH-OP (2.7 ± 0.7 to 1.7 ± 0.4 G). It is important to note that in this study, there might have been an over-estimation of coral growth rates, since rates used for the *ReefBudget* calculation were not site specific due to unavailable published literature on coral growth rates in the AG with the exception of

two species (*Platygyra daedalea* and *Cyphastrea microphthalma*; Howells *et al.*, 2018) . For the purpose of this study, growth rates from different bioregions were used for estimating the carbonate production rates. Similarly CCA and other secondary producers growth rates could be overestimated as utilizing different experimental substrates could yield different results (Mallela *et al.*, 2017). To our knowledge, to date, no study has been conducted to quantify carbonate budgets of reefs in Bahrain or the AG making this the first attempt. In general, Bahraini reef accretion rates (including pre and post bleaching; range between -0.3 to 2.7 G) were seen to be in the lower scale of accretion, most similar to the Caribbean (e.g. Jamaica = 1.1; Land, 1979 and Barbados = 4.5 G; Scoffin *et al.*, 1980). Both sites retained low gross erosion rates accompanying low gross production rates.

In conclusion, reefs in the AG are unique, particularly in relation to the capability of corals to sustain themselves in such extreme environmental conditions with seasonal temperature fluctuations. However, SST warming events, which are projected to increase in frequency and intensity with climate change, are jeopardizing the resilience of these reefs. Based on these trends, suppressed budgetary states are predicted for reefs in the AG. This, along with associated IPCC projected sea level rise, will limit the capacity of Bahraini reefs to perform their natural breakwater function and therefore may threaten island stability.

### 4.3 | STATUS & TREND OF REEF CARBONATE BUDGETS IN THE PROTECTED AREA OF CURIEUSE ISLAND, SEYCHELLES

#### ABSTRACT

Coral reefs rely on their structural complexity, which underpins their ecological functioning. Reefs in the Seychelles (Western Indian Ocean) were severely impacted by the thermal anomalies experienced in 2015-2016, which triggered intense bleaching globally. In this study, accretional health of reef sites are assessed around Curieuse Island post-2016 bleaching, including change in carbonate producer and eroder composition, their geomorphic state and a comparison of the reefs budgetary state is made to those reported prior to the 2016 event. Live coral cover was observed to decline by 51% overall between 2017-2018 resulting in a decrease in the mean net carbonate production from  $5.8 \pm 0.6$  to  $0.8 \pm 1.3$  kg CaCO<sub>3</sub> m<sup>2</sup> yr<sup>-1</sup> between 2017 – 2018, with the main contributors to gross carbonate production being stress-tolerant coral taxa (e.g. *Porites spp.*), with minimal contribution from the branching *Acropora spp.* When compared to rates reported prior to the 2016 event, the budgetary state of these reefs are observed to be shifting into a negative state. The current trajectories indicate a steady decline with low rates of recovery similar to those observed on the majority of reefs worldwide. The study highlights a rapid shift into an erosive state, threatening structural integrity and ability to cope with rising sea levels in light of global warming.

#### 4.3.1 | INTRODUCTION

Coral reefs are undeniably valuable worldwide from an ecological and economical aspect, benefiting approximately one billion people through their ecosystem services ranging from coastal protection to food security and the provision of livelihoods (Spalding *et al.*, 2017). Some of these services include benefiting ~200 million people who live below 10 m elevation and within 50 km of reefs as

these coral reefs dissipate 97% of the energy that would otherwise hit shorelines (Ferrario *et al.*, 2014; Woodhead *et al.*, 2019). In addition to reefs contributing towards generating income through reef tourism, estimated to be worth ca. US \$35.8 billion dollars per annum globally, reefs also contribute towards reducing annual expected damages from storms across reef coastlines, by more than \$4 billion (Woodhead *et al.*, 2019). Despite their high ecological and economic value, coral reefs worldwide are highly threatened and are witnessing a sharp and serious decline with an estimate of 30% of reefs already lost or severely damaged whilst predictions estimate that 60% of reefs will be lost by 2030 (Wilkinson, 2000; Hughes *et al.*, 2003). Coral reefs have been identified as the most vulnerable biome to the climate emergency according to probability estimates (with very high confidence) in the ‘*Ocean and Cryosphere in a Changing Climate*’ IPCC special report (IPCC, 2019). Ocean warming, a byproduct of global warming, is considered as the most significant threat to coral reefs, as elevated sea temperatures are associated with coral bleaching events which impact coral mortality depending on their intensity and frequency thereby hindering reefs long-term ability to survive (Hoegh-Guldberg, 1999; Donner *et al.*, 2005).

The severity and intensity of the recent global 2015-2016 El Niño-induced coral bleaching event has impacted reefs worldwide in a manner comparable to that observed following the 1997-1998 bleaching event on both spatial and magnitude scale (Hughes *et al.*, 2018a). Both events have severely impacted coral mortality and recovery rates on the majority of reefs worldwide (Ampou *et al.*, 2017; Hughes *et al.*, 2017a, 2018b; Monroe *et al.*, 2018); compromising their structural integrity due to the decrease in coral cover and changing species composition (Januchowski-Hartley *et al.*, 2017; Perry & Morgan, 2017; Lange & Perry, 2019). The recovery trajectories of reefs following a bleaching event is said to vary and is influenced by various factors including the degree of reef resilience and local anthropogenic stresses (Graham *et al.*, 2015; Courtney *et al.*, 2018).

Coral reefs' three-dimensional framework is constructed from a calcium carbonate ( $\text{CaCO}_3$ ) skeleton produced by primary carbonate reef builders (e.g. hermatypic corals) and bound together by secondary carbonate producers (e.g. coralline algae; Perry *et al.*, 2008). The ability of coral reefs to sustain their 3-D structural integrity is reliant on a delicate balance between the rate of carbonate production and erosion (removal), whereby reefs are said to be in a positive state if their carbonate production is higher than their erosion and are in a negative state vice-versa (Perry *et al.*, 2012). The consequence of declining reef carbonate production threatens reef accretion thus impacting the capacity of coral reefs to cope with sea level rise (SLR) (Perry *et al.*, 2018a). The question remains as to whether impacted reefs can recover from intense bleaching events and re-establish their vertical growth potential, and if so, what is the time frame required for such recovery? Few studies have quantified changes in reef carbonate production post-bleaching (Januchowski-Hartley *et al.*, 2017; Perry & Morgan, 2017; Ryan *et al.*, 2019) whilst even fewer examined the impacts on reefs' geomorphic state following severe bleaching events (Lange & Perry, 2019).

In 1994, the Seychelles (Western Indian Ocean) was documented to harbour reefs characterised by their high structural complexity and rich live branching and massive coral cover (Graham *et al.*, 2006). Unfortunately, reefs in the inner Seychelles were reported to have suffered >90% coral cover loss as a result of the 1998 bleaching event (Goreau *et al.*, 2000; Sheppard, 2003) leading to the collapse of their structural complexity with reports of slow recovery rates (Graham *et al.*, 2015). Januchowski-Hartley *et al.* (2017) assessed reef carbonate budgets in the Seychelles using a twenty-year dataset (1994 – 2014). Results indicated that the overall average net carbonate budget has declined from  $\sim 4 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  (pre-bleaching) to  $-1.5 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  (post-bleaching), which illustrates the extent of damage on these reefs. Even though some reefs have recovered post-bleaching, little evidence is available that indicates reefs will return to a net positive budget state in the future. In 2016, the Seychelles like many parts of the world, experienced a prolonged heat wave

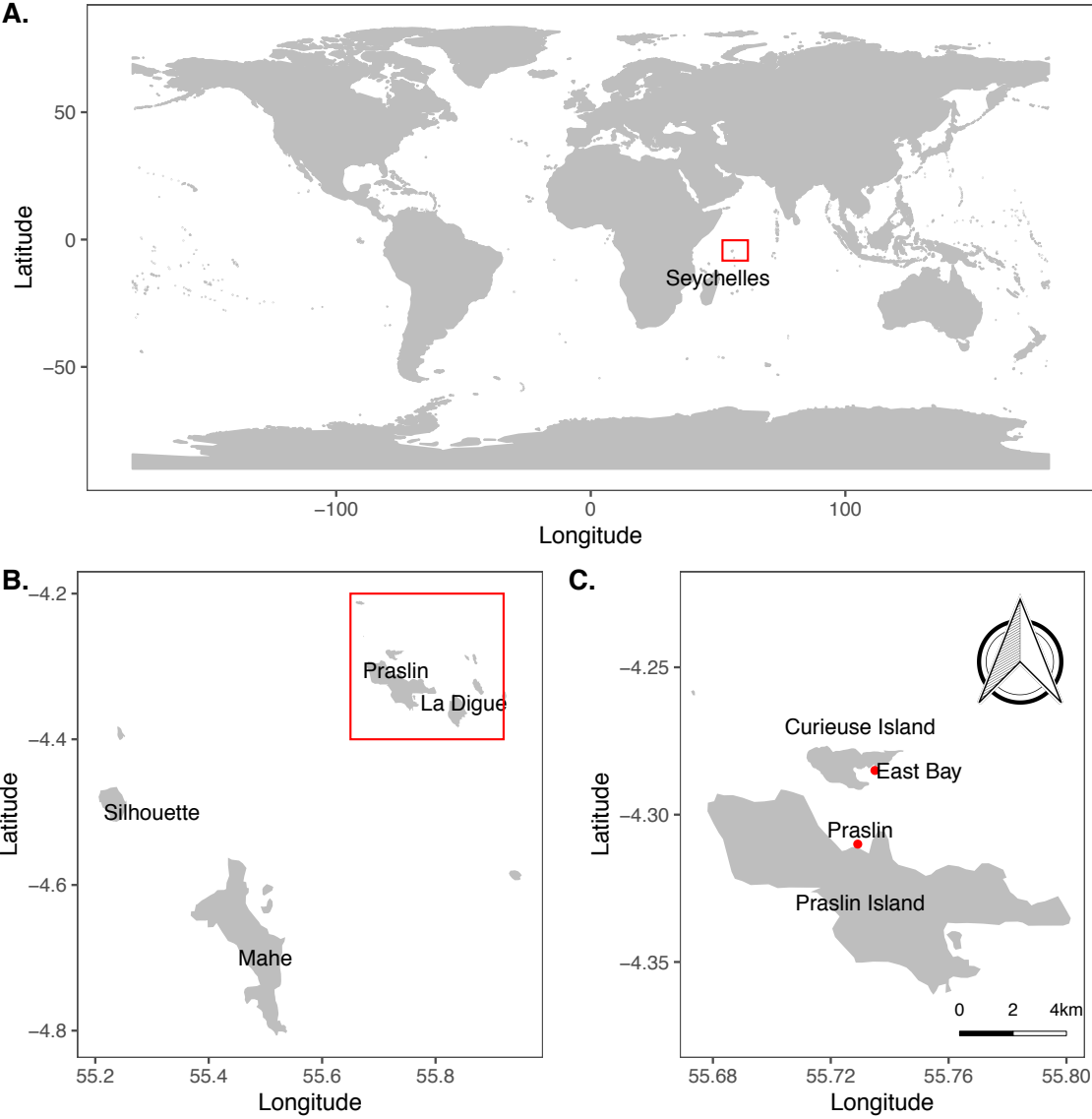
where cumulative heat stress on the reefs exceeded 10 Degree Heating Weeks (DHW), highly impacting coral mortality (Gardner *et al.*, 2018).

Januchowski-Hartley *et al.* (2017) is the first study on carbonate budgets in the Seychelles whereby their study tracked change in reef carbonate budgets over time through modeling with their last sampling point ending in 2014. Therefore, this research aims to (1) quantify reef carbonate production and erosion rate of reefs in the Seychelles following the 2015-2016 bleaching event; (2) examine the change in geomorphic state of reefs and; (3) compare the quantified budget post-bleaching to that reported in the previous study conducted in order to determine the magnitude of change and trajectory of these reefs.

### **4.3.2 | MATERIALS & METHODS**

#### **4.3.2.1 | Site descriptions**

Two fringing carbonaceous reef sites within Curieuse Marine National Park (CMNP) in the Seychelles (Figure 4.3.1) were investigated in April 2017 & 2018. Reefs from both turbid (Praslin Island; 4°18'35"S 55°43'28"E) and relatively clear-water (herein referred to as optimal - East Bay; 4°16'55"S 55°44'32"E) sites were selected with sampling occurring at approximately 10 m (see Table 4.3.1 for environmental characteristics of sites).



**Figure 4.3.1. Location of Study Sites – (a) Location of Seychelles; (b) Map of the main islands of the Seychelles and; (c) Location of selected study sites within the Seychelles [Site codes: East Bay (SY-OP) and Praslin (SY-TB)].**



**Table 4.3.1. Site description and characterisation of study sites within Curieuse Marine National Park, Seychelles.**

Site	Site Code	Depth (m)	Temp. (°C)	Salinity (ppt)	Sedimentation rates (g cm <sup>-2</sup> d <sup>-1</sup> ± SE)**	Light attenuation (K <sub>d</sub> PAR; m <sup>-1</sup> )***	Site Description
<b>Praslin (Turbid)</b>	SY-TB	5-10	25-29	~35	0.03±0.01	0.2-0.4	This reef is located ~1.5 km southwest Curieuse Island and is subjected to large sediment load since it is located closer to Praslin island, which has intensive tourist marine activities.
<b>East Bay (Optimal)*</b>	SY-OP	5-12					This reef is located ~1.5 km southeast Curieuse Island and is considered one of the least impacted sites with minimum anthropogenic impacts. Carbonate fringing reefs with minimal tourist activity.

\* Clear water in this study is referred to as optimal, so in this case site East Bay is considered to be an optimal site.

\*\* Sedimentation rates were measured at 10m depth across all sites using sediment traps, however, due to expedition time constraints the traps were only deployed for a total of 4 days.

\*\*\* Light attenuation coefficients (K<sub>d</sub> (PAR), m<sup>-1</sup>) for each site was obtained from Gardner *et al.*, (2018)

#### 4.3.2.2 | Quantifying the Carbonate Budgetary State

Quantitative data such as benthic composition, rugosity, carbonate producers and eroders were obtained through surveying field transects as outlined in Table S3.1 (see Supplementary Material; S3) along each reef site as per the standardised methodology for collecting budgetary data *ReefBudget* (Perry *et al.*, 2012, 2018b). Data collected was used to calculate CaCO<sub>3</sub> production and erosion rates (kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> hereafter expressed as G whilst ± represents the SE of all values stated). It is important to note that slight modifications were made to the *ReefBudget* methodology, which was originally designed for Caribbean reefs (Perry *et al.*, 2012) and then developed for the Indo-Pacific reefs (Perry *et al.*, 2018b). Details of these modifications are given and explained in the supplementary material section S3.1.

#### 4.3.2.3 | Data analysis

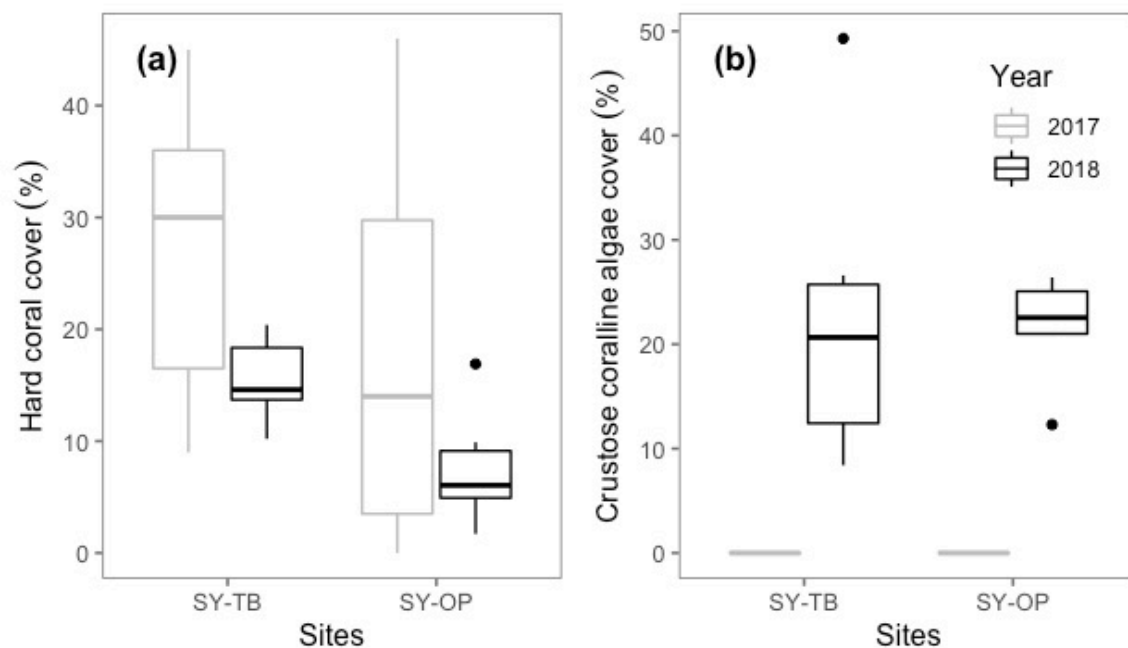
Data analysis was done using the software “R” and “RStudio” version 3.5.1 whereby different R statistical packages were used such as ggplot and tidyverse for plotting maps, processing data and statistical analysis (Hothorn *et al.*, 2008; R, 2018). In addition, the analysis of variance (ANOVA) was used to test for differences in gross carbonate production, gross carbonate erosion and net production between and within sites across years (2017-2018). Furthermore, to test for differences in carbonate production rates between branching and massive corals at each site, ANOVA was conducted.

### 4.3.3 | RESULTS

#### 4.3.3.1 | Site Characterization & Carbonate Budgetary State

##### *Carbonate Producers*

Live coral cover at both sites SY-OP and SY-TB declined by 43.4% and 58.3% respectively between April 2017 and April 2018 (Figure 4.3.2a). On the contrary, CCA cover increased at both sites from none observed in 2017 to  $22.7 \pm 6.1\%$  in SY-OP and  $21.7 \pm 2.1\%$  in SY-TB (Figure 4.3.2b). In addition, rugosity was noted to decrease by  $3.9 \pm 0.2\%$  and  $3.8 \pm 0.2\%$  in SY-OP and SY-TB respectively. Carbonate production rates by primary carbonate producers also decreased at both sites between 2017-2018 (Table 4.3.2) whilst production by secondary carbonate producers was noted to have a minimal contribution in 2018 whereas in 2017 no contribution was observed to carbonate production (Table 4.3.2).



**Figure 4.3.2. Mean percentage cover of carbonate producers between 2017-2018 (a) Hard coral cover (n=6) and (b) CCA = Crustose Coralline Algae (n=6).**

**Table 4.3.2. Carbonate production rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G) by primary and secondary producers in 2017 and 2018 at the study sites in the Seychelles (n=6; G $\pm$ SE).**

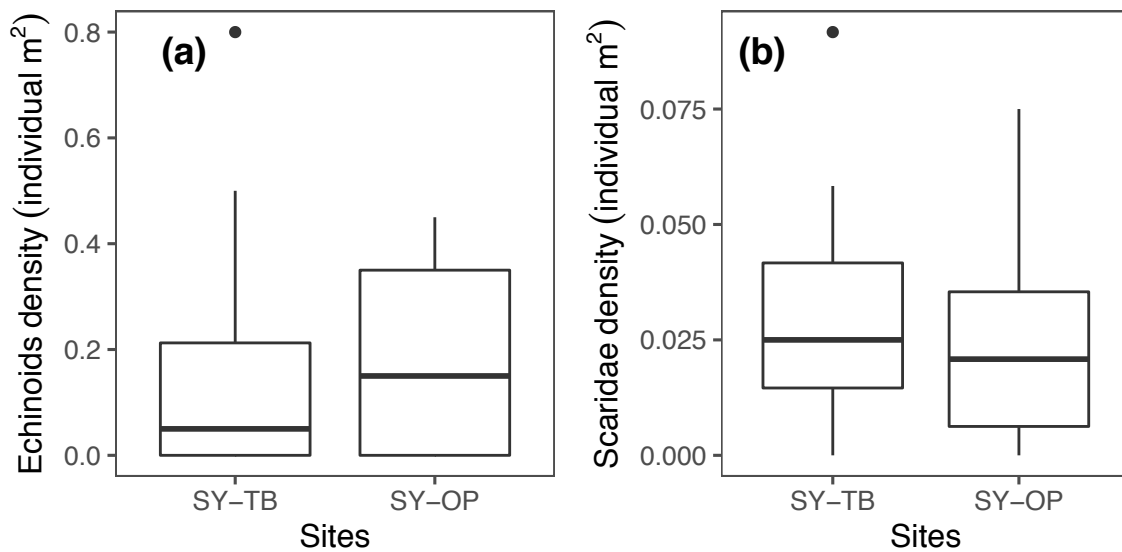
	SY-OP		SY-TB	
	2017	2018	2017	2018
<b>Primary Production</b>	3.9 $\pm$ 0.9	2.6 $\pm$ 0.2	2.6 $\pm$ 1.2	1.1 $\pm$ 0.3
<b>Secondary Production</b>	0 $\pm$ 0	0.1 $\pm$ 0.3	0 $\pm$ 0	0.1 $\pm$ 0.01

### ***Carbonate Eroders***

Echinoid densities were observed to remain fairly stable at SY-OP (2017 = 0.02  $\pm$  0.1; 2018 = 0.1  $\pm$  0.1 individuals per 20 m<sup>2</sup>) and SY-TB (2017 = 0.2  $\pm$  0.1; 2018 = 0.1  $\pm$  0.1 individuals per 20 m<sup>2</sup>) in both years (Figure 4.3.3a). Similarly, Scaridae densities remained stable at both SY-OP (2017 = 0.02  $\pm$  0.01; 2018 = 0.04  $\pm$  0.01 individuals per 120 m<sup>2</sup>) and SY-TB (2017 = 0.02  $\pm$  0.01; 2018 = 0.04  $\pm$  0.01 individuals per 120 m<sup>2</sup>) between 2017-2018 (Figure 4.3.3b). Species of echinoids noted along the transects at both sites were restricted to three, mainly: *Echinometra mathei*, *Diadema setosum* and *Echniothrix sp.* size classes of echinoids were at the higher range (81-100 mm) in both years at both study sites (Figure 4.3.4).

In 2017, excavator Scaridae were recorded in abundance at both sites (SY-OP = 65% and SY-TB = 83%) whilst the remaining were scrapers most of which were in their terminal phase of life (Figure 4.3.5). In 2018, the contrary was observed in SY-TB whereby, 57% were scrapers whilst the remaining 43% were excavators while in SY- OP, excavators fairly maintained their position (64%; Figure 4.3.5). Seven species of Scaridae were recorded in this study (*Cetoscarus biocolor*, *Chlorurus sordidus*, *Chlorurus bleekeri*, *Scarus ghobban*, *Scarus niger*, *Scarus oviceps* and *Scarus*

*flavipectoralis*). Most of the Scaridae recorded were observed to be in the terminal phase in 2017 at both sites however, in 2018, Scaridae were recorded in a variety of size class and in both the initial and terminal phase (Figure 4.3.5).



**Figure 4.3.3. Mean density (count per unit m<sup>2</sup>) of carbonate eroders (2018): (a) Echinoids (n=6; area=20m<sup>2</sup> per transect) and (b) Scaridae (n=6; area=120m<sup>2</sup> per transect) at both study sites.**

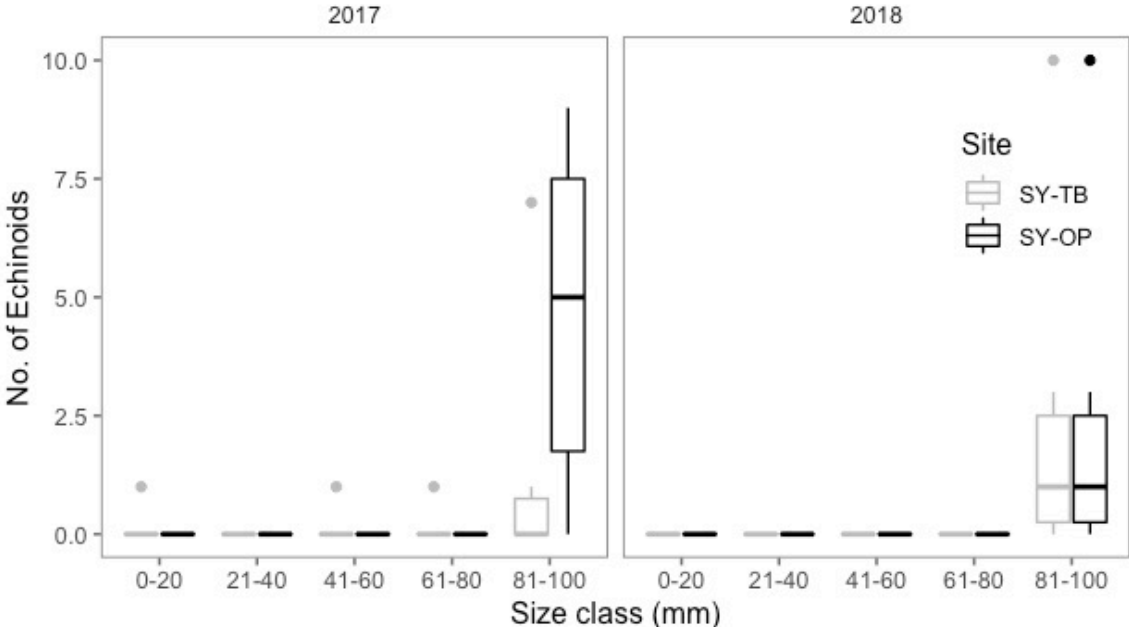


Figure 4.3.4. Total abundance of echinoids (2017-2018) recorded based on size class at both study sites (n=6).

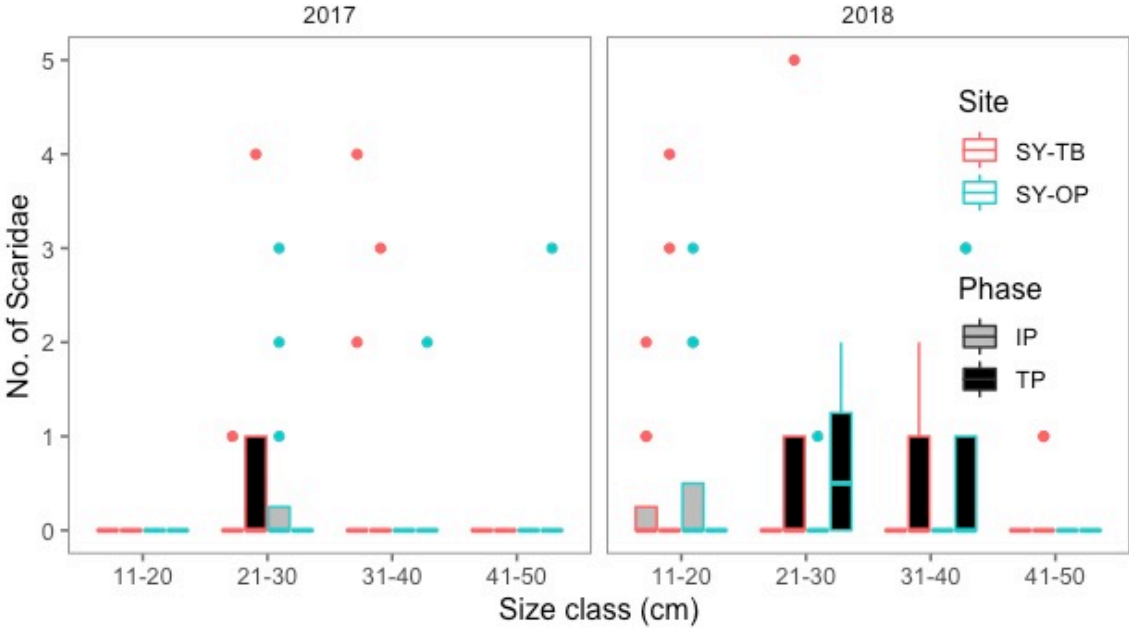
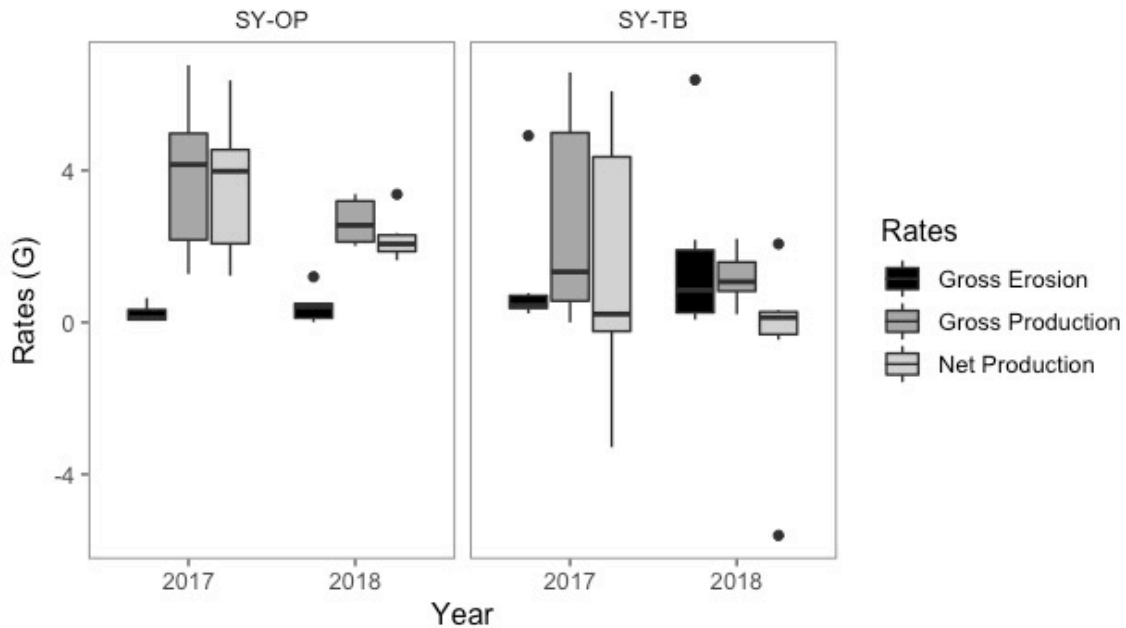


Figure 4.3.5. Total abundance of Scaridae (2017-2018) recorded based on size class (IP = initial phase / juveniles; TP = terminal phase / adults) pre and post bleaching at both study sites (n=6).

#### 4.3.3.2 | Carbonate Budgets

Gross carbonate production rates decreased in both study sites with SY-OP showing a decrease from  $3.9 \pm 0.9$  G in 2017 to  $2.6 \pm 1.2$  G in 2018 (Figure 4.3.6). Similarly, SY-TB reported a decline in gross carbonate production from  $2.6 \pm 0.3$  G in 2017 to  $1.2 \pm 0.3$  G in 2018 (Figure 4.3.6). There was a significant difference in gross carbonate production rates between sites in 2018 ( $F_{(1,10)} = 14.9$ ,  $p < 0.05$ ) but not in 2017 ( $F_{(1,10)} = 0.7$ ,  $p > 0.05$ ). Gross carbonate erosion at SY-TB was observed to have minimal change between 2017-2018 (2017 =  $1.2 \pm 0.7$  G; 2018 =  $1.7 \pm 1.0$  G), this was also observed in SY-OP (2017 =  $0.2 \pm 0.1$ ; 2018 =  $0.4 \pm 0.2$  G) although between the two sites, SY-TB had a higher rate of erosion (Figure 4.3.6). The majority of erosion at SY-OP is shared equally between echinoids and Scaridae with negligible erosion done by bioeroding sponges, whilst in SY-TB, erosion was mostly by Scaridae with some contribution from echinoids (Table 4.3.3). In general, bioerosion from echinoids and Scaridae is considered to be minimal at both sites (Table 4.3.3) whilst bioerosion caused by bio-eroding sponge is considered to be negligible (Table 4.3.3). Overall, major decreases in the net carbonate production rates were recorded on both reefs as a result of a decrease in live hard coral cover. SY-OP demonstrated a major but non-significant decline ( $F_{(1,10)} = 2.8$ ,  $p > 0.05$ ) in net carbonate production from  $3.6 \pm 0.8$  to  $1.4 \pm 1.5$  G, despite this, it remains in a low positive budgetary state (Figure 4.3.6). However, SY-TB showed a steep decline (although not statistically significant;  $F_{(1,10)} = 1.2$ ,  $p > 0.05$ ) in net carbonate production rate within a one-year period (2017 =  $2.2 \pm 0.3$ ; post =  $-0.6 \pm 1.1$  G) indicating a shift from a positive budget state to a negative budget state (Figure 4.3.6). Net carbonate production was observed to be significantly different between sites in 2017 ( $F_{(1,10)} = 6.5$ ,  $p < 0.05$ ) but not in 2018 ( $F_{(1,10)} = 1.6$ ,  $p > 0.05$ ) as SY-OP dips into the lower scale of net reef budgets.



**Figure 4.3.6. Reef carbonate budget rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G; 2017-2018) across study sites illustrating Gross Carbonate Production; Gross Carbonate Erosion and Reef Growth in the form of Net Carbonate Production.**

**Table 4.3.3. Erosion rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G) by major bio-eroders at study sites ( $n=6$ ;  $G \pm \text{SE}$ )**

	SY-OP		SY-TB	
	2017	2018	2017	2018
<b>Echinoids</b>	$0.1 \pm 0.2$	$0.2 \pm 0.3$	$0.3 \pm 0.2$	$0.2 \pm 0.3$
<b>Scaridae</b>	$0.1 \pm 0.1$	$0.2 \pm 0.3$	$0.9 \pm 2.0$	$1.5 \pm 2.5$
<b>Bio-eroding Sponge</b>	$0.03 \pm 0.04$	$0.01 \pm 0$	$0 \pm 0$	$0.01 \pm 0$



#### 4.3.3.3 | Change in Geomorphic State of Reefs

In 2017, massive corals were observed to be the dominate corals in both SY-OP ( $26.0 \pm 5.4\%$ ) and SY-TB ( $13.5 \pm 6.3\%$ ) followed by branching corals in SY-OP ( $1.6 \pm 1.2\%$ ) and encrusting corals in SY-TB ( $2.3 \pm 1.4\%$ ; Figure 4.3.7). In 2018, massive corals continued to be the dominated coral morphotype in the site SY-TB ( $6.9 \pm 2.4\%$ ) despite their decrease in comparison to the previous year. The percentage cover of branching corals decreased in SY-TB by 88.9% (2017 =  $1.8 \pm 1.6\%$ ; 2018 =  $0.2 \pm 0.2\%$ ) whilst it increased by 50% (2017 =  $1.6 \pm 1.2\%$ ; 2018 =  $2.4 \pm 1.1\%$ ) in SY-OP (Figure 4.3.7). Overall, the majority of carbonate production by primary carbonate producers was observed to done by massive stress-tolerant corals with contributions in 2017 of  $3.6 \pm 0.8$  G at SY-OP and  $2.2 \pm 1.1$  G at SY-TB (Figure 4.3.8). This was noted to decline in 2018 to  $2.1 \pm 0.2$  G at SY-OP and  $1.0 \pm 0.3$  G at SY-TB (Figure 4.3.8). Branching corals were seen to be the second contributors to carbonate production at both sites and years (Figure 4.3.8). When compared, there was no significant differences in the contribution of carbonate production between massive and branching corals in 2017 at SY-TB ( $F_{(1,10)} = 3.0$ ,  $p > 0.05$ ), however, with the general declines in production, a significant difference was detected indicating that massive corals were beginning to significantly outcompete branching corals in carbonate production by 2018 ( $F_{(1,10)} = 10.6$ ,  $p < 0.05$ ). On the other hand, massive corals were seen to significantly produce more carbonate in comparison to branching corals at SY-OP in both years (2017 =  $F_{(1,10)} = 17.0$ ,  $p < 0.05$ ; 2018 =  $F_{(1,10)} = 10.6$ ,  $p < 0.05$ ). In general, results indicate that massive corals contribute significantly (SY-OP =  $F_{(1,22)} = 30.2$ ,  $p < 0.05$ ; SY-TB =  $F_{(1,22)} = 6.5$ ,  $p < 0.05$ ) to carbonate production by primary carbonate producers at both sites.

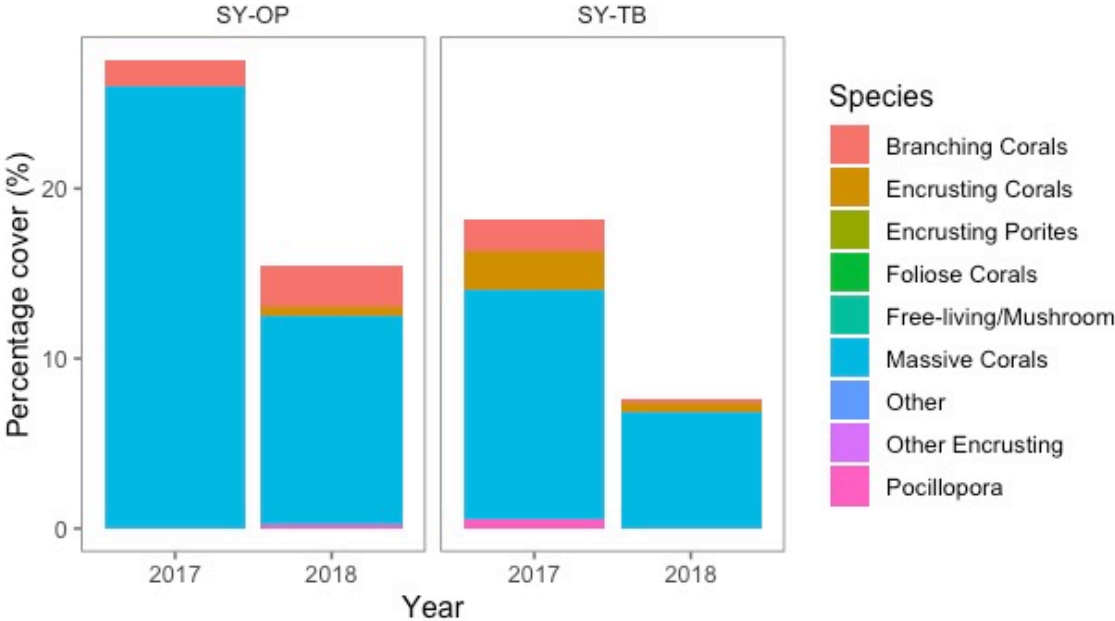


Figure 4.3.7. Mean percentage cover of primary carbonate producers (2017-2018) growth forms at the study sites (n=6).

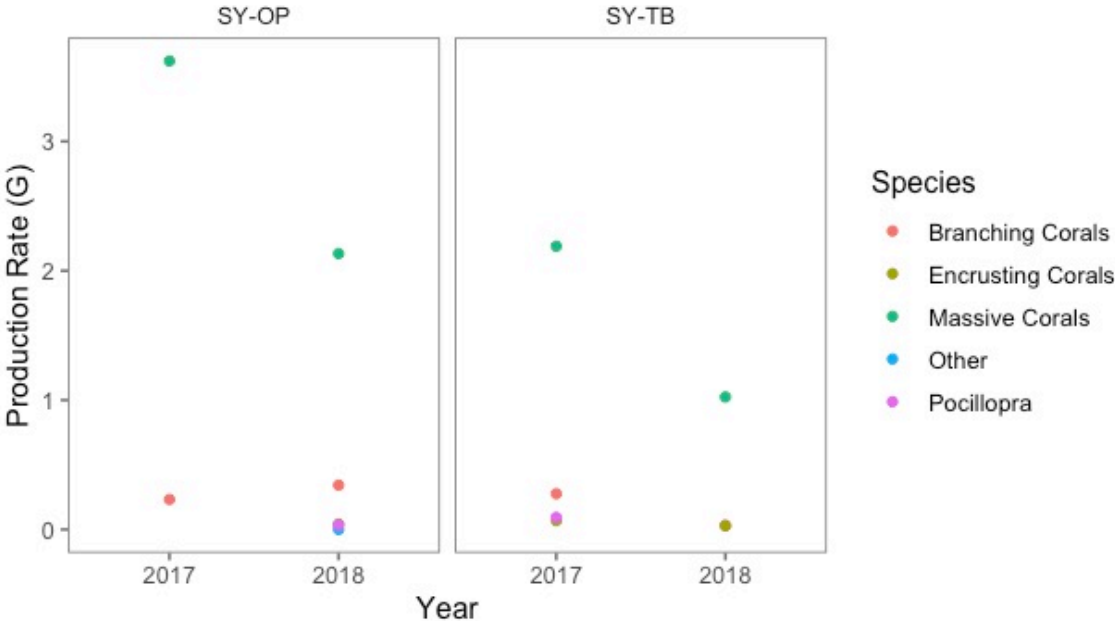


Figure 4.3.8. Carbonate Production Rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G; 2017-2018) by the different coral morphological groups at the study sites (n=6).

#### 4.3.3.4 | Change in Reef Carbonate Budget (2014-2018) pre and post – 2016 bleaching

When comparing the results derived from this study to that of the published paper, results indicate that within the 4 year period (2014 - 2018), the reef carbonate budgets in the Seychelles continue to maintain a low budget state with some reefs falling into a negative budgetary state ( $SY-TB = -0.6 \pm 1.1$  G) whilst others remain in a low positive budgetary state ( $SY-OP = 1.4 \pm 1.5$  G) with the trajectories indicating a steady decline with low rates of recovery.

#### 4.3.4 | DISCUSSION

This study aimed to quantifying the reef carbonate production and erosion rate of reefs in the Seychelles following the 2015-2016 bleaching event and how that has impacted the geomorphic state of reefs. The quantified budget post-bleaching was also compared to that reported by Januchowski-Hartley *et al.*, (2017) in order to determine the magnitude of change and trajectory of these reefs in the four year period between 2014-2018.

##### 4.3.4.1 | Carbonate Budgetary State

###### *Carbonate Producers & Production*

Hard live coral (primary reef producers) cover was observed to drastically decline in both sites SY-OP and SY-TB, heavily impacting the accretional health of these reefs. In 2016, prior to the bleaching event, it was reported that the live coral coverage at these sites were witnessing a steady increase from  $35 \pm 5\%$  to  $49 \pm 9\%$  in SY-OP and  $30 \pm 2\%$  to  $42 \pm 7\%$  in SY-TB during the seven year period between 2009-2016 (Gardner *et al.*, 2018). However, the 2016 bleaching event has resulted in a decline from  $49 \pm 9\%$  to  $22 \pm 2\%$  in SY-OP and  $42 \pm 7\%$  to  $13 \pm 3\%$  in SY-TB (Gardner *et al.*, 2018). Results obtained in 2018 from this study indicate that this reef is continuing to decline, where coral cover had reached  $15.5 \pm 1.6\%$  in SY-OP and  $7.6 \pm 2.1\%$ . This decline in

primary reef producers has naturally resulted in the decline of the gross carbonate production rate at both of the study sites.

Interestingly, CCA (secondary reef producers) percentage cover was observed to increase at both sites which could be due to the presence of rubble on the reefs, whereas 12 months on from the bleaching event, CCA was not observed at either of the sites. In addition to being an important carbonate producer, CCA is known for its important binding role which contributes extensively towards cementation and stabilizing reefs through creating suitable substrate for colonization (Fujita *et al.*, 2009; Langer, 2008; Perry & Hepburn, 2008; Rasser & Riegl, 2002). This in turn contributes towards enhancing larval recruitment of various organisms and maintaining wave resistance reef fronts thereby promoting accretion (Rasser & Riegl, 2002; Mallela & Perry, 2007). The appearance of CCA on the reefs is a positive indicator for the reefs ability for recovery despite encountering bleaching events in previous years especially seeing that previous studies have reported steady recovery prior to the 2016 bleaching (see Chapter 3).

### ***Carbonate Eroders & Bioerosion***

Overall erosion rates at both sites are considered to be on the lower scale, however, SY-TB is observed to have a higher erosion rate in comparison to SY-OP (2018 =  $1.7 \pm 1.0$  G and  $0.4 \pm 0.2$  G respectively). This could be attributed to the turbid nature of the site which is likely to affect erosion rates, as erosion is known to be influenced by various environmental parameters such as depth and turbidity (Mallela, 2007; Perry & Hepburn, 2008). These rates are comparable to those quantified for the Seychelles for the period 1994-2008 (mean =  $1.9 \pm 0.1$  G; Januchowski-Hartley *et al.*, 2017). Densities of both echinoids and Scaridae remain stable between 2017 and 2018 with echinoids maintaining their upper scale size class (80-100 mm) whilst Scaridae expanding in size class between 11-20 cm and 31-40 cm ranging between their initial and terminal life stages. The majority

of the Scaridae were seen to be in their terminal stage which links with the observation that the majority of the Scaridae were classified as excavators considering the species recorded and their large biomass. This indicates that Scaridae inhabit a safe environment to maintain their population which is unsurprising since the reefs are located within a marine national park whereby the laws prohibit fishing activities (Clifton *et al.*, 2019). Overall erosion rates by bioeroding sponges were noted to be low (0.03-0.01 G). Despite the low contribution, it is considered within the reported ranges when compared to other studies globally e.g. Bonaire (Caribbean) = 0.01-0.1 G (Perry *et al.*, 2012).

#### 4.3.4.2 | Change in Geomorphic State

It comes as no surprise that the majority of the carbonate production rate is contributed by stress tolerant massive corals following the bleaching event (Ryan *et al.*, 2019) as results have indicated that massive corals were dominant at both reefs throughout the period 2017 and 2018. Contributions from branching corals is considered minimal due to their low abundance in 2017 (SY-OP =  $1.6 \pm 1.2\%$  and SY-TB =  $1.8 \pm 1.6\%$ ), following the 2016 bleaching event, it is alarming that in 2018 *Acropora spp.* was observed to be in low abundance at SY-TB given that its loss is likely to impact reef capacity to track projected rates of sea-level rise since this will hinder the vertical extension growth of the reef (Perry *et al.*, 2015a). Branching corals were observed to increase in abundance at SY-OP in 2018 indicating possible recovery especially that this particular coral morphotype is known to be opportunistic and fast growing (Alvarez-Filip *et al.*, 2013; Anderson *et al.*, 2017). However, its recovery could be limited especially if subjected to further disturbance events (Burt *et al.*, 2011; Pratchett *et al.*, 2017; Lange & Perry, 2019). Furthermore, the overall decline in the rugosity at both reefs is likely attributed towards the decline in branching corals (Alvarez-Filip *et al.*, 2009).

#### 4.3.5.3 | Change in Reef Carbonate Budgets over Time

Reef accretion is known to be compromised due to bleaching events caused by thermal anomalies resulting in high coral mortality rates which in turn reduce calcification rates in coral (De'ath *et al.*, 2009). This is evidently observed in the Seychelles, whereby an assessment of a 20 year dataset illustrated a 62.5% difference in reef accretional rates post-bleaching ( $-1.5 \text{ G} = \text{erosive state}$ ) compared to pre-bleaching ( $\sim 4 \text{ G} = \text{positive state}$ ) (Januchowski-Hartley *et al.*, 2017). Results from this study indicate that within the 4-year period (2014-2018), reef carbonate budgets in the Seychelles continue to remain in a low budgetary state. Some reefs were seen dipping into an erosive negative budgetary state ( $\text{SY-TB} = -0.6 \pm 1.1 \text{ G}$ ) whilst others are in a critically low but positive budgetary state ( $\text{SY-OP} = 1.4 \pm 1.5 \text{ G}$ ), whereby any further impacts could tip the scale moving them into a negative state. The current trajectories indicate a steady decline with low rates of recovery similar to those seen in other places following the 2016 bleaching event (Perry & Morgan, 2017; Lange & Perry, 2019).

In conclusion, even though these reefs have demonstrated their capability to recover previously whereby live coral cover witnessed an increase between 2009-2016, one intense bleaching event was able to drastically decrease coral cover by half jeopardizing these reefs' accretion rates and thus their structural integrity. With thermal anomalies expected to increase in frequency and intensity in the near future, the question remains whether these reefs will be able to keep up with SLR and maintain the stability of the islands that they surround.

#### **4.4 | INTERANNUAL VARIABILITY OF REEF CARBONATE BUDGETS IN THE WAKATOBI MARINE NATIONAL PARK (WMNP), INDONESIA**

##### **ABSTRACT**

Calcium carbonate skeletons of hermatypic corals contribute towards reef formation and its 3-D framework, which drives the ecological functioning of coral reefs. However, combined global and local stressors, such as bleaching caused by rising temperatures, ocean acidification, overfishing and pollution have heavily impacted reefs worldwide. This has caused major declines in live coral cover with impacts on calcification rates and structural framework integrity. The ability of reefs to maintain their framework is associated with their ability to track sea level rise and hence, it is important to assess changes in the budgetary state of reefs. Carbonate budgets are measured by the balance between  $\text{CaCO}_3$  production and erosion. Utilising the standardised *ReefBudget* methodology, this study aims to assess the temporal changes in net reef carbonate accretion at two time points (2012 and 2018) at four reef sites with different environmental conditions in the Wakatobi Marine National Park, Indonesia. Results indicate a 76.5% decline in total net carbonate production across the study sites from  $36.9 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  in 2012 to  $9.9 \text{ kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  in 2018. Interestingly, the only site to maintain its net carbonate accretion rate is the highly turbid site. In addition, results of this study provide insights into the role of coral morphological groups in relation to reef carbonate production, indicating that change in the community composition of primary carbonate producers may be driving a shift in coral assemblages, thereby implicating calcification rates by different coral genera and their associated morphotypes.

#### 4.4.1 | INTRODUCTION

Coral reefs are experiencing rapid change on a global scale as a result of climate-induced disturbances (e.g. ocean warming and acidification; Anthony *et al.*, 2008; Hughes *et al.*, 2017), coupled with local pressures such as overfishing and declining water quality due to nutrient runoffs and excessive sedimentation (Hughes *et al.*, 2003; Hoegh-Guldberg, 2011; de Bakker *et al.*, 2019). These changes include loss of coral cover, which has implicated the 3-D framework of reefs through shifts from competitive corals (i.e. fast growing, branching e.g. Caribbean *Acropora spp.*) to weedy opportunistic and stress tolerant corals (i.e. low growing, thermally tolerant e.g. Caribbean *Porites spp.* and *Siderastrea spp.*; Baumann *et al.*, 2016), thereby compromising their structural integrity (Perry & Morgan, 2017). In addition, changes in the functionality of reef associated fish have been documented with links associating coral cover decline to fish diversity decline thereby impacting various functional groups e.g. obligate corallivores (*Chaetodon sp.*) associated with tabulate *Acropora spp.* (Pratchett *et al.*, 2011). Moreover, many reefs have been reported to witness shifts in their coral and associated species community composition e.g. shifts towards sponge dominated reefs (Bell *et al.*, 2013) and shifts towards massive stress tolerant reefs (Ryan *et al.*, 2019).

The ecological functioning of coral reefs is dependent on continuous accumulation of calcium carbonate (Graham & Nash, 2013; Kennedy *et al.*, 2013; Yanovski *et al.*, 2017; Perry *et al.*, 2018a) which is necessary for reefs to maintain their complex structural framework. Carbonate budgets measure the balance between  $\text{CaCO}_3$  production and erosion and provide a net figure, which informs whether a reef is in a positive or negative budgetary state. This information is particularly important when determining the vulnerability of particular reefs in relation to their ability to track sea level rise. Hence, current research is focused on understanding the magnitude of change in reef carbonate budgets whether it is through time, between regions or following disturbances.



The Coral Triangle, an area in the Indo-Pacific which covers provinces in Indonesia, Malaysia, the Philippines, East Timor, Papua New Guinea, and the Solomon Island, is considered the epicenter of global marine diversity (Sanciangco *et al.*, 2013). It hosts the highest diversity of hermatypic (reef building) corals (92%) on the planet (Veron, 2000) whilst harbouring 76% of the world's total species complement (Veron *et al.*, 2009). Despite the uniqueness of this area, reefs are not immune to global and local threats with reports suggesting that Indo-Pacific reefs are disappearing at a rate of 1% per year (Bruno & Selig, 2007). Over 80% of reefs are considered at risk from anthropogenic pressures in Southeast Asia (Burke *et al.*, 2002) whilst current projections suggest that thermal anomalies are expected to drive coral decline in the Coral Triangle (McManus *et al.*, 2019).

Change in reef benthic community structure is commonly reported when live coral cover (primary carbonate producers) declines and coral-dominant reefs shift towards organisms such as macroalgae, sponge and soft corals (Maliao *et al.*, 2008; Norström *et al.*, 2009). It is also important to consider shifting coral assemblages (e.g. from branching to massive) when investigating carbonate production on reefs, as this could indicate a decrease in calcification and reef complexity, which is independent of total coral abundance (Alvarez-Filip *et al.*, 2013). This is because, rapid growth of branching corals such as *Acropora* spp. are responsible for the majority of calcification and structural complexity due to their rapid growth (Lizard Island, GBR =  $\sim 7.31 \text{ cm yr}^{-1}$ ; Anderson *et al.*, 2017) and large forms, hence, complimenting reef vertical growth. Thus, they are considered an important functional group in terms of reef accretion as they contribute towards enabling reefs to track sea level rise (SLR) (Alvarez-Filip *et al.*, 2013; Roff, 2020) and their loss exacerbates reef framework decline. Nevertheless, massive stress tolerant corals have been reported to be able to maintain positive carbonate production on reefs e.g. reefs in the Maldives (Ryan *et al.*, 2019) despite their comparative lack of vertical growth extension.

In addition, reef calcification is also influenced by the variability in environmental factors such as temperature (Glynn, 1977; Lough & Barnes, 2000), light availability (Falkowski *et al.*, 1984; Suggett *et al.*, 2013), turbidity (Kendall *et al.*, 1985), sedimentation (Rogers, 1990), carbonate saturation state (Gattuso *et al.*, 1998; Silverman *et al.*, 2007) wave exposure and depth (Miller, 1995; Morgan *et al.*, 2016). In 2012, Franco (2014) made the first attempt at quantifying the carbonate budgets on four reefs that experience a range of reef conditions within the Wakatobi Marine National Park, Indonesia with results indicating that reefs in this region were in a positive budgetary state with reef budgets ranging between 16.6 and 3.8 kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup>. Therefore the aim of this study is to assess the temporal change in net reef carbonate production since 2012 at these four selected sites.

#### **4.4.2 | MATERIALS & METHODS**

##### **4.4.2.1 | Site descriptions**

The Wakatobi Marine National Park (hereafter referred to as Wakatobi) is located in South-East Sulawesi, Indonesia and encompasses four main islands: Wangi-Wangi, Kaledupa, Tomia and Binongko. These four islands together with other smaller islands and their surrounding waters covering 3.4 million acres of islands and waters comprise the Tukang Besi Archipelago (UNESCO, 2012). In 1996, the Wakatobi was declared a national park and was designated as a UNESCO Biosphere Reserve in 2012 due to its extremely high marine biodiversity that includes over 396 species of coral and 590 species of fish (Pet-Soede & Erdmann, 2003; UNESCO, 2012). In addition, it is the second largest marine national park in Indonesia and is located in the Coral Triangle (Hoeksema, 2007; Powell *et al.*, 2010). Covering ~ 50,000 hectares of coral reefs (Clifton *et al.*, 2010) which provides food and income to approximately 103,450 inhabitants spread across 64 villages (UNESCO, 2012) reflects the heavy local dependence on Wakatobi reefs for survival. This reliance, coupled with a history of poor resource management within the Wakatobi (Cullen-

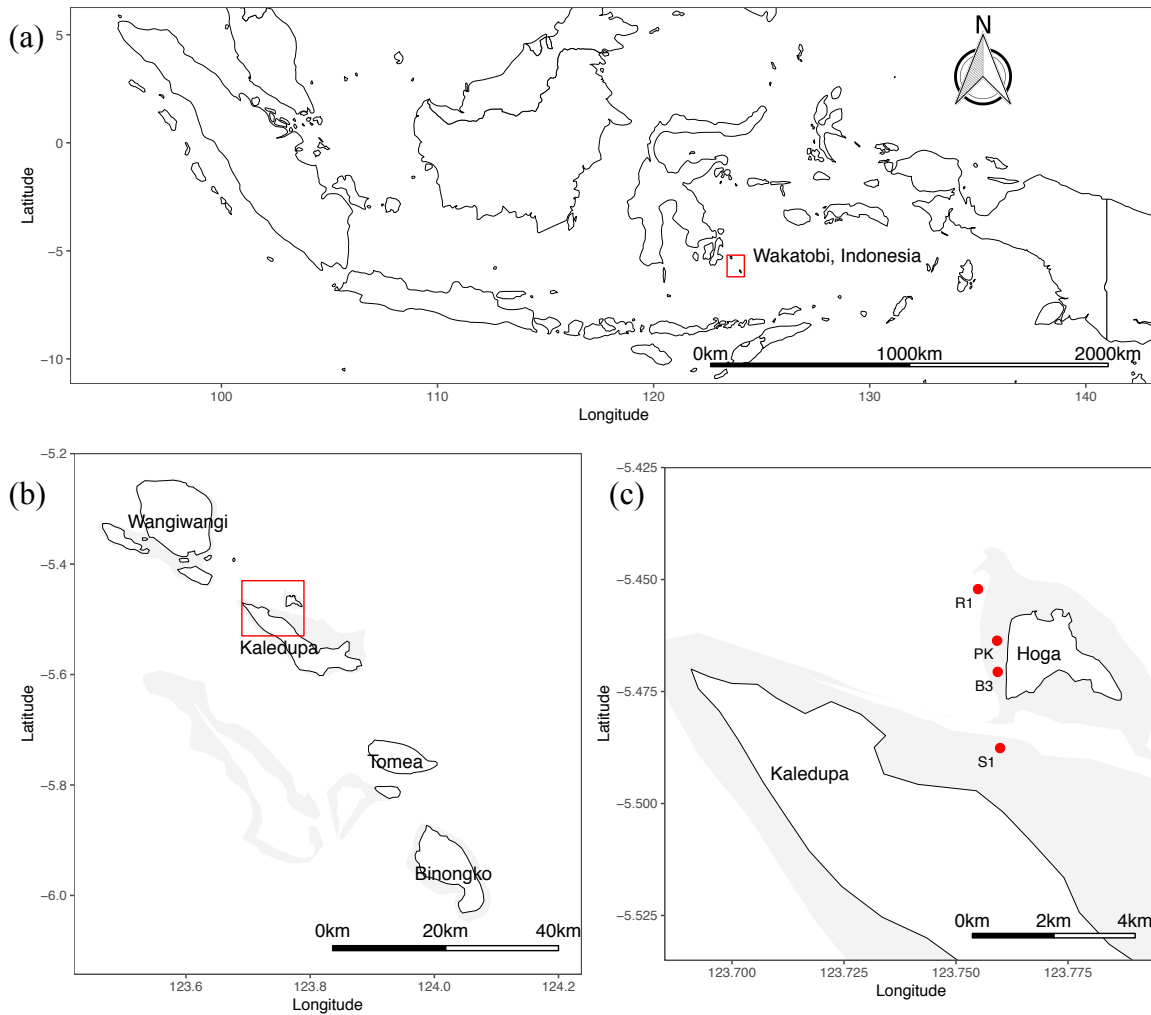
Unsworth, 2010), and regional/global pressures has resulted in declines in both coral cover and fish abundance (Gouraguine *et al.*, 2019). Reef degradation is reported to be patchy (Powell *et al.*, 2010) with some reefs severely degraded whilst others are in 'good' condition (Marlow *et al.*, 2019), making this area highly suitable to assess the variability in reef carbonate budgets. Four sites that experience a range of reef conditions within the Wakatobi (Table 4.4.1) were selected for this study namely: Ridge 1 (R1; outer exposed reefs), Buoy 3 (B3; inner fringing reef wall), Pak Kasims (PK; inner reef slopes) and Sampela 1 (S1; turbid lagoon reefs) (Figure 4.4.1).

**Table 4.4.1. Environmental characteristics of the selected study sites in the Wakatobi Marine National Park, Indonesia.**

Site	Site Code	Coordinates	Temp. (°C)	Salinity (ppt)	Sedimentation rates (mg cm <sup>-2</sup> d <sup>-1</sup> )*	Light attenuation (K <sub>PAR</sub> )**	Impacts
<b>Ridge 1</b>	R1	05-26.565 S 123-45.138 E	26-30	32-34	2.6 ± 1.0	0.02	R1 is located ~1 km northwest Hoga Island and runs north to south. Its crest is between 4-10 m wide with a depth of 5-10m. Its slope runs on either side of the crest at ~70° to over 100m on the outer slope and slightly shallower on the inner slope (Powell <i>et al.</i> , 2010). R1 is considered one of the least impacted sites within the area with some artisanal line fishing occurring.
<b>Buoy 3</b>	B3	05-28.4 S 123-45.45 E	26-30	32-34	4.3 ± 1.8	0.25	B3 is a fringing reef located ~150m off the west of Hoga island. Its reef flat and reef crest are at a depth of 1-6 m. The reef slope is characterised by walls, overhangs and caves which descends to a depth of ~60m where it levels out into sandy habitat (Powell <i>et al.</i> , 2010).
<b>Pak Kasims</b>	PK	05- 27.569 S 123-45.179 E	26-30	32-34	2.0 ± 0.8	0.01	PK is located 500m north of B3 along the same fringing reef. Its reef crest is located ~200m further offshore than B3 with its reef slope descending at an angle of 40-70° leading to gently sloping sand flats at ~50m (Powell <i>et al.</i> , 2010).
<b>Sampela 1</b>	S1	05-29.6 S 123-45.26 E	26-30	32-34	6.3 ± 2.7	0.01	S1 is located ~1.5 southwest of Hoga Island. Its reef flat occurs at 2-4m with a crest at 1-3m and a slope that descends at 45° to ~14m where it levels off into sand flats (Powell <i>et al.</i> , 2010). The site is adjacent to the Bajo village of Sama Bahari and is subjected to large sediment load and various anthropogenic activities, thus heavily impacted.

\*Sedimentation rates collected by Operation Wallacea between 2006-2011 (mean values are reported here along with ±SD and taken from Franco, 2014).

\*\*Light intensity was measured using hobo loggers that were deployed at two measurements 5 and 10m at all sites and then calibrated following the methods outlined in Long *et al.*, (2012) to calculate photosynthetically active radiation (PAR).



**Figure 4.4.1. Location of Study Sites – (a) Location of Indonesia; (b) Map of the Wakatobi Marine National Park (Wakatobi), South Sulawesi and; (c) Location of selected study sites around Hoga Island, Wakatobi.**

#### 4.4.2.2 | Quantifying the Carbonate Budgetary State

To assess calcium carbonate production and erosion rates on the selected reefs, quantitative data such as benthic composition, rugosity, carbonate producers and eroders was collected using the *ReefBudget* methodology. This method was originally designed for the Caribbean (Perry *et al.*, 2012) and then developed specifically for Indo-Pacific reefs (Perry *et al.*, 2018b). The data collected via benthic transects (Table S3.3; Supplementary Material) was then used to calculate CaCO<sub>3</sub> production and erosion rates (kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> hereafter expressed as G whilst ± represents the SE of all values stated) through utilizing a series of equations specific for carbonate producers and eroders as outlined and explained in the *ReefBudget* toolkit (Perry *et al.*, 2018b). The *ReefBudget* methodology for data collection in this study was followed in full with the exception of bioeroding sponge data and that transects were recorded at three depths rather than one depth (5, 10 and 15 m – 2 transects at each = 6 transects in total). Details of these modifications are given in section S3.2 of the supplementary material along with a brief explanation. The modification was necessary in this study to ensure that the data was comparable to that collected by Franco, (2014). Benthic composition was measured following the integrated method outlined in Perry *et al.*, (2012, 2018b). Budget data collected in 2012 which was used for the purpose of this study, is restricted to the budget rates (gross carbonate production, gross carbonate erosion and net carbonate production). Unfortunately, data collected in 2012 could not be obtained for comparison in terms of primary and secondary carbonate producers in addition to densities of major eroders.

#### 4.4.2.3 | Data analysis

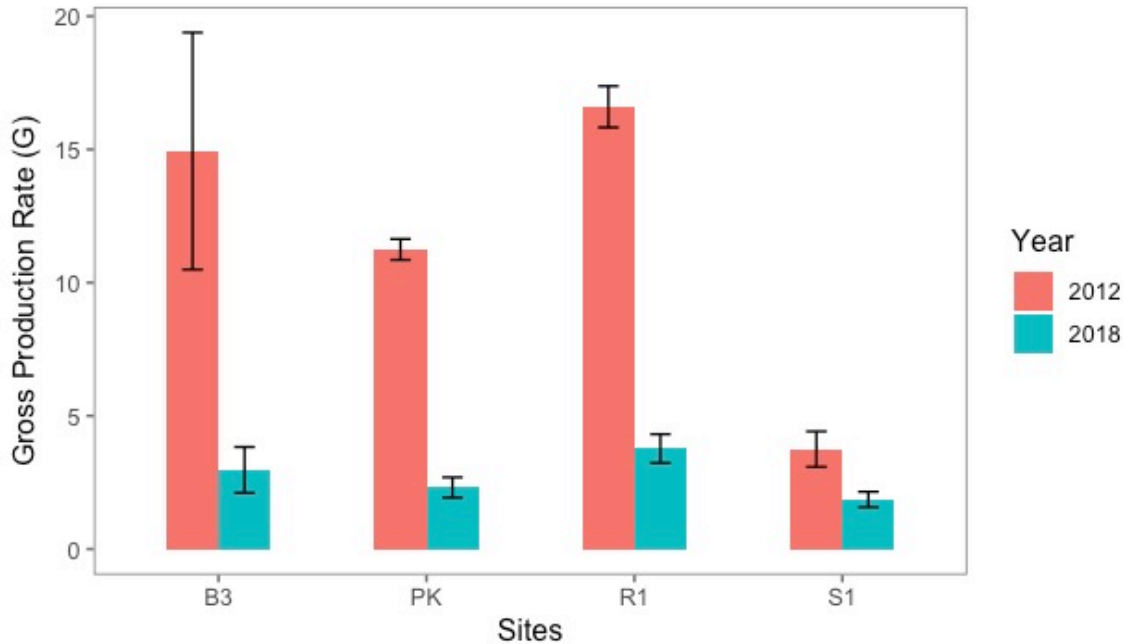
The software “R” and “RStudio” version 3.5.1 was used for data analysis, accompanied by various data processing and statistical packages including ggplot and tidyverse for plotting maps (Hothorn *et al.*, 2008; Wickham, 2009; R, 2018). It was impossible to test for statistical differences in the

percentage cover change of primary and secondary carbonate producers in addition to major eroders between sites over time since raw data (individual data points) could not be obtained for 2012. However, the analysis of variance (ANOVA) was used to test for differences in the gross carbonate production, erosion and net production between sites over time. In addition,  $\pm$ SE is stated throughout.

### 4.4.3 | RESULTS

#### 4.4.3.1 | Carbonate Production

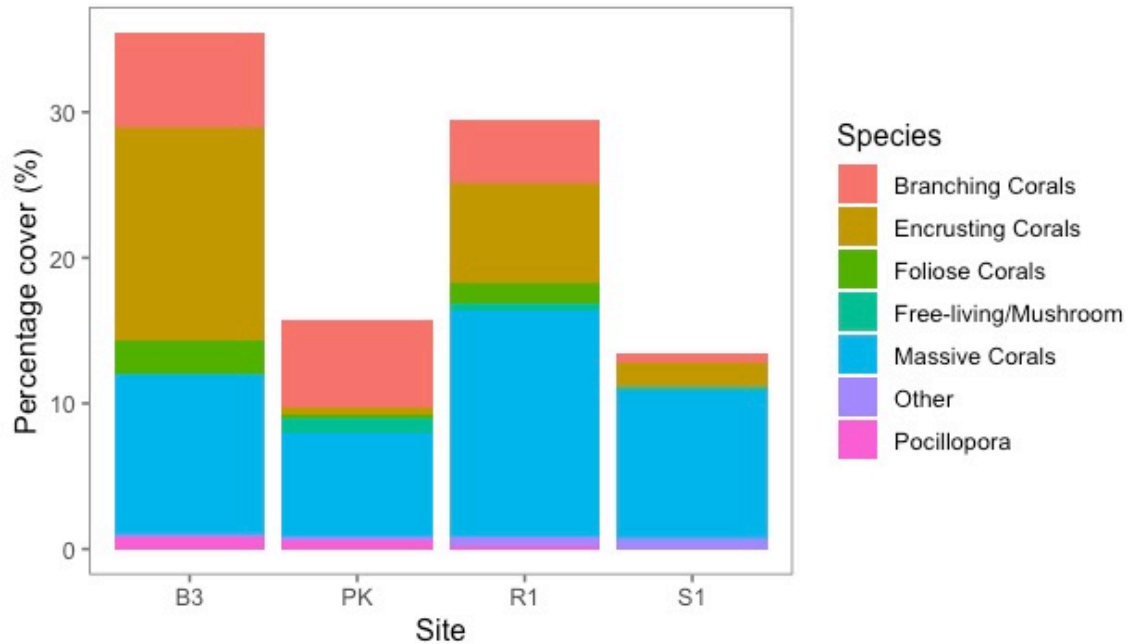
In 2012, all reefs surveyed were in a positive carbonate budgetary state, and the analysis from 2018 reported that these reefs have maintained this positive state. However, a reduction in their gross carbonate production rates was observed at all sites with the exception of S1 (Figure 4.4.2). Carbonate production rates significantly decreased by 77.7% at R1 (2012 =  $16.6 \pm 0.63$ ; 2018 =  $3.7 \pm 0.5$  G;  $F_{(1,6)} = 150.0$ ,  $p < 0.05$ ), 79.8% at B3 (2012 =  $14.9 \pm 4.5$ ; 2018 =  $3.0 \pm 0.9$  G;  $F_{(1,7)} = 14.2$ ,  $p < 0.05$ ) and 80.7% at PK (2012 =  $11.9 \pm 0.4$ ; 2018 =  $2.3 \pm 0.4$  G;  $F_{(1,7)} = 205.1$ ,  $p < 0.05$ ) while S1 witnessed a 50% decrease (2012 =  $3.8 \pm 0.7$ ; 2018 =  $1.9 \pm 0.3$  G;  $F_{(1,7)} = 9.6$ ,  $p < 0.05$ ; Figure 4.4.2). In terms of primary carbonate producers, in 2018, B3 ( $35.5 \pm 6.1\%$ ) had the highest percentage of hard corals followed by R1 ( $29.9 \pm 5.5\%$ ) and PK ( $15.6 \pm 2.7\%$ ) with S1 ( $13.6 \pm 1.9\%$ ) having the lowest. This pattern is also observed with secondary carbonate producers whereby B3 ( $6.2 \pm 2.0\%$ ) had the highest percentage of CCA followed by R1 ( $5.0 \pm 3.1\%$ ) and PK ( $2.6 \pm 2.2\%$ ) whilst no CCA was observed at S1.



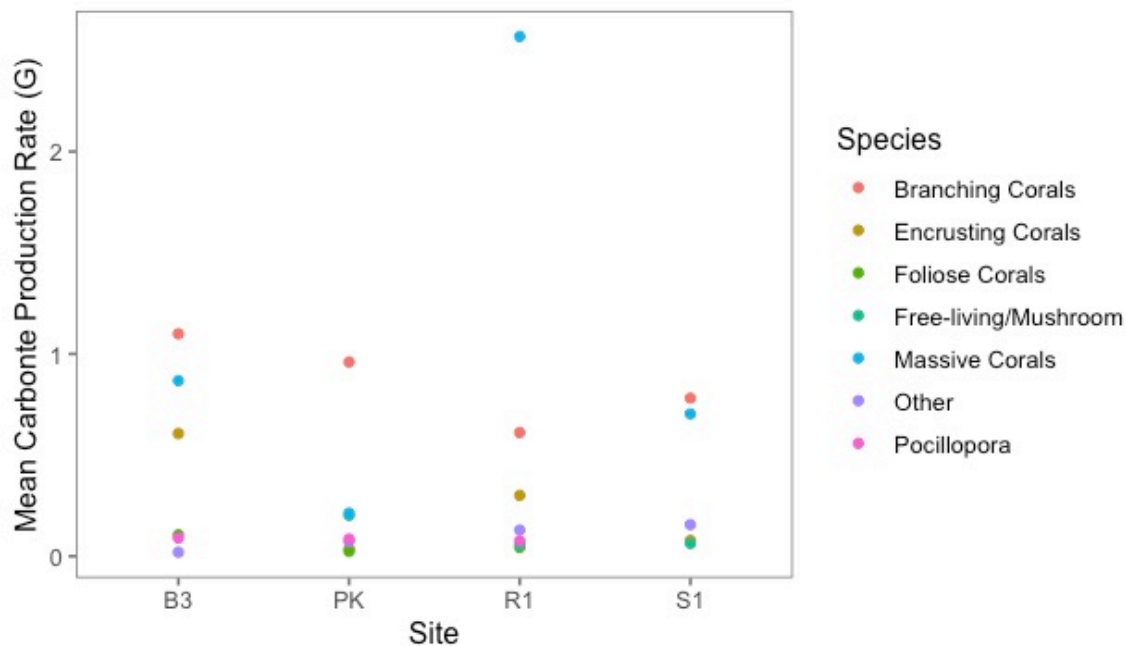
**Figure 4.4.2. Comparison of gross carbonate production rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G) across the four study sites between the period 2012-2018 ( $n=6$ ;  $G \pm \text{SE}$ ); B3 =  $F_{(1,7)} = 14.2$ ,  $p < 0.05$ ; PK =  $F_{(1,7)} = 205.1$ ,  $p < 0.05$ ; R1 =  $F_{(1,6)} = 150.0$ ,  $p < 0.05$ ; S1 =  $F_{(1,7)} = 9.6$ ,  $p < 0.05$ .**

In 2018, massive corals dominated all the study sites (Figure 4.4.3) with massive *Porites spp.* leading in each of B3 ( $6.6 \pm 2.6\%$ ), PK ( $5.1 \pm 1.4\%$ ) and R1 ( $9.9 \pm 2.3\%$ ) whilst in S1 other massive corals were dominant ( $5.8 \pm 1.3\%$ ) e.g. *Galaxea spp.*, *Diploastrea spp.* and *Favites spp.* Branching *Acropora spp.* were highest at PK ( $3.3 \pm 1.5\%$ ) followed by B3 ( $1.9 \pm 0.8\%$ ) and R1 ( $0.5 \pm 0.5\%$ ) whilst S1 had the lowest cover ( $0.2 \pm 0.2\%$ ). In addition, other branching corals of different genera (e.g. *Montipora spp.* and *Tubinaria spp.*) were dominant in both B3 ( $4.1 \pm 2.1\%$ ) and R1 ( $3.9 \pm 1.5\%$ ) (Figure 4.4.3).





**Figure 4.4.3. Mean percentage cover of primary carbonate producers in 2018 based on their morphological groups across the study sites (n=6).**



**Figure 4.4.4. Carbonate production rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G) in 2018 by the different coral morphological groups at the study sites (n=6).**

Despite the dominance of massive corals, carbonate production rates were highest by branching corals at B3 ( $1.1 \pm 0.4$  G;  $F_{(1,10)} = 0.2$ ,  $p > 0.05$ ) and PK ( $1.0 \pm 0.2$  G;  $F_{(1,10)} = 9.3$ ,  $p < 0.05$ ; Figure 4.4.4). Surprisingly, massive corals ( $2.5 \pm 0.6$  G) contribute to carbonate production significantly more than branching corals ( $0.6 \pm 0.2$  G) at R1 ( $F_{(1,10)} = 10.1$ ,  $p < 0.05$ ), whilst at S1 both massive ( $0.7 \pm 0.2$  G) and branching corals ( $0.8 \pm 0.2$  G) contribute similarly to carbonate production (Figure 4.4.4). Encrusting corals such as *Leptoseris spp.* and *Pachyseris spp.* were the third leading contributors towards carbonate production across all reefs (Figure 4.4.4).

#### 4.4.3.2 | Carbonate Erosion

In 2012, erosion was strongly influenced by Scaridae across all sites with the highest erosion occurring at PK and the lowest at R1 (Table 4.4.2). Although erosion rates by echinoids in 2012 are considered negligible across all sites, in 2018, almost no erosion is observed due to echinoid activity on these reefs (Table 4.4.2). Unfortunately, it was not possible to obtain bioeroding sponge data from Franco (2014) and therefore it is not possible to conduct a temporal comparison, however, data collected in 2018 illustrates that erosion by bioeroding sponge is minimal across all sites (Table 4.4.2).

**Table 4.4.2. Erosion rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G) by major bio-eroders at study sites (n=6;  $G \pm SE$ )**

	B3		PK		R1		S1	
	2012	2018	2012	2018	2012	2018	2012	2018
<b>Echinoids</b>	0.04±0.01	0 ± 0	0.1±0.1	0.01±0.01	0.02±0.01	0 ± 0	0.15±0.1	0.03±0.01
<b>Scaridae</b>	3.0±1.4	0.03±0.01	3.8±0.2	0.1±0.04	0.7±0.2	0.3±0.2	2.0±0.1	0.09±0.03
<b>Bioeroding Sponge</b>	NA*	0.1±0.03	NA	0.1±0.1	NA	0.1±0.04	NA	0.1±0.1

\*NA=Not Available

Echinoid densities were observed to be low across all sites (B3 =  $0.03 \pm 0.01$ ; PK =  $0.02 \pm 0.01$ ; R1 =  $0.03 \pm 0.02$ ; S1 =  $0.03 \pm 0.01$  individuals per 20 m<sup>2</sup>). Scaridae abundance was noted to be ~2 individuals per 120 m<sup>2</sup> across all sites with density records of  $0.01 \pm 0.002$ ,  $0.02 \pm 0.003$ ,  $0.02 \pm 0.01$  and  $0.01 \pm 0.002$  individuals per 120 m<sup>2</sup> at B3, PK, R1 and S1 respectively. Species of echinoids on transects at both sites were restricted to three, mainly: *Echinometra lucunter*, *Diadema spp.* and *Echniothrix spp.* Echinoids were largest at S1 (81-100 mm) whilst both PK and R1 had the smallest echinoids in size (0-20 mm; Figure 4.4.5).

The majority of Scaridae across the study sites were recorded to be scrapers (B3 = 57%; PK = 65%; R1 = 59%; S1 = 78%) most of which were in their terminal life phase (Figure 4.4.6). Excavator Scaridae were recorded to be the highest at B3 = 43% and R1 = 41% with S1 having the lowest number (21%) (Figure 4.4.6). Twelve species of Scaridae were recorded in this study: *Bolbometopon muricatum*, *Sparisoma griseorubrum*, *Chlorurus sordidus*, *Chlorurus bleekeri*, *Scarus ghobban*, *Scarus niger*, *Scarus frenatus*, *Scarus globiceps*, *Scarus dimidiatus*, *Scarus psittacus*, *Scarus oviceps* and *Scarus flavipectoralis*.

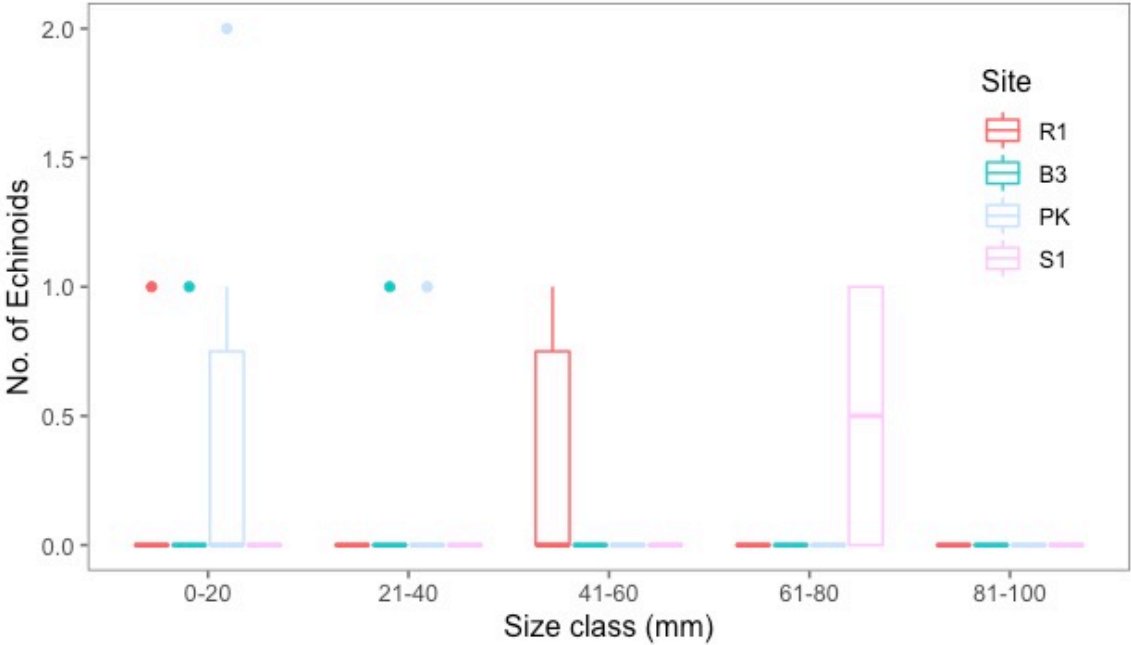


Figure 4.4.5. Total abundance of echinoids recorded in 2018 based on size class across study sites (n=6; area=20m<sup>2</sup> per transect).

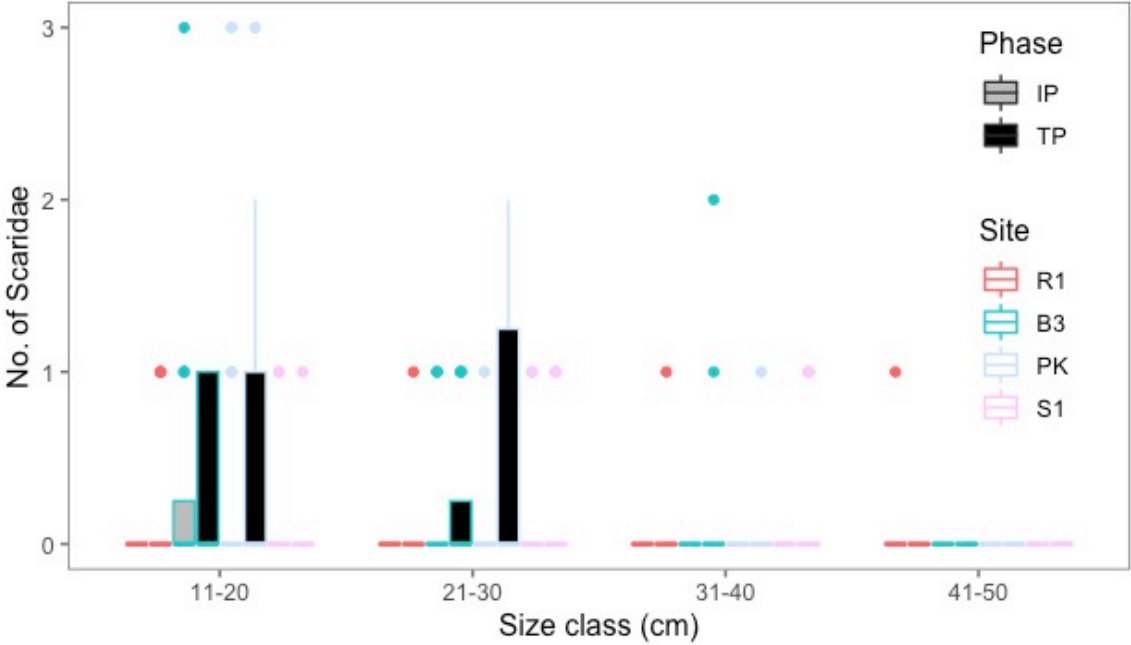
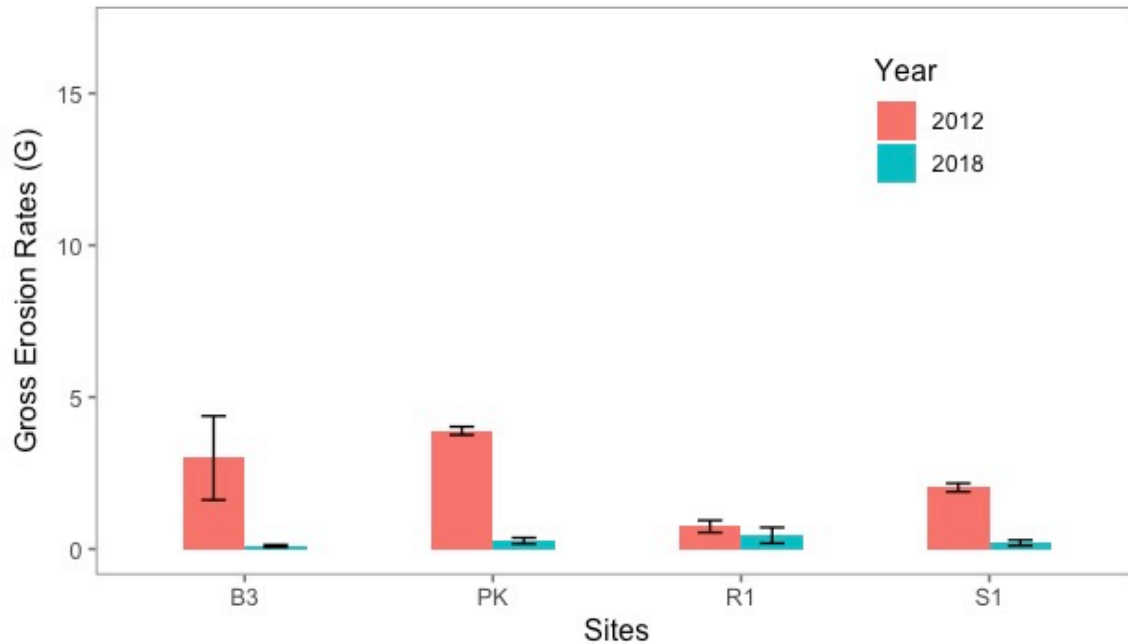


Figure 4.4.6. Total abundance of Scaridae in 2018 based on size class (IP = initial phase / juveniles; TP = terminal phase / adults) across study sites (n=6; area=120m<sup>2</sup> per transect).



**Figure 4.4.7. Comparison of gross carbonate erosion rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G) across the four study sites between the period 2012-2018 ( $n=6$ ;  $G \pm \text{SE}$ ).**

In 2012, gross carbonate erosion was the lowest at R1 ( $0.7 \pm 0.2 \text{ G}$ ) and the highest at PK ( $3.9 \pm 0.1 \text{ G}$ ) followed by B3 ( $3.0 \pm 1.4 \text{ G}$ ) and S1 ( $2.0 \pm 0.1 \text{ G}$ ; Figure 4.4.7). On the contrary, in 2018, R1 had the highest rate ( $0.5 \pm 0.3 \text{ G}$ ) of erosion amongst the four sites although the rate remains similar to that recorded six years ago whilst B3 had the lowest ( $0.1 \pm 0.04 \text{ G}$ ) witnessing a 97% decrease in erosion rates. Nevertheless, overall all sites have witnessed an insignificant decrease in the gross carbonate erosion rates between the period 2012-2018 (R1 =  $F_{(1,6)} = 0.8$ ,  $p > 0.05$ ; B3 =  $F_{(1,7)} = 1.2$ ,  $p > 0.05$ ; PK =  $F_{(1,7)} = 3.5$ ,  $p > 0.05$ ; Sampela =  $F_{(1,7)} = 0.8$ ,  $p > 0.05$ ; Figure 4.4.7).

#### 4.4.3.3 | Carbonate Budgetary State

Over the period 2012-2018, reefs across all study sites have successfully maintained their positive budgetary state, despite the decline in net carbonate production between time points (Figure 4.4.8). R1 was observed to have the highest net carbonate production rate (2012 =  $15.9 \pm 0.5$ ; 2018 =  $3.3 \pm 0.3$  G), followed by B3 (2012 =  $11.9 \pm 4.4$ ; 2018 =  $2.9 \pm 0.8$  G) and PK (2012 =  $7.4 \pm 0.4$ ; 2018 =  $2.0 \pm 0.3$  G) whilst interestingly; S1 maintained its net production rate (2012 =  $1.7 \pm 0.8$ ; 2018 =  $1.7 \pm 0.2$  G; Figure 4.4.8). In addition, all reefs maintained their rank (with R1 leading and S1 the lowest) throughout the six-year period (2012-2018; Figure 4.4.8). However, R1's net production rate has witnessed a decline by 79.2% ( $F_{(1,6)} = 4.4$ ,  $p > 0.05$ ) whilst B3 ( $F_{(1,7)} = 8.4$ ,  $p < 0.05$ ) and PK ( $F_{(1,7)} = 12.7$ ,  $p < 0.05$ ) also suffered a decrease by 75.6% and 73% respectively.



**Figure 4.4.8.** Reef carbonate budget rates ( $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$  expressed as G) across study sites illustrating Gross Carbonate Production; Gross Carbonate Erosion and Reef Growth in the form of Net Carbonate Production for the period 2012-2018 ( $n=6$ ;  $G \pm \text{SE}$ ).

#### 4.4.4 | DISCUSSION

This study examined the temporal change in net carbonate accretion on reefs in the Wakatobi at two time points (2012 and 2018), six years apart. The decline in net carbonate production recorded (>75% on the majority of these reefs) could be attributed to the decrease in hard coral cover (primary carbonate producers) over time. Although data collected in 2012 could not be presented in this study, a decreasing trend in hard coral cover has been reported in previous studies on these specific reefs, e.g. studies reported hard coral cover in PK as 50% (Hennige *et al.*, 2008) decreasing to 27% (Powell *et al.*, 2010), which has further decreased to 15.5% as per data collected in 2018 for this study (also see Chapter 3). This was also observed to be the case in B3 which was reported to have 51% hard coral cover (Powell *et al.*, 2010) whereas this study has revealed that the cover has dropped to 35%. Overall, a decline of 69.3% in hard coral was documented over a 11-year period (2002-2012) on a total of six reefs surveyed in the Wakatobi (Gouraguine *et al.*, 2019). This decline is driven by a number of different factors such as physical destruction of coral cover through the use of destructive fishing practices (e.g. dynamite fishing; Clifton *et al.*, 2010), bleaching events and coral disease (Haapkylä *et al.*, 2009). Interestingly, although S1 witnessed a sharp decline in previous years from 31.7% (Hennige *et al.*, 2008) to 13% (Powell *et al.*, 2010) attributed to destructive fishing practices (Clifton *et al.*, 2010); it has maintained its coral cover over the last eight years (13.3% in 2018). This could be due to the adaptive mechanisms of corals in such extreme conditions to high turbid environments which includes responses to temporal fluctuations in the environment (Anthony & Larcombe, 2000). Moreover, recent models suggest that extreme environmental conditions, characteristic of reefs with fluctuating turbidity, light, and temperature, may acclimate corals to the thermal anomalies associated with bleaching (Hughes *et al.*, 2017a), thereby, enabling them to build resilience.

Furthermore, the variation in environmental conditions and levels of anthropogenic impact across the study sites could contribute towards primary carbonate producers (hard corals) being the highest at B3, followed by R1, PK and lowest at S1, this pattern was also observed in CCA (secondary

carbonate producer). Since light availability, temperature and turbidity influences coral diversity and abundance (Hennige *et al.*, 2011) which is reported to decrease from optimal (clear water) to marginal (considered more “turbid”) environments (Bak & Meesters, 2000; Vermeij & Bak, 2002; Schleyer & Celliers, 2003; Hennige *et al.*, 2011), this pattern is observed on the study sites and is consistent with previous studies. In addition, CCA is known to have an inverse relationship with sediment whereby reefs with high sedimentation rates have lower recruitment of CCA-specialised organisms thereby impacting reef calcification (Fabricius & De’ath, 2001; Mallela, 2013) and as such reef carbonate production. This is also in line with the results from this study whereby no CCA was observed at S1 whilst the highest cover was observed to occur at the reef with optimal environmental conditions amongst the four sites declining in cover as the conditions become more marginal between the sites.

Surprisingly, even though the highest cover of primary carbonate producers was recorded at B3, the highest carbonate production rate was observed to be at R1 followed by B3. This was observed in both years (2012 and 2018) and could be attributed to the high contribution of carbonate production by massive corals which dominates the R1 site while branching corals dominate B3 (although not significantly) as indicated by the results of this study. However, carbonate production on reefs is independent of total coral abundance, whereby change in coral community calcification and reef complexity could be in response to shifting coral assemblages (branching to massive; Alvarez-Filip *et al.*, 2013). In addition, although branching corals are major contributors towards the vertical expansion especially due to their rapid growth rates, hermatypic corals are reported to exhibit extensive plasticity (Todd, 2008). For example, each morphotype within the massive *Porites lobata* colonies differ in physiological responses to environmental conditions thereby harbouring 15-33% faster annual growth rates in comparison to other coral morphological groups (e.g. columnar and free-living) thereby contributing towards reef structure (Tortolero-Langarica *et al.*, 2016). Morphoplasticity in colony structure is an adaptive strategy used by coral species to benefit from changes in their environment (Foster, 1979; Muko *et al.*, 2000; Smith *et al.*, 2007; Forsman *et al.*, 2009; Tortolero-Langarica *et al.*, 2016). This plasticity and morphological variation contributes towards



reef structure and complexity while strengthening species survival (Spalding *et al.*, 2001; Alvarez-Filip *et al.*, 2009). In addition, massive corals have been reported to be able to maintain positive carbonate production on reefs (Ryan *et al.*, 2019) despite their lack of vertical growth extension, this is noted at S1 whereby branching corals are less than 1% and is mainly dominated by massive corals. Therefore, exploring carbonate production in relation to the variation in morphological groups could provide new insights into the functionality of reef builders and redefine major contributors towards carbonate production.

On the other hand, in 2018, erosion across all sites were observed to be low in general, this could be attributed to low densities of macro-eroders especially echinoids and Scaridae populations across all sites. However, over the six-year period (2012-2018), there is a clear decline in erosion rates at all the sites with the exception of R1. This site maintains erosion rates over time despite it having the lowest erosion rate in 2012, whereas in 2018, it is the highest in comparison to the other sites. This could be due to minimal change in the eroder populations at R1 overtime; uncertainties remain since temporal data on eroder populations could not be obtained for comparison. However, B3 witnessed a 97% decrease in its erosion rates over time, this was also observed at PK and S1 all of which indicates a change in their eroder population. In terms of the overall budget, S1 was the only site that managed to maintain its net carbonate production rate whilst the remaining reefs witnessed a drastic sharp decline, which is associated mainly with the decline in their gross production rate. In terms of S1, although its gross production rate had decreased by 50%, its erosion rate has also declined thereby enabling the reef to maintain its budgetary state. This also indicates that reefs in turbid environments maybe able to sustain themselves through a combination of adaptive mechanisms, such as their responses to temporal environmental fluctuations (Anthony & Larcombe, 2000), ability to acclimatize to thermal disturbances (Hughes *et al.*, 2017a) and the dominance of massive stress tolerant corals which have been observed to contribute towards maintaining a positive

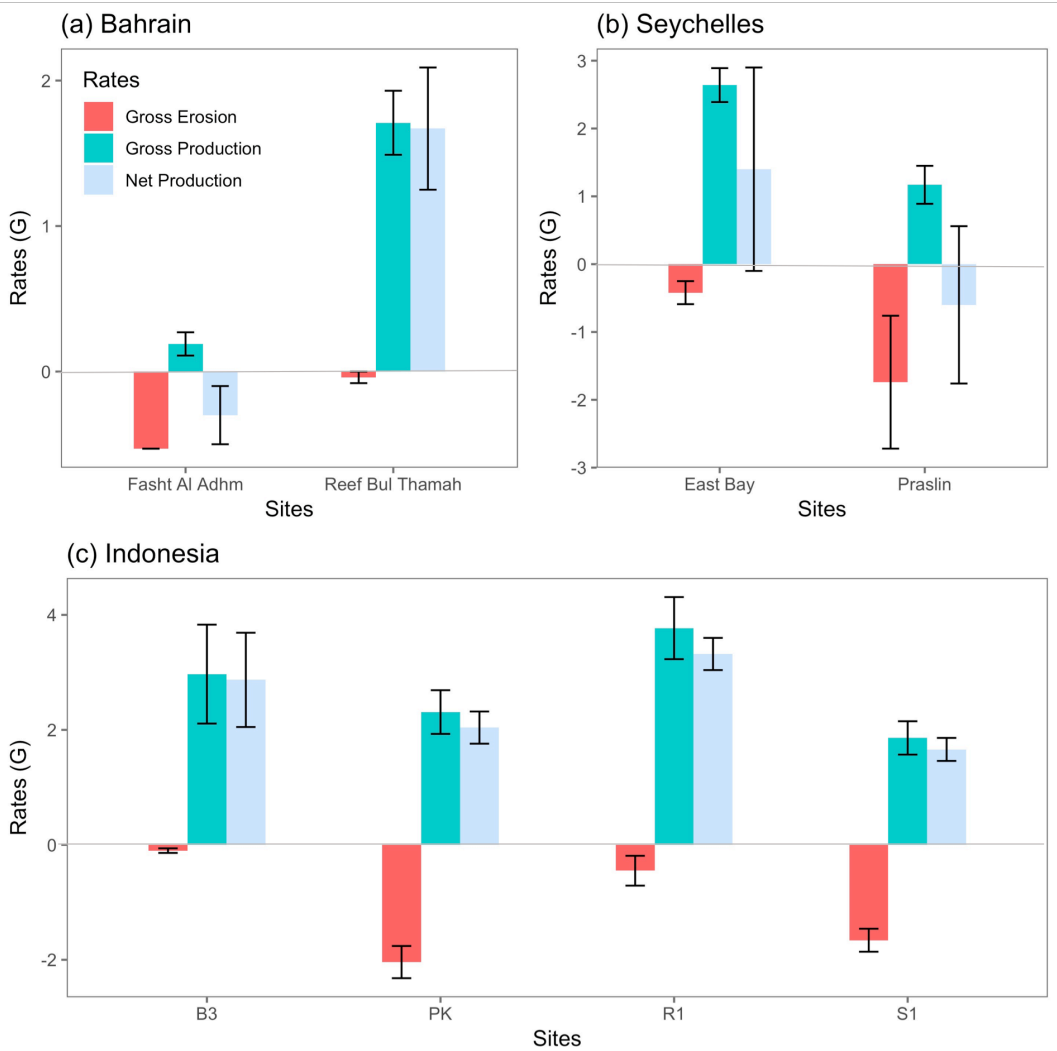
budgetary state (Ryan *et al.*, 2019). This combined, as well as, the limited erosion experienced on these reefs contribute towards making them more robust and resilient to change.

In conclusion, overall budgetary states across all reefs remain positive, although the sharp decline in net carbonate production across all sites from the period 2012 through to 2018 is alarming. This indicates rapid change in the functional performance of these reefs, which highlight spatial and temporal variations in their reef framework formation and growth. The results of this study presents new insights as to the role of various coral morphological groups in relation to reef carbonate production and indicates that perhaps a shift in coral assemblages is driving a change in the community composition of primary carbonate producers.

#### 4.5 | CONCLUSION: REEF CARBONATE BUDGETS ACROSS BIOREGIONS

It is without doubt that this study on reef carbonate budgets has provided valuable insights as to the current accretional health of reefs in the three selected bioregions: AG, WIO and CIP (Figure 4.5.1). These reefs offer a unique opportunity to examine carbonate budgets from diverse environmental and species richness spectrums within a given time period. On a global level, results have indicated that reefs that exist in extreme environmental conditions, such as those in Bahrain (AG), where reefs are exposed to high temperatures that reach 36°C, have either dipped into a negative budgetary state (BH-TB =  $-0.3 \pm 0.2$  G) or maintain a low positive budgetary state (BH-OP =  $1.7 \pm 0.4$  G). This is also observed in the Seychelles (WIO), which has encountered multiple disturbances i.e. extreme bleaching events over the last few years resulting in a total net carbonate budget of 1.6 G, similar to that of Bahraini reefs. However, in Indonesia (CIP), although the Coral Triangle has been reported to experience multiple thermal anomalies, the intensity and duration of these events remains much lower than the other two locations (see Chapter 2). This is also reflected in the carbonate budgets whereby all reefs explored maintain a positive budgetary state ranging between 1.7 and 3.3 G. Nevertheless, the temporal comparison has shown that despite the minimal net positive state, these reefs have experienced an alarming decline over the last few years that should not be ignored. Results obtained from the hottest sea could provide insights as to the future of global reefs since reefs in the AG currently survive in temperatures similar to those projected (1.5-2°C above pre-industrial levels) to occur globally by 2100 (IPCC, 2014b). Although temperatures in the Seychelles are milder than those in Bahrain, the disturbances faced have put the reefs in a vulnerable position. The question remains as to whether these reefs will adapt and become resilient through shifting their coral assemblages and communities towards massive stress tolerant corals and still achieve/maintain a positive budgetary state like some of the reefs in Bahrain? What are the implications of this in the

face of SLR? How will reefs in the Wakatobi adapt to their changing environment and how will that impact their budgets? Would the change in their budgets also mean that their species richness index will be affected and by how much? These are questions that should be prioritized and explored in future carbonate reef budget studies.



**Figure 4.5.1. Overall carbonate budget rates of reefs in 2018 across sites: (a) Bahrain, (b) Seychelles and; (c) Indonesia.**

**CHAPTER FIVE: SYMBIODINIACEAE DIVERSITY ACROSS  
THERMAL REGIMES AND LATITUDINAL GRADIENTS**

This page was left intentionally blank

## 5 | SYMBIODINIACEAE DIVERSITY ACROSS THERMAL REGIMES AND LATITUDINAL GRADIENTS

### ABSTRACT

Reef-building corals are under serious threat from ocean warming, which directly impacts their symbiotic partnership with dinoflagellates from the family Symbiodiniaceae; a relationship that is integral for the survival of coral reefs. Symbiodiniaceae species vary in their levels of tolerance to heat and light, with some reported to enhance a coral's thermal tolerance. This study examines the composition and diversity of Symbiodiniaceae species across different thermal regimes and latitudinal gradients in three bioregions: Bahrain (Arabian Gulf), the Seychelles (Western Indian Ocean) and Indonesia (Central Indo-Pacific). Results acquired through next generation sequencing (NGS) targeting the ITS2 rDNA region, have identified the presence of three main genera: *Cladocopium* (dominant across all sites), *Durusdinium*, and *Symbiodinium*. Biogeographical patterns revealed that Symbiodiniaceae diversity and richness is lower in higher latitude reefs compared to those in the lower latitude. Shifts in Symbiodiniaceae community composition from prevalent thermally sensitive symbionts types in the low thermal regime reefs (thermal stress =  $\leq 4^{\circ}\text{C-DHW}$ ) to thermally tolerant types in the high thermal regime reefs (thermal stress =  $>4^{\circ}\text{C-DHW}$ ) were also noted. Results include the first reporting of ITS2 types present in Bahrain, along with a novel observation of the presence of ITS2 type C3-Gulf in the Seychelles. Overall, Symbiodiniaceae species diversity, distribution, and community composition are influenced by multiple variables, including environmental factors, thermal regimes, and latitudinal gradients.

## 5.1 | INTRODUCTION

Corals host a complex composition of microbes including microalgae, bacteria, viruses, fungi and archaea in their mucus layer, skeleton, and tissues (Blackall *et al.*, 2015). This collective diverse and dynamic group of microbial communities is referred to as the coral holobiont (Rohwer *et al.*, 2002; Blackall *et al.*, 2015; Thompson *et al.*, 2015). These microorganisms provide their host with benefits via various mechanisms, including photosynthesis, nitrogen fixation, the provision of nutrients and infection prevention, all of which contributes towards coral health (Trench, 1979; Rohwer *et al.*, 2002; Rosenberg *et al.*, 2007). These symbiont microbial populations may reach densities of several million or more per square centimeter of host tissue (LaJeunesse, 2002). The coral holobiont functions as a dynamic system whereby external environmental conditions determines its members (Shashar *et al.*, 1993; Tanner, 1996; Thompson *et al.*, 2015; Roik *et al.*, 2016). Therefore, any change in environmental conditions will change the relative abundance of microbial species to facilitate the coral holobiont to adapt to the new condition (Reshef *et al.*, 2006).

The mutualistic association between hermatypic corals (reef-building) and endosymbiont dinoflagellates (commonly known as zooxanthellae) in the family Symbiodiniaceae is said to underpin the survival of coral reefs (Hume *et al.*, 2015; Rouzé *et al.*, 2017; LaJeunesse *et al.*, 2018). The Symbiodiniaceae species inhabits the vacuoles (known as symbiosome) which are present within the endodermic layer of the coral polyp tissue (Trench, 1979). Corals are supplied by photosynthetic products such as sugars, fatty and amino acids, carbohydrates, and small peptides from the Symbiodiniaceae species who contribute towards nutritional provision (Trench, 1979; Papina *et al.*, 2003; Morris *et al.*, 2019). This energy supply from the Symbiodiniaceae species is related to the amount of energy available for coral calcification (Jones & Berkelmans, 2010). In return, the Symbiodiniaceae species receives crucial plant



nutrients such as ammonia and phosphate from the coral's waste metabolism (Furla *et al.*, 2000; Al-Hammady, 2013).

The last twenty years of molecular technique advancements has revealed an array of Symbiodiniaceae species diversity hosted within cnidarians and invertebrate populations (Rowan & Powers, 1991; LaJeunesse, 2001, 2002; Pochon *et al.*, 2001; Coffroth & Santos, 2005; Sampayo *et al.*, 2009; Hill *et al.*, 2011). Subsequently, recent phylogenetic reconstructions have revealed nine widely recognized divergent phylogenetic lineages of Symbiodiniaceae species referred to as “clades” (A-I) which, based on the 18S rDNA and internal transcribed spacer regions (ITS) analyses (Rowan & Powers, 1991; LaJeunesse, 2001, 2002; Pochon *et al.*, 2006; Pochon & Gates, 2010; Hill *et al.*, 2011; Yang *et al.*, 2012; Rouzé *et al.*, 2017), are further divided into sub-clades or types (Rowan & Knowlton, 1995). Over the years, several new species of Symbiodiniaceae (currently 22) have been formally described, classified and named (Table 5.1; Trench & Blank, 1987; Jeong *et al.*, 2014; LaJeunesse *et al.*, 2014, 2015, 2018; Hume *et al.*, 2015; Parkinson *et al.*, 2015; Ramsby *et al.*, 2017). Studies have revealed that Symbiodiniaceae fulfill the prerequisites of the multiple species concept which requires its species (clades and/or sub-clades – hereafter referred to as types) to exhibit distinct genetic, physiological, and ecological variation (Lajeunesse *et al.*, 2012; LaJeunesse *et al.*, 2018).

Symbiodiniaceae types vary in their levels of tolerance to heat and light (Stat *et al.*, 2006; Hennige *et al.*, 2011; Silverstein *et al.*, 2012). Coral-Symbiodiniaceae species associations have been seen to include mono or multi-clade associations (Fabina *et al.*, 2012; Silverstein *et al.*, 2012; Rouzé *et al.*, 2017), with their type and ecological dominance influenced by regional and local environmental factors (Baker, 2003; Ziegler *et al.*, 2017). Corals are seen to be most commonly associated with Symbiodiniaceae in type A-D (LaJeunesse, 2001), rarely with F and G (Ramsby *et al.*, 2017). During favourable environmental conditions the host and its associated symbiosis function in harmony. However, this symbiotic relationship is sensitive to

environmental change and can breakdown when subjected to various stressors caused by natural and/or anthropogenic sources, all of which is determined based on the stress tolerance of either partner (Yang *et al.*, 2012; Rouzé *et al.*, 2017). Coral bleaching refers to the partial or complete loss of the Symbiodiniaceae species from coral tissues, which occurs when corals are under severe stress from elevated temperatures, thereby exceeding their thermal tolerance levels (Hoegh-Guldberg, 1999; Donner *et al.*, 2005; Hoegh-Guldberg *et al.*, 2007). An increase by one or two degrees Celsius is enough for corals to expel their associated Symbiodiniaceae (Lesser, 2007; Desalvo *et al.*, 2008; Ricaurte *et al.*, 2016). This phenomena can be reversed with no major consequences to the coral, depending on the length of exposure and severity of temperature elevation (Baker *et al.*, 2008).

**Table 5.1. Symbiodiniaceae genera, assigned clades and species (\*lacks ITS alphanumeric designation-could be a different/new species)**

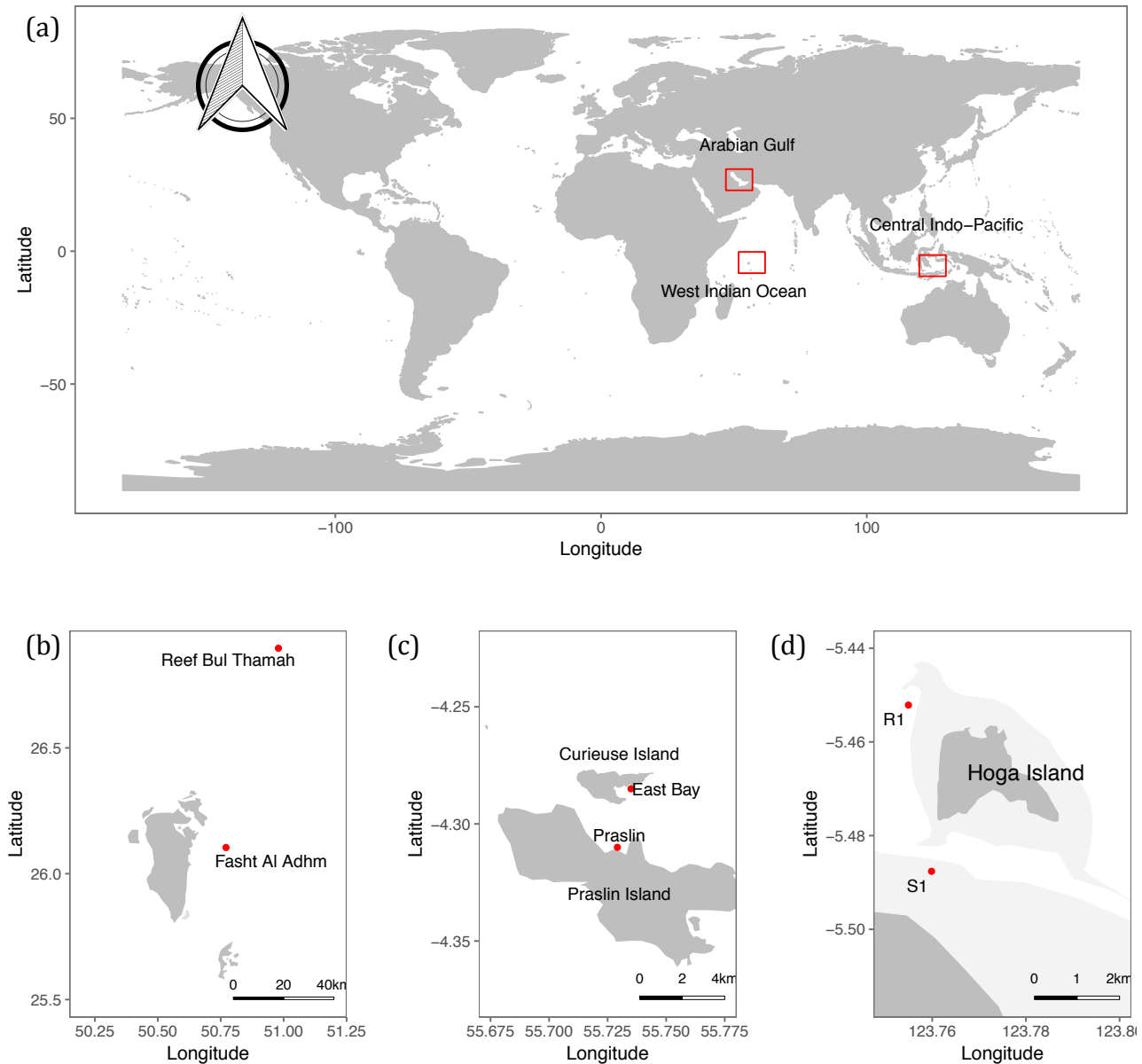
Clade/Type	Species	Source
A	<i>Symbiodinium sp.</i>	LaJeunesse <i>et al.</i> , 2018
A*	<i>Symbiodinium natans</i>	Hansen & Daugbjerg, 2009
A1/A1.1	<i>Symbiodinium microadriaticum</i>	Lee <i>et al.</i> , 2015
A2	<i>Symbiodinium pilosum</i>	Lee <i>et al.</i> , 2015
A3/A3 <sup>Pacific</sup> /A3a/ A3x/A6	<i>Symbiodinium tridacnidorum</i>	Lee <i>et al.</i> , 2015
A4	<i>Symbiodinium linuchae</i>	Trench & Thinh, 1995
A13/A1.1	<i>Symbiodinium necroappetens</i>	LaJeunesse <i>et al.</i> , 2015
B	<i>Breviolum sp.</i>	LaJeunesse <i>et al.</i> , 2018
B*	<i>Breviolum aenigmaticum</i>	Parkinson <i>et al.</i> , 2015
B1	<i>Breviolum antilogorgium</i>	Parkinson <i>et al.</i> , 2015
B1	<i>Breviolum minutum</i>	Lajeunesse <i>et al.</i> , 2012
B1	<i>Breviolum pseudominutum</i>	Parkinson <i>et al.</i> , 2015
B2	<i>Breviolum psygmophilum</i>	Lajeunesse <i>et al.</i> , 2012
B7	<i>Breviolum endomadracis</i>	Parkinson <i>et al.</i> , 2015
C	<i>Cladocopium sp.</i>	LaJeunesse <i>et al.</i> , 2018
C1	<i>Cladocopium goreau</i>	Davies <i>et al.</i> , 2018
C3-Gulf	<i>Cladocopium thermophilum</i>	Hume <i>et al.</i> , 2015
D	<i>Durusdinium sp.</i>	LaJeunesse <i>et al.</i> , 2018
D1	<i>Durusdinium glynnii</i>	Wham <i>et al.</i> , 2017
D1a	<i>Durusdinium trenchii</i>	Davies <i>et al.</i> , 2018
D15	<i>Durusdinium boreum</i>	LaJeunesse <i>et al.</i> , 2014
D8/D12-13/D13	<i>Durusdinium eurythalpos</i>	LaJeunesse <i>et al.</i> , 2014
E1	<i>Effrenium voratum</i>	Jeong <i>et al.</i> , 2014
F1	<i>Fugacium kawagutii</i>	Trench, 2000
G/G3/G3.3	<i>Gerakladium sp.</i>	LaJeunesse <i>et al.</i> , 2018
G*	<i>Gerakladium spongiolum</i>	Ramsby <i>et al.</i> , 2017
G*	<i>Gerakladium endoclonum</i>	Ramsby <i>et al.</i> , 2017

Bleaching has been proposed to be a survival mechanism used by corals to overcome severe stress through dynamic modification of their Symbiodiniaceae species community composition; a concept termed the “Adaptive Bleaching Hypothesis” (Buddemeier & Fautin, 1993). This is done by either switching their Symbiodiniaceae type with those more resistant and present in the surrounding environment, or through shuffling the pre-existing types with those more resistant (Rowan & Powers, 1991; Baker *et al.*, 2004; Rouzé *et al.*, 2017). For example, in a study on a common Indo-Pacific branching coral species (*Acropora millepora*), it was found that switching to thermally tolerant Symbiodiniaceae species type D increased the coral’s thermal tolerance between 1.0-1.5°C (Berkelmans & Van Oppen, 2006). However, this ability to switch to thermally tolerant symbionts comes with a cost or trade off. Previous studies have indicated that accretion rates of reef-building corals are likely to be significantly compromised due to the process of symbiont shuffling to more thermally tolerant types caused by thermal stress before bleaching coupled by the bleaching stress (Little *et al.*, 2004; Mieog *et al.*, 2009; Jones & Berkelmans, 2010). Moreover, it has been suggested that coral calcification rates are affected in hosts harbouring thermally tolerant symbiont when compared to those with a thermally sensitive type (Jones & Berkelmans, 2010; Pettay *et al.*, 2015) showcasing a cost-benefit relationship between corals and their symbionts. Therefore, it is necessary to understand the various associations between the assemblages of Symbiodiniaceae species and host in different environmental conditions as this could provide important insights as to how this relationship affects future reef accretion rates in the face of predicted global environmental change and sea level rise. This study examines the composition and diversity of Symbiodiniaceae species across different thermal regimes and latitudinal gradients in three bioregions, namely: Bahrain (Arabian Gulf / AG), the Seychelles (Western Indian Ocean / WIO) and Indonesia (Central Indo-Pacific / CIP).

## 5.2 | METHODOLOGY

### 5.2.1 | Site Selection & Description

Six study sites located in three bioregions (i.e. two in each): Bahrain (AG), the Seychelles (WIO) and Indonesia (CIP) were selected (Figure 5.1). Considering the latitudinal differences in these bioregions, the sites have been characterized into three thermal regions based on data derived from Chapter 2 (Table 5.2). Reefs from both turbid and clear-water (herein referred to as optimal) sites were chosen to represent different environmental gradients (Table 5.3). Reefs in Bahrain endure extreme SST temperatures ranging between 16-35°C whilst reefs in the Seychelles and Indonesia experience fairly narrow SST differences ranging between 24-29°C (Hume *et al.*, 2013; Rowley *et al.*, 2015); with El Niño events occurring irregularly at intervals of 3.5 to 5.5 years (Charles *et al.*, 1997). This difference in thermal regime is said to influence the variations in diversity and richness of coral species in Bahrain and Indonesia (Coles, 2003).



**Figure 5.1. Location of Study Sites – (a) Location of Bahrain (Arabian Gulf), the Seychelles (Western Indian Ocean) and Indonesia (Central Indo-Pacific); (b) Location of study sites within Bahrain; (c) Location of study sites within Curieuse Marine National Park, Seychelles; (d) Location of study sites within the Wakatobi Marine National Park, Indonesia.**

**Table 5.2. Characterization of thermal regime in each of the bioregions (refer to Chapter 2 for equations used to derive the data displayed below; brief definitions of the variables are outlined below the table). All values are temperature in °C with the exception of DHW which is in °C-weeks.**

Thermal Regime*	Study Site	Min. SST	Max. SST	Annual Mean	Min. Climatology	Max. Climatology	Seasonal Range	Bleaching Threshold	Max DHW	Mean DHW
High	Reef Bul Thamah (Bahrain)	16.5	36.2	26.2	19.1	33.1	14	34.1	18.2	4.8
	Fasht Al Adhm (Bahrain)	15.5	37	26	17.9	33.5	15.6	34.5	20.8	4.7
Moderate	Ridge (Indonesia)	24.5	32.7	28.5	26.5	29.7	3.2	30.7	6.1	2.2
	Sampela (Indonesia)	24.6	33.5	28.4	26.6	29.9	3.3	30.9	14.7	3.7
Low	East Bay (Seychelles)	23.4	32.2	28	25.8	30.1	4.2	31.1	6.5	1.7
	Praslin 2 (Seychelles)	23.3	31.9	28	25.7	30	4.3	31.1	5.6	1.6

\**Thermal regimes* have been assigned based on the combination of the maximum SST, Bleaching threshold and DHW expressed on the reefs.

*Climatology* the long-term mean of SST conditions over time.

*Seasonal Range* the difference between the minimum and maximum SST over time.

*Bleaching threshold* is the value where SST have exceeded maximum long-term mean by 1°C.

*Degree Heating Week (DHW)* is defined as of accumulated daily hotspots over 12 consecutive weeks when the thermal stress anomaly is  $\geq 1^\circ\text{C}$ .

DHW values of  $\geq 4^\circ\text{C}$  and  $< 8^\circ\text{C}$ -weeks, corresponds to delineation between coral bleaching and mortality levels (\*unit= $^\circ\text{C}$ -weeks)

**Table 5.3. Environmental characteristics of the selected study sites.**

Site	Site Code	Depth (m)	Temp. (°C)	Salinity (ppt)	Sedimentation rates (g cm <sup>-2</sup> d <sup>-1</sup> )**	Light attenuation (K <sub>d</sub> PAR)***	Distance	Impacts
<b>Bahrain (AG)</b>								
<b>Fasht Al Adhm (Turbid)</b>	BH-TB	5-7	16-35	42-44	0.23±0.04	0.02	~11 km east of the main island.	Heavily impacted due to various anthropogenic activities mainly reclamation and dredging.
<b>Reef Bul Thamah (Optimal)*</b>	BH-OP	10-12						
<b>Seychelles (WIO) - Curieuse National Park</b>								
<b>Praslin (Turbid)</b>	SY-TB	5-10	25-29	~35	0.03±0.01	0.2-0.4	~1.5 km southwest Curieuse Island	Site is subjected to large sediment load since it is located closer to Praline island, which has intensive tourist marine activities.
<b>East Bay (Optimal)*</b>	SY-OP	5-12						
<b>Indonesia (CIP) – Wakatobi Marine National Park, South East Sulawesi</b>								
<b>Sampela (Turbid)</b>	IN-TB	3-10	26-30	32-34	6.3±2.7	0.01	~1.5 km southwest Hoga Island	Site is adjacent to the Bajo village of Sama Bahari and is subjected to large sediment load and various anthropogenic activities, thus heavily impacted.
<b>Ridge (Optimal)*</b>	IN-OP	5-20						

\* Optimal in this study is referred to as clear waters.

\*\* **Bahrain:** Due to time restrictions, sedimentation rates (g cm<sup>-2</sup> d<sup>-1</sup>) were measured at 10m depth using sediment traps (n=6). Traps were deployed for a period of three days at each of the study sites in May 2018; **Seychelles:** Sedimentation rates (g cm<sup>-2</sup> d<sup>-1</sup>) were measured at 10m depth using sediment traps, however, due to expedition time constraints the traps were only deployed for a total of 4 days in April 2018; **Indonesia:** Sedimentation rates (mg cm<sup>-2</sup> d<sup>-1</sup>) collected by Operation Wallacea between 2006-2011 (mean values are reported here along with ±SD and taken from Franco, 2014).

\*\*\* **Bahrain & Indonesia:** Light intensity was measured using hobo loggers that were deployed at two measurements 3 and 7m in Bahrain and 5 and 10m in Indonesia, then calibrated following the methods outlined in (Long *et al.*, 2012) to calculate photosynthetically active radiation (PAR). **Seychelles:** Light attenuation coefficients (K<sub>d</sub> (PAR), m<sup>-1</sup>) for each site was obtained from Gardner *et al.*, (2018).



### 5.2.2 | Sample Collection

Coral fragments of ~2 cm from selected coral species (Table 5.4) were collected over a two-year period (2017-2018) from Bahrain and the Seychelles; Indonesian samples were only collected in 2017. Coral fragments came from different colonies with sampling depth between 5-10 m at each site; various numbers of replicates were collected based on availability at site (Table 5.4). To attain more site-specific representation, coral samples were collected randomly whilst ensuring a minimum of 1 m distance between sample colonies thereby randomizing host genetic effects and micro-environments. The coral fragments were preserved in RNAlater at room temperature and/ 3-6°C (in fridge) upon collection on the field and on ice during transit. Once samples arrived at the University of Essex they were then stored at -20°C.

**Table 5.4. List of coral specimens along with total number of individual replicates (n).**

<b>Bahrain (AG)* (April 2017 &amp; 2018)</b>	<b>Seychelles (WIO) (May 2017 &amp; 2018)</b>	<b>Indonesia (CIP) (July 2017)</b>
<i>Porites lutea</i> (n=16)	<i>Porites lutea</i> (n=19)	<i>Porites lutea</i> (n=9)
<i>Dipsastraea speciosa</i> (n=2)	<i>Dipsastraea speciosa</i> (n=17)	<i>Dipsastraea speciosa</i> (n=10)
<i>Platygra daedalea</i> (n=11)	<i>Favites pentagona</i> (n=17)	<i>Favites pentagona</i> (n=10)
<i>Cyphastrea microphtalma</i> (n=10)	<i>Acropora muricata</i> (n=13)	<i>Acropora muricata</i> (n=10)
<i>Tubinaria peltata</i> (n=3)	<i>Acropora gemmifera</i> (n=8)	<i>Acropora gemmifera</i> (n=10)
	<i>Pavona cactus</i> (n=4)	<i>Pocillopora verrucosa</i> (n=9)
		<i>Pocillopora damicornis</i> (n=5)

**\*NB:** Samples were collected following the mass bleaching in Bahrain in 2017 which impacted the study reefs severely, making it very difficult to find live coral with signs of Symbiodiniaceae species presence for sampling. In 2018, samples were collected for *P. lutea*, *P. daedalea* and *C. microphtalma* from Bahraini reefs.

### 5.2.3 | Molecular Analysis

DNA was extracted from the collected coral tissue of each sampled species (Table 5.4) using Qiagen DNeasy Blood & Tissue Kit following the manufacturer's instructions with minor modifications (see Supplementary Material; S4.1). Symbiodiniaceae communities were characterized using a Nextera XT dual-indexing strategy, which involved PCR amplification of a phylogenetic marker gene, followed by a secondary short-cycle PCR amplification in which dual Nextera indices are added to the amplicon for multiplexing of samples. The ITS rRNA gene was targeted (~234-266 bp region) with Symbiodiniaceae specific primers SYM\_VAR\_5.8S2: (5'-GAATTGCAGAACTCCGTGAACC-3') and SYM\_VAR\_REV: (5'-CGGGTTCWCTTGTYTGACTTCATGC-3; Hume *et al.*, 2018) both of which were modified to contain Illumina specific overhang sequences. The ITS rRNA gene was amplified in 25 µl reactions with 12.5 µl of appTAQ Polymerase (Appleton Woods LTD.), 1 µl of each primer (10 µM), 2 µl of Bovine Serum Albumin (BSA; 0.8 mg per reaction; Sigma Aldrich Co.), 6.5 µl of PCR water and 2 µl of template DNA. The PCR protocol included an initial denaturation step at 95°C for 3 minutes, followed by 35 cycles of 95°C for 30 seconds, 58°C for 30 seconds and 72°C for 30 seconds. After a final extension step of 72°C for 5 minutes, PCR products were held at 4°C. PCR products were purified using Agencourt AMPure XP PCR Purification beads (Beckman Coulter Ltd, High Wycombe, UK) following Illumina's "16S Metagenomic Sequencing Library Preparation" Protocol (<https://bit.ly/1Ns4tAD>).

The index PCR was carried out in 25 µl reactions with 12.5 µl of appTAQ Polymerase (Appleton Woods LTD.), 2.5 µl each of sample specific Series A & B Nextera XT index (Illumina), 5 µl of PCR water (Bioline Reagents Ltd, UK) and 2.5 µl of purified PCR product. PCR was conducted with an initial denaturation at 95°C for 3 minutes, followed by 8 cycles of 95°C for 30 seconds,

55°C for 30 seconds and 72°C for 30 seconds. A final extension step was included at 72°C for 5 minutes, after which PCR products were held at 4°C. PCR products were purified using Agencourt AMPure XP PCR Purification beads (Beckman Coulter Ltd, High Wycombe, UK) and quantified on a POLARstar Omega (BMG LABTECH GmbH, Germany) plate reader using the PicoGreen® dsDNA assay. PCR products were then pooled in equimolar concentrations. The size and concentration of the resulting pool was checked twice, once using a NEBNext® Library Quant Kit following the manufacturer's protocol (<https://bit.ly/2Z0kmjf>) on the BioRAD - CFXConnect Real Time System (96 well plate); and the second using the PicoGreen® dsDNA assay on a NanoDrop 3300 Fluorospectrometer following the manufacturer's protocol (<https://bit.ly/2YY8iz5>) to validate the concentration levels prior to sequencing. Next Generation Sequencing (NGS) was carried out on an Illumina HiSeq 2500 on rapid-run mode, producing 2 x 301 bp sequences, at the University of Essex, UK.

#### **5.2.4 | Bioinformatic Analysis**

The generated NGS ITS raw sequence amplicon libraries were processed using the SymPortal analytical framework (<https://symportal.org> - described in Hume *et al.*, 2019). Sequencing data was submitted to the SymPortal database for quality control (including the removal of non-Symbiodiniaceae sequences) and analysis. Symbiodiniaceae genera were identified as part of the SymPortal analysis, which is conducted within a framework supported by a database containing sequencing data of each genus acquired from all previous run analyses cataloged within that database. The SymPortal database utilizes the sequence data submitted to it by global researchers to improve its ability to identify Symbiodiniaceae genotype-representative ITS2 type profiles (hereafter referred to as ITS2 types) based on their presence and abundance in the samples and within the database. Unique combinations of intragenomic variations in sequences, commonly

referred to as defining intragenomic [sequence] variants (DIVs), are used for profile characterization considering both sequence abundances and identities whereby sets of sequences found to re-occur in multiple samples are searched for algorithmically (Howells *et al.*, 2020). For more details regarding the SymPortal pipeline, quality control and algorithms used for ITS2 profile identification refer to Hume *et al.* (2019) and/or the accompanying GitHub site ([https://github.com/didillysquat/SymPortal\\_framework](https://github.com/didillysquat/SymPortal_framework) ; Hume *et al.*, 2020).

### 5.2.5 | Data and Statistical Analysis

Symbiodiniaceae genera were analysed using the output dataset derived from the SymPortal analysis to examine the symbiont community composition in different host species across bioregions. All of which was conducted using R (R Development Core Team, 2016); all plots were created using the ggplot function in the “tidyverse” package in R (Wickham *et al.*, 2019). ITS2 type abundance, relative abundance, species richness, and Shannon’s ( $H'$ ) and Simpson’s (1-D) diversity indices (which account for both abundance and evenness) were calculated using the “vegan” package in R (Oksanen *et al.*, 2018). Analysis of variance (ANOVA) was used to test for significant difference in the diversity indices amongst bioregions and corals host species.

Principal coordinate analysis (PCA) was used to further analyse the variation in the ITS2 sequence abundance by utilising the *between profiles distances* and *between sample distances* matrices produced by SymPortal. These matrices were generated by calculating the average distance-to-centroid values for genus-separated distances (*Cladocopium* and *Durusdinium*; formerly, clade C and clade D respectively) using the UniFrac derived matrices. The distance matrices were calculated by SymPortal using a square root transformation, which is commonly used to increase the weight of lesser abundant sequences during analysis.

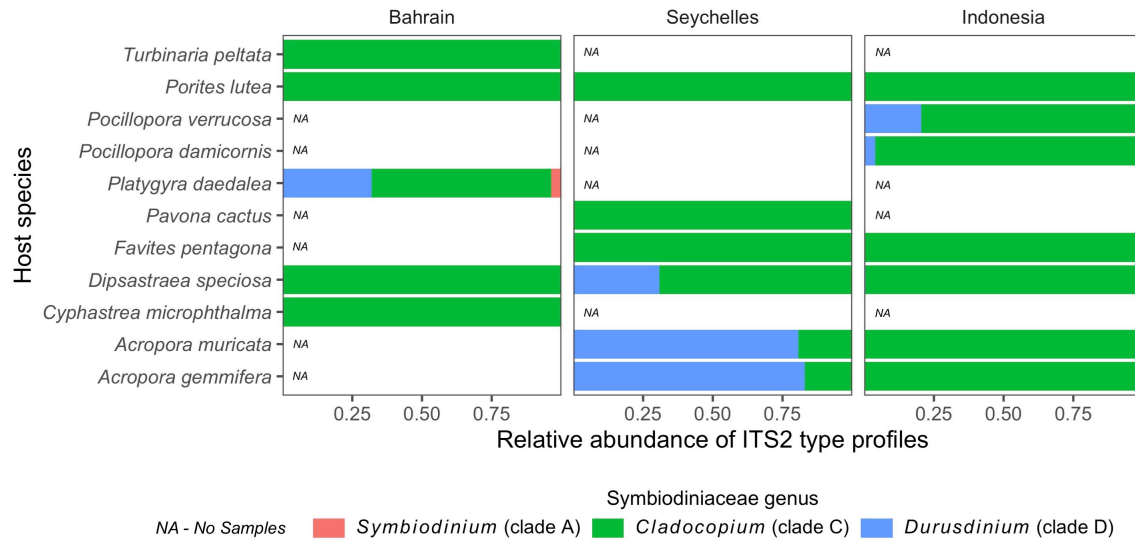
To further examine the potential drivers of the symbiont communities, variance partitioning in four cross factors were analysed: coral host species, bioregion/site, thermal regime, and latitude. This was done using a permutational multivariate analysis of variance (PERMANOVA) to test for differences in Symbiodiniaceae community composition across bioregions within each coral host species (considered as a nested factor). The PERMANOVA models were performed using the *adonis* method from the “vegan” package in R (Oksanen *et al.*, 2018).

## 5.3 | RESULTS

### 5.3.1 | Symbiodiniaceae Diversity & Abundance Across Bioregions

The amplicon sequencing produced a total of 5,622,444 unique sequences of which 3,551,814 were assigned as ITS2 types which identified three genera: *Cladocopium*, *Durusdinium* and *Symbiodinium* (Figure 5.2). Regardless of site/bioregion, the genus *Cladocopium* (corresponding clade C) is the most abundant endosymbiont accounting for 86.3% of sequences retained, followed by *Durusdinium* (corresponding clade D; 13.5%), whilst *Symbiodinium* (corresponding clade A) was observed to be the least abundant (0.2%) and detected only in one bioregion (AG). *Cladocopium* is present in all eleven-sampled host species whilst *Durusdinium* and *Symbiodinium* are present in seven and one host species, respectively (Figure 5.2; see Table 5.4 for full list of coral host species). Relative abundance of Symbiodiniaceae genera associations with coral host species was observed to differ depending on bioregions, whereby, all sampled colonies from the thermally extreme Bahrain (AG) were associated fully with *Cladocopium* (100%), with the exception of *Platygra daedalea* which was observed to have multiple associations: *Cladocopium* (65%), *Durusdinium* (32%) and *Symbiodinium* (4%; Figure 5.2). On the contrary, most coral colonies in the Seychelles (WIO) and Indonesia (CIP) were observed to be associated with more than one Symbiodiniaceae genera

depending on the coral host species. In the Seychelles, both *Favites pentagona* and *Pavona cactus* are associated with solely *Cladocopium* (100%) whereas the remaining colony hosts co-occurred with *Cladocopium* and *Durusdinium* (Figure 5.2). In Indonesia, *F. pentagona* retains a similar pattern of single association along with *Porites lutea* (*Cladocopium*; 100%), whereas the remaining colonies had co-occurrences of *Cladocopium* and *Durusdinium* (Figure 5.2). Interestingly, in the Seychelles, *Durusdinium* is more dominant (81%) in the coral host *Acropora* (*A. muricata* and *A. gemmifera*) whilst *Cladocopium* (19%) is much lower in abundance. However, in Indonesia, the opposite is observed with *Cladocopium* (99.98%) being the dominant endosymbiont in the coral host *A. muricata* whilst *Durusdinium* is observed to be in limited abundance (0.02%); *A. gemmifera* is associated with only *Cladocopium* (100%; Figure 5.2). In addition, the genus *Pocillopora* associated with *Cladocopium* and *Durusdinium* (Figure 5.2). *Symbiodinium* was only detected in Bahrain (relative abundance = 0.2%) and in one coral host species (*P. daedalea*) and was absent in other host species, whether in Bahrain or other regions. Unfortunately, samples could not be acquired from the Seychelles and Indonesia for this species; hence no comparisons are made (Figure 5.2).



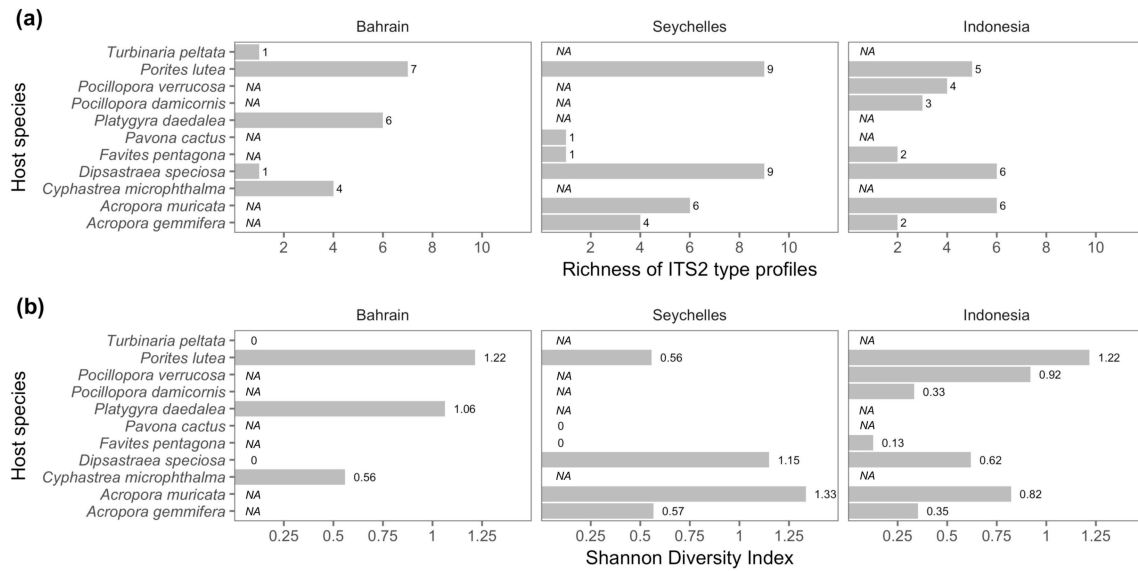
**Figure 5.2.** The relative abundance (>0.1% of total community) of ITS2 types of Symbiodiniaceae genera (clades) within each coral genus (host) at sites within Bahrain (Arabian Gulf), Seychelles (Western Indian Ocean) and Indonesia (Central Indo-Pacific). Individual colonies were sampled in both 2017 and 2018 for Bahrain and the Seychelles whilst Indonesian colonies were sampled in 2017 only.

In Bahrain, ITS2 type richness was observed to be highest in *P. lutea* and *P. daedalea* (Figure 5.3a). Shannon's ( $H'$ ) and Simpson's (1-D) diversity indices were noted to be highest in *P. lutea* ( $H' = 1.2$ ; 1-D = 0.7) followed by *P. daedalea* ( $H' = 1.1$ ; 1-D = 0.6), whilst only one ITS2 type was detected in *D. speciosa* and *Tubinaria peltata* (Figure 5.3b). In the Seychelles, *P. lutea*, *D. speciosa* and *Acropora* (*A. muricata* and *A. gemmifera*) had the richest ITS2 types, with Indonesia following a similar trend with *D. speciosa*, *P. lutea* and *A. muricata* acting as a hub for richness (Figure 5.3a). In the Seychelles, *A. muricata* had the highest diversity ( $H' = 1.3$ ; 1-D = 0.7), followed by *D. speciosa* ( $H' = 1.2$ ; 1-D = 0.6; Figure 5.3b). *Acropora gemmifera* was observed to host half the diversity ( $H' = 0.6$ ; 1-D = 0.3) of *A. muricata*, despite belonging to the same genus; whilst *F. pentagona* and *P. cactus* only hosted one ITS2 type (Figure 5.3b). In Indonesia *P. lutea* had the highest diversity ( $H' =$

1.2; 1-D = 0.7), followed by *A. muricata* ( $H' = 0.8$ ; 1-D = 0.4), whilst the least diversity was detected in *F. pentagona* ( $H' = 0.1$ ; 1-D = 0.1; Figure 5.3b).

Out of the three bioregions, *P. lutea* in the Seychelles was observed to host half the diversity of ITS2 types than *P. lutea* in Indonesia and Bahrain (Figure 5.3b). Similar to the pattern noted previously with diversity indices in the *Acropora* species, the diversity of ITS2 types in *A. muricata* in both the Seychelles and Indonesia are 50% higher than in *A. gemmifera*, despite belonging to the same genus (Figure 5.3b). In addition, ITS2 types are highly diverse in the host coral *D. speciosa* in the Seychelles, whereas, in Bahrain, no diversity was observed, and in Indonesia the diversity of the ITS2 types were approximately 40% lower than that in the Seychelles (Figure 5.3b). Lastly, the ITS2 types hosted in *P. verrucosa* ( $H' = 0.9$ ; 1-D = 0.5) were 60% more diverse than *P. damicornis* ( $H' = 0.3$ ; 1-D = 0.2) in Indonesia (Figure 5.3b). In general, no significant variation in the diversity of ITS types was observed across bioregions (ANOVA:  $F_{2,17} = 0.02$ ,  $p = 0.98$ ) or coral host species (ANOVA =  $F_{10,17} = 1.67$ ,  $p=0.26$ ).





**Figure 5.3. (a) Richness of coral associated-Symbiodiniaceae ITS2 types across all sites in Bahrain, Seychelles and Indonesia. (b) Shannon's Diversity Index ( $H'$ ) of coral associated-Symbiodiniaceae ITS2 types across all sites (NA = no samples acquired from respective sites). Individual colonies were sampled in both 2017 and 2018 for Bahrain and the Seychelles whilst Indonesian coral colonies were sampled in 2017 only.**

### 5.3.2 | Community Composition and Biogeographical Patterns of Symbiodiniaceae

Overall, 50 different Symbiodiniaceae ITS2 types were identified and associated with eleven coral host species in the three selected bioregions. *Cladocopium* (clade C) dominated all the associations in Bahrain, Seychelles, and Indonesia. The abundance of ITS2 types varied amongst host species and sites where the maximum number of associations in a host species was observed to be 9 (e.g. *P. lutea* in the Seychelles) and the lowest was 1 (e.g. *D. speciosa* in Bahrain; Figure 5.4). It is important to note that many of the associations detected were infrequent, occurring once or twice within a host; hence, it is only possible to see the more abundant ITS2 types in Figure 5.4.

In Bahrain, site-specific unique associations of ITS2 type C3-Gulf (*Cladocopium thermophilum*) were found in all coral hosts that exist in this thermal extreme bioregion (Figure 5.4). This association with ITS2 type C3-Gulf is influenced by thermal regime, individual site, and latitudinal transect (Figure 5.6a; Table 5.5). In total, 15 ITS2 types (the lowest in abundance amongst the three bioregions) make up the community composition of Symbiodiniaceae associations in Bahrain, based on the sampled coral hosts; with *P. lutea* hosting the most abundant associations (7 out of 15), followed by *P. daedalea* (6 out of 15), and *C. microphtalma* (4 out of 15; Figure 5.4). Both *D. speciosa* and *T. peltata* hosted only 1 ITS2 type. Overall, the community in Bahrain is predominantly made up of the C3-Gulf (*Cladocopium thermophilum*) type followed by C15, D1 (*Durusdinium glynnii*), and D5.

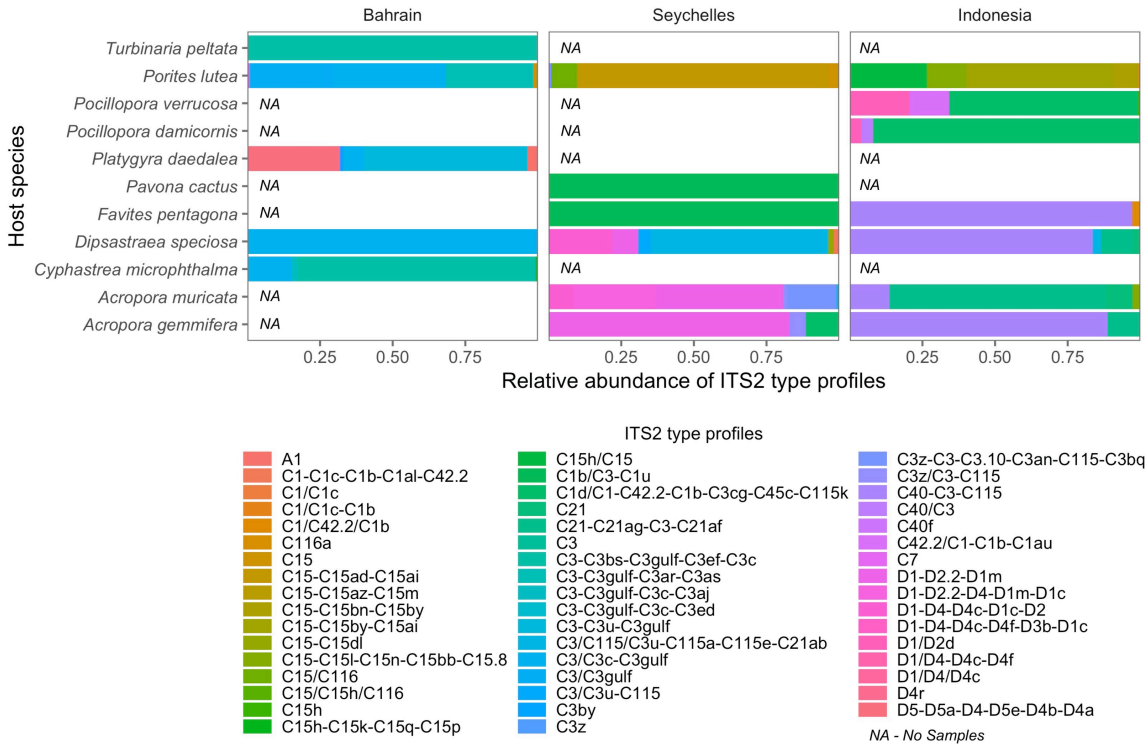
Since Indonesia is located in the coral triangle, epicenter of marine biodiversity, it is unsurprising that it also harbours the most diverse community composition of Symbiodiniaceae ITS2 types (19 types) amongst the three study bioregions with both *A. muricata* and *D. speciosa* hosting the most abundant number of ITS2 types (n=6). Differences in community composition between both

*Acropora* species were also noted whereby *A. gemmifera* was observed to have a community composition that is low in species abundance, being associated with only two ITS2 types belonging to the *Cladocopium* group (Figure 5.4).

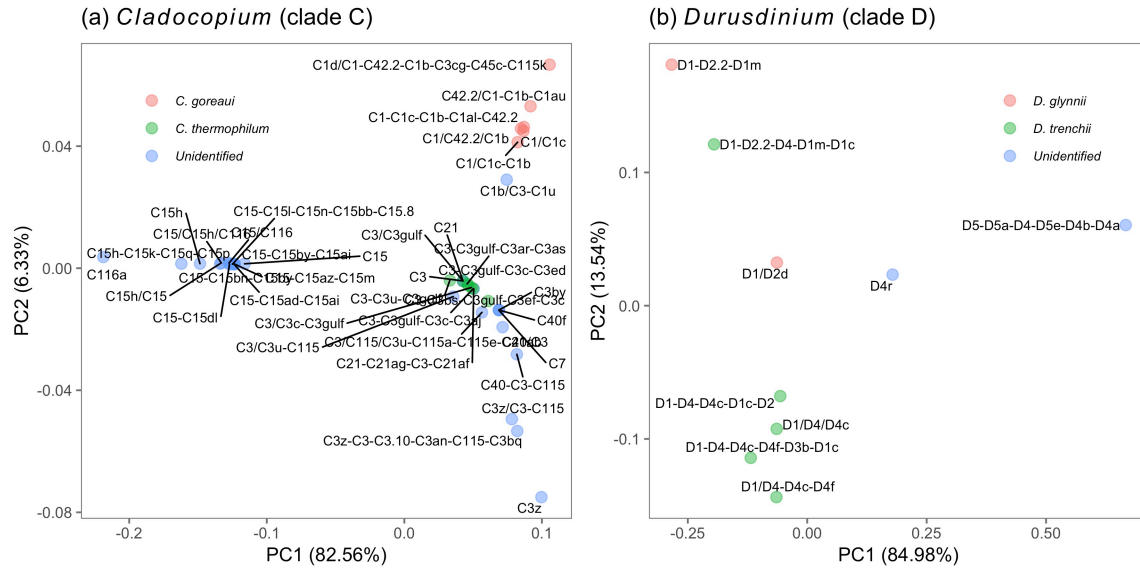
This pattern where *A. gemmifera* associates with lower species abundance than *A. muricata* is also observed in the Seychelles; in addition, the community composition of Symbiodiniaceae ITS2 types is also diverse and abundant in the Seychelles with an overall total of 18 ITS2 types associated across sampled host species. *Porites lutea* and *D. speciosa* have rich and abundant community compositions with 9 ITS2 type associations with both *Cladocopium* and *Durusdinium*, making the community richer in abundance than that observed in Indonesia (Figure 5.4). In addition, *D. speciosa* was noted to host the unique ITS2 type C3-Gulf despite its low contribution (0.1%) amongst its nine ITS2 type symbionts (S4.2). Nevertheless, communities within host specific corals such as *P. cactus* and *F. pentagona* are observed to associate with only one ITS2 type (Figure 5.4).

Overall, there seems to be a shift to lower diversity of ITS2 types (e.g. in *P. lutea* and *D. speciosa*) from sites with lower thermal regimes towards high thermal extremes (Figure 5.4). In Indonesia, community composition is dominated by C15, C21, C3 and D4 whilst the Seychelles is dominated by C3, C1 and C15 with notable contribution from D1 (*Durusdinium glynnii*; Figure 5.4; S4.2). Overall, coral host species is observed to be a strong driver of Symbiodiniaceae communities (Figure 5.6), however, other drivers with significant roles include thermal regime and latitudinal transects (Table 5.5). Moreover, some coral species, for example, *P. lutea* in the Seychelles and Indonesia is noted to have very different ITS types which suggests that bioregions/sites is also a potential strong driver since there is minimal difference between these two bioregion's thermal regimes and latitudinal position. In comparison to other Symbiodiniaceae genera, diversity in the genus *Cladocopium* is noted to be large (Figure 5.5), despite the many unidentified genotypes,

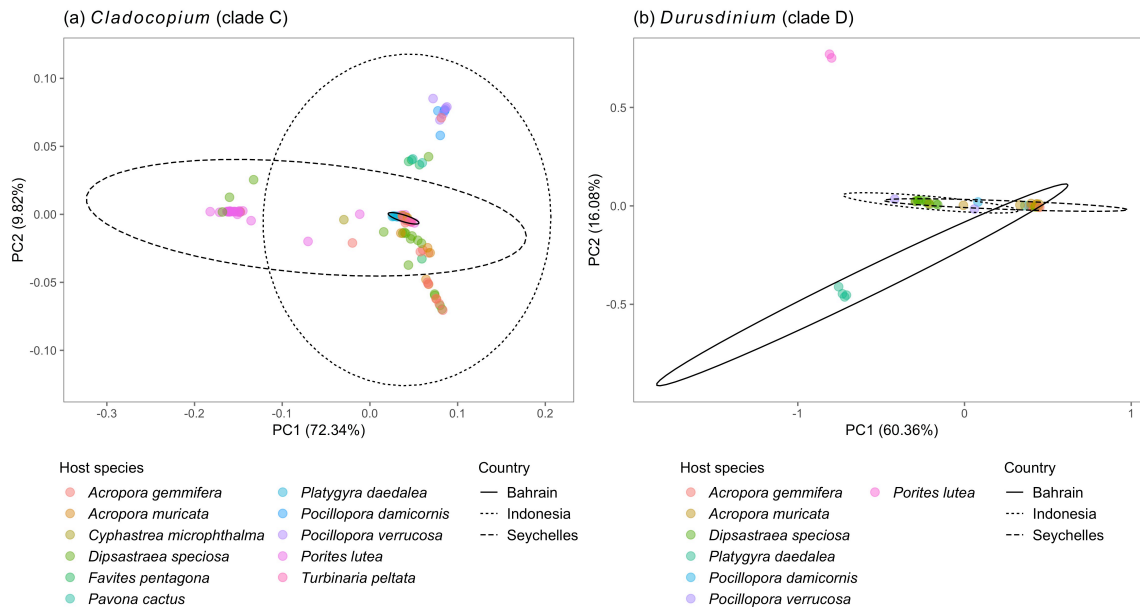
which infers that there are more new Symbiodiniaceae species than currently described in LaJeunesse *et al.* (2018).



**Figure 5.4.** The relative abundance of ITS2 types within each coral genus (host) at sites within the three bioregions. Individual colonies were sampled in both 2017 and 2018 for Bahrain and the Seychelles whilst Indonesian colonies were sampled in 2017 only.



**Figure 5.5.** Principal coordinate analysis (PCA) of Symbiodiniaceae ITS2 profiles across bioregions: (a) *Cladocopium* (clade C); (b) *Durusdinium* (clade D). Percentages on each axis indicate the amount of variation explained by each axis (UniFrac distance matrix).



**Figure 5.6.** Principal coordinate analysis (PCA) plots of Symbiodiniaceae community composition highlighting coral host and bioregions: Bahrain (Arabian Gulf), Seychelles (Western Indian Ocean), Indonesia (Central Indo-Pacific); (a) *Cladocopium* (clade C); (b) *Durusdinium* (clade D), utilising a UniFrac distance matrix; Adonis *p* values indicate significant results of PERMANOVA tests outlined in Table 5.5.

**Table 5.5. Results of PERMANOVA on PCA of Symbiodiniaceae communities between coral species by thermal regime, individual site, and latitudinal transect. Significant  $p$ -values ( $p < 0.05$ ) are marked in (\*), ( $p < 0.001$ ) are marked in (\*\*) and ( $p < 0$ ) are marked in (\*\*\*)**

Model	PERMANOVA p-value
<i>Cladocopium</i> (clade C)	
Between coral host species	$F_{10,116} = 4127.8, R^2 = 0.99, P = 9.999e-05$ ***
Coral host species* thermal regime	$F_{10,116} = 2261.17, R^2 = 0.99, P = 0.001$ **
Coral host species* individual site	$F_{10,116} = 4459.5, R^2 = 0.99, P = 0.001$ **
Coral host species* latitude	$F_{10,116} = 1209.3, R^2 = 0.99, P = 0.04$ *
<i>Durusdinium</i> (clade D)	
Between coral host species	$F_{6,38} = 478.2, R^2 = 0.99, P = 3e-04$ ***
Coral host species* thermal regime	$F_{6,38} = 511.5, R^2 = 0.99, P = 0.001$ **
Coral host species* individual site	$F_{6,38} = 466.1, R^2 = 0.99, P = 0.01$ *
Coral host species* latitude	$F_{6,38} = 1009.5, R^2 = 0.99, P = 0.0002$ ***

## 5.4 | DISCUSSION

This study investigates the diversity and distribution of coral-Symbiodiniaceae associations of different coral host species, bioregions, thermal regimes, and latitudinal gradients using next-generation sequencing.

### 5.4.1 | Symbiodiniaceae Diversity & Abundance Across Bioregions

Overall, three distinct genera (i.e. *Cladocopdium*, *Durusdinium*, and *Symbiodinium*) of coral-Symbiodiniaceae associations were found regardless of site. In general, *Cladocopdium* (clade C) was the most dominant whilst *Durusdinium* (clade D) was observed to co-occur across the three bioregions. Prevalence of *Cladocopdium* is observed to be a common feature of Symbiodiniaceae communities in the Arabian Gulf (Ziegler *et al.*, 2017; Howells *et al.*, 2020), Central Indo-Pacific (LaJeunesse, 2005; Thomas *et al.*, 2014), and Western Indian Ocean (Gardner *et al.*, 2018; Leveque *et al.*, 2019).

Previous studies have documented the occurrence of *Cladocopium goreau* (C1) and ITS2 type C3 worldwide; both of which are considered to be a generalist type (Lajeunesse *et al.*, 2004; Lajeunesse, 2005; Wham *et al.*, 2014; Leveque *et al.*, 2019). Results presented here reflect previous studies that record C3 dominance within the bioregions of the site-specific reefs, with reports of a dramatic shift in C3 prevalence depending on the reefs' latitudinal position whereby the usually common (on low latitude reefs) C3 was reported to be extremely rare or absent on high-latitude reefs (Lajeunesse *et al.*, 2004). The results presented here support this previous observation as they indicate a shift from the common C3 generalist genotypes (e.g. C3/C115, C3z/C3-C115, C3/C34-C115) observed in the Seychelles and/or Indonesia sites to a more specialised differentiated monophyletic lineage, referred to as C3-Gulf (*Cladocopium thermophilum*; Hume *et al.*, 2015) in

Bahrain. The ITS2 C3-Gulf type has been reported to increase the host coral's tolerance to the thermal extremes (~36°C) the reefs are exposed to (D'Angelo *et al.*, 2015). Extreme thermal regime also explains why all coral host species in Bahrain except *P. daedalea* were only associated with ITS2 C3-Gulf types. Our data is the first to confirm and report the presence of *Cladocopium thermophilum* in Bahrain. In addition, results from this study showcase that the proportion of the common generalist *Cladocopium* (C3) is observed to decrease by 50% in the Seychelles when compared to Indonesia. This could be because symbiont representatives from the *Cladocopium* group are considered to be thermally sensitive; *Cladocopium* is usually the dominant type when water temperatures are below the bleaching threshold (Smith *et al.*, 2017). This sensitivity to temperature change would also explain the decrease in the proportion of *Cladocopium* types in the Seychelles despite their dominance since water temperatures there experience notably warmer and longer episodes, that induce bleaching (DHW=7°C-weeks in 2016), than in Indonesia (DHW=5°C-weeks in 2016). *Durusidinum glynnii* (D1) was associated with coral host species in Bahrain and the Seychelles. *Durusidinum* symbionts are generally considered stress/thermally tolerant (Stat *et al.*, 2013); this lineage is observed to contribute notably to the abundance and richness of ITS2 types in the Seychelles. Furthermore, *Durusidinum trenchii* is often associated with recently bleached and/or recovering corals (Baker, 2001; Baker *et al.*, 2004) which can be replaced or outcompeted through the process of “shuffling” following recovery (Thornhill *et al.*, 2006; Baumann *et al.*, 2018). This association in warmer thermal regimes could be a result of the recent site specific bleaching event which occurred in the Seychelles in 2016 (Gardner *et al.*, 2018) and is reported in other regions (Kemp *et al.*, 2014; Smith *et al.*, 2017). Hosting these stress tolerant symbionts can increase the coral's thermal tolerance by 1.0-2.0°C (Stat & Gates, 2011) when compared to the common *Cladocopium* generalist (C3 type), which is more thermally sensitive (Berkelmans & Van Oppen, 2006). However, this enhanced resilience caused by representatives from the *Durusidinum* type



comes at an energetic cost to the coral host, impacting their growth and accretion rate (Baker, 2001; LaJeunesse *et al.*, 2009; Pettay *et al.*, 2015).

Furthermore, the genus *Symbiodinium* (clade A) was observed to occur in the high latitude sites (i.e. Bahrain) which mirrors previous reports that it occurs mostly at higher latitude reefs (Savage *et al.*, 2002; Baker, 2003; Leveque *et al.*, 2019). *Symbiodinium* associates are characterized as high temperature specialists with high irradiance (LaJeunesse, 2002). Previous studies have demonstrated that numerous *Symbiodinium* associates are tolerant to high light and temperature whilst being facilitated by enhanced photo-acclimation and photo-protective pathways (Robison & Warner, 2006; Reynolds *et al.*, 2008; Takahashi *et al.*, 2009; Kemp *et al.*, 2014). Therefore, it comes to no surprise that this group was detected in *P. daedalea* (a common thermal stress tolerant coral in the AG; Kirk *et al.*, 2018) in Bahrain which, amongst the coral species, had the most diverse and richest symbiont association (C = 65%, D = 32% and A = 4%).

Out of the three bioregions, Indonesia had the richest and most abundant ITS2 types. Located in the coral triangle, Indonesia is not only the epicenter of coral diversity, it is also considered the center of Symbiodiniaceae ITS2 genotype diversity (LaJeunesse *et al.*, 2012; Chen *et al.*, 2019), hence results are in line with previous observations. Indonesian corals host a mixture of *Cladocopium* types, some of which are thermally sensitive generalists (e.g. C3) whilst others are more thermally tolerant (e.g. C15; Pochon *et al.*, 2004). Moreover, observations of symbiont types within *P. verrucosa* and *P. damicornis* in Indonesia support those made by others whereby C1 is the most prevalent ITS2 type (Lajeunesse *et al.*, 2004; Yang *et al.*, 2012). Although previous studies reported the detection of C1c within *Pocillipora* sp. in the Pacific, we detected ITS2 C1d type. In addition, it remains unclear as to why Symbiodiniaceae assemblages differ in diversity between *A. muricata* and *A. gemmifera* despite belonging to the same genus and being collected from the same site/bioregion and thermal regime; a

suggestion maybe that this is related to heritability and the symbionts were horizontally (acquired from the environment) or vertically (passed on maternally) transferred (Quigley *et al.*, 2017).

Overall, diversity of ITS2 types varied between the same coral host species across bioregions; for example *P. lutea* in the Seychelles was observed to host half the diversity of ITS2 types found in Bahrain and Indonesia. This was also noted in *D. speciosa*, which hosted the highest diversity of symbionts in the Seychelles in contrast to Bahrain, which hosted just one ITS2 type; in Indonesia, its symbiont community was 40% lower than the Seychelles. This is probably because, although the identity of coral host species may contribute immensely towards determining Symbiodiniaceae diversity and distribution, previous studies report environmental factors to have a greater influence on diversity and distribution (Tonk *et al.*, 2013; Baumann *et al.*, 2018; Wang *et al.*, 2019) which is evident in our data lending support to this theory.

#### **5.4.2 | Community Composition and Biogeographical Patterns of Symbiodiniaceae**

Biogeographical patterns are evident in the distribution and community composition of Symbiodiniaceae species worldwide, influenced and driven by the difference in latitude and thermal regimes. Overall, a shift is clearly observed in the diversity and abundance of ITS2 types from high to low; when comparing symbionts in low latitude/thermal regime reefs (e.g. Indonesia) to high latitude/thermal regime reefs (e.g. Bahrain). This pattern supports previous studies on this topic (Chen *et al.*, 2019). In addition, Symbiodiniaceae community composition in Bahrain was relatively even, with C3-Gulf dominating across all species, whereas in Indonesia and the Seychelles compositionally distinct and variable Symbiodiniaceae communities were observed amongst coral species. This is likely driven by the difference in thermal regimes and geographical distances. Chen *et al.* (2019) have recently suggested that geographical distance could limit the spread of

Symbiodiniaceae species since evidence indicates that they have an *in situ* life span of approximately seven days (Nitschke, 2015). Their short life-span and ability to swim short distances (3-10 m/day; Fitt & Trench, 1983), depending on sea currents for their dispersal (Wirshing *et al.*, 2013; Thornhill *et al.*, 2017; Chen *et al.*, 2019), could offer a hypothesis as to why Symbiodiniaceae diversity and richness is lower in higher latitude reefs compared to those in low latitude reefs (Chen *et al.*, 2019). These factors (i.e. currents, geographical distance, short-life span) could limit the spread of Symbiodiniaceae species from the epicentre of genotype diversity to other bioregions. In addition, other limiting factors such as environmental stressors (e.g. extreme thermal regimes and high salinity levels in the AG) have also been suggested to limit Symbiodiniaceae diversity and distribution (D'Angelo *et al.*, 2015; Ziegler *et al.*, 2017) whilst dictating the symbiont type hosted (Smith *et al.*, 2017).

Symbiodiniaceae community composition in the Seychelles comprises largely of thermally tolerant symbionts, despite the prevalence of *Cladocopium* (thermally sensitive). The thermally tolerant *Durusdinium* symbiont contributes notably to the community composition. In addition, ITS2 type C3-Gulf in *D. speciosa*, was noted to be present despite its low abundance in the community (0.1%). This is the first observation (to our knowledge) confirming the presence of this ITS2 type C3-Gulf (also referred to as *Cladocopium thermophilum*) outside the three known niche regions (the AG, the Gulf of Oman and the Red Sea; Hume *et al.*, 2016). Suggestions have been made that the Gulf of Oman could play a role in facilitating the adaptation of corals in the Indian Ocean to rising temperatures in light of a warming planet through providing a potential source of these thermotolerant symbionts (D'Angelo *et al.*, 2015). Furthermore, evidence suggests that Symbiodiniaceae species composition in Bahrain tends to shift from thermal sensitive ITS2 types (e.g. common generalist *Cladocopium*) to thermally tolerant types (e.g. *Durusdinium*) as a

mechanism to adapt and acclimatise to long term exposure to elevated temperatures (Berkelmans & Van Oppen, 2006; Palumbi *et al.*, 2014; Wang *et al.*, 2019). *Cladocopium thermophilum* is said to be cryptically distributed outside its niche areas (the AG, the Gulf of Oman and the Red Sea) since it is a member of the highly diverse and ancient Symbiodiniaceae group (Hume *et al.*, 2016). The group can be traced back to the Mesozoic Era (~160 mya) which is suspected to be the earliest known diversification period of this family (LaJeunesse *et al.*, 2018). The observations made regarding the presence of this highly specialised coral symbionts in Bahrain supports previously reported phylogeographic evidence which indicated that this symbiont is a member of a sub-population of an ancestral taxonomic group that is stress-tolerant which harbours high genetic diversity that is present at hardly detectable levels outside the AG (Hume *et al.*, 2016). Therefore, the findings and observations made across the three bioregions especially the novel detected of C3-Gulf in the Seychelles suggests that perhaps, hermatypic corals outside the three niche areas cryptically harbour specialised stress tolerant symbionts which shall evolve to detectable levels as the oceans get warmer worldwide enabling coral reefs to adapt to rising SST.

## 5.5 | CONCLUSION

In conclusion, biogeographical patterns of Symbiodiniaceae species diversity, distribution, and community composition are affected by a number of variables including environmental factors, thermal regimes, and latitudinal gradients. Our results provide the first analysis of ITS2 types present in Bahrain (the world's hottest reefs) and a novel observation of ITS2 type C3-Gulf in the Seychelles. In addition, results from Indonesia indicate that lower latitude reefs with low thermal regimes harbour diverse and abundant ITS2 types across species. These observations of diverse and abundant ITS2 types in Indonesia support previously reported observations, contributing towards a

coherent and in depth understanding of Symbiodiniaceae communities and factors that influence them. Overall, this study further supports scientific understanding of coral-Symbiodiniaceae associations in light of a rapidly changing climate.

This page was left intentionally blank

## **CHAPTER SIX: GENERAL DISCUSSION**

This page was left intentionally blank



## 6. GENERAL DISCUSSION

### 6.1 | SUMMARY OF KEY FINDINGS

The overall aim of this thesis was to assess reef accretional health and explore Symbiodiniaceae diversity of site-specific reefs in Bahrain (Arabian Gulf; AG), the Seychelles (Western Indian Ocean; WIO) and Indonesia (Central Indo-Pacific; CIP). In order to begin assessing the accretional health of these reefs, it was important to establish and define the environmental conditions that inhibit these selected reefs especially when comparing Bahrain in the AG to the other two bioregions. When it is stated that reefs in higher latitudes (in this thesis the AG) experience extreme thermal stress, the question arises, how extreme is extreme? It is standard practice to report thermal stress using specific measures such as DHW<sup>1</sup>. Since ocean warming is one of the biggest threats to coral reefs worldwide, it was necessary to examine and compare the thermal stress history of the selected reefs in the three bioregions to quantify these measurements (Chapter 2). To do this, I explored the thermal history of these reefs through deriving SST data from the CoRTAD satellite for the period 1982-2017 (35 years). Results illustrated that thermal stress anomalies were observed to increase over time in all three bioregions whilst confirming that reefs in high latitudes (i.e. the AG) experienced high and intense temperature disturbances (mean =  $\geq 4^{\circ}\text{C-DHW}$ ) in comparison to those in the lower latitudes (i.e. Seychelles and Indonesia), which experienced low intensity increase in temperatures ( $< 4^{\circ}\text{C-DHW}$ ) but at a higher frequency (Figure 6.1). Following this, it was necessary to determine the current status and trends of reefs in these bioregions in addition to our site-specific reefs. Conducting a systematic review of the available published literature to identify data points that report percentage cover of live hard coral between 1985-2018, has allowed the tracking of

---

<sup>1</sup> **Degree Heating Week (DHW)** is defined as of accumulated daily hotspots over 12 consecutive weeks when the thermal stress anomaly is  $\geq 1^{\circ}\text{C}$ . DHW values of  $\geq 4^{\circ}\text{C}$  and  $< 8^{\circ}\text{C-weeks}$ , corresponds to delineation between coral bleaching and mortality levels (\*unit= $^{\circ}\text{C-weeks}$ ).

temporal change of primary reef carbonate producers (i.e. hard corals) in reefs across the three bioregions. This was an interesting exercise as it strongly highlighted the extent of damage caused on these reefs as a consequence of intense thermal stress, which triggers bleaching. Overall trends illustrated non-linear fluctuations in coral cover over time with reefs experiencing an increasing trend at certain periods followed by declines across all bioregions (Chapter 3). The declines in both the AG and the Seychelles can be linked to major bleaching events (i.e. 1998 and 2016) whilst the decline in Indonesia can be attributed to anthropogenic impacts. In addition, recovery rates of reefs in these regions were estimated at 0.9, 1.2 and 2.0 % per year on reefs in the AG, the Seychelles (WIO) and Wakatobi, Indonesia (CIP) respectively. Interestingly, the recovery rate of reefs in Indonesia is double the rate of reefs in Bahrain. It is unsurprising though considering that we are comparing reefs in the hottest sea on the planet to those living in what is deemed as “optimal” reef thermal conditions. Nevertheless, the uniqueness of reefs in the AG is very striking especially when we take a closer look at the status and trend in live coral cover on all our site-specific reefs across all bioregions. All of our reef sites demonstrate a continuous decline especially when we compare the first data point that documents their coral cover to the last one, whether this decline is caused by bleaching events or anthropogenic impacts. However, there is one exception that is noteworthy - Reef Bul Thamah in Bahrain was able to maintain its coral cover over time despite numerous disturbances, thus, revealing a potential future refugia reef due to its high resilience to environmental change.

Now that the basic understanding of the reefs’ history was explored, I proceeded towards assessing the accretional health of reefs through quantifying their carbonate budgets utilising the standardised *ReefBudget* methodology (Chapter 4). Initially, the aim was to compare the reef budgets across bioregions however, throughout the budget quantification period for each study site, at a closer

examination, the data was uncovering very interesting outputs that presented different local reef stories. From this, a decision was made to present the carbonate budget chapter as a paper series, as it is important for local details not to be lost or overshadowed when global comparisons are made. The overall results that present the 2018 reef carbonate budgetary state of these site specific reefs indicated that some reefs in the thermal extreme (Bahrain), have either dipped into a negative budgetary state ( $-0.3 \pm 0.1$  G) or maintained a low positive budgetary state ( $1.9 \pm 0.2$  G). Interestingly, reefs in the Seychelles had a total net reef carbonate budget of 1.6 G, similar to that of Bahraini reefs. On the other hand, Indonesian reefs maintained a positive budgetary state, with a total net carbonate production budget ranging between  $1.7 \pm 0.2$  G and  $3.3 \pm 0.3$  G (Figure 6.1). These results highlight three main observations:

- The systematic review illustrated higher coral cover in Indonesia than Bahrain and the Seychelles. The percentage cover of primary carbonate producers (i.e. hard corals) influences reef budgets. Since coral cover was observed to be higher in general in Indonesia than the other two bioregions, it is no surprise that reefs in Indonesia had higher net carbonate budgets than Bahrain and the Seychelles.
- Interestingly, the lower range of the net carbonate budget in Indonesia represents reefs with marginal conditions (i.e. turbid), which is comparable to the reefs in Bahrain and the Seychelles. This perhaps suggests that reefs experiencing harsher conditions may be able to sustain themselves through developing resilience to change. Another observation is that these marginal reefs in Indonesia seem to have low bioerosion rates, which could also be a contributing factor towards them maintaining a positive budgetary state despite the low carbonate production rate.
- On the other hand, the higher range of the Indonesian net carbonate reef budgets is double the reef budget of those in Bahrain and the Seychelles.

When we consider that coral growth rates are influenced by their associated symbiont, the above observations indicate complex yet strong links between reef accretional health and associated coral-symbionts. Previous research has demonstrated that thermally tolerant symbionts reduce the growth rates of their coral host. Therefore, in an environment such as the AG, which is subjected to dramatic swings in temperatures (5-6°C) higher than the majority of reef systems in other parts of the globe, the ability of primary carbonate producers (i.e. corals) to survive in these environments will depend on a certain trade-off with their symbionts, hence creating a cost-benefit deal. This presents the question of whether the association with thermally tolerant symbionts enables long-term survival but limits reef development. Currently, there are no published growth rates for corals in the AG, with the exception of two species (*Platygyra daedalea* and *Cyphastrea microphthalma*; Howells *et al.*, 2018). However, due to the nature of the reefs and assuming the hypothesis that thermally tolerant symbionts decrease the rate in coral growth; coral growth rates in the AG would naturally be lower than other bioregions. This hypothesis would support our results that indicate higher reef carbonate budgets on reefs in Indonesia as a consequence of faster coral growth rates that results in double the recovery rate of coral cover on these reefs in comparison to those in Bahrain. Since measuring coral growth rates in the three bioregions was not feasible as part of this thesis, we did take things further by examining the composition and diversity of Symbiodiniaceae species across the three bioregions. This was done through next-generation sequencing with results including the first reporting of the unique associations with ITS2 type profile (C3-Gulf) of the thermo-tolerant species *Cladocopium thermophilum* in Bahrain, along with a novel observation of the presence of this ITS2 type C3-Gulf in the Seychelles. In addition, results showcased that the community composition of Symbiodiniaceae in Indonesia was very diverse and was mainly associated with symbionts that were generalists or opportunistic such as C1 which is linked to enhance growth rates (Little *et al.*, 2004) thereby impacting accretion rates. This contributes to

supporting the hypothesis that thermally tolerant symbionts decrease coral growth rates and aid in providing an answer to the question, whether certain symbiont associations enable long-term survival of reefs but limits their development. However, this gives rise to another question, if thermally symbiont association enable long-term survival of these reefs in light of ocean warming, but limits their development, how will these reefs keep up in the face of another challenge facing reefs – sea level rise (SLR)?

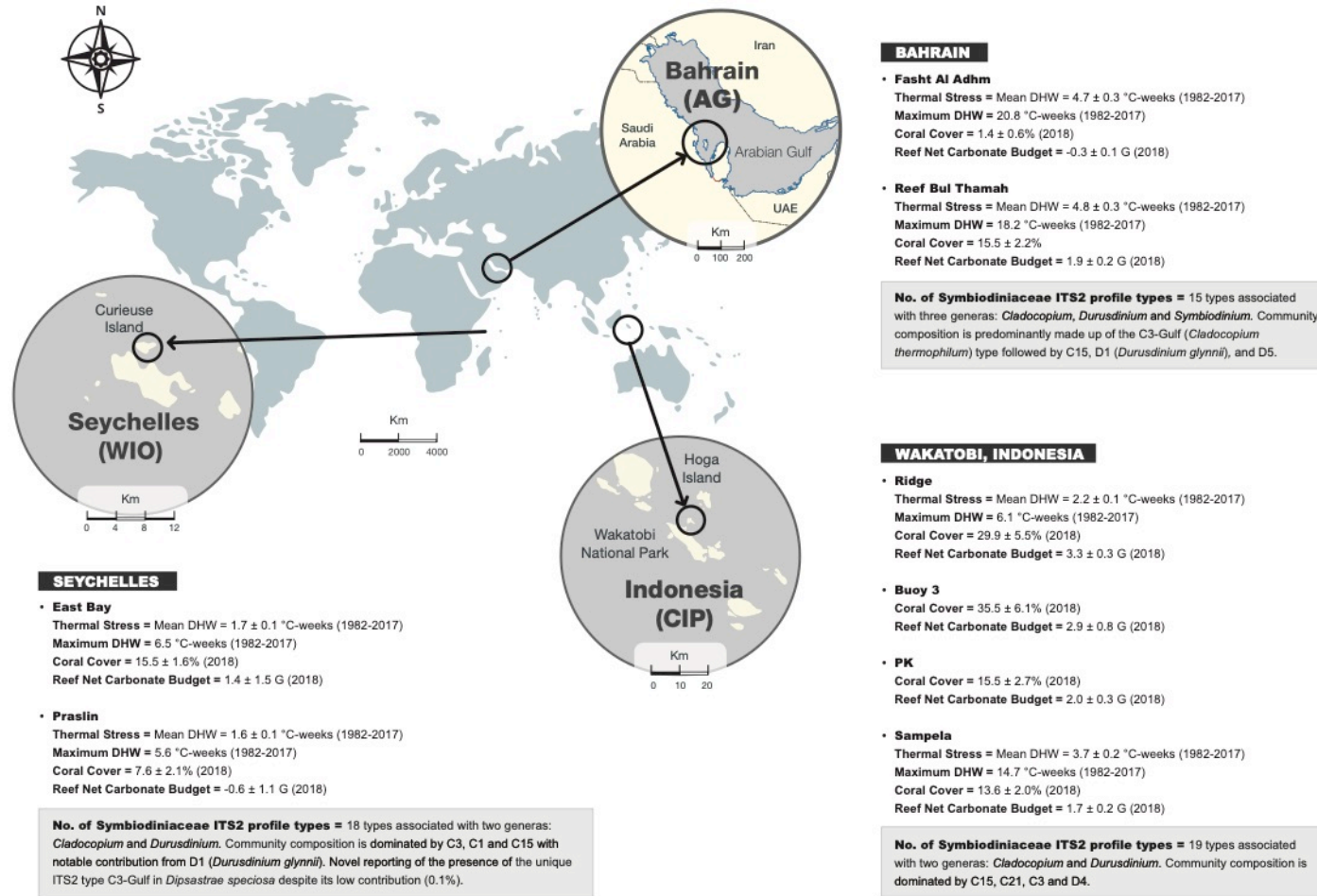


Figure 6.1. Summary of Overall Findings

## 6.2 | LIMITATIONS

Similar to any other piece of scientific research, this study has faced numerous challenges and limitations. For example, tools such as systematic reviews and/or meta-analysis are useful in enabling quantitative assessments to estimate the rates of ecological change (in this context, change in coral cover) in different habitats. This also allows the detection of temporal and spatial trends that track this change. However, results derived from these tools are sensitive to data availability and so the accuracy of the calculated rates of change is dependent and influenced by sample size and sites. This was apparent during the data collection process as many large gaps between the data points were identified within each of the three bioregions. Examples include lack or limited data between 1987-1999 in the AG and no documented data prior to 2001 in the Wakatobi, Indonesia. Nevertheless, it is felt that the calculated rates are a fair representation of what is currently known and serves as a preliminary insight to allow for possible projections of the future of these reefs. In terms of using remote sensing, the main limitation faced was using data with large spatial resolution making it difficult to accurately estimate the site-specific values related to thermal history, this was evident with data from the Seychelles. It is important to note that in this study, there might have been an over-estimation of coral growth rates, since rates used for the *ReefBudget* calculation were not site specific due to unavailable published literature on coral growth rates in the AG with the exception of two species (*Platygyra daedalea* and *Cyphastrea microphthalma*). This also applies to the *ReefBudget* calculation of reefs in the Seychelles, and so for the purpose of this study, growth rates from different bioregions were used for estimating the carbonate production rates for these two regions. Although the Indonesian carbonate budgets were calculated using regional specific rates in terms of gross carbonate production, limitations were encountered using the adopted rubble assessment method to calculate the erosion rate of bioeroding sponge. Since it was difficult to

determine how much of the erosion was done solely by bioeroding sponge without the contribution of other bioeroders (e.g. bivalves), this could have lead to an under/overestimation of the actual erosion rates. Nevertheless, despite these limitations and challenges, to our knowledge, this is the first attempt at quantifying reef carbonate budgets in the AG providing an important baseline for future studies. Similar challenges were also encountered in the studies conducted prior to our study, which marks the second in both the Seychelles and the Wakatobi, Indonesia. Further challenges were encountered in collecting the appropriate replicates of samples for the genetics work as in some bioregions our sampling periods were right after the bleaching events. This made acquiring samples very difficult due to limited availability of our initial target species (e.g. no *Acropora* sp. was found in Bahrain during the survey periods). Further challenges were faced throughout the library preparation phase in the lab, which required intense and frequent troubleshooting. Lastly, time constraints during fieldwork meant that the collection of environmental data (e.g. light attenuation, sedimentation rates etc.) was very limited and does not reflect the state of the reefs during seasonal changes and over a longer period of time.

### **6.3 | KEY MESSAGES & FUTURE DIRECTION OF RESEARCH**

This thesis focused on providing the baseline data necessary to understand the current ecological state of the site-specific reefs in the three selected bioregions (Figure 6.1). This was done through quantifying their reef carbonate budgets, investigating their thermal history and how that linked to coral cover change over time resulting in their current status. Latitudinal positions drive thermal regimes, which in turn plays a large role in driving reef carbonate budgets and coral symbiont communities. As a member of a sub-population of an ancestral taxonomic group that is stress-tolerant and based on recent evidence (Hume *et al.*, 2016) suggesting that *Cladocopium thermophilum* maybe cryptically distributed outside its niche areas (the AG, the Gulf of Oman and



the Red Sea), these specialised stress tolerant symbionts which are currently in levels that are hard to detect outside the AG will soon become prevalent as SST continues to rise. It is already known that coral symbionts undergo the process of shuffling when the coral encounters stress and expels its symbiont during bleaching events. This indicates that perhaps these coral symbionts could adopt another method to aid their hosts in adapting to climatic changes through the process of switching on their stress tolerant mode from “cryptic to visible/activated”. This train of thought stems from the pattern observed in the differences across coral symbiont community composition which witnesses a shift from the high diversity but thermally sensitive symbionts in lower thermal regimes to low diversity but thermally specialised symbionts in high thermal regimes. It is known that calcification rates are impacted when corals host thermo-tolerant species, which is evident when considering the reef carbonate budgets of both Bahrain and the Seychelles that were much lower than Indonesia. When investigated, their coral symbiont community consisted of a larger composition of stress tolerant symbionts than Indonesia, which can be linked to the severe bleaching events experienced on those reefs in recent years. Although, carbonate budgets are impacted by bleaching events (mean  $\geq 4^{\circ}\text{C-DHW}$ ) causing shifts in the coral symbiont communities which may impact calcification rates, other factors which are part of the reef ecology also influence the carbonate budgets. This includes carbonate producers (e.g. corals and CCA) and bioeroder populations (e.g. urchins, parrotfish and bioeroding sponges), which are in turn influenced by environmental conditions and anthropogenic pressures. For example, if primary carbonate producers (i.e. corals) continue to decline due to continuous intense bleaching events but erosion remains low, then this might mean that reefs could potentially have an opportunity to maintain themselves. Opportunities include the recruitment of juveniles however, if the site experiences heavy sedimentation (coral spats require hard substrates to attach to and do not do well in sediment surfaces or soft substrates) or erosion rate exceeds carbonate production rate then reefs will continue to experience impacts that hinder

accretion disabling them from keeping pace with SLR. In general, within all three bioregions the mean coral cover on a regional level was over 10%, which is the threshold for reefs to keep up with SLR. If reefs are able to keep their coral cover at or above 10% whilst stress tolerant coral symbionts become prevalent at reefs worldwide in light of rising sea temperatures then, reefs may have the opportunity to adapt and survive through this era of Anthropocene. I believe that coral reefs will evolve in an image that is not familiar to us as they begin to adopt their new structure. Since coral reefs date back ~500 million years (Dorf, 1960) and survived the climatic changes witnessed across time including the late Cambrian period and the Paleozoic era, their evolutionary traits are not to be underestimated. Hence, reefs in Bahrain, which exist in the hottest sea on the planet, provide an excellent opportunity to explore the possibility of how coral reefs around the world might cope with the climatic changes experienced worldwide.

Future work should explore modeling carbonate budget rates based on our current findings to examine the future of our site-specific reefs under the projected SLR scenarios coupled with the predictions of more frequent and intense bleaching events across the three bioregions. These models will provide insights as to the future of these reefs and aid reef managers in creating resilient reefs. It would also be interesting to continue investigating the genetic aspect of the coral-symbiont association expanding the comparison beyond the Symbiodiniaceae communities to the entire coral microbiome (which includes bacteria, viruses, fungi). This might provide important outlooks into how the AG coral microbiome has adapted to its extreme environment in comparison to the corals in other bioregions. Lastly, skeletal growth rates for corals in the AG and the Seychelles must be established to be able to provide accurate values for modeling future projections.

## 6.4 | CONCLUDING REMARKS

To conclude, reefs in the three bioregions show an alarming decreasing trend in coral cover that in turn impacts reef accretion rates. Some reefs in the AG and the Seychelles are already dipping into a negative eroding state whilst others are maintaining a low positive budgetary state following major disturbances. This substantial reduction in reef accretion could result in ecological and economical consequences impacting reef ecology and the coastal communities that depend on them for their livelihoods. To mitigate these consequences, local monitoring should include periodic assessments of reef carbonate budgets to best inform local reef management. Results such as those included in this thesis could benefit decision makers through establishing informed policies. All of our study sites are within the vicinity of marine protected areas (MPAs) with the exception of Fasht Al Adhm in Bahrain. However, a declining trend is seen in all of our site-specific reefs highlighting the need to enhance reef resilience through increasing law enforcement in MPAs and regulating fishing activities and other anthropogenic impacts. Compromised reef structural frameworks as a consequence of declining coral cover and reduced reef accretion has been linked to declines in smaller bodied fish species and smaller size classes of larger fish, which has been suggested to cause reductions in fish yields in the long-term (Graham, 2014; Rogers *et al.*, 2014). This in turn negatively impacts the socio-economic aspects of reefs and associated stakeholders. It is hence important to regulate fishing practices within MPAs to ensure the sustainability of the reefs. Decision makers can also benefit from utilising data from our research to create models that will aid these island nations in planning their adaptation strategies to track SLR that threaten the coasts and stability of these islands, along with their associated reef systems that offer protection from natural disasters such as storms. However, it is important to acknowledge as voiced by many researchers that without substantial reductions in atmospheric carbon emissions, even the best coral reef

management strategies will not prevent further coral mortalities. In addition, there is a need to recognize the clear difference between local and global stressors on reef sites worldwide to address them through embracing a holistic approach in reef conservation and management.

## **SUPPLEMENTARY MATERIAL**

This page was left intentionally blank

**S1| EXPLORING THERMAL HISTORY OF A CORAL REEF WITH THE PACKAGE IN R*****Introduction & Rationale***

To date, efforts have been made to describe thermal patterns that induce coral stress and mortality in a global and/or regional context using remote sensing data (Purkis & Riegl, 2005; Selig *et al.*, 2010; Hoegh-Guldberg *et al.*, 2014; Pramanik, 2014; Claar *et al.*, 2018). However, the process of extrapolating, summarising and visualising data is tedious and time consuming. Therefore, there is a need to develop tools that can easily aid in this process whilst being time efficient. With this in mind, here, we produced an R package called “*THE*” which provides a suite of functions to retrieve, summarise, and visualise the thermal history of coral reefs. This package is useful in coral reef conservation and management.

***Software/Package Availability***

The software is freely available through github (<https://github.com/brisneve/THE>) and is implemented in R. The package was written by Brisneve Edullantes ([bedullantes@up.edu.ph](mailto:bedullantes@up.edu.ph)) and reviewed by Reem AlMealla.

***Software Overview***

The *THE* (Thermal History Exploration) package:

- (1) Retrieves publicly available sea surface temperature (SST) datasets from CORTAD, Coral Watch, and Giovanni;
- (2) Calculates thermal history metrics such as climatology (long term monthly mean, minimum, and maximum SST; °C), SST Anomaly (SSTA; °C), Thermal Stress Anomaly (TSA; °C), and Degree Heating Weeks (DHW, °C-weeks);
- (3) Creates visualization plots that illustrate the thermal history of the chosen site-specific reefs.

## **Conclusion**

In order to develop a better understanding of the effect of climate change, particularly ocean warming, on coral bleaching and associated coral mortalities, advance tools are needed to process and visualise remotely sensed sea surface data in an efficient manner. To our knowledge, the *THE* package is the first exploration tool of its kind that is dedicated towards tracing the thermal history of coral reefs, which is fully implemented in R. Furthermore, the package presented here contributes towards the enhancement of coral reef management and conservation in response to the climate change.

## **S2 | LIST OF STUDIES USED IN THE SYSTEMATIC REVIEW**

### **S2.1 | LIST OF STUDIES CORRESPONDING TO THE ARABIAN GULF DATA**

Alhazeem SH, Burt JA, Alsaffar AH, Chen W, Al-Kandari MA (2017) Long-term coral community stability in a disturbed marginal reef in Kuwait. *Journal of Water Resources and Ocean Science*, **6(6)**: 85-89. [https://doi: 10.11648/j.wros.20170606.12](https://doi.org/10.11648/j.wros.20170606.12)

AlMealla, R (2020) – Findings from this thesis

Bauman AG, Baird AH, Burt JA, Pratchett MS, Feary DA (2014) Patterns of coral settlement in an extreme environment: The southern Persian Gulf (Dubai, United Arab Emirates). *Marine Ecology Progress Series*, **499**: 115-126.

Bento R, Hoey AS, Bauman AG, Feary DA, Burt JA (2016) The implications of recurrent disturbances within the world's hottest coral reef. *Marine Pollution Bulletin*, **105(2)**: 466-472. [https://doi:10.1016/j.marpolbul.2015.10.006](https://doi.org/10.1016/j.marpolbul.2015.10.006)

Benzoni F, Pichon M, Hazeem SA, Galli, P (2006) The coral reefs of the northern Arabian Gulf: Stability over time in extreme environmental conditions. In: *Proceedings of 10th International Coral Reef Symposium*, pp. 969-975.

Burt J, Al-Khalifa K, Khalaf E, Alshuwaikh B, Abdulwahab A (2013) The continuing decline of coral reefs in Bahrain. *Marine Pollution Bulletin*, **72(2)**: 357-63.

Burt JA, Smith EG, Warren C, Dupont J (2015) An assessment of Qatar's coral communities in a regional context. *Marine Pollution Bulletin*, **105**: 473-479

Fatemi S, Shokri M (2001) Iranian coral reefs status with particular reference to Kish Island, Persian Gulf. Indian Ocean Regional Workshop: The International Coral Reef Initiative, pp. 1-13.

Grizzle RE, Ward KM, AlShihi RMS, Burt, JA (2016) Current status of coral reefs in the United Arab Emirates: Distribution, extent, and community structure with implications for



management. *Marine Pollution Bulletin*, **105(2)**: 515–523.  
<https://doi.org/10.1016/j.marpolbul.2015.10.005>

- Kavousi J, Seyfabadi J, Rezai H, Fenner D (2011) Coral reefs and communities of Qeshm Island, the Persian Gulf. *Zoological Studies*, **50(3)**: 276-283.
- Pratchett MS, Hoey AS, Feary DA, Bauman AG, Burt JA, Riegl BM (2013). Functional composition of Chaetodon butterflyfishes at a peripheral and extreme coral reef location, the Persian Gulf. *Marine Pollution Bulletin*, **72(2)**: 333-341.
- Rezai H, Samimi K, Kabiri K, Kamrani E, Jalili M, Mokhtari M (2010) Distribution and Abundance of the Corals around Hengam and Farurgan Islands, the Persian Gulf. *Journal of Persian Gulf*, **1(1)**: 7-16.
- Shokri MR, Fatemi SMR, Crosby MP (2005) The status of butterflyfishes (Chaetodontidae) in the northern Persian Gulf, I.R. Iran. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **15**: 91-99.
- Uwate KR, Bader H, Torabi M, Bailey S, Keenan P (2000) *Reef Check 2000 Surveys in Bahrain, Arabian Gulf*. Directorate of Fisheries and Marine Resources, Ministry of Works and Agriculture, Manama, Bahrain.

## S2.2 | LIST OF STUDIES CORRESPONDING TO THE SEYCHELLES DATA

- AlMealla, R (2020) – Findings from this thesis
- Buckley RM, Downing N, Stobart B, Teleki K, Pistorius PA (2008) Was the 1998 coral bleaching in the Southern Seychelles a catastrophic disturbance? 1999–2006 Reef fish responses to coral substrate changes. In: *Proceedings of the 11th International Coral Reef Symposium*, pp. 696–700.
- Chong-Seng KM, Graham NAJ, Pratchett MS (2014) Bottlenecks to coral recovery in the Seychelles. *Coral Reefs*, **33(2)**, 449–461. doi:10.1007/s00338-014-1137-2
- Engelhardt U, Russell M, Wendling B (2002) *Coral Communities around the Seychelles Islands 1998-2002*. Linden O, Souter D, Wilhelmsson D and Obura D (eds.). Coral degradation in the Indian Ocean: Status Report 2002. CORDIO, Department of Biology and Environmental Science, University of Kalmar, Kalmar, Sweden. pp 212-231.
- Friedlander AM, Obura D, Aumeeruddy R, Ballesteros E, Church J, Cebrian E, Sala E (2014) Coexistence of Low Coral Cover and High Fish Biomass at Farquhar Atoll, Seychelles. *PLoS ONE*, **9(1)**. doi:10.1371/journal.pone.0087359
- Gardner SG, Camp EF, Smith DJ, Kahlke T, Osman EO, Gendron G, Hume B, Pogoreutz C, Voolstra CR, Suggett, DJ (2019) Coral microbiome diversity reflects mass coral bleaching susceptibility during the 2016 El Niño heat wave. *Ecology and evolution*, **9(3)**: 938–956. <https://doi.org/10.1002/ece3.4662>
- Graham NAJ, Jennings S, Macneil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, **518**, 94–97.

- GVI Seychelles (2018). Global Vision International, Seychelles - *Mahé Report Series* No. 181-184 ISSN 1751-2255 (Print).
- Hagan AB, Spencer T (2008) Reef resilience and change 1998–2007. Alphonse Atoll, Seychelles. In: *Proceedings of the 11th International Coral Reef Symposium*, pp. 388–392.
- Harris A, Wilson S, Graham N, Sheppard C (2014) Scleractinian coral communities of the inner Seychelles 10 years after the 1998 mortality event. *Aquatic Conservation: Marine and Freshwater Ecosystem*, **24(5)**: 667-679.
- Januchowski-Hartley FA, Graham NAJ, Wilson SK, Jennings S, Perry CT (2017) Drivers and predictions of coral reef carbonate budget trajectories. *Proceedings of the Royal Society of London B*, **284**, 20162533.
- Jeliazkov A, Mijatovic D, Chantepie S, Andrew N, Arlettaz R, Barbaro L, Barsoum N, Bartonova A, Belskaya E, Bonada N, Brind'Amour A, Carvalho R, Castro H, Chmura D, Choler P, Chong-Seng K, Cleary D, Cormont A, Cornwell W, de Campos R, de Voogd N, Doledec S, Drew J, Dziocck F, Eallonardo A, Edgar MJ, Farneda F, Hernandez DF, Frenette-Dussault C, Fried G, Gallardo B, Gibb H, Goncalves-Souza T, Higuti J, Humbert JY, Krasnov BR, Le Saux E, Lindo Z, Lopez-Baucells, A, Lowe E, Marteinsdottir B, Martens K, Meffert P, Mellado-Diaz A, Menz MHM *et al.* (2020) A global database for metacommunity ecology, integrating species, traits, environment and space. *Science Data*, **7(6)**. <https://doi.org/10.1038/s41597-019-0344-7>
- Jennings S, Grandcourt EM, Polunin, NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs*, **14(4)**: 225–235. <https://doi:10.1007/bf00334346>
- Ledlie MH, Graham NAJ, Bythell JC, Wilson SK, Jennings S, Polunin NVC, Hardcastle, J (2007) Phase shifts and the role of herbivory in the resilience of coral reefs. *Coral Reefs*, **26(3)**: 641–653. <https://doi:10.1007/s00338-007-0230-1>
- Smith DJ, Etienne M, Springer N, Suggett DJ (2008) Tolerance, refuge and recovery of coral communities to thermal bleaching: evidence from reefs of the Seychelles. In: *Proceedings of the 11th International Coral Reef Symposium*. Vol **12**, pp. 7-11.
- Spencer T, Teleki KA, Bradshaw C, Spalding, MD (2000) Coral Bleaching in the Southern Seychelles During the 1997–1998 Indian Ocean Warm Event. *Marine Pollution Bulletin*, **40(7)**: 569–586. [https://doi:10.1016/s0025-326x\(00\)00026-6](https://doi:10.1016/s0025-326x(00)00026-6)
- Stobart B, Teleki K, Buckley R, Downing N, Callow M (2005) Coral recovery at Aldabra Atoll, Seychelles: five years after the 1998 bleaching event. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, **363(1826)**: 251–255. <https://doi:10.1098/rsta.2004.1490>

## S2.3 | LIST OF STUDIES CORRESPONDING TO THE WAKATOBI, INDONESIA DATA

- AlMealla, R (2020) – Findings from this thesis
- Bell J, Jompa J, Haris A, Werorilangi S, Shaffer M, Mortimer C (2018) Domination of mesophotic ecosystems in the Wakatobi Marine National Park (Indonesia) by sponges, soft corals and other non-hard coral species. *Journal of the Marine Biological Association of the United Kingdom*, 1–5.
- Crabbe C, Karaviotis S, Smith DJ (2004) Preliminary comparison of three coral reef sites in the Wakatobi Marine National Park (S.E.Sulawesi, Indonesia): Estimated recruitment dates compared with Discovery Bay, Jamaica. *Bulletin of Marine Science*, **74**, 469–476.
- Clifton J, Unsworth RKF, Smith DJ (2010) *Marine research and conservation in the Coral Triangle, The Wakatobi Marine National Park*. Nova Science, New York, 1–258 pp.
- Franco C (2014) *Modelling the dynamics of CaCO<sub>3</sub> budgets in changing environments using a Bayesian Belief Network approach*. PhD thesis, University of Essex, UK.
- Haapkylä J, Unsworth RKF, Seymour AS, Melbourne-Thomas J, Flavell M, Willis BL, Smith DJ (2009) Spatio-temporal coral disease dynamics in the Wakatobi Marine National Park, South-East Sulawesi, Indonesia. *Diseases of Aquatic Organisms*, **87**, 105–115.
- Haapkylä J, Melbourne-Thomas J, Flavell M (2015) The association between coral communities and disease assemblages in the Wakatobi Marine National Park, south-eastern Sulawesi, Indonesia. *Marine and Freshwater Research*, **66**, 948–955.
- Hennige SJ, Smith DJ, Perkins R, Consalvey M, Paterson DM, Suggett DJ (2008) Photoacclimation, growth and distribution of massive coral species in clear and turbid waters. *Marine Ecology Progress Series*, **369**, 77–88.
- Marlow J, Haris A, Jompa J, Werorilangi S, Bates T, Bennett H, Bell JJ (2019) Spatial variation in the benthic community composition of coral reefs in the Wakatobi Marine National Park, Indonesia: updated baselines and limited benthic community shifts. *Journal of the Marine Biological Association of the United Kingdom*, 1–8. <https://doi.org/10.1017/S0025315419001012>
- Powell A, Hepburn LJ, Smith DJ, Bell JJ (2010) Patterns of Sponge Abundance Across a Gradient of Habitat Quality in the Wakatobi Marine National Park, Indonesia. *The Open Marine Biology Journal*, **4**, 31–38.
- Powell A, Smith DJ, Hepburn LJ, Jones T, Berman J, Jompa J, Bell, JJ (2014) Reduced diversity and high sponge abundance on a sedimented Indo-Pacific reef system: Implications for future changes in environmental quality. *PLoS ONE*. **9**(1).
- Roth SK, Powell A, Smith DJ, Roth F, Schierwater B (2018) The highly competitive ascidian *Didemnum sp.* threatens coral reef communities in the Wakatobi Marine National Park, Southeast Sulawesi, Indonesia. *Regional Studies in Marine Science*, **24**, 48–54. doi:10.1016/j.rsma.2018.07.001
- Rovellini A (2020). *Modelling regime shifts of coral reefs to sponge reefs*. Victoria University of Wellington. PhD Thesis. pp 276.
- Scaps P, Denis V (2008) Can organisms associated with live scleractinian corals be used as indicators of coral reef status? *Atoll Research Bulletin*, **566**: 1-18.

### S3| REEF CARBONATE BUDGETS

#### S3.1 | SEYCHELLES - QUANTIFYING METHODOLOGY FORTH THE CARBONATE BUDGET

Quantitative data such as benthic composition, rugosity, carbonate producers and eroders were obtained through surveying field transects as outlined in Table S4.1 along each reef site as per the standardised methodology for collecting budgetary data *ReefBudget* (Perry *et al.*, 2012, 2018b). Data collected was used to calculate CaCO<sub>3</sub> production and erosion rates (kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> hereafter expressed as G whilst ± represents the SE of all values stated). It is important to note that slight modifications were made to the *ReefBudget* methodology (in terms of growth rates used, & number of replicates (due to time constraints)), which was originally designed for Caribbean reefs (Perry *et al.*, 2012) and then developed for the Indo-Pacific reefs (Perry *et al.*, 2018b). Details of these modifications are given below along with a brief explanation. Benthic composition was measured following the integrated method outlined in Perry *et al.*, (2012 and 2018b) whereby benthic cover and surface rugosity data were collected using a modified version of the standard linear intercept methodology where benthic cover was recorded along every 1 cm increment of the tape. Rugosity was calculated from the total surface distance for each linear 1m of reef.

**Table S3.1. Carbonate budget components and number of replicates at each study site in the Seychelles.**

Carbonate Budget Component	Variable*	Number of transects	Length of transect (m)
Carbonate production rate	Benthic composition assessment	6	10
	Rugosity	6	10
	Carbonate producers	6	10
Carbonate erosion rate	Echinoids (Urchins)	6	10
	Scaridae (Parrotfish)	6	30
	Bioeroding sponges (Clionidae)	6	10

### **Carbonate Producers**

In order to calculate carbonate production rates, primary carbonate producers (coral colonies) recorded along the transects were identified to genus level (e.g. *Porites spp*) with their morphological growth form noted and to ensure comparability, growth rates were taken from the published literature as listed and used in Januchowski-Hartley *et al.*, (2017) of which a summary is listed in Table S4.2. The data was then inserted in datasheets that have been set up with standardized *ReefBudget* equations that automatically calculate the carbonate production rates for each transect. Datasheets can be downloaded for use through: <http://geography.exeter.ac.uk/reefbudget/indopacific/>. To quantify secondary producers (e.g. crustose coralline algae (CCA)), six PVC pipes measuring 35 cm x 16 cm (length x circumference of the pipe) were deployed at each study site (~10m depth) and were retrieved following a one-year period as per the *ReefBudget* methodology (Perry *et al.*, 2012). Prior to retrieval, all pipes were photographed underwater, placed in a plastic bag secured with cable ties over the upper part of the pipe. Once in the lab, pipes were examined and photographed in detail following which they were placed in 10% sodium hypochlorite (bleach) for 72 hours. Once removed from the bleach, the pipes were left to dry after which, they were weighed in replicates of three, following which they were soaked in 10% HCl for another 36 hours. Once all the calcium carbonate was dissolved, the pipes were taken out and weighted for a second time (in replicates of three), enabling a weight per unit area to be derived. The weight per unit area value was inserted in the *ReefBudget* carbonate production calculation sheet in the growth rates column thereby automatically included in the overall production budget calculation.

**Table S3.2. Skeletal densities and growth rates / linear extension rate of corals derived from the supplementary material of Januchowski-Hartley *et al.*, (2017) ( $\pm 95\%$  CI).**

Coral Genera / Species	Morphology	Skeletal Density (g/cm <sup>3</sup> )	Growth rate (cm/yr)
<i>Acropora spp.</i>	branching	1.3 $\pm$ 0.2	4.2 $\pm$ 1.2
<i>Galaxea fascicularis</i>	encrusting, massive	1.9 $\pm$ 0.5	0.9 $\pm$ 0.2
<i>Goniatrea spp.</i>	massive	1.7 $\pm$ 0.2	1.2 $\pm$ 0.2
<i>Diplostrea/Favia spp.</i>	encrusting, massive	1.4 $\pm$ 0.2	0.6 $\pm$ 0.2
<i>Favites spp.</i>	encrusting, massive	1.4 $\pm$ 0.2	0.6 $\pm$ 0.2
<i>Leptoseris spp.</i>	encrusting	1.7 $\pm$ 0.2	1.7 $\pm$ 0.2
<i>Lobophyllia spp.</i>	massive	1.4 $\pm$ 0.3	1.5 $\pm$ 0.8
<i>Montipora spp.</i>	encrusting	1.2 $\pm$ 0.7	1.6 $\pm$ 0.3
<i>Platygyra spp.</i>	encrusting, massive	1.5 $\pm$ 0.5	0.9 $\pm$ 0.1
<i>Pocillopora spp.</i>	submassive	1.4 $\pm$ 0.1	2.7 $\pm$ 0.7
<i>Porites spp.</i>	massive	1.4 $\pm$ 0.1	1.2 $\pm$ 0.2

### Carbonate Eroders

For calculating carbonate erosion rates, species, density and size class measurements were recorded for grazers such as echinoids (n = 6; area = 20 m<sup>2</sup> per transect) and Scaridae (n = 6; area = 120 m<sup>2</sup> per transect) along the transect area.

- **Echinoids:** The area surveyed along each of the six transects was 1 m on either side of the 10 m transect line covering a total of 20 sq m per transect. The number of individuals along each transect were counted, identified to species level and recorded in the following size class: 0-20 mm, 21-40 mm, 41-60 mm, 61-80 mm, 81-100 mm. Data was then inputted into the datasheets downloaded from: <http://geography.exeter.ac.uk/reefbudget/indopacific/>
- **Scaridae:** The area surveyed along each of the three transect was 4 m in width of the 30 m transect line covering a total of 120 sq m per transect. The number of individuals encountered along each transect were counted, identified to species level and recorded in the

following size class: <10 cm, 10-20 cm, 21-30 cm, 31-40 cm and 41-50 cm. Biomass of Scaridae was calculated using published species-specific length-weight relationships as per the rates outlined in the *ReefBudget* datasheets which can be downloaded from: <http://geography.exeter.ac.uk/reefbudget/indopacific/>

- **Bioeroding sponge:** The area surveyed along each of the six transects was 0.5 m width of the 10 m transect line covering a total of 10 sq m per transect. The area of individual bioeroding sponge colonies with visual papillae were estimated using a transparent sheet with a printed 1x1cm grid along the transect, however identification to species level was difficult as there is no bio-eroding sponge guide available for the WIO. In order to confirm that the sponges recorded were bioeroding, a hammer and chisel were used to verify boring activity. Due to the limitation in data availability globally on internal microbioerosion rates of coral substrate, for this study the rates were taken as outlined in Perry *et al.*, (2012). Data from this study was then inserted into the datasheets, which are available, online for use: <https://geography.exeter.ac.uk/reefbudget/caribbean/>.

### S3.2 | INDONESIA - QUANTIFYING METHODOLOGY FORTH THE CARBONATE BUDGET

In order to gather quantitative data such as benthic composition, rugosity, carbonate producers and eroders to assess calcium carbonate production and erosion on the selected reefs, *ReefBudget*, a census-based methodology was used. It was originally designed for the Caribbean (Perry *et al.*, 2012) and then developed specifically for Indo-Pacific reefs (Perry *et al.*, 2018b). The data collected via transects (Table S4.3) was then used to calculate CaCO<sub>3</sub> production and erosion rates (kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> hereafter expressed as G whilst ± represents the SE of all values stated) through utilizing a series of equations specific for carbonate producers and eroders as outlined and explained in the *ReefBudget* toolkit (Perry *et al.*, 2018b). The *ReefBudget* methodology for data collection in this

study was followed in full with the exception of bioeroding sponge data and that transects were recorded at three depths (5, 10 and 15 m – 2 transects at each = 6 transects in total). Details of these modifications are given below along with a brief explanation. The modification was necessary in this study to ensure that the data was comparable to that collected by Franco, (2014). Benthic composition was measured following the integrated method outlined in (Perry *et al.*, 2012, 2018b). Benthic cover data was collected using a modified version of the standard linear intercept methodology with benthic organisms recorded every 1 cm using video footage of the transect. Rugosity was calculated from the total surface distance for each linear 1m of reef using SCUBA and a 1.5 m flexi tape. Budget data collected in 2012 used for the purpose of this study, is restricted to the budget rates (gross carbonate production, gross carbonate erosion and net carbonate production). Data could not be obtained for comparison in terms of primary and secondary carbonate producers in addition to densities of major eroders.



**Table S3.3. Details of carbonate budget components and number of replicates at each study site in the Wakatobi, Indonesia.**

Carbonate Budget Component	Variable*	Number of transects	Length of transect (m)
Carbonate production rate	Benthic composition assessment	6	10
	Rugosity	6	10
	Carbonate producers	6	10
Carbonate erosion rate	Echinoids (Urchins)	6	10
	Scaridae (Parrotfish)	10	30
	Bioeroding sponges (Clionidae)	10 pieces of rubble collected from each transect	

### Carbonate Producers

In order to calculate carbonate production rates, primary carbonate producers (coral colonies) were recorded along the transects at three depths and identified to genus level (e.g., *Porites* spp.) with their morphological growth form noted. The data was then used in datasheets that have been set up with standardized *Reefbudget* equations, which automatically calculate the carbonate production rate for each transect. Datasheets can be downloaded for use through: <http://geography.exeter.ac.uk/reefbudget/indopacific/>. To quantify secondary producers (e.g. crustose coralline algae (CCA)), six PVC pipes measuring 35 cm x 16 cm (length x circumference of the pipe) were deployed at each study site (~10m depth) and were retrieved following a one-year period as per the *ReefBudget* methodology (Perry *et al.*, 2012). Prior to retrieval, all pipes were photographed underwater, placed in a plastic bag secured with cable ties over the upper part of the pipe. Once in the lab, pipes were examined and photographed in detail following which they were placed in 10% sodium hypochlorite (bleach) for 36 hours. Once removed from the bleach, the pipes were left to dry after which, they were weighed in replicates of three, then they were soaked in 10%

HCl for another 36 hours. Once all the calcium carbonate was dissolved, the pipes were taken out and weighted for a second time (in replicates of three), this allowed for a weight per unit area to be derived. The weight per unit area value was inserted in the *Reefbudget* carbonate production calculation sheet in the growth rates column thereby automatically included in the overall production budget calculation.

### **Carbonate Eroders**

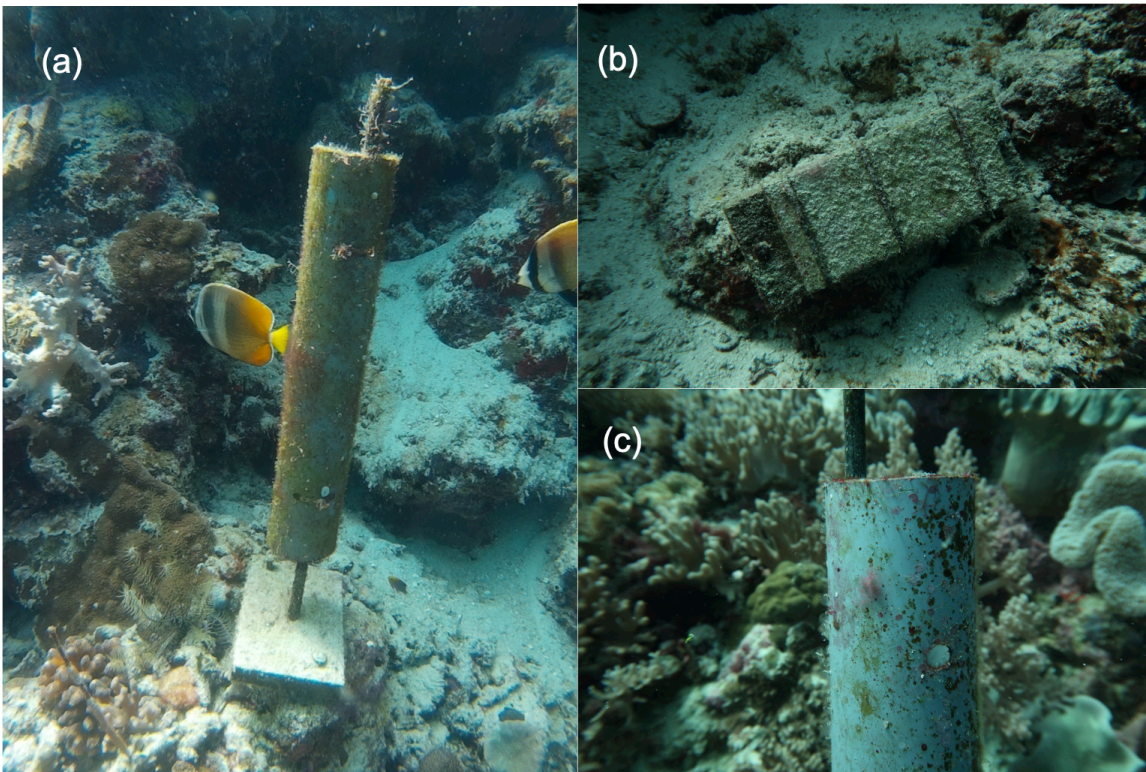
For calculating carbonate erosion rates, species, density and size class measurements were recorded for grazers such as echinoids (n=6; area=20 m<sup>2</sup> per transect) and Scaridae (n=10; area= 120 m<sup>2</sup> per transect) along the transect area.

- **Echinoids:** The area surveyed along each of the six transects was 1 m on either side of the 10 m transect line covering a total of 20 sq m per transect. The number of individuals along each transect were counted, identified to species level and assigned one of the following size class: 0-20 mm, 21-40 mm, 41-60 mm, 61-80 mm, 81-100 mm. Data was then inputted into the datasheets downloaded from: <http://geography.exeter.ac.uk/reefbudget/indopacific/>
- **Scaridae:** The area surveyed along each of the three transect was 4 m in width of the 30 m transect line covering a total of 120 sq m per transect. The number of individuals encountered along each transect were counted, identified to species level, assigned a life phase (juvenile, initial or terminal phase) and recorded in the following size class: <10 cm, 10-20 cm, 21-30 cm, 31-40 cm and 41-50 cm. Biomass of parrotfish was calculated using published species-specific length-weight relationships as per the rates outlined in the *ReefBudget* datasheets which can be downloaded from: <http://geography.exeter.ac.uk/reefbudget/indopacific/>

- **Bioeroding sponge:** Macrobioerosion caused by bioeroding sponge was assessed following the same method used by Franco (2014) which is through direct rubble investigation. At each of the three depths (5, 10 and 15 m) ten rubble pieces were randomly collected within the transect areas. The collected rubble pieces were then cut in half for investigation. Macro-invertebrates living within one half were removed for identification while the second half was photographed and borehole surface areas and percentages were assessed. Scaled images were analysed using the Image J tool while the total surface areas ( $\text{cm}^2$ ) of boreholes and rubble were used to calculate the total volume of carbonate removed ( $\text{cm}^3$ ) by macroborers. One of the limitations encountered using this rubble assessment method was that it was difficult to determine how much of the erosion was done solely by bioeroding sponge without the contribution of other bioeroders (e.g. bivalves). This could have lead to an overestimation of the actual rates of bio-eroding sponge erosion occurring at the study sites.

### **S3.3 | RESULTS OF SECONDARY CARBONATE PRODUCTION RATES**

To quantify secondary carbonate producers (e.g. CCA, bryozoans, foraminifera and serpulids), six PVC pipes and six ceramic tiles (Figure S4.1) were deployed for a period of one-year (2017-2018) at each study site in Bahrain and Indonesia whereas in the Seychelles, only six PVC pipes were deployed. For the purpose of this study, only the results of the PVC pipes were used to ensure consistency with the *ReefBudget* methodology. However, results using both substrates are reported from this one-year experiment in Table S3.4.



**Figure S3.1 Quantification experiment of carbonate production by secondary producers:** (a) One of the PVC pipes deployed in Indonesia with signs of algal growth and CCA following a one-month period; (b) One of the tiles deployed in Indonesia with signs of turf algal growth following a one-month period; (c) Close up of one of the PVC pipes deployed in Indonesia with CCA establishment following a one-month period.

**Table S3.4. Carbonate Production Rates (kg CaCO<sub>3</sub> m<sup>-2</sup> y<sup>-1</sup> expressed as G) by Secondary Carbonate Producers between 2017-2018 at each of the study sites across the three bioregions.**

Site	PVC Pipes	Ceramic Tiles (Cryptic side)	Ceramic Tiles (Exposed side)
<i>Bahrain*</i>			
Fasht Al Adhm	0.03 ± 3.2	0.02 ± 1.5	0.01 ± 0.5
Reef Bul Thamah	0.01	NA	NA
<i>Seychelles**</i>			
East Bay	0.0001 ± 6.7	NA	NA
Praslin	0.00001 ± 2.7	NA	NA
<i>Indonesia***</i>			
Ridge	0.1 ± 0.01	0.02 ± 0.01	0.02 ± 0.01
Sampela	0.03 ± 0.01	0.1 ± 5.7	0.02 ± 0.8

\***Bahrain:** number of replicates n=6 (pipes) and n=5 (tiles) at 7m in Fasht Al Adhm and n = 1 (pipe) at 10 m, the remaining of the pipes and tiles were not found following the one-year period with signs of destructive fishing on the reefs that could have caused the tiles and pipes to be displaced.

\*\***Seychelles:** number of replicates n=6 (pipes) at 10m at East Bay and n=6 (pipes) at 10m at Praslin.

\*\*\***Indonesia:** number of replicates n=7 (pipes) and n=5 (tiles) at 10m in Sampela and n=7 (pipes) and n=7 (tiles) at 10m in the Ridge.

## **S4 | SYMBIODINIACEAE DNA EXTRACTION PROTOCOL & RELATIVE ABUNDANCE OF ASSOCIATED ITS2 TYPES**

### **S4.1 | QIAGEN DNEASY BLOOD & TISSUE KIT – PROTOCOL METHOD MODIFICATION**

- Add 180 µl of ATL Buffer to a 1.5 ml micro-centrifuge tube.
- Place coral tissue into the micro-centrifuge tube, grind coral tissue sample in the tube to mix with ATL Buffer.
- Add 30 µl of proteinase K to the sample and vortex.
- Incubate in thermomixer at 56°C overnight at 400 rpm.
- Add 4 µl of RNAase A and leave to incubate at room temperature for 2 minutes
- Add 200 µl of AL Buffer and vortex.
- Add 200 µl of 100% ethanol, vortex and centrifuge.
- Pipette mixture into spin column in 2 ml collection tube. Centrifuge at 8000 rpm for 1 min. Discard flow through and collection tube.
- Place spin column into new 2 ml collection tube and add 500 µl of AW1 Buffer. Centrifuge at 8000 rpm for 1 minute. Discard flow through and collection tube.
- Place spin column into new 2ml collection tube and add 500 µl of AW2 Buffer. Centrifuge for 3 minutes at 14000 rpm. Discard flow through and collection tube.
- Transfer spin column to new 1.5 / 2 ml micro-centrifuge tube.
- Elute the DNA by adding 70 µl AE Buffer to center of spin column membrane, incubate for 5 mins at room temperature then centrifuge for 1 minute at 8000 rpm.
- Pipette solution from the micro-centrifuge tube back into spin column, incubate for 5 mins at room temperature then centrifuge for 1 minute at 8000 rpm.
- Discard of filter top and spin column.
- DNA is now in the bottom of the 1.5 µl micro-centrifuge tube ready for use.

## S4.2 | RELATIVE ABUNDANCE OF ITS2 TYPE PROFILES IN EACH CORAL HOST SPECIES AND BIOREGION

**Table S4.2.** Relative abundance of ITS2 type profiles in each coral host species and bioregion. Row in red highlights the novel observation of C3-Gulf in the Seychelles.

Species	ITS2 Type	Relative abundance (%)
<b>Bahrain (high latitude &amp; thermal regime)</b>		
<i>Cyphastrea microphthalma</i>	C15h-C15k-C15q-C15p	0.7
	C3-C3bs-C3gulf-C3ef-C3c	82.15
	C3-C3gulf-C3c-C3aj	1.91
	C3/C3c-C3gulf	15.21
<i>Dipsastraea speciosa</i>	C3/C3c-C3gulf	100
<i>Platygra daedalea</i>	A1	3.63
	C3-C3u-C3gulf	56.1
	C3/C3c-C3gulf	7.4
	C3by	1.1
	D1-D2.2-D1m	0.2
	D5-D5a-D4-D5e-D4b-D4a	31.6
<i>Porites lutea</i>	C15	1.7
	C3-C3gulf-C3ar-C3as	29.8
	C3-C3gulf-C3c-C3ed	0.3
	C3/C3c-C3gulf	0.4
	C3/C3gulf	0.2
	C40f	0.6
	C17	28.9
<i>Tubinaria peltata</i>	C3-C3bs-C3gulf-C3ef-C3c	100
<b>Seychelles (mid latitude &amp; moderate thermal regime)</b>		
<i>Acropora gemmifera</i>	C15	0.03
	C1d/C1-C42.2-C1b-C3cg-C45c-C115k	11.4
	C3z/C3-C115	5.6
	D1-D2.2-D1m	82.9
<i>Acropora muricata</i>	C3/C115/C3u-C115a-C115e-C21ab	0.9
	C3z-C3-C3.10-C3an-C115-C3bq	16.9
	C3z/C3-C115	1.5

	D1-D2.2-D1m	43.6
	D1-D2.2-D4-D1m-D1c	28.6
	D1-D4-D4c-D1c-D2	8.5
<i>Dipsastraea speciosa</i>	C1-C1c-C1b-C1al-C42.2	1.7
	C1/C1c	0.03
	C1/C1c-C1b	0.2
	C15-C15dl	1.8
	C3/C115/C3u-C115a-C115e-C21ab	70
	<b>C3/C3gulf</b>	<b>0.1</b>
	C3/C3u-C115	4.3
	D1-D2.2-D1m	9
	D1-D4-D4c-D1c-D2	21.8
	<i>Favites pentagona</i>	C1b/C3-C1u
<i>Pavona cactus</i>	C1b/C3-C1u	100
<i>Porites lutea</i>	C15	3.8
	C15-C15ad-C15ai	86.2
	C15-C15az-C15m	0.2
	C15-C15dl	0.3
	C15/C116	8.4
	C15/C15h/C116	0.2
	C3z	0.3
	C3z/C3-C115	0.6
	D4r	0.2
<b>Indonesia (low latitude &amp; thermal regime)</b>		
<i>Acropora gemmifera</i>	C21-C21ag-C3-C21af	11.3
	C40-C3-C115	88.7
<i>Acropora muricata</i>	C15-C15l-C15n-C15bb-C15.8	2.7
	C21	9.1
	C21-C21ag-C3-C21af	74.3
	C3	0.2
	C40-C3-C115	13.6
	D1/D4-D4c-D4f	0.02
<i>Dipsastraea speciosa</i>	C21	2.6
	C21-C21ag-C3-C21af	10.8
	C3/C115/C3u-C115a-C115e-C21ab	2.9



	C40-C3-C115	83.2
	D1-D4-D4c-D4f-D3b-D1c	0.4
	D1/D4/D4c	0.07
<i>Favites pentagona</i>	C1/C42.2/C1b	2.8
	C40-C3-C115	97.2
<i>Pocillopora damicornis</i>	C1d/C1-C42.2-C1b-C3cg-C45c-C115k	92
	C40/C3	4.1
	D1/D2d	3.9
<i>Pocillopora verrucosa</i>	C15h	0.9
	C1d/C1-C42.2-C1b-C3cg-C45c-C115k	64.9
	C42.2/C1-C1b-C1au	13.8
	D1/D2d	20.5
<i>Porites lutea</i>	C116a	0.7
	C15-C15bn-C15by	8.8
	C15-C15by-C15ai	50.4
	C15-C15l-C15n-C15bb-C15.8	13.6
	C15h/C15	26.5

This page was left intentionally blank

## **REFERENCES**

This page was left intentionally blank

## REFERENCES

- Al-Hammady MAM (2013) The effect of zooxanthellae availability on the rates of skeletal growth in the Red Sea coral *Acropora hemprichii*. *Egyptian Journal of Aquatic Research*, **39**, 177–183.
- Al-kuwari Z (2006) *Bahrain First National Report to the Convention on Biological Diversity*. Manama, Bahrain.
- Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR (2009) Flattening of Caribbean coral reefs: Region-wide declines in architectural complexity. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 3019–3025.
- Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R (2013) Shifts in coral-assemblage composition do not ensure persistence of reef functionality. *Scientific Reports*, **3**, 1–5.
- Ampou EE, Johan O, Menkes CE, Nino F, Birol F, Ouillon S, Andrefouet S (2017) Coral mortality induced by the 2015-2016 El-Niño in Indonesia: the effect of rapid sea level fall. *Biogeosciences*, **14**, 817–826.
- Anderson KD, Cantin NE, Heron SF, Pisapia C, Pratchett MS (2017) Variation in growth rates of branching corals along Australia’s Great Barrier Reef. *Scientific Reports*, **7**, 1–13.
- Anthony K, Larcombe P (2000) Coral reefs in turbid waters: sediment-induced stresses in corals and likely mechanisms of adaptation. *Proceedings of the 9th International Coral Reef Symposium*, **I**, 239–244.
- Anthony KRN, Kline DI, Diaz-Pulido G, Dove S, Hoegh-Guldberg O, Karl DM (2008) Ocean acidification causes bleaching and productivity loss in coral reef builders. *PNAS*, **105**, 17442–17446.
- Appana SD, Vuki CV (2004) Bioerosion Patterns and Abundance and Spatial Distribution of *Echinometra sp. A* (green white tip) ecomorph on Nukubuco Reef, Fiji. *Proceedings of the 10th International Coral Reef Symposium, Okinawa, Japan*, **2**, 938–934.
- Attalla TM, Hanafy MH, Aamer MA (2011) Growth rates of the two reef-building species, *Acropora humilis* and *Millepora platyphylla* at Hurghada, Red Sea, Egypt. *Egyptian Journal of Aquatic Biology & Fish*, **15**, 1–15.
- Baird A, Madin J, Álvarez-Noriega M, Cumbo VR, Connolly SR, Dornelas M, Madin JS (2018) A decline in bleaching suggests that depth can provide a refuge from global warming in most coral taxa. *Marine Ecology Progress Series*, **603**, 257–264.
- Bak RPM (1990) Patterns of echinoid bioerosion in two Pacific coral reef lagoons. *Marine Ecology Progress Series*, **66**, 267–272.
- Bak RPM (1994a) Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. *Coral Reefs*, **13**, 99–103.
- Bak RPM (1994b) Sea urchin bioerosion on coral reefs: place in the carbonate budget and relevant variables. *Coral Reefs*, **13**, 99–103.
- Bak RPM, Meesters EH (2000) Acclimatization/adaptation of coral reefs in a marginal environment. *Proceedings 9th International Coral Reef Symposium*, **1**.
- Baker AC (2001) Reef corals bleach to survive change. *Nature*, **411**, 765–766.

- Baker AC (2003) Flexibility and Specificity in Coral - Algal Symbiosis: Diversity, Ecology, and Biogeography of Symbiodinium. *Annual Review of Ecology, Evolution and Systematics*, **34**, 661–89.
- Baker AC, Starger CJ, McClanahan TR, Glynn PW (2004) Coral reefs: corals' adaptive response to climate change. *Nature*, **430**, 741.
- 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. *Estuarine, Coastal and Shelf Science*, **80**, 435–471.
- De Bakker DM, van Duyl FC, Perry CT, Meesters EH (2019) Extreme spatial heterogeneity in carbonate accretion potential on a Caribbean fringing reef linked to local human disturbance gradients. *Global Change Biology*, **25**, 4092–4104.
- De Bakker DM, Webb AE, van den Bogaart LA, Van Heuven SMAC, Meesters EH, van Duyl FC (2018) Quantification of chemical and mechanical bioerosion rates of six Caribbean excavating sponge species found on the coral reefs of Curaçao. *PLoS ONE*, **13**, 1–22.
- Bank W (2018) Data: Land area (sq.km). *World Bank*.
- Bates D, Mächler M, Bolker B, Walker S (2015) Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, **67**.
- Baumann JH, Townsend JE, Courtney TA, Aichelman HE, Davies SW, Lima FP, Castillo KD (2016) Temperature regimes impact coral assemblages along environmental gradients on lagoonal reefs in Belize. *PLoS ONE*, **11**, 1–19.
- Baumann JH, Davies SW, Aichelman HE, Castillo KD (2018) Coral *Symbiodinium* Community Composition Across the Belize Mesoamerican Barrier Reef System is Influenced by Host Species and Thermal Variability. *Microbial Ecology*, **75**, 903–915.
- Beger M, Sommer B, Harrison PL, Smith SDA, Pandolfi JM (2014) Conserving potential coral reef refuges at high latitudes. *Diversity and Distributions*, **20**, 245–257.
- Bell J, Galzin R (1984) Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progress Series*, **15**, 265–274.
- Bell JJ, Davy SK, Jones T, Taylor MW, Webster NS (2013) Could some coral reefs become sponge reefs as our climate changes? *Global Change Biology*, **19**, 2613–2624.
- Bellwood D (1995) Direct estimate of bioerosion by two parrotfish species on the Great Barrier Reef, Australia. *Marine Biology*, **121**, 419–429.
- Bellwood DR, Hoey AS, Choat JH (2003) Limited functional redundancy in high diversity systems: Resilience and ecosystem function on coral reefs. *Ecology Letters*, **6**, 281–285.
- Bellwood DR, Hughes TP, Folke C, Nyström M (2004) Confronting the coral reef crisis. *Nature*, **429**, 827–833.
- Bento R, Hoey AS, Bauman AG, Feary DA, Burt JA (2016) The implications of recurrent disturbances within the world's hottest coral reef. *Marine Pollution Bulletin*, **105**, 466–472.
- Benzoni F, Pichon M, Hazeem S Al, Galli P (2006) The Coral Reefs of the Northern Arabian Gulf: stability over time in extreme environmental conditions? **975**, 7.
- Berg H, Francis J, Souter P (2002) Support to marine research for sustainable management of marine and coastal resources in the Western Indian Ocean. *Ambio*, **31**, 597–601.

- Berkelmans R (2002) Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. *Marine Ecology Progress Series*, **229**, 73–82.
- Berkelmans R, Oliver JK (1999) *Large-scale bleaching of corals on the Great Barrier Reef*, Vol. 18. Springer-Verlag, 55–60 pp.
- Berkelmans R, Van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a “nugget of hope” for coral reefs in an era of climate change. *Proceedings of the Royal Society B*, **273**, 2312.
- van Beukering PJH, Sarkis S, McKenzie E, Hess S, Brander L, Roelfsema M, der Putten LL, Bervoets, T (2010) Total economic value of Bermuda’s coral reefs: valuation of ecosystem services.
- Blackall L, Wilson B, Van Oppen MJH (2015) Coral — The World’s Most Diverse Symbiotic Ecosystem. *Molecular Ecology*, 5330–5347.
- Blanchon P, Jones B (1997) Hurricane control on shelf-edge-reef architecture around Grand Cayman. *Sedimentology*, **44**, 479–506.
- Bowen BW, Rocha LA, Toonen RJ, Karl SA (2013) The origins of tropical marine biodiversity. *Trends in Ecology & Evolution*, **28**, 359–366.
- Bridge TCL, Hoey AS, Campbell SJ, Muttaqin E, Rudi E, Fadli N, Baird AH (2014) Depth-dependent mortality of reef corals following a severe bleaching event: implications for thermal refuges and population recovery. *F1000Research*, **2**, 187.
- Browne N (2011) *A carbonate and terrigenous sediment budget for inshore turbid reefs on the Great Barrier Reef*. James Cook University, 222 pp.
- Browne N (2012) Spatial and temporal variations in coral growth on an inshore turbid reef subjected to multiple disturbances. *Marine Environmental Research*, **77**, 71–83.
- Browne NK, Smithers SG, Perry CT (2012a) Coral reefs of the turbid inner-shelf of the Great Barrier Reef, Australia: An environmental and geomorphic perspective on their occurrence, composition and growth. *Earth-Science Reviews*, **115**, 1–20.
- Browne NK, Smithers SG, Perry CT, Ridd P V (2012b) A field-based technique for measuring sediment flux on coral reefs: application to turbid reefs on the Great Barrier Reef. *Journal of Coastal Research*, **28**, 1247–1262.
- Bruggemann JH, Kuyper MWM, Breeman AM (1994) Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Marine Ecology Progress Series*, **112**, 51–66.
- Bruggemann JH, Van Kessel AM, Van Rooij JM, Breeman AM (1996) Bioerosion and sediment ingestion by the caribbean parrotfish *Scarus vetula* and *Sparisoma viride*: Implications of fish size, feeding mode and habitat use. *Marine Ecology Progress Series*, **134**, 59–71.
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: Timing, extent, and subregional comparisons. *PLoS ONE*, **2**.
- Bruno JF, Petes LE, Harvell CD, Hettinger A (2003) Nutrient enrichment can increase the severity of coral diseases. *Ecology Letters*, **6**, 1056–1061.
- Buddemeier RW, Fautin DG (1993) Coral Bleaching as an adaptive mechanism. *BioScience*, **43**, 320–326.

- Buddemeier RW, Maragos JE, Knutson DW (1974) Radiographic studies of reef coral exoskeletons: Rates and patterns of coral growth. *Journal of Experimental Marine Biology and Ecology*, **14**, 179–199.
- Burke L, Selig E, Spalding M (2002) *Reefs at Risk in Southeast Asia*. 76 pp.
- Burnett WJ (2002) Longitudinal variation in algal symbionts (zooxanthellae) from the Indian Ocean zoanthid *Palythoa caesia*. *Marine Ecology Progress Series*, **234**, 105–109.
- Burt JA (2013) The growth of coral reef science in the Gulf: A historical perspective. *Marine Pollution Bulletin*, **72**, 289–301.
- Burt JA (2014) The environmental costs of coastal urbanization in the Arabian Gulf. *City*, **18**, 760–770.
- Burt J, Al-Harhi S, Al-Cibahy A (2011) Long-term impacts of coral bleaching events on the world's warmest reefs. *Marine Environmental Research*, **72**, 225–229.
- Burt J, Bartholomew A, Feary D (2012) Coral Reefs of the Gulf. *Coral Reefs of the World*, **3**, 170–186.
- Burt JA, Al-Khalifa K, Khalaf E, AlShuwaikh B, Abdulwahab A (2013) The continuing decline of coral reefs in Bahrain. *Marine Pollution Bulletin*, **72**, 357–363.
- Burt JA, Coles S, van Lavieren H, Taylor O, Looker E, Samimi-Namin K (2016) Oman's coral reefs: A unique ecosystem challenged by natural and man-related stresses and in need of conservation. *Marine Pollution Bulletin*, **105**, 498–506.
- Burt JA, Paparella F, Al-Mansoori N, Al-Mansoori A, Al-Jailani H (2019) Causes and consequences of the 2017 coral bleaching event in the southern Persian/Arabian Gulf. *Coral Reefs*, **38**, 567–589.
- Camp EF, Schoepf V, Mumby PJ, Hardtke LA, Rodolfo-Metalpa R, Smith DJ, Suggett DJ (2018) The future of coral reefs subject to rapid climate change: Lessons from natural extreme environments. *Frontiers in Marine Science*, **5**, 1–21.
- Carpenter KE, Abrar M, Aeby G, Aronson RB, Banks S, Bruckner A, Chiriboga A, Cortes J, Delbeek JC, DeVantier L, Edgar, GJ, Edwards AJ, Fenner D, Guzman HM, Hoeksema BW, Hodgson G, Johan O, Licuanan WY, Livingstone SR, Lovell ER, Moore JA, Obura DO, Ochavillo D, Polidoro BA, Precht WF, Quibilian MC, Reboton C, Richards ZT, Rogers AD, Sanciangco, Sheppard A, Sheppard C, Smith J, Stuart S, Turak E, Veron JEN, Wallace C, Weil E, Wood E (2008) One-third of reef-building corals face elevated extinction risk from climate change and local impacts. *Science (New York, N.Y.)*, **321**, 560–3.
- Cesar HSJ, Herman SJ, van Beukering P (2004) Economic valuation of the coral reefs of Hawai'i. *Pacific Science*, **58**, 231–242.
- Charles CD, Hunter DE, Fairbanks RG (1997) Interaction between the ENSO and the Asian monsoon in a coral record of tropical climate. *Science*, **277**, 925–928.
- Chazottes V, Champion-Alsumard TL, Peyrot-Clausade M (1995) Bioerosion rates on coral reefs: interactions between macroborers, microborers and grazers (Moorea, French Polynesia). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **113**, 189–198.
- Chazottes V, Champion-Alsumard T, Peyrot-Clausade M, Cuet P (2002) The effects of eutrophication-related alterations to coral reef communities on agents and rates of bioerosion



- (Reunion Island, Indian Ocean). *Coral Reefs*, **21**, 375–390.
- Chen B, Yu K, Liang J, Huang W, Wang G, Su H, Qin Z, Huang X, Pan Z, Luo W, Luo Y, Wang Y (2019) Latitudinal variation in the molecular diversity and community composition of Symbiodiniaceae in coral from the South China Sea. *Frontiers in Microbiology*, **10**, 1278.
- Choi DR, Ginsburg RN (1983) Distribution of coelobites (cavity-dwellers) in coral rubble across the Florida Reef Tract. *Coral Reefs*, **2**, 165–172.
- Cinner JE, Huchery C, Darling ES, Humphries AT, Graham NA, Hicks C, Marshall N, McClanahan TR (2013) Evaluating social and ecological vulnerability of coral reef fisheries to climate change. *PLoS ONE*, **8**, e74321.
- Claar DC, Szostek L, Mcdevitt-irwin JM, Schanze JJ, Baum K (2018) Global patterns and impacts of El Niño events on coral reefs : A meta-analysis. *PLoS ONE*, **13**, e0190957.
- Clifton J, Unsworth RKF, Smith DJ (2010) *Marine research and conservation in the Coral Triangle, The Wakatobi Marine National Park*. Nova Science, New York, 1–258 pp.
- Clifton J, Osman EO, Suggett DJ, Smith DJ (2019) Resolving conservation and development tensions in a small island state: A governance analysis of Curieuse Marine National Park, Seychelles. *Marine Policy*, 103617.
- Coffroth MA, Santos SR (2005) Genetic diversity of symbiotic dinoflagellates in the genus *Symbiodinium*. *Protist*, **156**, 19–34.
- Coles SL (2003) Coral species diversity and environmental factors in the Arabian Gulf and the Gulf of Oman: A comparison to the Indo-Pacific region. *Atoll Research Bulletin*, 1–19.
- Coles SL, Fadlallah YH (1991) Reef coral survival and mortality at low temperatures in the Arabian Gulf: new species-specific lower temperature limits. *Coral Reefs*, **9**, 231–237.
- Coles SL, Jokiel PL (1978) Synergistic effects of temperature, salinity and light on the hermatypic coral *Montipora verrucosa*. *Marine Biology*, **49**, 187–195.
- Coles SL, Riegl BM (2013) Thermal tolerances of reef corals in the Gulf: A review of the potential for increasing coral survival and adaptation to climate change through assisted translocation. *Marine Pollution Bulletin*, **72**, 323–332.
- Collier JS, Humber SR (2012) Fringing Reefs of the Seychelles Inner Granitic Islands, Western Indian Ocean. *Seafloor Geomorphology as Benthic Habitat*, 339–347.
- 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**, 1–27.
- Courtney TA, De Carlo EH, Page HN, Bahr KD, Barro A, Howins N, Tabata R, Terlouw G, Rodgers KS, Andersson AJ (2018) Recovery of reef-scale calcification following a bleaching event in Kāneʻohe Bay, Hawaiʻi. *Limnology and Oceanography Letters*, **3**, 1–9.
- Crabbe C, Karaviotis S, Smith DJ (2004) Preliminary comparison of three coral reef sites in the Wakatobi Marine National Park (S.E.Sulawesi, Indonesia): Estimated recruitment dates compared with Discovery Bay, Jamaica. *Bulletin of Marine Science*, **74**, 469–476.
- Cullen-Unsworth LC (2010) Marine resource dependence and natural resource use patterns in a small Indo-Pacific Island community: Implications for Management. In: *Marine Research and Conservation in the Coral Triangle: the Wakatobi National Park, Environmental science*,

- engineering and technology* (eds Cullen-Unsworth R, Clifton J, Smith DJ), pp. 171–191. Nova Science, New York.
- Curtis-Quick JA (2013) *Drivers of change of reef fish assemblages within the coral triangle*. PhD thesis, University of Essex, UK.
- D'Angelo C, Hume BCC, Burt J, Smith EG, Achterberg EP, Wiedenmann J (2015) Local adaptation constrains the distribution potential of heat-tolerant *Symbiodinium* from the Persian/Arabian Gulf. *The ISME journal*, **9**, 2551–60.
- Darling ES, McClanahan TR, Côté IM (2010) Combined effects of two stressors on Kenyan coral reefs are additive or antagonistic, not synergistic. *Conservation Letters*, **3**, 122–130.
- Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côté IM (2012) Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, **15**, 1378–1386.
- Davies P (1989) Short-term growth measurements of corals using an accurate buoyant weighing technique. *Marine Biology*, **101**, 389–395.
- Davies SW, Ries JB, Marchetti A, Castillo KD (2018) *Symbiodinium* functional diversity in the Coral *Siderastrea siderea* is influenced by thermal stress and reef environment, but not ocean acidification. *Frontiers in Marine Science*, **5**, 1–14.
- Daw TM, Hicks CC, Brown K, Chaigneau T, Januchowski-Hartley FA, Cheung WWL, Rosendo S, Crona B, Coultard S, Sandbrook C, Perry C, Bandeira S, Muthiga NA, Schulte-Herbruggen B, Bosire J, McClanahan TR (2016) Elasticity in ecosystem services: exploring the variable relationship between ecosystems and human well-being. *Ecology and Society*, **21**, 11.
- De'ath G, Lough JM, Fabricius KE (2009) Declining coral calcification on the Great Barrier Reef. *Science (New York, N.Y.)*, **323**, 116–9.
- Desalvo MK, Voolstra CR, Sunagawa S et al. (2008) Differential gene expression during thermal stress and bleaching in the Caribbean coral *Montastraea faveolata*. *Molecular Ecology*, **17**, 3952–3971.
- Dibattista JD, Howard Choat J, Gaither MR, Hobbs JP, Lozano-Cortes DF, Myers RF, Paulay G, Rocha LA, Toonen RJ, Westneat MW, Berumen ML (2016) On the origin of endemic species in the Red Sea. *Journal of Biogeography*, **43**, 13–30.
- Donner S, Skirving W, Little C, Oppenheimer M, Hoegh-Guldbergs O (2005) Global assessment of coral bleaching and required rates of adaptation under climate change. *Global Change Biology*, **11**, 2251–2265.
- Dorf E. (1960) Climatic changes of the past and present. *American Scientist*, **48(3)**, 341–364.
- Douglas A. (2003) Coral bleaching - how and why? *Marine Pollution Bulletin*, **46**, 385–392.
- Duckworth AR, West L, Vansach T, Stubler A, Hardt M (2012) Effects of water temperature and pH on growth and metabolite biosynthesis of coral reef sponges. *Marine Ecology Progress Series*, **462**, 67–77.
- Eakin C (1992) Post El Niño Panamanian Reefs: less accretion, more erosion and damselfish protection. In: *Proceedings of the 7th International Coral Reef Symposium*, Vol. 1, pp. 387–396.
- Eakin CM (1996) Where have all the carbonates gone? A model comparison of calcium carbonate budgets before and after the 1982–1983 El Niño at Uva Island in the eastern Pacific. *Coral*

- Reefs*, **15**, 109–119.
- Edinger EN, Limmon G V, Jompa J, Widjatmoko W, Heikoopà JM, Riskà MJ (2000) Normal coral growth rates on dying reefs: Are coral growth rates good indicators of reef health? *Marine Pollution Bulletin*, **40**, 404–425.
- Elizalde-Rendón EM, Horta-Puga G, González-Díaz P, Carricart-Ganivet JP (2010) Growth characteristics of the reef-building coral *Porites astreoides* under different environmental conditions in the Western Atlantic. *Coral Reefs*, **29**, 607–614.
- Emara HI, El-Samra MI, El-Debb KZ, Ahmed IF (1985) A preliminary study of the chemical characteristics of the coral reef areas in the Qatari waters (Gulf area). In: *Proceedings of the 5th International Coral Reef Congress*, pp. 13–16. vol. 6, Tahiti.
- Enochs IC, Manzello DP, Tribollet A, Valentino L, Kolodziej G, Donham EM, Fitchett MD, Carlton R, Price NN (2016) Elevated colonization of microborers at a volcanically acidified coral reef. *PLoS ONE*, **11**, e0159818.
- Fabina NS, Putnam HM, Franklin EC, Stat M, Gates RD (2012) Transmission mode predicts specificity and interaction patterns in Coral-*Symbiodinium* Networks. *PLoS ONE*, **7**(9): e44970.
- Fabricius K, De'ath G (2001) Environmental factors associated with the spatial distribution of crustose coralline algae on the Great Barrier Reef. *Coral Reefs*, **19**, 303–309.
- Fabricius K, De'ath G, Mccook L, Turak E, Williams DM (2005) Changes in algal, coral and fish assemblages along water quality gradients on the inshore Great Barrier Reef. *Marine Pollution Bulletin*, **51**, 384–398.
- Fabry VJ, Seibel BA, Feely RA, Fabry JCO, Fabry VJ (2008) Impacts of ocean acidification on marine fauna and ecosystem processes. *ICES Journal of Marine Science*, **65**, 414–432.
- Falkowski PG, Dubinsky Z, Muscatine L, Porter JW (1984) Light and the bioenergetics of a symbiotic coral. *BioScience*, **34**, 705–709.
- Fan L, Liu M, Simister R, Webster NS, Thomas T (2013) Marine microbial symbiosis heats up: the phylogenetic and functional response of a sponge holobiont to thermal stress. *The ISME Journal*, **7**, 991–1002.
- Fang JKH, Mello-Athayde MA, Schönberg CHL, Kline DI, Hoegh-Guldberg O, Dove S (2013) Sponge biomass and bioerosion rates increase under ocean warming and acidification. *Global Change Biology*, **19**, 3581–3591.
- Ferrario F, Beck MW, Storlazzi CD, Micheli F, Shepard CC, Airoidi L (2014) The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nature Communications*, **5**, 1–9.
- Fitt W, Trench R (1983) The relation of diel patterns of cell division to diel patterns of motility in the symbiotic dinoflagellate *Symbiodinium microadriaticum* freudenthal in culture. *New Phytologist*, **94**, 421–432.
- Forsman ZH, Barshis DJ, Hunter CL, Toonen RJ (2009) Shape-shifting corals: Molecular markers show morphology is evolutionarily plastic in *Porites*. *BMC Evolutionary Biology*, **9**, 1–9.
- Foster AB (1979) Phenotypic plasticity in the reef corals *Montastraea annularis* (Ellis and Solander) and *Siderastrea siderea* (Ellis and Solander). *Journal of Experimental Marine Biology and Ecology*, **39**, 25–54.
- Franco C (2014) *Modelling the dynamics of CaCO<sub>3</sub> budgets in changing environments using a*

- Bayesian Belief Network approach*. PhD thesis, University of Essex, UK.
- Franco C, Hepburn LA, Smith DJ, Nimrod S, Tucker A (2016) A Bayesian Belief Network to assess rate of changes in coral reef ecosystems. *Environmental Modelling & Software*, **80**, 132–142.
- Franklin E, Jokiel P, Donahue M (2013) Predictive modeling of coral distribution and abundance in the Hawaiian Islands. *Marine Ecology Progress Series*, **481**, 121–132.
- Fujita K, Osawa Y, Kayanne H, Ide Y, Yamano H (2009) Distribution and sediment production of large benthic foraminifers on reef flats of the Majuro Atoll, Marshall Islands. *Coral Reefs*, **28**, 29–45.
- Furla P, Allemand D, Orsenigo M (2000) Involvement of H<sup>+</sup>-ATPase and carbonic anhydrase in inorganic carbon uptake for endosymbiont photosynthesis. *American Journal of Physiol Regulatory Integrative Comp*, **279**, R870–R881.
- Gardner SG, Camp EF, Smith DJ, Kahlke T, Osman EO, Gendron G, Hume BCC, Pogoreutz C, Woolstra CR, Suggett, DJ (2018) Coral microbiome diversity reflects mass coral bleaching susceptibility during the 2016 El Niño heat wave. *Ecology and Evolution*, **9**, 938–956.
- Gattuso J-P, Frankignoulle M, Bourge I, Romaine S, Buddemeier RW (1998) Effect of calcium carbonate saturation of seawater on coral calcification. *Global and Planetary Change*, **18**, 37–46.
- Ghavam Mostafavi P, Fatemi SMR, Shahhosseiny MH, Hoegh-Guldberg O, Loh WKW (2007) Predominance of clade D *Symbiodinium* in shallow-water reef-building corals off Kish and Larak Islands (Persian Gulf, Iran). *Marine Biology*, **153**, 25–34.
- Glynn PS (1977) Coral growth in the upwelling and non-upwelling areas of the Pacific coast of Panama. *Journal of Marine Research*, **35**, 567–585.
- Glynn P. (1997) Bioerosion and coral reef growth : A dynamic balance. In: *Life and Death on Coral Reefs* (ed In: Birkeland C), pp. 68–95. Chapman and Hall, New York.
- Goreau TF (1963) Calcium carbonate deposition by coralline algae and corals in relation to their roles as reef builders. *Annals of the New York Academy of Sciences*, **109**, 127–167.
- Goreau T, Hartman W (1963) Boring sponges as controlling factors in the formation and maintenance of coral reefs. *American Association for the Advancement of Science*, **75**, 25–54.
- Goreau T, McClanahan TR, Hayes R, Strong A (2000) Conservation of coral reefs after the 1998 global bleaching event. *Conservation Biology*, **14**, 5–15.
- Gouraguine A, Moranta J, Ruiz-Frau A, Hinz H, Renones O, Ferse SCA, Jompa J, Smith DJ (2019) Citizen science in data and resource-limited areas: A tool to detect long-term ecosystem changes. *PLoS ONE*, **14(1)**: e0210007.
- Graham NAJ (2014) Habitat complexity: Coral structural loss leads to fisheries declines. *Current Biology*, **24**, 359–361.
- Graham NAJ, Nash KL (2013) The importance of structural complexity in coral reef ecosystems. *Coral Reefs*, **32**, 315–326.
- Graham NAJ, Wilson SK, Jennings S, Polunin NVC, Bijoux JP, Robinson J (2006) Dynamic fragility of oceanic coral reef ecosystems. *PNAS*, **103**, 8425–8429.
- Graham NAJ, Jennings S, Macneil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature*, **518**, 94–97.

- Grizzle RE, Ward KM, AlShihi RMS, Burt JA (2016) Current status of coral reefs in the United Arab Emirates: Distribution, extent, and community structure with implications for management. *Marine Pollution Bulletin*, **105**, 515–523.
- Gudka M, Obura O, Mwaura J, Porter S, Yahya S, Mabwa R (2018) *Impact of the 3rd global coral bleaching event on the Western Indian Ocean Impact of the 3rd Global Coral Bleaching Event on the Western Indian Ocean in 2016*. 67 pp.
- Gudka M, Obura D, Mbugua J, Ahamada S, Kloiber U, Holter T (2020) Participatory reporting of the 2016 bleaching event in the Western Indian Ocean. *Coral Reefs*, **39**, 1–11.
- Guzmán H, Cortés J (1989) Growth rates of eight species of scleractinian corals in the eastern Pacific (Costa Rica). *Bulletin of Marine Science*, **44**, 1186–1194.
- GVI Seychelles (2018) *GVI Seychelles – Mahé Marine Conservation Expedition January - December 2018*, Vol. 2255. Mahé.
- Haapkylä J, Unsworth RKF, Seymour AS, Melbourne-Thomas J, Flavell M, Willis BL, Smith DJ (2009) Spatio-temporal coral disease dynamics in the Wakatobi Marine National Park, South-East Sulawesi, Indonesia. *Diseases of Aquatic Organisms*, **87**, 105–115.
- Haapkylä J, Melbourne-Thomas J, Flavell M (2015) The association between coral communities and disease assemblages in the Wakatobi Marine National Park, south-eastern Sulawesi, Indonesia. *Marine and Freshwater Research*, **66**, 948–955.
- Hansen G, Daugbjerg N (2009) *Symbiodinium natans* sp. nov.: A “free-living” dinoflagellate from tenerife (northeast-Atlantic ocean). *Journal of Phycology*, **45**, 251–263.
- Harney JN, Fletcher CH (2003) A budget of carbonate framework and sediment production, Kailua Bay, Oahu, Hawaii. *Journal of Sedimentary Research*, **73**, 856–868.
- Harriott VJ (1999) Coral growth in subtropical eastern Australia. *Coral Reefs*, **18**, 281–291.
- Harris A, Wilson S, Graham N, Sheppard C (2014) Scleractinian coral communities of the inner Seychelles 10 years after the 1998 mortality event. *Aquatic Conservation: Marine and Freshwater Ecosystems*, **24**, 667–679.
- Hennige SJ, Smith DJ, Perkins R, Consalvey M, Paterson DM, Suggett DJ (2008) Photoacclimation, growth and distribution of massive coral species in clear and turbid waters. *Marine Ecology Progress Series*, **369**, 77–88.
- Hennige SJ, Smith DJ, Walsh SJ, McGinley MP, Warner ME, Suggett DJ (2010) Acclimation and adaptation of scleractinian coral communities along environmental gradients within an Indonesian reef system. *Journal of Experimental Marine Biology and Ecology*, **391**, 143–152.
- Hennige SJ, McGinley MP, Grottoli AG, Warner ME (2011) Photoinhibition of *Symbiodinium* spp. within the reef corals *Montastraea faveolata* and *Porites astreoides*: implications for coral bleaching. *Marine Biology*, **158**, 2515–2526.
- Hepburn LJ (2006) *Processes of bioerosion and calcareous encrustation on a Mexican Caribbean reef: implications for framework development*. PhD thesis, Manchester Metropolitan University, Manchester, UK.
- Hepburn LJ, Blanchon P, Murphy G, Cousins L, Perry CT (2015) Community structure and palaeoecological implications of calcareous encrusters on artificial substrates across a Mexican Caribbean reef. *Coral Reefs*, **34**, 189–200.

- Heron SF, Maynard JA, Van Hooidek R, Eakin CM (2016) Warming trends and bleaching stress of the world's coral reefs 1985-2012. *Scientific Reports*, **6**, 1–14.
- Herrán N, Narayan GR, Reymond CE, Westphal H (2017) Calcium carbonate production, coral cover and diversity along a distance gradient from Stone Town: A case study from Zanzibar, Tanzania. *Frontiers in Marine Science*, **4**, 1–14. doi: 10.3389/fmars.2017.00412.
- Highsmith R (1979) Coral growth rates and environmental control of density banding. *Journal of Experimental Marine Biology and Ecology*, **37**, 105–125.
- Hill M, Allenby A, Ramsby B, Schönberg C, Hill A (2011) *Symbiodinium* diversity among host clonoid sponges from Caribbean and Pacific reefs: Evidence of heteroplasmy and putative host-specific symbiont lineages. *Molecular Phylogenetics and Evolution*, **59**, 81–88.
- Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. *Marine and Freshwater Research*, **50**, 839–866.
- Hoegh-Guldberg O (2011) Coral reef ecosystems and anthropogenic climate change. *Regional Environmental Change*, **11**, S215–S227.
- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzitolos ME (2007) Coral Reefs Under Rapid Climate Change and Ocean Acidification. *Science*, **318**, 1737–1742.
- Hoegh-Guldberg O, Cai R, Poloczanska ES et al. (2014) The ocean. *Climate Change 2014: Impacts, Adaptation, and Vulnerability. Part B: Regional Aspects. Contribution of Working Group II to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change*, 1655–1732.
- Hoegh-Guldberg O, Poloczanska ES, Skirving W, Dove S (2017) Coral reef ecosystems under climate change and ocean acidification. *Frontiers in Marine Science*, **4**, 158.
- Hoeksema B (2007) Delineation of the Indo-Malayan centre of maximum marine biodiversity. In: *The coral triangle biogeography, time, and place: Distributions, Barriers, and Islands*, pp. 117–178. Springer, The Netherlands.
- Hoey AS, Bellwood DR (2008) Cross-shelf variation in the role of parrotfishes on the Great Barrier Reef. *Coral Reefs*, **27**, 37–47.
- Hoey A, Howells E, Johansen J, Hobbs JP, Messmer V, McCowan DM, Wilson S, Pratchett MS (2016) Recent advances in understanding the effects of climate change on coral reefs. *Diversity*, **8**, 12.
- Holmes KE, Edinger EN, Hariyadi, Limmon GV, Risk MJ (2000) Bioerosion of live massive corals and branching coral rubble on Indonesian coral reefs. *Marine Pollution Bulletin*, **40**, 606–617.
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal*, **50**, 346–363.
- Howells EJ, Abrego D, Vaughan GO, Burt JA (2014) Coral spawning in the Gulf of Oman and relationship to latitudinal variation in spawning season in the northwest Indian Ocean. *Scientific reports*, **4**, 7484.
- Howells EJ, Dunshea G, McParland D, Vaughan GO, Heron SF, Pratchett MS, Burt JA, Bauman AG (2018) Species-specific coral calcification responses to the extreme environment of the Southern Persian Gulf. *Frontiers in Marine Science*, **5**, 1–13.

- Howells EJ, Bauman AG, Vaughan GO, Hume BCC, Voolstra CR, Burt JA (2020) Corals in the hottest reefs in the world exhibit symbiont fidelity not flexibility. *Molecular Ecology*, **00**, 1-13.
- Huang D, Roy K (2015) The future of evolutionary diversity in reef corals. *Philosophical Transactions Royal Society B*, **370**, 20140010.
- Hubbard DK, Miller AI, Scaturro D (1990) Production and cycling of calcium carbonate in a shelf-edge reef system (St.Croix, U.S. Virgin Islands): Applications to the nature of reef systems in the fossil record. *Journal of Sedimentary Research*, **60**, 335–360.
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleympas J, Lough JM, Marshall P, Nystrom M, Palumbi SR, Pandolfi JM, Rosen B, Roughgarden J (2003) Climate change, human impacts, and the resilience of coral reefs. *Science*, **301**, 929–933.
- Hughes TP, Kerry J, Álvarez-Noriega M et al. (2017a) Global warming and recurrent mass bleaching of corals. *Nature*, **543**, 373–377.
- Hughes L, Steffen W, Alexander D, Rice M (2017b) *Climate Change: A Deadly Threat to Coral Reefs*. Climate Council of Australia Limited, 28 pp.
- Hughes TP, Anderson KD, Connolly SR et al. (2018a) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science*, **359**, 80–83.
- Hughes TP, Kerry JT, Simpson T (2018b) Large-scale bleaching of corals on the Great Barrier Reef. *Ecology*, **99**, 501.
- Hume B, D'Angelo C, Burt J, Baker AC, Riegl B, Wiedenmann J (2013) Corals from the Persian/Arabian Gulf as models for thermotolerant reef-builders: Prevalence of clade C3 *Symbiodinium*, host fluorescence and ex situ temperature tolerance. *Marine Pollution Bulletin*, **72**, 313–322.
- Hume BCC, Angelo CD, Smith EG, Stevens JR, Burt J, Wiedenmann J (2015) *Symbiodinium thermophilum* sp. nov., a thermotolerant symbiotic alga prevalent in corals of the world's hottest sea, the Persian/Arabian Gulf. *Scientific Reports*, **5**, 8562.
- Hume BCC, Voolstra CR, Arif C, D'Angelo C, Burt JA, Eyal G, Loya Y, Wiedenmann (2016) Ancestral genetic diversity associated with the rapid spread of stress-tolerant coral symbionts in response to Holocene climate change. *PNAS*, **113**, 4416–4421.
- Hume BCC, Ziegler M, Poulain J, Pochon X, Romac S, Boissin E, deVargas C, Planes S, Wincker P, Voolstra CR (2018) An improved primer set and amplification protocol with increased specificity and sensitivity targeting the *Symbiodinium* ITS2 region. *PeerJ*, **6**, e4816.
- Hume BCC, Smith EG, Ziegler M, Warrington HJM, Burt JA, LaJeunesse TC, Wiedenmann J, Voolstra CR (2019) SymPortal: A novel analytical framework and platform for coral algal symbiont next-generation sequencing ITS2 profiling. *Molecular Ecology Resources*, **19**, 1063–1080.
- Hume BCC, Mejia-Restrepo A, Voolstra CR, Berumen ML (2020) Fine-scale delineation of Symbiodiniaceae genotypes on a previously bleached central Red Sea reef system demonstrates a prevalence of coral host-specific associations. *Coral Reefs 2020*, 1–19.
- Hunter IG (1977) Sediment production by *Diadema antillarum* on a Barbados fringing reef. In: *Proceedings of the 3rd International Coral Reef Symposium*, pp. 106–109.

- Hutchings PA (1986) Biological destruction of coral reefs. *Coral Reefs*, **4**, 239–252.
- Hutchings PA, Bamber L (1985) Variability of bioerosion rates at Lizard Island, Great Barrier Reef: preliminary attempts to explain these rates and their significance. In: *Proceedings of the 5th Coral Reef Symposium*, pp. 333–338. Tahiti.
- IPCC (2013) *Climate Change 2013: The physical science basis working group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change* (eds Stocker TF, Qin D, Plattner G-K, Tignor MMB, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM). Cambridge University Press, Cambridge, UK and New York, USA, 1535 pp.
- IPCC (2014) Climate Change 2014 Synthesis Report Summary Chapter for Policymakers. *Ipcc*, 31.
- IPCC (2015) *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*. IPCC, Geneva, Switzerland, 151 pp.
- IPCC (2019) *IPCC Special Report on the Ocean and Cryosphere in a Changing Climate*. 37–70 pp.
- Januchowski-Hartley FA, Graham NAJ, Wilson SK, Jennings S, Perry CT (2017) Drivers and predictions of coral reef carbonate budget trajectories. *Proceedings of the Royal Society of London B*, **284**, 20162533.
- Jeong HJ, Lee SY, Kang NS, Yoo YD, Lim AS, Lee MJ, Kim HS, Yih W, Yamashita H, LaJeunesse TC (2014) Genetics and morphology characterize the dinoflagellate *Symbiodinium voratum*, n. sp., (dinophyceae) as the Sole representative of *Symbiodinium* clade E. *Journal of Eukaryotic Microbiology*, **61**, 75–94.
- Jokiel PL, Rodgers KS, Brown EK, Kenyon JC, Aeby G, Smith WR, Farrell F (2015) Comparison of methods used to estimate coral cover in the Hawaiian Islands. *PeerJ*, **3**, e954.
- Jones A, Berkelmans R (2010) Potential costs of acclimatization to a warmer climate: Growth of a reef coral with heat tolerant vs. sensitive symbiont types. *PLoS ONE*, **5**.
- Jones RJ, Steven AL (1997) Effects of cyanide on corals in relation to cyanide fishing on reefs. *Marine and Freshwater Research*, **48**, 517–522.
- Jones NS, Ridgwell A, Hendy EJ (2015) Evaluation of coral reef carbonate production models at a global scale. *Biogeosciences*, **12**, 1339–1356.
- Kavousi J, Tavakoli-Kolour P, Mohammadzadeh M, Bahrami A, Barkhordari A (2014) Mass coral bleaching in the northern Persian Gulf, 2012. *Scientia Marina*, **78**, 397–404.
- Kemp DW, Hernandez-Pech X, Iglesias-Prieto R, Fitt WK, Schmidt GW (2014) Community dynamics and physiology of *Symbiodinium* spp. before, during, and after a coral bleaching event. *Limnology and Oceanography*, **59**, 788–797.
- Kendall JJ, Powell EN, Connor SJ, Bright TJ, Zastrow CE (1985) Effects of turbidity on calcification rate, protein concentration and the free amino acid pool of the coral *Acropora cervicornis*. *Marine Biology*, **87**, 33–46.
- Kennedy EV, Perry CT, Halloran PR, Iglesias-Prieto R, Schonberg CHL, Wisshak M, Form AU, Carricart-Ganivet JP, Fine M, Eakin CM, Mumby PJ (2013) Avoiding coral reef functional collapse requires local and global action. *Current Biology*, **23**, 912–918.
- Kiene WE (1988) A model of bioerosion on the Great Barrier Reef. In: *Proceedings of the 6th International Coral Reef Symposium*, Vol. 3, pp. 449–454. Townsville, Australia.



- Kiene WE, Hutchings PA (1994) Bioerosion experiments at Lizard Island, Great Barrier Reef. *Coral Reefs*, **13**, 91–98.
- Kirk NL, Howells EJ, Abrego D, Burt JA, Meyer E (2018) Genomic and transcriptomic signals of thermal tolerance in heat-tolerant corals (*Platygyra daedalea*) of the Arabian/Persian Gulf. *Molecular Ecology*, **27**(24), 5180–5194.
- Kleypas JA, Langdon C (2006) *Coral Reefs and Changing Seawater Carbonate Chemistry*. American Geophysical Union, Washington, DC, 73–110 pp.
- Kleypas JA, Buddemeier RW, Archer D, Gattuso JP, Langdon C, Opdyke BN (1999a) Geochemical consequences of increased atmospheric carbon dioxide on coral reefs. *Science*, **284**, 118–120.
- Kleypas JA, Mcmanus JW, Menez LAB (1999b) Environmental limits to coral reef development : where do we draw the line ? *American Zoologist*, **146**, 1–15.
- Lafferty KD, Porter JW, Ford SE (2004) Are Diseases Increasing in the Ocean? *Annual Review of Ecology, Evolution, and Systematics*, **35**, 31–54.
- Lajeunesse TC (2005) ‘Species’ radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Molecular Biology and Evolution*, **22**, 570–581.
- Lajeunesse TC, Thornhill DJ, Cox EF, Stanton FG, Fitt WK, Schmidt GW (2004a) High diversity and host specificity observed among symbiotic dinoflagellates in reef coral communities from Hawaii. *Coral Reefs*, **23**, 596–603.
- Lajeunesse TC, Bhagooli R, Hidaka M et al. (2004b) Closely related *Symbiodinium* spp. differ in relative dominance in coral reef host communities across environmental, latitudinal and biogeographic gradients. *Marine Ecology-Progress Series*, **284**, 147–161.
- Lajeunesse TC, Parkinson JE, Reimer JD (2012) A genetics-based description of *Symbiodinium minutum* sp. nov. and *S. psygmophilum* sp. nov. (dinophyceae), two dinoflagellates symbiotic with cnidaria. *Journal of Phycology*, **48**, 1380–1391.
- LaJeunesse TC (2001) Investigating the biodiversity, ecology and phylogeny of endosymbiotic dinoflagellates in the genus *Symbiodinium* using the ITS Region: In search of a “species” level marker. *Journal of Phycology*, **37**, 866–880.
- LaJeunesse TC (2002) Diversity and community structure of symbiotic dinoflagellates from Caribbean coral reefs. *Marine Biology*, **141**, 387–400.
- LaJeunesse TC (2005) “Species” radiations of symbiotic dinoflagellates in the Atlantic and Indo-Pacific since the Miocene-Pliocene transition. *Molecular Biology and Evolution*, **22**, 570–581.
- LaJeunesse TC, Smith RT, Finney J, Oxenford H (2009) Outbreak and persistence of opportunistic symbiotic dinoflagellates during the 2005 Caribbean mass coral “bleaching” event. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 4139–4148.
- LaJeunesse T, John E, Robert K (2012) *Symbiodinium*. Available Online < <http://tolweb.org/Symbiodinium/12605/2012.0704>> Last accessed: 29 March 2020.
- LaJeunesse TC, Wham DC, Pettay DT, Parkinson JE, Keshavmurthy S, Chen CA (2014) Ecologically differentiated stress-tolerant endosymbionts in the dinoflagellate genus *Symbiodinium* (Dinophyceae) Clade D are different species. *Phycologia*, **53**, 305–319.
- LaJeunesse TC, Lee SY, Gil-Agudelo DL, Knowlton N, Jeong HJ (2015) *Symbiodinium necroappetens* sp. nov. (Dinophyceae): an opportunist ‘zooxanthella’ found in bleached and

- diseased tissues of Caribbean reef corals. *European Journal of Phycology*, **50**, 223–238.
- LaJeunesse TC, Parkinson JE, Gabrielson PW, Jeong HJ, Reimer JD, Voolstra CR, Santos SR (2018) Systematic Revision of Symbiodiniaceae Highlights the Antiquity and Diversity of Coral Endosymbionts. *Current Biology*, **28**, 2570–2580.e6.
- Land LS (1979) The fate of reef-derived sediment on the northern Jamaican island slope. *Marine Geology*, **29**, 55–71.
- Lange ID, Perry CT (2019) Bleaching impacts on carbonate production in the Chagos Archipelago: influence of functional coral groups on carbonate budget trajectories. *Coral Reefs*, **38**, 619–624.
- Langer MR (2008) Assessing the contribution of foraminiferan protists to global ocean carbonate production. *Journal of Eukaryotic Microbiology*, **55**, 163–169.
- Laurans Y, Pascal N, Binet T, Brander L, Clua E, David G, Rojat D, Seidl A (2013) Economic valuation of ecosystem services from coral reefs in the South Pacific: Taking stock of recent experience. *Journal of Environmental Management*, **116**, 135–144.
- Lee SY, Jeong HJ, Kang NS, Jang TY, Jang SH, Lajeunesse TC (2015) *Symbiodinium tridacnidorum* sp. nov., a dinoflagellate common to Indo-Pacific giant clams, and a revised morphological description of *Symbiodinium microadriaticum* freudenthal, emended Trench & Blank. *European Journal of Phycology*, **50**, 155–172.
- Leon JX, Woodroffe CD (2013) Morphological characterisation of reef types in Torres Strait and an assessment of their carbonate production. *Marine Geology*, **338**, 64–75.
- Lesser MP (2007) Coral reef bleaching and global climate change: can corals survive the next century? *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 5259–5260.
- Lesser MP, Stochaj WR, Tapley DW, Shick JM (1990) Coral Reefs effects of irradiance, ultraviolet radiation and temperature. *Coral Reefs*, **8**, 225–232.
- Leveque S, Afiq-Rosli L, Ip YCA, Jain SS, Huang D (2019) Searching for phylogenetic patterns of Symbiodiniaceae community structure among Indo-Pacific Merulinidae corals. *PeerJ*, **2019**, 1–23.
- Little A, Van Oppen M, Willis B (2004) Flexibility in algal endosymbioses shapes growth in reef corals. *Science*, **304**, 1492–1494.
- Littman R, Willis BL, Bourne DG (2011) Metagenomic analysis of the coral holobiont during a natural bleaching event on the Great Barrier Reef. *Environmental Microbiology Reports*, **3**, 651–660.
- Liu G, Strong AE, Skirving WJ, Arzayus LF (2006) Overview of NOAA Coral Reef Watch Program's near-real-time satellite global coral bleaching monitoring activities. *Proceedings of the 10th International Coral Reef Symposium*, **1793**, 1783–1793.
- Loh TL, McMurray SE, Henkel TP, Vicente J, Pawlik JR (2015) Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. *PeerJ*, **3**, e901.
- Long MH, Rheuban JE, Berg P, Zieman JC (2012) A comparison and correction of light intensity loggers to photosynthetically active radiation sensors. *Limnology and Oceanography: Methods*, **10**, 416–424.

- Lough JM (2000) 1997–1998: unprecedented thermal stress to coral reefs? *Geophysical Research Letters*, **27**, 3901–3904.
- Lough JM, Barnes DJ (2000) Environmental controls on growth of the massive coral *Porites*. *Journal of Experimental Marine Biology and Ecology*, **245**, 225–243.
- Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs: 1871–2017. *Scientific Reports*, **8**, 1–8.
- Loya Y (1976) Effects of water turbidity and sedimentation. *Bulletin of Marine Science*, **26**, 450–466.
- Mace GM, Reyers B, Alkemade R, Biggs R, Chapin FS, Cornell SE, Diaz S, Jennings S, Leadley P, Mumby PJ, Purvis A, Scholes RJ, Seddon AWR, Solan M, Steffen W, Woodward G (2014) Approaches to defining a planetary boundary for biodiversity. *Global Environmental Change*, **28**, 289–297.
- Magnusson SH, Fine M, Kühl M (2007) Light microclimate of endolithic phototrophs in the scleractinian corals *Montipora monasteriata* and *Porites cylindrica*. *Marine Ecology Progress Series*, **332**, 119–128.
- Maliao RJ, Turingan RG, Lin J (2008) Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. *Marine Biology*, **154**, 841–853.
- Mallela J (2004) *Coral reef communities and carbonate production in a fluvially-influenced embayment, RioBueno, Jamaica*. PhD thesis, Manchester Metropolitan University, UK.
- Mallela J (2007) Coral reef encruster communities and carbonate production in cryptic and exposed coral reef habitats along a gradient of terrestrial disturbance. *Coral Reefs*, **26**, 775–785.
- Mallela J (2013) Calcification by reef-building sclerobionts. *PLoS ONE*, **8**, e60010.
- Mallela J, Perry ACT (2007) Calcium carbonate budgets for two coral reefs affected by different terrestrial runoff regimes, Rio Bueno, Jamaica. *Coral Reefs*, **26**, 129–145.
- Mallela J, Milne BC, Martinez-Escobar D (2017) A comparison of epibenthic reef communities settling on commonly used experimental substrates: PVC versus ceramic tiles. *Journal of Experimental Marine Biology and Ecology*, **486**, 290–295.
- Marlow J, Smith D, Werorilang S, Bell J (2018) Sedimentation limits the erosion rate of a bioeroding sponge. *Marine Ecology*, **39**, 1–7.
- Marlow J, Haris A, Jompa J, Werorilangi S, Bates T, Bennett H, Bell JJ (2019) Spatial variation in the benthic community composition of coral reefs in the Wakatobi Marine National Park, Indonesia: Updated baselines and limited benthic community shifts. *Journal of the Marine Biological Association of the United Kingdom*, 1–9.
- Marquez JC, Zea S (2012) Parrotfish mediation in coral mortality and bioerosion by the encrusting, excavating sponge *Cliona tenuis*. *Marine Ecology*, **33**, 417–426.
- Mcclanahan TR, Baker A, Ateweberhan M (2011) Preparing for climate change in the Western Indian Ocean. Identifying climate refugia, biodiversity responses and preferred management. *WIOMSA. Western Indian Ocean Marine Science Association*, 62.
- McManus LC, Vasconcelos VV, Levin SA, Thompson DM, Kleypas JA, Castruccio FS, Curchitser EN, Watson JR (2019) Extreme temperature events will drive coral decline in the Coral Triangle. *Global Change Biology*, gcb.14972.

- Mieog JC, Olsen JL, Berkelmans R, Bleuler-Martinez SA, Willis BL, Van Oppen MJH, Bruno JF (2009) The Roles and Interactions of Symbiont, Host and Environment in Defining Coral Fitness. *PLoS ONE*, **4**, e6364.
- Miller MW (1995) Growth of a temperate coral: Effects of temperature, light, depth, and heterotrophy. *Marine Ecology Progress Series*, **122**, 217–226.
- Milliman JD (1993) Production and accumulation of calcium carbonate in the ocean: Budget of a nonsteady state. *Global Biogeochemical Cycles*, **7**, 927–957.
- Moberg F, Folke C (1999) Ecological goods and services of coral reef ecosystems. *Ecological Economics*, **29**, 215–233.
- Monroe AA, Ziegler M, Roik A et al. (2018) In situ observations of coral bleaching in the central Saudi Arabian Red Sea during the 2015/2016 global coral bleaching event. *PLoS ONE*, **13**, 1–13.
- Morgan G (2006) *Country review: Bahrain*. In: DeYoung, C. (Ed.), *Review of the State of World Marine Capture Fisheries Management: Indian Ocean*. FAO Fisheries Technical Paper 488. Rome, 187–194 pp.
- Morgan KM, Kench PS (2012) Skeletal extension and calcification of reef-building corals in the central Indian Ocean. *Marine Environmental Research*, **81**, 78–82.
- Morgan KM, Perry CT, Smithers SG, Johnson JA, Gulliver P (2016) Transitions in coral reef accretion rates linked to intrinsic ecological shifts on turbid-zone nearshore reefs. *Geology*, **44**, 995–998.
- Morris LA, Voolstra CR, Quigley KM, Bourne DG, Bay LK (2019) Nutrient availability and metabolism affect the stability of Coral–Symbiodiniaceae symbioses. *Trends in Microbiology*, **27**, 678–689.
- Muko S, Kawasaki K, Sakai K, Takasu F, Shigesada N (2000) Morphological plasticity in the coral *Porites sillimaniani* and its adaptive significance. *Bulletin of Marine Science*, **66**, 225–239.
- Murty TS, El-Sabh MI (1984) Cyclones and storm surges in the Arabian Sea: A brief review. *Deep Sea Research Part A. Oceanographic Research Papers*, **31**, 665–670.
- Naser HA (2012) Evaluation of the Environmental Impact Assessment System in Bahrain. *Journal of Environmental Protection*, **03**, 233–239.
- Neumann AC (1966) Observations on coastal erosion in Bermuda and measurements of the boring rate of the sponge, *Cliona Lampa*. *Limnology Oceanography*, **11**, 92–107.
- Nitschke M (2015) *The Free-Living Symbiodinium Reservoir and Scleractinian Coral Symbiont Acquisition*. PhD thesis, University of Queensland, St Lucia, Australia.
- Norström AV, Nyström M, Lokrantz J, Folke C (2009) Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series*, **376**, 293–306.
- Nugues MM, Roberts CM (2003) Coral mortality and interaction with algae in relation to sedimentation. *Coral Reefs*, **22**, 507–516.
- Obura DO (2005) Resilience and climate change: lessons from coral reefs and bleaching in the Western Indian Ocean. *Estuarine, Coastal and Shelf Science*, **65**, 353–372.
- Obura DO (2012) The diversity and biogeography of Western Indian Ocean reef-building corals. *PLoS ONE*, **7**, e45013.

- Obura DO (2016) An Indian Ocean centre of origin revisited: Palaeogene and Neogene influences defining a biogeographic realm. *Journal of Biogeography*, **43**, 229–242.
- Obura DO, Gudka M, Rabi FA, Gian SB, Bijoux J, Freed S, Maharavo J, Mwaura J, Porter S, Sola E, Wickel J, Yahya S, Ahamada S (2017) *Coral Reef Status Report for the Western Indian Ocean (2017)*. 144 pp.
- Odum HT, Odum EP (1955) Trophic Structure and Productivity of a Windward Coral Reef Community on Eniwetok Atoll. *Ecological Monographs*, **25**, 291–320.
- Oksanen AJ, Blanchet FG, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, Stevens MHH, Szoecs E, Wagner H (2018) Package 'vegan'. Available Online: <<https://cran.r-project.org>, <https://github.com/vegandevs/vegan>> Last accessed: 27 April 2020.
- Orr JC, Fabry VJ, Aumont O, Bopp L, Doney SC, Feely RA, Gnanadesikan A, Gruber N, Ishida A, Joos F, Key RM, Lindsay K, Maier-Reimer E, Matear R, Monfray P, Mouchet A, Najjar RG, Plattner GK, Rodgers KB, Sabine CL, Sarmiento JL, Schlitzer R, Slater RD, Totterdell IJ, Weirig MF, Yamanaka Y, Yool A (2005) Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature*, **437**, 681–686.
- Palumbi SR, Barshis DJ, Traylor-Knowles N, Bay RA (2014) Mechanisms of reef coral resistance to future climate change. *Science*, **344**, 895–898.
- Pandolfi JM, Connolly SR, Marshall DJ, Cohen AL (2011) Acidification projecting coral reef futures under global warming and ocean acidification. *Science*, **333**, 418–422.
- Paparella F, Xu C, Vaughan GO, Burt JA (2019) Coral bleaching in the Persian/Arabian Gulf is modulated by summer winds. *Frontiers in Marine Science*, **6**, 1–15.
- Papina M, Meziane T, Van Woesik R (2003) Symbiotic zooxanthellae provide the host - coral *Montipora digitata* with polyunsaturated fatty acids. *Comparative Biochemistry and Physiology Part B*, **135**, 533–537.
- Parkinson JE, Coffroth MA, Lajeunesse TC (2015) New species of Clade B Symbiodinium (Dinophyceae) from the greater Caribbean belong to different functional guilds: *S. aenigmaticum* sp. nov., *S. antillogorgium* sp. nov., *S. endomadracis* sp. nov., and *S. pseudominutum* sp. nov. *Journal of Phycology*, **51**, 850–858.
- Payri C (1997) *Hydroliton reinboldii rodolith* distribution, growth and carbon production of a French Polynesian reef. In: *Proceedings of the 8th Coral Reef Symposium*, Vol. 1, pp. 775–760. Smithsonian Tropical Research.
- Perry CT, Hepburn LJ (2008) Syn-depositional alteration of coral reef framework through bioerosion, encrustation and cementation: Taphonomic signatures of reef accretion and reef depositional events. *Earth-Science Reviews*, **86**, 106–144.
- Perry CT, Spencer T, Kench PS (2008) Carbonate budgets and reef production states: a geomorphic perspective on the ecological phase-shift concept. *Coral Reefs*, **27**, 853–866.
- Perry CT, Edinger EN, Kench PS, Murphy GN, Smithers SG, Steneck RS, Mumby PJ (2012) Estimating rates of biologically driven coral reef framework production and erosion: A new census-based carbonate budget methodology and applications to the reefs of Bonaire. *Coral*

- Reefs*, **31**, 853–868.
- Perry CT, Murphy GN., Kench PS, Smithers SG, Edinger EN, Steneck RS, Mumby PJ (2013) Caribbean-wide decline in carbonate production threatens coral reef growth. *Nature Communications*, **4**, 1–7. doi: 10.1038/ncomms2409.
- Perry CT, Murphy GN, Kench PS, Edinger EN, Smithers SG, Steneck RS, Mumby PJ (2014) Changing dynamics of Caribbean reef carbonate budgets: emergence of reef bioeroders as critical controls on present and future reef growth potential. *Proceedings of the Royal Society B*, **281**, 20142018.
- Perry CT, Murphy GN, Graham NAJ, Wilson SK, Januchowski-Hartley FA, East HK (2015a) Remote coral reefs can sustain high growth potential and may match future sea-level trends. *Scientific Reports*, **5**, 18289.
- Perry C, Murphy G, Edinger E, Kench P, Mumby P, Smithers S, Steneck B (2015b) *ReefBudget: Methodology*. 1–36 pp.
- Perry CT, Morgan KM (2017) Bleaching drives collapse in reef carbonate budgets and reef growth potential on southern Maldives reefs. *Scientific Reports*, **7**, 40581.
- Perry CT, Alvarez-Filip L, Graham NAJ, Mumby PJ, Wilson SK, Kench PS, Manzello DP, Morgan KM, Slangen ABA, Thomson DP, Januchowski-Hartley F, Smithers SG, Steneck RS, Carlton R, Edinger EN, Enochs IC, Estrada-Saldivar N, Haywood MDE, Kolodziej G, Murphy GN, Perez-Cervantes E, Suchley A, Valentino L, Boenish R, Wilson M, Macdonald C (2018a) Loss of coral reef growth capacity to track future increases in sea level. *Nature*, **558**, 396–400.
- Perry C, Lange I, Januchowski-Hartley F (2018b) *ReefBudget: online resource and methodology*.
- Pescud A (2012) *An empirical evaluation of the relationship between coral reef calcium carbonate production and wave energy using geospatial techniques at Lizard Island, Great Barrier Reef, Australia*. BSc thesis, University of Wollongong, Australia 94 pp.
- Pet-Soede L, Erdmann M (2003) *Rapid Ecological Assessment Wakatobi National Park*. Bali, Indonesia.
- Pettay DT, Wham DC, Smith RT, Iglesias-Prieto R, LaJeunesse TC (2015) Microbial invasion of the Caribbean by an Indo-Pacific coral zooxanthella. *Proceedings of the National Academy of Sciences*, **112**, 7513–7518.
- Peyrot-Clausade M, Hutchings P, Richard G (1992) Temporal variations of macroborers in massive *Porites lobata* on Moorea, French Polynesia. *Coral Reefs*, **11**, 161–166.
- Pineda J, Starczak V, Tarrant A, Blythe J, Davis K, Farrar T, Berumen M, da Silva JCB (2013) Two spatial scales in a bleaching event: Corals from the mildest and the most extreme thermal environments escape mortality. *Limnology and Oceanography*, **58**, 1531–1545.
- Plucer-Rosario G, Randall RH (1987) Preservation of rare coral species by transplantation and examination of their recruitment and growth. *Bulletin of Marine Science*, **41**, 585–593.
- Pochon X, Gates RD (2010) A new *Symbiodinium* clade (Dinophyceae) from soritid foraminifera in Hawai'i. *Molecular Phylogenetics and Evolution*, **56**, 492–497.
- Pochon X, Pawlowski J, Zaninetti L, Rowan R (2001) High genetic diversity and relative specificity among *Symbiodinium*-like endosymbiotic dinoflagellates in soritid foraminiferans. *Marine Biology*, **139**, 1069–1078.

- Pochon X, LaJeunesse TC, Pawlowski J (2004) Biogeographic partitioning and host specialization among foraminiferan dinoflagellate symbionts (*Symbiodinium*; Dinophyta). *Marine Biology*, **146**, 17–27.
- Pochon X, Montoya-Burgos JI, Stadelmann B, Pawlowski J (2006) Molecular phylogeny, evolutionary rates, and divergence timing of the symbiotic dinoflagellate genus *Symbiodinium*. *Molecular Phylogenetics and Evolution*, **38**, 20–30.
- Powell A, Hepburn LJ, Smith DJ, Bell JJ (2010) Patterns of Sponge Abundance Across a Gradient of Habitat Quality in the Wakatobi Marine National Park, Indonesia. *The Open Marine Biology Journal*, **4**, 31–38.
- Prada F, Caroselli E, Mengoli S, Brizi L, Fantazzini P, Capaccioni B, Pasquini L, Fabricius KE, Dubinsky Z, Falini G, Goffredo S (2017) Ocean warming and acidification synergistically increase coral mortality. *Scientific Reports*, **7**, 40842.
- Pramanik MK (2014) Climate change and sea surface temperature: Modelling the effects on coral bleaching. *Journal of Earth Science & Climatic Change*, **5**, 9.
- Pratchett MS, Hoey AS, Wilson SK, Messmer V, Graham NAJ (2011) Changes in biodiversity and functioning of reef fish assemblages following coral bleaching and coral loss. *Diversity*, **3**, 424–452.
- Pratchett M, Baird A, Bauman A, Burt J (2017) Abundance and composition of juvenile corals reveals divergent trajectories for coral assemblages across the United Arab Emirates. *Marine Pollution Bulletin*, **114**, 1031–1035.
- Purkis SJ, Riegl B (2005) Spatial and temporal dynamics of Arabian Gulf coral assemblages quantified from remote-sensing and in situ monitoring data. *Marine Ecology Progress Series*, **287**, 99–113.
- Purkis SJ, Riegl BM, Andrefouet S (2005) Remote Sensing of Geomorphology and Facies Patterns on a Modern Carbonate Ramp (Arabian Gulf, Dubai, U.A.E.). *Journal of Sedimentary Research*, **75**, 861–876.
- Purkis SJ, Rowlands GP, Riegl BM, Renaud PG (2010) The paradox of tropical karst morphology in the coral reefs of the arid Middle East. *Geology*, **38**, 227–230.
- Quigley KM, Willis BL, Bay LK (2017) Heritability of the *Symbiodinium* community in vertically and horizontally transmitting broadcast spawning corals. *Scientific Reports*, **7**, 8219.
- R (2018) R: A language and environment for statistical computing.
- Ramsby BD, Hill MS, Thornhill DJ, Steenhuizen SF, Achlatis M, Lewis AM, LaJeunesse TC (2017) Sibling species of mutualistic *Symbiodinium* clade G from bioeroding sponges in the western Pacific and western Atlantic oceans. *Journal of Phycology*, **53**, 951–960.
- Rasser MW, Riegl AB (2002) Holocene coral reef rubble and its binding agents. *Coral Reefs*, **21**, 57–72.
- Reis MAC, Leão ZMAN (2000) Bioerosion rate of the sponge *Cliona celata* (Grant 1826) from reefs in turbid waters, north Bahia, Brazil. *Proceedings 9th International Coral Reef Symposium*, 23–27.
- Reshef L, Koren O, Loya Y, Zilber-Rosenberg I, Rosenberg E (2006) The coral probiotic hypothesis. *Environmental Microbiology*, **8**, 2068–2073.

- Reynolds JMC, Bruns BU, Fitt WK, Schmidt GW (2008) Enhanced photoprotection pathways in symbiotic dinoflagellates of shallow-water corals and other cnidarians. *Proceedings of the National Academy of Sciences of the United States of America*, **105**, 13674–13678.
- Rezai H, Wilson S, Claereboudt M, Riegl B (2004) Coral reef status in the ROPME sea area: Arabian/Persian Gulf, Gulf of Oman and Arabian Sea. In: *Status of Coral Reefs of the World* (ed Wilkinson C), pp. 155–169. Australian Institute of Marine Science, Townsville.
- Ricaurte M, Schizas NV, Ciborowski P, Boukli NM (2016) Proteomic analysis of bleached and unbleached *Acropora palmata*, a threatened coral species of the Caribbean. *Marine Pollution Bulletin*, **107**, 224–232.
- Ridgway T, Sampayo EM (2005) Population genetic status of the Western Indian Ocean: What do we know? *Journal of Marine Science*, **4**, 1–9.
- 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). *Marine Biology*, **140**, 29–40.
- Riegl B (2003) Climate change and coral reefs: Different effects in two high-latitude areas (Arabian Gulf, South Africa). *Coral Reefs*, **22**, 433–446.
- Riegl B, Purkis S (2012) *Adaptations to climatic extremes in the world's hottest sea - Coral Reefs of the Gulf*. Springer Netherlands, Dordrecht, Netherlands, 1–4 pp.
- Riegl B, Purkis S (2015) Coral population dynamics across consecutive mass mortality events. *Global Change Biology*, **21**, 3995–4005.
- Riegl BM, Purkis SJ, Al-Cibahy AS, Abdel-Moati MA, Hoegh-Guldberg O (2011) Present limits to heat-adaptability in corals and population-level responses to climate extremes. *PLoS ONE*, **6**, e24802.
- Riegl B, Johnston M, Purkis S, Howells E, Burt J, Steiner SCC, Sheppard CRC, Bauman A (2018) Population collapse dynamics in *Acropora downingi*, an Arabian/Persian Gulf ecosystem-engineering coral, linked to rising temperature. *Global Change Biology*, **24**, 2447–2462.
- Roberts LG, Harriott VJ (2003) Can environmental records be extracted from coral skeletons from Moreton Bay, Australia, a subtropical, turbid environment? *Coral Reefs*, **22**, 517–522.
- Robinson JPW, Wilson SK, Graham NAJ (2019) Abiotic and biotic controls on coral recovery 16 years after mass bleaching. *Coral Reefs*, **38**, 1255–1265.
- Robison JD, Warner ME (2006) Differential impacts of photoacclimation and thermal stress on the photobiology of four different phylotypes of *Symbiodinium* (Pyrrophyta). *Journal of Phycology*, **42**, 568–579.
- Roff G (2020) Reef accretion and coral growth rates are decoupled in Holocene reef frameworks. *Marine Geology*, **419**.
- Rogers CS (1990) Responses of coral reefs and reef organisms to sedimentation. *Marine Ecology Progress Series*, **62**, 185–202.
- Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. *Current Biology*, **24**, 1000–1005.
- Rohatgi A (2019) WebPlot Digitizer Version 4.2.
- Rohwer F, Seguritan V, Azam F, Knowlton N (2002) Diversity and distribution of coral-associated bacteria. *Marine Ecology Progress Series*, **243**, 1–10.



- Roik A, Röthig T, Roder C et al. (2016) Year-Long Monitoring of Physico-Chemical and Biological Variables Provide a Comparative Baseline of Coral Reef Functioning in the Central Red Sea. *PLOS ONE*, **11**, e0163939.
- Roik A, Röthig T, Pogoreutz C, Voolstra CR (2017) Coral reef carbonate budgets and ecological drivers in the naturally high temperature and high alkalinity environment of the Red Sea. *BiorXiv*, **1**, 1–42.
- Rosenberg E, Koren O, Reshef L, Efrony R, Zilber-Rosenberg I (2007) The role of microorganisms in coral health, disease and evolution. *Nature Reviews Microbiology*, **5**, 355–362.
- Rouzé H, Lecellier GJ, Saulnier D, Planes S, Gueguen Y, Wirshing HH, Berteaux-Lecellier V (2017) An updated assessment of *Symbiodinium* spp. that associate with common scleractinian corals from Moorea (French Polynesia) reveals high diversity among background symbionts and a novel finding of clade B. *PeerJ*, **5**, e2856.
- Rowan B, Knowlton N (1995) Intraspecific diversity and ecological zonation in coral-algal symbiosis. *Proceedings of the National Academy of Sciences of the United States of America*, **92**, 2850–2853.
- Rowan R, Powers DA (1991) Molecular genetic identification of symbiotic dinoflagellates (zooxanthellae). *Marine Ecology Progress Series*, **71**, 65–73.
- Rowley SJ, Robinson L, Pochon X, Watling L (2015) Environmental influences on the Indo-Pacific octocoral *Isis hippuris* Linnaeus 1758 (Alcyonacea: Isididae): genetic fixation or phenotypic plasticity? *Peer J*, DOI 10.7717/peerj.1128.
- Rützler K (1975) The role of burrowing sponges in bioerosion. *Oecologia*, **19**, 203–216.
- Ryan EJ, Hanmer K, Kench PS (2019) Massive corals maintain a positive carbonate budget of a Maldivian upper reef platform despite major bleaching event. *Scientific Reports*, **9**, 1–11.
- Salm R (1993) Coral reefs of the Sultanate of Oman. *Atoll Research Bulletin*, **379–389**.
- Sammarco PW, Risk MJ, Rose C (1987) Effects of grazing and damselfish territoriality on internal bioerosion of dead corals: indirect effects. *Journal of Experimental Marine Biology and Ecology*, **112**, 185–199.
- Sampayo EM, Dove S, Lajeunesse TC (2009) Cohesive molecular genetic data delineate species diversity in the dinoflagellate genus *Symbiodinium*. *Molecular Ecology*, **18**, 500–519.
- Sanciango JC, Carpenter KE, Etnoyer PJ, Moretzsohn F (2013) Habitat availability and heterogeneity and the Indo-Pacific warm pool as predictors of marine species richness in the tropical Indo-Pacific. *PLoS ONE*, **8**.
- Savage AM, Goodson MS, Visram S, Trapido-Rosenthal H, Wiedenmann J, Douglas AE (2002) Molecular diversity of symbiotic algae at the latitudinal margins of their distribution: Dinoflagellates of the genus *Symbiodinium* in corals and sea anemones. *Marine Ecology Progress Series*, **244**, 17–26.
- Scaps P, Denis V (2008) Can organisms associated with live scleractinian corals be used as indicators of coral reef status? *Atoll Research Bulletin*, 1–18.
- Schleyer MH, Celliers L (2003) Coral dominance at the reef-sediment interface in marginal coral communities at Sodwana Bay, South Africa. *Marine and Freshwater Research*, **54**, 967–972.
- Schmidt GM, Richter C (2013) Coral growth and bioerosion of *Porites lutea* in response to large

- amplitude internal waves. *PLoS ONE*, **8**.
- Scoffin TP, Stearn CW, Boucher D, Frydl P, Hwakins CM (1980) Calcium carbonate budget of a fringing reef on the west coast of Barbados. *Bulletin of Marine Science*, **30**, 475–508.
- Seemann J, González CT, Carballo-Bolaños R, Berry K, Heiss GA, Struck U, Leinfelder RR (2014) Assessing the ecological effects of human impacts on coral reefs in Bocas del Toro, Panama. *Environmental Monitoring and Assessment*, **186**, 1747–1763.
- Selig ER, Casey KS, Bruno JF (2010) New insights into global patterns of ocean temperature anomalies: implications for coral reef health and management. *Global Ecology and Biogeography*, **19**, 397–411.
- Shashar N, Cohen Y, Loya Y (1993) Extreme diel fluctuations of oxygen in diffusive boundary layers surrounding stony corals. *The Biological Bulletin*, **185**, 455–461.
- Sheppard CR (2000) Coral reefs of the Western Indian Ocean: An overview. In: *Coral reefs of the Indian Ocean: Their ecology and conservation* (eds McClanahan T, Sheppard C, Obura D), pp. 3–38. Oxford University Press, New York.
- Sheppard CRC (2003) Predicted recurrences of mass coral mortality in the Indian Ocean. *Nature*, **425**, 294–297.
- Sheppard C (2016) Coral reefs in the Gulf are mostly dead now, but can we do anything about it? *Marine Pollution Bulletin*, **105**, 593–598.
- Sheppard C, Loughland R (2002) Coral mortality and recovery in response to increasing temperature in the southern Arabian Gulf. *Aquatic Ecosystem Health & Management*, **5**, 395–402.
- Sheppard C, Price A, Roberts C (1992) *Marine ecology of the Arabian region: patterns and processes in extreme tropical environments*. Academic Press, London, 359 pp.
- Sheppard C, Al-Husiani M, Al-Jamali F, Al-Yamani F, Baldwin R, Bishop J, Benzoni F, Dutrieux E, Dulvy NK, Durvasula SRV, Jones DA, Loughland R, Medio D, Nithyanandan M, Pilling GM, Polikarpov I, Price ARG, Purkis S, Riegl B, Saburova M, Namin KS, Taylor O, Wilson S, Zainal K (2010) The Gulf: A young sea in decline. *Marine Pollution Bulletin*, **60**, 13–38.
- Shi Q, Zhao M, Zhang Q, Yu K, Chen T, Li S, Wang H (2009) Estimate of carbonate production by scleractinian corals at Luhuitou fringing reef, Sanya, China. *Chinese Science Bulletin*, **54**, 696–705.
- Shuail D, Wiedenmann J, D'Angelo C, Baird AH, Pratchett MS, Riegl B, Burt JA, Petrov P, Amos C (2016) Local bleaching thresholds established by remote sensing techniques vary among reefs with deviating bleaching patterns during the 2012 event in the Arabian/Persian Gulf. *Marine Pollution Bulletin*, **105**, 654–659.
- Silverman J, Lazar B, Erez J (2007) Effect of aragonite saturation, temperature, and nutrients on the community calcification rate of a coral reef. *Journal of Geophysical Research*, **112**, C05004.
- Silverstein RN, Correa AMS, Baker AC (2012) Specificity is rarely absolute in coral – algal symbiosis: implications for coral response to climate change. *Proceedings of the Royal Society B*, 2609–2618.
- Smith SV (1978) Coral-reef area and the contributions of reefs to processes and resources of the world's oceans. *Nature*, **273**, 225–226.

- Smith LW, Barshis D, Birkeland C (2007) Phenotypic plasticity for skeletal growth, density and calcification of *Porites lobata* in response to habitat type. *Coral Reefs*, **26**, 559–567.
- Smith D, Etienne M, Spring N, Suggett D (2008) Tolerance, refuge and recovery of coral communities to thermal bleaching: evidence from reefs of the Seychelles. *Proceedings of the 11th International Coral Reef Symposium*, 7–11.
- Smith EG, Vaughan GO, Ketchum RN, Mcparland D, Burt JA (2017) Symbiont community stability through severe coral bleaching in a thermally extreme lagoon. *Scientific Reports*, **7**, 2428.
- Spalding MD, Grenfell AM (1997) New estimates of global and regional coral reef areas. *Coral Reefs*, **16**, 225–230.
- Spalding MD, Ravolius C, Green EP (2001) *World Atlas of Coral Reefs*. UNEP-WCMC, University of California Press, EUA.
- Spalding MD, Fox HE, Allen GR, Davidson N, Ferdana ZA, Finlayson M, Halpern BS, Jorge MA, Lombana A, Lourie SA, Martin KD, Mcmanus E, Molnar J, Recchia CA, Robertson J (2007) Marine Ecoregions of the World: A Bioregionalization of Coastal and Shelf Areas. *BioScience*, **57**, 573.
- Spalding M, Burke L, Wood SA, Ashpole J, Hutchison J, zu Ermgassen P (2017) Mapping the global value and distribution of coral reef tourism. *Marine Policy*, **82**, 104–113.
- Spencer T, Teleki KA, Bradshaw C, Spalding MD (2000) Coral bleaching in the Southern Seychelles during the 1997-1998 Indian Ocean warm event. *Marine Pollution Bulletin*, **40**, 569–586.
- Stat M, Gates RD (2011) Clade D *Symbiodinium* in Scleractinian Corals: A “Nugget” of Hope, a Selfish Opportunist, an Ominous Sign, or All of the Above? *Journal of Marine Biology*, **2011**, 1–9.
- Stat M, Carter D, Hoegh-Guldberg O (2006) The evolutionary history of *Symbiodinium* and scleractinian hosts—Symbiosis, diversity, and the effect of climate change. *Perspectives in Plant Ecology, Evolution and Systematics*, **8**, 23–43.
- Stat M, Pochon X, Franklin EC, Bruno JF, Casey KS, Selig ER, Gates RD (2013) The distribution of the thermally tolerant symbiont lineage (*Symbiodinium* clade D) in corals from Hawaii: Correlations with host and the history of ocean thermal stress. *Ecology and Evolution*, **3**, 1317–1329.
- Stearn C, Scoffin T (1977) Carbonate budget of fringing reef, Barbados. In: *Proceedings of the 3rd International Coral Reef Symposium*, pp. 471–476. Miami, Florida.
- Suggett DJ, Smith DJ (2010) Interpreting the sign of coral bleaching as friend vs. foe. *Global Change Biology*.
- Suggett DJ, Dong LF, Lawson T, Lawrenz E, Torres L, Smith DJ (2013) Light availability determines susceptibility of reef building corals to ocean acidification. *Coral Reefs*, **32**, 327–337.
- Sully S, Burkepille DE, Donovan MK, Hodgson G, van Woesik R (2019) A global analysis of coral bleaching over the past two decades. *Nature Communications*, **10**, 1–5.
- Takahashi S, Whitney SM, Badger MR (2009) Different thermal sensitivity of the repair of photodamaged photosynthetic machinery in cultured *Symbiodinium* species. *Proceedings of the*

- National Academy of Sciences of the United States of America*, **106**, 3237–3242.
- Tanner JE (1996) Seasonality and lunar periodicity in the reproduction of Pocilloporid corals. *Coral Reefs*, **15**, 59–66.
- Thomas L, Kendrick GA, Kennington WJ, Richards ZT, Stat M (2014) Exploring *Symbiodinium* diversity and host specificity in *Acropora* corals from geographical extremes of Western Australia with 454 amplicon pyrosequencing. *Molecular Ecology*, **23**, 3113–3126.
- Thompson JR, Rivera HE, Closek CJ, Medina M (2015) Microbes in the coral holobiont: partners through evolution, development, and ecological interactions. *Frontiers in Cellular and Infection Microbiology*, **4**, 176.
- Thornhill DJ, LaJeunesse TC, Kemp DW, Fitt WK, Schmidt GW (2006) Multi-year, seasonal genotypic surveys of coral-algal symbioses reveal prevalent stability or post-bleaching reversion. *Marine Biology*, **148**, 711–722.
- Thornhill DJ, Howells EJ, Wham DC, Steury TD, Santos SR (2017) Population genetics of reef coral endosymbionts (*Symbiodinium*, Dinophyceae). *Molecular Ecology*, **26**, 2640–2659.
- Todd PA (2008) Morphological plasticity in scleractinian corals. *Biological Reviews*, **83**, 315–337.
- Tonk L, Sampayo EM, Weeks S, Magno-Canto M, Hoegh-Guldberg O (2013) Host-Specific Interactions with Environmental Factors Shape the Distribution of *Symbiodinium* across the Great Barrier Reef. *PLoS ONE*, **8**, e68533.
- Tortolero-Langarica JJA, Cupul-Magaña AL, Carricart-Ganivet JP, Mayfield AB, Rodríguez-Troncoso AP (2016) Differences in Growth and calcification rates in the reef-building coral *Porites lobata*: The implications of morphotype and gender on coral growth. *Frontiers in Marine Science*, **3**, 179.
- Trench RK (1979) The Cell Biology of Plant-Animal Symbiosis. *Annual Review of Plant Physiology*, **30**, 485–531.
- Trench R (2000) Validation of some currently used invalid names of dinoflagellates. *Journal of Phycology*, **36**, 972.
- Trench RK, Blank RJ (1987) *Symbiodinium microadriaticum* freudenthal, *S. goreauii* sp. nov., *S. kawagutii* sp. nov. and *S. pilosum* sp. nov.: Gymnodinioid dinoflagellate symbionts of marine invertebrates. *Journal of Phycology*, **23**, 469–481.
- Trench RK, Thinh L (1995) *Gymnodinium linucheae* sp. nov.: The dinoflagellate symbiont of the jellyfish *Linuche unguiculata*. *European Journal of Phycology*, **30**, 149–154.
- Tribollet A, Golubic S (2005) Cross-shelf differences in the pattern and pace of bioerosion of experimental carbonate substrates exposed for 3 years on the northern Great Barrier Reef, Australia. *Coral Reefs*, **24**, 422–434.
- Tribollet A, Payri C (2001) Bioerosion of the coralline alga *Hydrolithon onkodes* by microborers in the coral reefs of Moorea, French Polynesia. *Oceanologica Acta*, **24**, 329–342.
- Tucker ME, Wright P (1990) *Carbonate Sedimentology*. Blackwell Publishing Ltd, Oxford, 482 pp.
- UNEP (2016) *GEO-6 Regional Assessment for West Asia*. UNEP, 145 pp.
- UNESCO (2012) Biosphere Reserves - Wakatobi, Indonesia. *Ecological Sciences - Man and Biosphere Programme*.
- Uwate KR, Shams AJ (1999) *Summary of Recent Coral and Coral Reef Related Activities in*

- Bahrain, Regional Meeting on the Assessment of the Health of Coral reefs*. Manama, Bahrain, 1–6 pp.
- Uwate KR, Bader H, Torabi M, Bailey S, Keenan P (2000) *Reef Check Surveys in Bahrain, Arabian Gulf*. Manama, Bahrain.
- van Lavieren H, Burt J, Feary DA et al. (2011) *Managing the growing impacts of development on fragile coastal and marine ecosystems: Lessons from the Gulf*. Hamilton, ON, Canada, 100 pp.
- Vargas-Ángel B, Richards CL, Vroom PS, Price NN, Schils T, Young CW, Smith J, Johnson MD, Brainard RE (2015) Baseline Assessment of Net Calcium Carbonate Accretion Rates on U.S. Pacific Reefs (ed Voolstra CR). *PLoS ONE*, **10**, e0142196.
- Vecsei A (2004) A new estimate of global reefal carbonate production including the fore-reefs. *Global and Planetary Change*, **43**, 1–18.
- Vermeij MJA, Bak RPM (2002) How are coral populations structured by light? Marine light regimes and the distribution of *Madracis*. *Marine Ecology Progress Series*, **233**, 105–116.
- Veron JEN (2000) *Corals of the World*, Vol 1-3 edn. Australian Institute of Marine Science, Townsville, Australia.
- Veron J, Devantier M, Turak E, Green A, Kininmonth S, Stafford-Smith M, Peterson N (2009) Delineating the Coral Triangle. *Journal of Coral Reef Studies*, **11**, 91–100.
- Vousden DH (1988) The Bahrain marine habitat survey: a study of the marine environment of Bahrain using remote sensing as a rapid assessment methodology. In: *Proceedings of the ROPME Workshop on Coastal Area Development* (United Nations Environment Programme), pp. 3–34. Regional Seas Reports and Studies No. 90/ROPME. Publication No. GC-5/006.
- Vousden DH (1995) *Bahrain Marine Habitats and Some Environmental Effects on Seagrass Beds: A Study of the Marine Habitats of Bahrain With Particular Reference to the Effects of Water Temperature, Depth and Salinity on Seagrass Biomass and Distribution*. PhD thesis, University of Wales (Bangor), UK, 261 pp.
- Wang JT, Wang YT, Keshavmurthy S, Meng PJ, Chen CA (2019) The coral *Platygyra verweyi* exhibits local adaptation to long-term thermal stress through host-specific physiological and enzymatic response. *Scientific Reports*, **9**, 1–11.
- Webster NS, Botté ES, Soo RM, Whalan S (2011) The larval sponge holobiont exhibits high thermal tolerance. *Environmental Microbiology Reports*, **3**, 756–762.
- Wellington GM, Glynn PW, Strong AE, Navarrete SA, Wieters E, Hubbard D (2001) Crisis on coral reefs linked to climate change. *Eos, Transactions American Geophysical Union*, **82**, 1–5.
- Wham DC, Carmichael M, LaJeunesse TC (2014) Microsatellite loci for *Symbiodinium goreau* and other Clade C *Symbiodinium*. *Conservation Genetics Resources*, **6**, 127–129.
- Wham DC, Ning G, LaJeunesse TC (2017) *Symbiodinium glynnii* sp. nov., a species of stress-tolerant symbiotic dinoflagellates from pocilloporid and montiporid corals in the Pacific Ocean. *Phycologia*, **56**, 396–409.
- Wickham H (2009) *ggplot2: elegant graphics for data analysis*. Springer US, New York.
- Wickham H, Averick M, Bryan J et al. (2019) Welcome to the Tidyverse. *Journal of Open Source Software*, **4**, 1686.
- Wilkinson C (1998) The 1997-1998 mass bleaching event around the world. In: *Status of coral reefs*

- of the world: 1998*, pp. 15–38. Townsville, Australia.
- Wilkinson C (2000) *Status of Coral Reefs of the World*. Australian Institute of Marine Science, Townsville, Australia, 363 pp.
- Wilkinson C, Linden O, Cesar H, Hodgson G, Rubens J, Strong A (1999) Ecological and socioeconomic impacts of 1998 coral mortality in the Indian Ocean: An ENSO impact and a warning of future change? *Ambio*, **28**, 188–196.
- Wilson SK, Graham NAJ, Fisher R, Robinson J, Nash K, Chong-Seng K, Polunin NVC, Aumeeruddy R, Quatre R (2012) Effect of macroalgal expansion and marine protected areas on coral recovery following a climatic disturbance. *Conservation Biology*, **26**, 995–1004.
- Wirshing HH, Feldheim KA, Baker AC (2013) Vectored dispersal of *Symbiodinium* by larvae of a Caribbean gorgonian octocoral. *Molecular Ecology*, **22**, 4413–4432.
- Wisshak M, Schönberg CHL, Form A, Freiwald A (2014) Sponge bioerosion accelerated by ocean acidification across species and latitudes? *Helgoland Marine Research*, **68**, 253–262.
- Wolanski E, De 'ath G (2005) Predicting the impact of present and future human land-use on the Great Barrier Reef. *Estuarine, Coastal and Shelf Science*, **64**, 504–508.
- Woodhead AJ, Hicks CC, Norström AV, Williams GJ, Graham NAJ (2019) Coral reef ecosystem services in the Anthropocene. *Functional Ecology*, **33**, 1023–1034.
- Wooldridge SA (2009) Water quality and coral bleaching thresholds: Formalising the linkage for the inshore reefs of the Great Barrier Reef, Australia. *Marine Pollution Bulletin*, **58**, 745–751.
- Wouthuyzen S, Abrar M, Lorwens J (2018) A comparison between the 2010 and 2016 El-Ninō induced coral bleaching in the Indonesian waters. *IOP Conference Series: Earth and Environmental Science*, **118**.
- Yang SY, Keshavmurthy S, Obura D, Sheppard CRC, Visram S, Chen CA (2012) Diversity and Distribution of *Symbiodinium* Associated with Seven Common Coral Species in the Chagos Archipelago, Central Indian Ocean. *Central Indian Ocean. PLoS ONE*, **7**, e35836.
- Yanovski R, Nelson PA, Abelson A (2017) Structural Complexity in Coral Reefs: Examination of a Novel Evaluation Tool on Different Spatial Scales. *Frontiers in Ecology and Evolution*, **5**.
- Zawada KJA, Madin JS, Baird AH, Bridge TCL, Dornelas M (2019) Morphological traits can track coral reef responses to the Anthropocene. *Functional Ecology*, **33**, 962–975.
- Ziegler M, Arif C, Burt JA, Dobretsov S, Roder C, Lajeunesse TC, Voolstra CR (2017) Biogeography and molecular diversity of coral symbionts in the genus *Symbiodinium* around the Arabian Peninsula. *Journal of Biogeography*, **44**, 674–686.
- Zinke J, Pfeiffer M, Park W, Schneider B, Reuning L, Dullo WC, Camoin GF, Mangini A, Schroeder-Ritzrau A, Garbe-Schonberg D, Davies GR (2014) Seychelles coral record of changes in sea surface temperature bimodality in the western Indian Ocean from the Mid-Holocene to the present. *Climate Dynamics*, **43**, 689–708.
- Zundeleovich A, Lazar B, Ilan M (2007) Chemical versus mechanical bioerosion of coral reefs by boring sponges - lessons from *Pione cf. vastifica*. *The Journal of Experimental Biology*, **210**, 91–96.