Assessing the risk of ocean acidification for scleractinian corals on the Great Barrier Reef

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School of the Environment

Certificate of original authorship

I certify that the work in this thesis has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree except as fully acknowledged within the text.

I also certify that the thesis has been written by me. Any help that I have received in my research work and the preparation of the thesis itself has been acknowledged. In addition, I certify that all information sources and literature used are indicated in the thesis.

Signature of Student:

Date:

This thesis is dedicated to my son, Javier Patrick Lloyd. His arrival into this world during my PhD was a timely reminder that we do not inherit this earth from our ancestors; we borrow it from our children. Javier, I wrote this thesis in the hope that it will serve to maintain the beauty of the Great Barrier Reef for your generation and many more to come.

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Publications arising directly from this thesis

Chapter 2:

Lloyd A, Kline DI, Larkum AWD, Ralph, PJ, Dove SG. A working hypothesis to describe the mechanism of coral bleaching under ocean acidification. Submitted to Global Change Biology.

Chapter 3:

Lloyd A, Dunn S, Kline DI, Dove SG, Ralph PJ. Diurnal carbonate chemistry variability impacts the sensitivity of *Acropora millepora* to ocean acidification. Submitted to Coral Reefs.

Chapter 4:

Lloyd A, Tonk L, Doropoulos C, Dove SG, Ralph PJ, Ward S. Coral bleaching in *Acropora millepora* juveniles under ocean acidification. Submitted to PLoS One.

Publications during candidature

Crawley A, Kline DI, Dunn S, Anthony K, Dove S (2010) The effect of ocean acidification on symbiont photorespiration and productivity in *Acropora formosa*. Global Change Biology. 15: 851-863. doi: 10.1111/j.1365-2486.2009.01943.x

Reymond CE, **Lloyd A**, Kline DI, Dove SG, Pandolfi JM (2013) Decline in growth of foraminifer *Marginopora rossi* under eutrophication and ocean acidification scenarios. Global Change Biology. 19:291-302. doi: 10.1111/gcb.12035

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Abbreviations

α: photosynthetic efficiency at sub-saturating irradiance

ATP: adenosine triphosphate

ADP: adenosine diphosphate

A_T: total alkalinity

CA: carbonic anhydrase

CAP: canonical analysis of principle coordinates

CCA: crustose coralline algae

CCM: carbon concentration mechanism

Chl *a*: Chlorophyll *a*

CPCe: Coral Point Count with Excel extensions

DBL: diffusion boundary layer

DGGE: denaturing gradient gel electrophoresis

DbRDA: distance based redundancy analysis

Dd: diadinoxanthin

DIC: dissolved inorganic carbon

DISTLM: distance based linear model

Dt: diatoxanthin

E_k: minimum saturating irradiance

ECM: extracellular calcifying medium

fCO_2: fugacity CO_2

F_0: minimum fluorescence

F_m: maximum fluorescence

F_m': light-adapted maximum fluorescence

F_t: steady-state fluorescence

ΔF: light-adapted variable fluorescence

F_v: variable fluorescence

F_v/F_m: maximum dark-adapted quantum yield of PSII

$\Delta F/F_m'$: effective dynamic quantum yield of PSII

FP: fluorescent proteins

G3P: glyceraldehyde 3-phosphate

GFP: green fluorescent protein

HIRS: Heron Island Research Station

HPLC: high performance liquid chromatography

iPAM: imaging pulse amplitude modulation fluorometer

IPCC: Intergovernmental Panel on Climate Change

ITS1/2: internal transcribed spacer regions of rDNA

K'_{sp}: solubility constant

LEC: light enhanced calcification

LEDR: light enhanced dark respiration

LHC: light harvesting complex

LIRS: Lizard Island Research Station

LR: Loomis Reef

MC: Mermaid Cove

$NAD(P)^+$: nicotinamide adenine dinucleotide (phosphate)

NADPH: nicotinamide adenine dinucleotide phosphate

NPQ: non-photochemical quenching

OA: ocean acidification

Ω_{calc}: saturation state of calcite

Ω_{arag}: saturation state of aragonite

P_{680}: PSII primary donor

PCR: polymerase chain reaction

PG: phsophoglycolate

PGA: phosphoglycerate

PGPase: phosphoglycolate phosphatase

Phe: phaeophytin

P_{net}: net photosynthesis

$P_n max$: maximum rate of net photosynthesis

pCO_2: partial pressure of carbon dioxide

P:E curve: photosynthesis-irradiance curve

PERMANOVA: permutational analysis of variance

P_g: gross photosynthesis

P_g:R: gross photosynthesis to respiration ratio

$pH = -\log [H^+]$

pH_T: total pH

PQ: plastoquinone

PRIMER: Plymouth routines in multivariate ecological research

PSII: photosystem II

PSU: practical salinity unit

Q_A: quinone acceptor

Q_m: excitation pressure

RC: reaction centre

R_{dark}: dark respiration

ROS: reactive oxygen species

RuBisCO: ribulose bisphosphate carboxylase/oxygenase

RuBP: ribulose-1,5-bisphosphate

SR: Station Reef

SST: sea surface temperatures

Φ_{NO}: yield of fluorescence

Φ_{NPQ}: yield of non-photochemical quenching

Abstract

Ocean acidification will impact the photo-physiology of reef-building corals as it can lead to dysfunction of the symbiosis and loss of productivity. The major objective of this thesis was to provide insight into the mechanism of CO_2-induced bleaching and productivity loss across multiple life-history stages and interpret these findings in an ecological context.

Chapter 1 provides a review of the literature investigating the photo-physiological impact of ocean acidification, emphasizing the experimental conditions in studies that observed *Symbiodinium* dysfunction and productivity loss. Chapter 2 presents a working hypothesis to describe the fundamental physiological aspects of coral bleaching under ocean acidification. This research investigates the response of *Acropora aspera* using pulse amplitude modulation (PAM) fluorometry and oxygen respirometry under increased pCO_2 with concomitant high light conditions. The dinoflagellate density and HPLC pigment analysis are utilised to characterise the CO_2-induced bleaching response. We present a conceptual model linking photorespiration to CO_2-induced bleaching and productivity loss.

The impact of ocean acidification on coral reef ecosystems is likely to deviate from oceanic climate models due to diel modification of carbonate chemistry by community metabolism. Chapter 3 characterises the diurnal variation in carbonate chemistry at sites around Lizard Island and links this to the ocean acidification response of *Acropora millepora* collected from these sites. Furthermore, we utilise permutational multivariate statistical analyses to partition the variation in carbonate chemistry attributable to community composition at these sites. It was hypothesized that greater diurnal variation in carbonate chemistry may improve resilience of scleractinian corals to future ocean acidification conditions. This chapter highlights that site-specific physiological trade-offs may influence the response of reef-building corals to future ocean acidification scenarios.

Chapter 4 reports a visual bleaching response in *A. millepora* juveniles under future ocean acidification conditions. The effect of ocean acidification on coral juveniles is

hypothesised to impact *Symbiodinium* uptake and photochemical efficiency. We utilised the iPAM to align the photochemistry in the juveniles with their visual bleaching response and *Symbiodnium* type, as assessed by denaturing gradient gel electrophoresis (DGGE) of the internal transcribed spacer region 1 (ITS1) of the ribosomal genes. This study links the bleaching response with recruits containing a dominant population of *Symbiodinium* type D1 or D1-4, with potential implications for post-settlement survivorship and population dynamics.

Lastly, in Chapter 5 the key findings of this thesis are discussed in light of the ecological implications for the Great Barrier Reef. The synopsis outlines the effect of ocean acidification on the photo-physiology, productivity, calcification, reproduction and symbiont acquisition of reef-building corals. Future avenues for research are suggested based on new research gaps revealed by this thesis with the aim to continue to provide up-to-date scientific information to policy makers and reef managers.