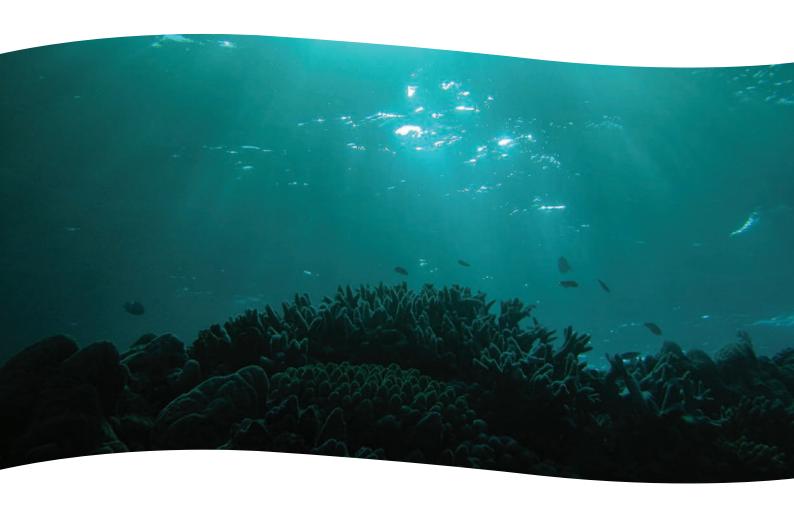


National **Environmental Science** Programme

Benthic light as ecologically-validated GBR-wide indicator for water quality

Barbara Robson, Marites Canto, Catherine Collier, Stephanie di Perna, Murray Logan, Patricia Menendez, Lachlan McKinna, Sam Noonan and Katharina Fabricius







Benthic light as ecologically-validated GBR-wide indicator for water quality

Barbara Robson¹, Marites Canto^{1,2}, Catherine Collier², Stephanie di Perna^{1,2}, Murray Logan¹, Patricia Menendez¹, Lachlan McKinna³, Sam Noonan¹ and Katharina Fabricius¹

¹ Australian Institute of Marine Science ² James Cook University ³ Go2Q Consulting





Supported by the Australian Government's
National Environmental Science Program
Project 2.3.1 Benthic light as ecologically-validated GBR-wide indicator for water quality:
drivers, thresholds and cumulative risks

© Australian Institute of Marine Science, 2019



Creative Commons Attribution

Benthic light as ecologically-validated GBR-wide indicator for water quality is licensed by the Australian Institute of Marine Science for use under a Creative Commons Attribution 4.0 Australia licence. For licence conditions see: https://creativecommons.org/licenses/by/4.0/

National Library of Australia Cataloguing-in-Publication entry: 978-1-925514-37-7

This report should be cited as:

Robson, B., Canto, M., Collier, C., di Perna, S., Logan, M., Menendez, P., McKinna, L., Noonan, S. and Fabricius, K. *Benthic light as an ecologically-validated GBR-wide indicator for water quality.* Report to the National Environmental Science Program. Reef and Rainforest Research Centre Limited, Cairns (40 pp.).

Published by the Reef and Rainforest Research Centre on behalf of the Australian Government's National Environmental Science Program (NESP) Tropical Water Quality (TWQ) Hub.

The Tropical Water Quality Hub is part of the Australian Government's National Environmental Science Program and is administered by the Reef and Rainforest Research Centre Limited (RRRC). The NESP TWQ Hub addresses water quality and coastal management in the World Heritage listed Great Barrier Reef, its catchments and other tropical waters, through the generation and transfer of world-class research and shared knowledge.

This publication is copyright. The Copyright Act 1968 permits fair dealing for study, research, information or educational purposes subject to inclusion of a sufficient acknowledgement of the source.

The views and opinions expressed in this publication are those of the authors and do not necessarily reflect those of the Australian Government.

While reasonable effort has been made to ensure that the contents of this publication are factually correct, the Commonwealth does not accept responsibility for the accuracy or completeness of the contents, and shall not be liable for any loss or damage that may be occasioned directly or indirectly through the use of, or reliance on, the contents of this publication.

Cover photographs: (front) Ben Reef credit LTMP, AIMS; (back) Light experiment aquaria, AIMS.

This report is available for download from the NESP Tropical Water Quality Hub website: http://www.nesptropical.edu.au

CONTENTS

Contents	i
List of Figures	ii
Acronyms	V
Glossary	vi
Executive Summary	1
1.0 Introduction	3
2.0 Evaluation of bPAR thresholds for Seagrass and coral health	6
2.1 Review of seagrass light thresholds	6
2.2 Effects of low and variable light on growth of two species of coral	8
Abstract	8
Conclusions and key figures	8
2.3 Effects of variable light and elevated pCO ₂ on the growth and physiology of and adult <i>Acropora</i> corals	-
Objective	11
Methods	11
Results	14
Conclusions	20
2.4 Responses of the coral <i>Acropora tenuis</i> to moderate and strong Light limitat waters	
Abstract	22
Conclusions	22
2.5 Summary of findings: PAR thresholds and responses	23
3.0 Development of a remote sensing algorithm for benthic light (bPAR) in the	
Abstract	24
Key figures	24
Conclusions	28
4.0 Development of a benthic-light based Water quality index (WQI)	29
5.0 Conclusions and Future Work	36

LIST OF FIGURES

Figure 1:	bPAR Water Quality Index values for each region over time. Regions are arranged from north to south (top to bottom) and from nearshore to offshore (left to right). Results are not shown for the Offshore Burnett Mary as the depth of water in this region precludes the occurrence of photosynthetic benthic habitats (including seagrasses and corals) at the 1 km grid scale of this analysis. Letter grades are assigned from A (i.e. excellent, index > 0.8) to E (i.e. poor, index < 0.2)
Figure 2:	Diverse coral and seagrass habitats rely on light reaching the bottom of the water column to drive photosynthesis. Changes in water quality can reduce the penetration and quality of light at the sea floor. Photo: Ben Reef. Latitude: -20.00833. Longitude: 150.325. Credit: LTMP. Copyright Australian Institute of Marine Science.
Figure 3:	Photosynthetic potential, light stress and non-photochemical quenching under constant high and low DLI, and under two variable DLI treatments. Mean maximum quantum yield (Fv/Fm), excitation pressure on PSII (Qm) and non-photochemical quenching (NPQ) of <i>Pachyseris speciosa</i> (A, C, E)—and <i>Acropora millepora</i> (B, D, F), over the 20-days experiment in high DLI treatment (HL, orange), low DLI treatment (LL, purple), variable DLI 1 treatment (VL1, blue dashed lines) and variable DLI 2 treatment (VL2, green dashed lines). Values represent means over 16 colonies per treatment per species, with shaded areas representing standard error. https://doi.org/10.1371/journal.pone.0203882.g001
Figure 4:	Effects of constant and variable light on pigment concentrations. Concentration of chlorophyll a (μg cm ⁻²) and total carotenoids (μg cm ⁻²) in <i>Pachyseris speciosa</i> (N = 5–6 nubbins/treatment) and <i>Acropora millepora</i> (N = 16 nubbins/treatment) under high DLI (white), low DLI (black), and variable DLI (VL1, light gray, and VL2, dark gray) treatments at the end of the 20-days experiment. Tukey HSD post-hoc results from one-way ANOVA comparison superimposed. Error bars represent standard error. https://doi.org/10.1371/journal.pone.0203882.g002
Figure 5:	Photosynthesis-irradiance curves describing the contrasting photosynthetic features of the study species. Mean light-dependent oxygen production or consumption (µmol O ₂ cm ⁻² h ⁻¹) for <i>Pachyseris speciosa</i> (A) and Acropora millepora (B) at the end of the 20-day experiment in the high DLI (HL, solid grey), low DLI (LL, solid black), and variable DLI (VL1, dashed light gray, and VL2, dashed dark gray) treatments. N = 2–3 colonies/treatment/species. https://doi.org/10.1371/journal.pone.0203882.g003
Figure 6:	Relative growth of <i>Acropora millepora</i> between constant and variable DLI treatments. Mean percent change of <i>Acropora millepora</i> buoyant weight in the high DLI (HL, white), low DLI (LL, black), and two variable DLI treatments (VL1, light grey & VL2, dark grey) after 12 days. Tukey HSD post-hoc results from one-way ANOVA comparisons superimposed. Error bars represent standard error, n = 16 per treatment. https://doi.org/10.1371/journal.pone.0203882.g005

Figure 7:	Experimental room to assess the effects of low, variable, medium and high daily
	light integrals on coral recruits and adults11
Figure 8:	Effects of constant and variable daily light integrals on the growth of two species
	of Acropora recruits over a 9-weeks period13
Figure 9:	Representative seawater pHT and pCO ₂ in the experimental aquaria over a five
	day period. Values of pHT are averaged between aquaria (n = 8 per treatment),
	and error bars are standard errors15
Figure 10:	Effects of constant (solid points) and variable (open crossed points) daily light
	integrals on the growth of adult Acropora tenuis (a) and A. hyacinthus colonies
	after 49 days of experimental exposure. Grey points represent the 900 ppm
	pCO2 treatment, while black points are the 400 ppm treatment15
Figure 11:	Effects of constant (solid points) and variable (open crossed points) daily light
	integrals on the protein content of adult Acropora tenuis (a) and A. hyacinthus
	colonies after 49 days of experimental exposure. Grey points represent the 900
	ppm pCO2 treatment, while black points are the 400 ppm treatment16
Figure 12:	Effects of constant (solid points) and variable (open crossed points) daily light
	integrals on the chlorophyll a content of adult Acropora tenuis (a) and A.
	hyacinthus colonies after 49 days of experimental exposure. Grey points
	represent the 900 ppm pCO ₂ treatment, while black points are the 400 ppm
	treatment17
Figure 13:	The effective quantum yield (ϕ_{PSII}) of photosystem II in <i>Acropora tenuis</i> (a, c, e
	and g) and A. hyacinthus (b, d, f and h) in the variable (a and b), low (c and d)
	constant medium (e anf f) and high (g and h) light intensity treatments over the
	final ten days of the 49 day experiment. This time period covered a complete
	light-cycle in the variable treatment. Grey points represent the 900 ppm pCO ₂
	treatment, while black points are the 400 ppm treatment. The black lines
	represent the modelled means, while the grey lines are confidence intervals.
	The φ _{PSII} shows the proportion of available light that is being used for
	photosynthesis (i.e. a value of 0.6 indicates 60% of light is being
	photosynthesised)
Figure 14:	The relative electron transport rate (rETR) in Acropora tenuis (a, c, e and g)
•	and A. hyacinthus (b, d, f and h) in the variable (a and b), low (c and d), constant
	medium (e anf f) and high (g and h) light intensity treatments over the final ten
	days of the 49 day experiment. This time period covered a complete light-cycle
	in the variable treatment. Grey points represent the 900 ppm pCO ₂ treatment.
	while black points are the 400 ppm treatment. The black lines represent the
	modelled means, while the grey lines are confidence intervals. rETRs give an
	estimate of photosynthetic rates20
Figure 15:	Location map of the four validation sites within the GBR region along the north
J	eastern coast of Australia (inset map). The colour indicates depth contours
	within the shelf. The rectangle indicates the boundary of the small regional box
	Burdekin region, used for temporal evaluation of the model (as detailed in
	section 3.5) with the corresponding subset bathymetry showing the complex
	topographic features in the model region. Gray masked regions indicate land
	and coral reefs25
Figure 16:	Scatterplots of concurrent log-transformed instantaneous satellite-derived and
_	in situ bPAR for the four test regions of varying optical properties. The colour
	gradient of the data points correspond to the month of the concurrent
	•

	observations. The thin and thick black solid lines indicate the 1:1 line and the reduced major axis regression slope, respectively
Figure 17:	Example bPAR (benthic light) map showing the amount of light reaching the bottom of the water column on 1 January 2004, using data derived from NASA's
	MODIS satellite and an inherent optical property-based algorithm developed during the course of this project
Figure 18:	Bathymetry map showing areas where depth is less than 61m, the depth to which sparse seagrass beds have been observed in the Great Barrier Ree (Coles et al., 2009). Boundaries of regions are shown as black outlines30
Figure 19:	(left) Map showing areas where mean daily integrated light >5 mol m ⁻² d ⁻¹ (purple, potentially able to support at least sparse seagrass beds) and areas where mean daily integrated light >7.5µmol m ⁻² d ⁻¹ (light blue, potentially able to support sustained coral growth) in 2002-2003 indicating areas of potential suitable seagrass and coral habitat. (right) Figure copied from Petus et al. (2016) under Creative Commons by Attribution (CC-BY) licenses (http://creativecommons.org/licenses/by/4.0/). The GBR (Great Barrier Reef) World Heritage Area, Natural Resource Management (NRM) regions and marine portions, and major rivers (Normanby: No, Barron: Ba, Tully: Tu, Herbert: He, Burdekin: Bur, Pioneer: Pi, Fitzroy: Fi and Burnett: Bu). Key marine ecosystems: coral reefs and seagrass meadows. Coral reef outlines used are per the GBR Marine Park Authority Spatial Data Centre official reefs spatial data layer 2013. Seagrass areas show where meadows boundaries have been mapped (map: composite of surveyed data as at November, 1984–June, 2010) and the modelled (mod.) probability (50%–100%, pixel size 2 km2) of deepwater seagrass habitat [17]. The seagrass and coral reef sites monitored though the Great Barrier Reef Marine Monitoring Program are indicated with
Figure 20:	green asterisks and white dots, respectively
Figure 21:	bPAR Water Quality Index values for each region over time. Regions are arranged from north to south (top to bottom) and from nearshore to offshore (left to right). Results are not shown for the Offshore Burnett Mary as the depth of water in this region precludes the occurrence of photosynthetic benthic habitats at the 1 km grid scale of this analysis.
Figure 22:	Alternative visualisation of WQI letter grades, highlighting spatial distribution of scores
Figure 23:	An alternative visualisation of the bPAR WQI scores, highlighting the general trend of improving water quality when moving from south to north (top to bottom) and from nearshore to offshore (left to right)

ACRONYMS

AIMS Australian Institute of Marine Science

bPAR Benthic Photosynthetically Available Radiation

bPAR WQI.... Benthic Light Water Quality Index

CCA Crustose Coralline Algae

CDOM Coloured Dissolved Organic Matter

DLI Daily Light Integral

ETR..... Electron Transport Rates

GAMMs Generalised Additive Mixed Models

GBR..... Great Barrier Reef

GBRMPA..... Great Barrier Reef Marine Park Authority

GLMs..... Generalised Linear Models

IMOS Integrated Marine Observing System

IOPs...... Inherent Optical Properties

LTMP Long Term Monitoring Program

MMP Marine Monitoring Program

MODIS Moderate Resolution Imaging Spectroradiometer **NASA**...... National Aeronautics and Space Administration

NESP National Environmental Science Program

NRM Natural Resource Management TWQ Tropical Water Quality Hub

PAR Photosynthetically Active Radiation

POM..... Particulate Organic Matter **WQI**..... Water Quality Indicator

ABBREVIATIONS

cm..... Centimetres **CO**₂ Carbon dioxide

km..... kilometres

m..... metres

m⁻² s⁻¹..... per square metre per second

mol m⁻² d⁻¹ moles (of photons) per square metre per day

NH₄ Ammonium **NO**₃ Nitrate

NO₂ Nitrite

PO₄ Phosphate SiO₂ Silica dioxide

GLOSSARY

bPAR

The amount of photosynthetically available radiation (PAR – see glossary entry) that reaches the bottom of the water column (the surface of the sediments or benthic habitat).

DLI

The integrated Photosynthetically Available Radiation (PAR) dose received over the course of a day.

eAtlas

A website and mapping system for presenting environmental research data in an accessible form (https://eatlas.org.au/).

Indicator

"An overall characteristic of interest, e.g. water quality" (Robillot et al., 2018).

Index

"Standardised representation of a measure typically expressed relative to a benchmark, guideline or threshold" (Robillot et al., 2018).

Metric

"Mathematical formula or expression used to generate an index" (Robillot et al., 2018).

Marine Monitoring Program (MMP)

A long-term program of regular water quality and ecological health measurement activities established by GBRMPA in 2005 to measure the health of the nearshore Great Barrier Reef (http://www.gbrmpa.gov.au/our-work/our-programs-and-projects/reef-2050-marine-monitoring-program).

MODIS

A satellite-based earth observing system run by NASA. With instruments on two satellites (Terra and Aqua), each with daily over-passes providing multiple spectral bandwidths at a 1 km resolution, MODIS is widely used for ocean colour applications (https://modis.gsfc.nasa.gov/).

PAR

The amount of light within the wave-lengths that drive photosynthesis by plants and coral symbionts (400-700 nanometres).

Region

Natural Resource Management (NRM) Region.

Remote Sensing

Use of instruments located at a distance from the system to be observed. Most commonly (and in this report), this refers to satellite-based observations.

SeaSim

Australia's National Sea Simulator, world-leading experimental marine aquarium facilities housed at the Australian Institute of Marine Science (https://www.aims.gov.au/seasim).

Secchi Depth

The depth at which an 8-inch (20 cm) disk of alternating white and black quadrants is no longer visible from the surface of fluid.

Water quality index

An *index* used to track the indicator, water quality, relative to a benchmark.

ACKNOWLEDGEMENTS

This project was jointly funded by the Australian Government's National Environmental Science Program and the Australian Institute of Marine Science. The development of the remote sensing bPAR algorithm received additional support from an AIMS@JCU scholarship, a joint initiative of the Australian Institute of Marine Science and James Cook University.

The Integrated Marine Observing System (IMOS) provided collaborative support for the deployment, maintenance and retrieval of the benthic light loggers. Thanks in particular to Chris Bartlett (AIMS) for his role in this.

Many thanks to Tommy Owens of the NASA Ocean Biology Processing Group (OBPG) for processing support of MODIS time-series data for Yongala.

We gratefully acknowledge the staff at the National Sea Simulator for their technical assistance setting up the laboratory experiments, as well as their aid in troubleshooting issues as they arose during the experiments. We would also like to acknowledge the AIMS Weather Station Program for long-term light data at Davies' Reef as seen in the supporting information. Many thanks to our volunteer Oscar Ward who helped with the first experiment, and to Reynaldo Arteaga for support.

We also gratefully acknowledge our collaborators, Julia Strahl and Melissa Rocker at the University of Oldenburg, who led the third coral response experiment discussed in this report.

EXECUTIVE SUMMARY

Light is required by seagrasses and coral symbionts to provide the energy needed to drive photosynthesis. Light within the 400 to 700nm wavelength range is known as photosynthetically active radiation (PAR). Poor water quality reduces the penetration of light to the sea-floor and reef habitats that may otherwise support corals and seagrass beds.

This project included three major components with the over-arching goal of producing a scientifically-supported Water Quality Indicator (WQI) for benthic light (bPAR). These components were:

- Evaluation of bPAR thresholds for coral and seagrass health by reviewing existing ecophysiological data and conducting aquarium experiments to assess the response of key corals and seagrasses to low light and variable light.
- 2) Development of a remote sensing algorithm to estimate bPAR from satellite ocean colour observations, validated against *in situ* optical measurements, to provide a cost-effective means to monitor variations in benthic light across the whole Great Barrier Reef.
- 3) Development of a new Water Quality Index to relate bPAR to ecological outcomes across the whole Great Barrier Reef (GBR), which will be made routinely available for incorporation into the Great Barrier Reef Marine Park Authority (GBRMPA) Report Cards.

Using laboratory experiments and field data, we define bPAR thresholds for measures of ecosystem health and develop guideline values. Responses of different coral and seagrass species to low and moderate light vary. Coral growth and recruitment for key species studied are considerably reduced below 10 mol photons m⁻², though some species thrive in lower light conditions. Seagrasses are at risk of light limitation when bPAR declines below 5 or 6 mol m⁻² d⁻¹. Growth rates are reduced in both low and variable light and daily integrated light (DLI) is important.

A new remote sensing algorithm is presented, which allows benthic PAR to be estimated from satellite ocean colour observations. This algorithm, which uses National Aeronautics and Space Administration (NASA) satellite data products, has been validated against *in* situ openwater irradiance data obtained in collaboration with IMOS. It has been used to quantify and map benthic irradiance throughout the GBR, near-daily over 14 years.

Combining threshold values for ecological health with remote sensing benthic PAR, we are able to map year-to-year changes in areas that receive sufficient light to support strong growth and recruitment of common coral and seagrass species. The maps show declines in suitable habitat in years following major flood events, especially in coastal regions influenced by the Fitzroy and Burdekin Rivers.

Using this information, we propose a new benthic light water quality index (bPAR WQI). The index is a measure of changes in the area of benthic habitat that receive sufficient light to support strong photosynthetic growth of common coral species and is equally relevant to seagrass health. The index does not require expensive *in situ* monitoring, is responsive to

human activities and year-to-year variations in runoff, can be easily automated for incorporation into GBRMPA Report Cards, and is of direct ecological relevance.

The proposed bPAR WQI is used to produce letter grades for each NRM region, from enclosed coastal to offshore areas, for the period from 2003 to 2018 (Figure 1).

The bPAR WQI and bPAR maps produced during this project will also provide an additional data layer which can feed into assessments of cumulative risks and recovery potential in the context of coral bleaching and Crown of Thorns Starfish outbreaks. Work will continue through NESP TWQ Hub Project 5.3 to ensure that these outcomes are achieved.

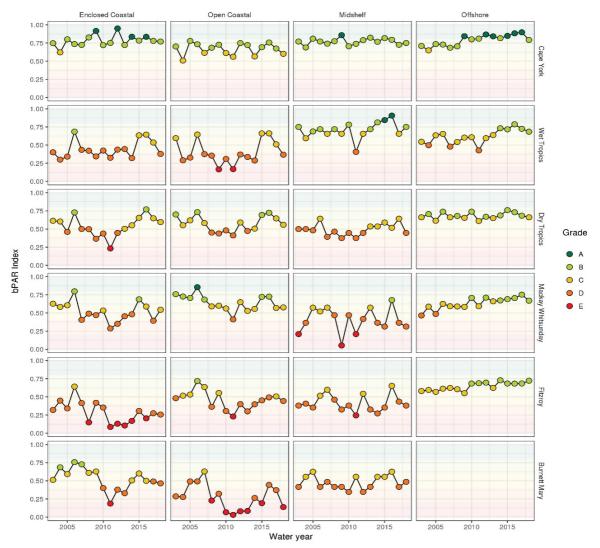


Figure 1: bPAR Water Quality Index values for each region over time. Regions are arranged from north to south (top to bottom) and from nearshore to offshore (left to right). Results are not shown for the Offshore Burnett Mary as the depth of water in this region precludes the occurrence of photosynthetic benthic habitats (including seagrasses and corals) at the 1 km grid scale of this analysis. Letter grades are assigned from A (i.e. excellent, index > 0.8) to E (i.e. poor, index <0.2).

1.0 INTRODUCTION

The Great Barrier Reef (GBR) is subject to multiple pressures, from climate change to crown of thorns starfish outbreaks. It is essential for management agencies to have tools that allow them to identify the causes of observed change in ecosystem health. Understanding the factors contributing to ecosystem decline or ecosystem resilience provides a sound basis for targeted management responses.

Water quality indices (WQIs) can be used to link changes in ecosystem health to declining water quality. Under the Reef 2050 Water Quality Improvement Plan 2017-2022 (State of Queensland, 2018) and under the preceding Reef Water Quality Protection Plan 2013 (Reef Water Quality Protection Plan Secretariat, 2013), the Australian and Queensland Governments produce annual report cards describing the health of the Great Barrier Reef. These report cards consider marine water quality and ecology, management practices, catchment indicators and catchment loads. These are informed by indices of water quality in each marine region, such as the frequency at which chlorophyll a and Secchi depth fail to meet target values.

An overview of the recently updated process to produce GBR report cards is given by Robillot et al. (2018). The new report cards will consider both nearshore water quality monitoring data from the Marine Monitoring Program (J Waterhouse et al., 2018) and results from the data-assimilating version of the eReefs marine models (Baird et al., 2017; Jones et al., 2016; Skerratt et al., 2018). The updated report cards improve upon previous versions by ensuring that the thresholds used are ecologically relevant and regionally specific and that water quality changes can be monitored not only in the well-monitored nearshore region, but also in the mid- and outer-shelf regions of the Great Barrier Reef.

The report cards, however, do not currently include an index of benthic light, and this is the gap that the work describes here seeks to address.

The availability of sufficient light is essential for photosynthesis, the foundation of all food webs and the dominant source of energy for corals and seagrasses. The most important part of the light spectrum for marine organisms is photosynthetically active radiation (PAR), which is the amount of light within the 400 to 700nm wavelength range. As light penetrates the water column, optically active constituents such as suspended sediments, plankton, particulate organic matter (POM) and coloured dissolved organic matter (CDOM) reduce light and change its character (Brando, Dekker, Park, & Schroeder, 2012; Cherukuru et al., 2017). The amount of photosynthetically active light reaching the sea floor is known as 'benthic PAR' (bPAR) and is influenced by both water quality and depth.

PAR is critical for corals, seagrass and other photosynthetic benthic organisms, and light reduction is known to reduce ecosystem health (Albright et al., 2016). Benthic and water-column PAR may be reduced by terrestrial run-off via rivers that often bring high loads of fine sediments, nutrients and organic matter. PAR can also be reduced by tidal resuspension of sediments, by cyclone-induced vertical mixing, and by human activities such as dredging in the coastal zone. Water clarity is therefore believed to be a key mediator of the effects of

human activities on ecological outcomes for the Great Barrier Reef (Fabricius, Logan, Weeks, Lewis, & Brodie, 2016).

Metrics to calculate the exposure of GBR reef and seagrass habitats to flood plumes from satellite ocean colour observations have been developed (Devlin et al., 2015) and have been discussed as a possible basis for a PAR WQI. Detection of primary, secondary and tertiary flood plumes and calculation of the duration of exposure of nearshore reefs to each category has provided a metric that integrates multiple potential impacts of flood plumes, from reduced water clarity to freshwater exposure to the potential impacts of pesticide exposure and sedimentation.

While Secchi depth is included in the current GBR Report Card as an index of water clarity (Reef Water Quality Protection Plan Secretariat, 2013), the ecological relevance of Secchi depth varies regionally because the amount of light reaching corals and seagrasses also varies as a function of water depth. Using benthic light (bPAR) instead of Secchi depth will allow the interacting effects of water clarity and spatially variable bathymetry (water depth) to be taken into account.

Previous work by Logan et al. (2013) and Fabricius, Logan, Weeks, and Brodie (2014); (2016) however, has demonstrated that light penetration and photic depth varies across the whole Great Barrier Reef (GBR) in response to inter-annual variations in river discharge, not only in the areas directly affected by flood plumes, but also in mid- and outer-shelf areas of some regions. These effects can be observed more than six months after flood plumes have dispersed, suggesting that flood plume detection is not in itself sufficient to characterise the likely spatial and temporal extent of the ecological impacts of river runoff and human activities in Queensland catchments and coastal regions.

Variations in photic depth (commonly measured as Secchi depth) can be characterised using existing remote sensing data products developed for the Great Barrier Reef and available as NASA data products (Weeks et al., 2012). However, translating variations in photic depth to ecological outcomes such as the area of benthic habitat potentially suitable for growth of seagrasses and corals and recovery from bleaching events is not straightforward. Ecologically-relevant, GBR-specific light thresholds for corals and ecosystem health have not previously been determined. A cost-effective means to estimate benthic light across the whole GBR has not been available. Further, a responsive, ecologically-relevant WQI that describes the benthic light environment at local and GBR-wide scales has not previously been devised. It is the goal of this project to address these gaps as part of the broader NESP Tropical Water Quality Hub commitment to developing effective and cost-effective catchment and marine water quality indexes, thresholds and sub-lethal health-indicators for key marine organisms and processes in support of the Reef.

This project included three major components:

- Evaluation of bPAR thresholds for coral and seagrass health by reviewing existing ecophysiological data and conducting SeaSim experiments to assess the response of key organisms to low light and variable light in various conditions.
- 2) Development of a remote sensing algorithm to estimate bPAR from satellite ocean colour observations, working with NASA's SeaDAS L2GEN processing framework and using locally-measured inherent optical properties, IMOS and MMP water quality

- monitoring data, and *in situ* PAR loggers. The algorithm will be made available for other uses through collaboration with NASA.
- 3) Development of a new Water Quality Index to relate bPAR to ecological outcomes across the whole GBR, which will be made routinely available through eAtlas as map layers that can be incorporated into GBRMPA Report Cards and used to help evaluate and improve eReefs bPAR estimates.

Each of these components will be discussed in more detail in the chapters that follow.



Figure 2: Diverse coral and seagrass habitats rely on light reaching the bottom of the water column to drive photosynthesis. Changes in water quality can reduce the penetration and quality of light at the sea floor. Photo: Ben Reef. Latitude: -20.00833. Longitude: 150.325. Credit: Long Term Monitoring Program (LTMP). Copyright Australian Institute of Marine Science.

2.0 EVALUATION OF BPAR THRESHOLDS FOR SEAGRASS AND CORAL HEALTH

2.1 Review of seagrass light thresholds

Benthic light is one of the most important environmental conditions affecting seagrass distribution and changing abundances over seasonal and inter-annual time-scales (Catherine Collier & Waycott, 2009). Seagrasses have higher light requirements than other benthic marine plants (macroalgae) (Dennison et al.), partly because of their complex structure including sexual reproduction and the large amount of non-photosynthetic below-ground tissues (Collier et al., *in prep.*). Their high light requirements and their sensitivity to periods of low light have given seagrass meadows a reputation for being sentinels of inshore water quality (Catherine Collier & Waycott, 2009; Dennison et al., 1993; Ralph, Durako, Enriquez, Collier, & Doblin, 2007).

Benthic light thresholds that relate to seagrass loss have been developed and summarised in previous NESP projects (CJ Collier, Adams, et al., 2016). These have been adopted for management of port activities (Chartrand, Bryant, Carter, Ralph, & Rasheed, 2016), in the interpretation of wet season flood impacts (CJ Collier, Chartrand, Honchin, Fletcher, & Rasheed, 2016; C. J. Collier, Waycott, & McKenzie, 2012), and in the revision of sediment load targets for flood-plume affected areas of the GBR (Brodie et al., 2017).

Previous research to characterise seagrass bPAR requirements has focused on the impact of short- to medium-term (weeks to months) impacts of 'continuous' low light exposure mimicking extreme wet seasons, and/or for determining thresholds for management of port activities. Most of this research was carried out *in-situ* (Chartrand et al., 2016; C. J. Collier et al., 2012) or in aquaria-based experiments (CJ Collier, Adams, et al., 2016) with naturally varying incoming radiation, but has not directly measured acclimation times and sensitivity to variable light. These studies have focused on four out of fifteen seagrass species, including *Z. muelleri*, *H. uninervis*, *C. serrulata* and *H. ovalis*, because of the dominance of these species in inshore regions in the southern two-thirds of the GBR (Wet Tropics to Burnett Mary) where the risk of low benthic light is greatest (J. Waterhouse et al., 2017). These short-term light thresholds were summarised for NESP TWQ Hub Project 3.3 (CJ Collier, Chartrand, et al., 2016).

If bPAR declines below 5 or 6 mol m⁻² d⁻¹, then seagrasses are at risk of light limitation. However, there are differences among species in the risk of morality below this threshold based on the *duration of exposure* with larger 'persistent' species (sensu Kilminster et al., 2015) surviving longer than 'colonising' or 'opportunistic' species (O'Brien et al., 2018). Halophila species growing in deep water (>10 m) are smaller and have lower light requirements, and are impacted if light falls below 3.2 mol m⁻² d⁻¹ (Chartrand, Szabo, Sinutok, Rasheed, & Ralph, 2018; CJ Collier, Adams, et al., 2016).

The effects of low light can also depend strongly on other environmental conditions. Warmer temperatures drive faster rates of respiratory carbon loss (Catherine J Collier et al., 2017) and increase bPAR requirements (CJ Collier, Adams, et al., 2016). Light requirements may also be compounded by other cumulative impacts such PSII herbicides, which reduce the efficiency

of photosystem II and carbon fixation, and therefore also exacerbate light stress (Negri, Flores, Mercurio, Mueller, & Collier, 2015).

There are extensive and ecologically-important seagrass meadows in intertidal habitats of the GBR. Intertidal seagrasses can receive periods of very high light during low tide exposure. However during the wet season, when extreme turbidity tends to occur more often, the low tides that expose intertidal seagrasses occur during the night. Therefore, even these very shallow meadows suffer light stress during the warm wet summers and are vulnerable to decline (Chartrand et al., 2016; McKenzie et al., 2018; Rasheed, McKenna, Carter, & Coles, 2014).

Tolerance to periods of low light are affected by seagrass resilience, which is influenced by the amount of stored carbohydrate reserves that seagrasses can use to sustain metabolic requirements when photosynthetic carbon fixation is insufficient (O'Brien et al., 2018). To build these reserves, seagrasses require periods of higher light. Seagrasses have their maximum growth period from September to November, and this period of growth is critical for recovery from wet season senescence. Therefore, it is essential that benthic light thresholds consider bPAR throughout the year and thresholds defined for annual light levels and/or seasonal benthic light levels. There is some limited evidence that benthic light of 10 mol m⁻² d⁻¹ is needed for annual maintenance of growth and resilience. However, there are some apparently healthy seagrass meadows that form when annual bPAR is lower than this, for example the subtidal meadows around Magnetic Island (McKenzie et al., 2018). Furthermore the exposure and vulnerability to low light levels varies regionally throughout the GBR (J. Waterhouse et al., 2017), and sensitivity to low light can be affected by exposure history (Maxwell et al., 2014). Determination of long-term light requirements should therefore consider variability among species and locations.

2.2 Effects of low and variable light on growth of two species of coral

This work has been published as DiPerna, Hoogenboom, Noonan and Fabricius (2018). The abstract and key figures are provided below. The <u>published paper</u> includes a full description of methods and results.

Abstract

Phototrophic sessile organisms, such as reef corals, adjust their photosynthetic apparatus to optimize the balance of light capture versus protection in response to variable light availability (photoacclimation). In shallow marine environments, daily light integrals (DLI) can vary several-fold in response to water clarity and clouds. This laboratory study investigated the responses of two coral species to fluctuations in DLI. Corals were exposed to four contrasting DLI treatments: 'high-light' (potentially photoinhibiting conditions. 32 mol photons m⁻² d⁻¹), 'lowlight' (potentially light-limiting conditions, 6 mol photons m⁻² d⁻¹), and two 'variable light' treatments that alternated between high and low conditions every 5 days. In the variable treatments, the shade-tolerant coral *Pachyseris speciosa* displayed cycles of rapid declines in maximum quantum yield during high-light and subsequent recoveries during low-light, showing photoacclimation at a time scale of 3-5 days. In contrast, the shallow-water coral Acropora millepora showed slow (>20 days) photoacclimation, and minimal changes in photosynthetic yields despite contrasting light exposure. However, growth (change in buoyant weight) in A. millepora was significantly slower under variable light, and even more so under low-light conditions, compared with high-light conditions. The responses of yields in P. speciosa match their preference for low-light environments, but suggest a vulnerability to even short periods of high-light exposure. In contrast, A. millepora had better tolerance of high-light conditions, however its slow photoacclimatory responses limit its growth under low and variable conditions. The study shows contrasting photoacclimatory responses in variable light environments, which is important to identify and understand as many coastal and midshelf reefs are becoming increasingly more turbid, and may experience higher variability in light availability.

Conclusions and key figures

Although the results show different responses for two species of coral to high and low light, and different capacity for photoacclimation, there is both species show dramatically reduced growth in low-light conditions (6 mol photons m⁻² d⁻¹) and intermediate growth rates in variable-light conditions. Overall, daily integrated light is a better predictor of growth rates than maximum or minimum instantaneous light. Physiological responses to different light conditions are shown in Figure 3, effects on pigmentation are shown in Figure 4 and photosynthesis-irradiance curves are shown in Figure 5, showing maximum photosynthesis in both species at around 300 µmol photons m⁻² s⁻¹. Even at 6 mol photons m⁻² d⁻¹, some increase in polyp weight is observed in both species (Figure 6).

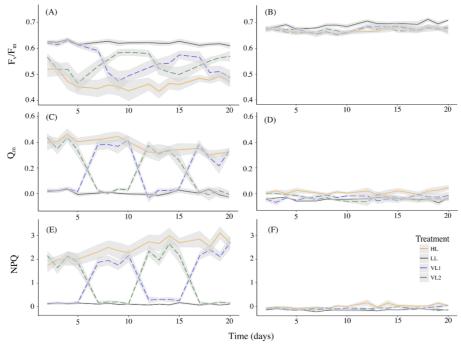


Figure 3: Photosynthetic potential, light stress and non-photochemical quenching under constant high and low DLI, and under two variable DLI treatments. Mean maximum quantum yield (Fv/Fm), excitation pressure on PSII (Qm) and non-photochemical quenching (NPQ) of *Pachyseris speciosa* (A, C, E)—and *Acropora millepora* (B, D, F), over the 20-days experiment in high DLI treatment (HL, orange), low DLI treatment (LL, purple), variable DLI 1 treatment (VL1, blue dashed lines) and variable DLI 2 treatment (VL2, green dashed lines). Values represent means over 16 colonies per treatment per species, with shaded areas representing standard error. https://doi.org/10.1371/journal.pone.0203882.g001

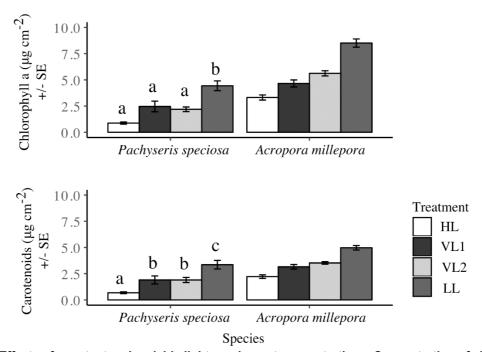


Figure 4: Effects of constant and variable light on pigment concentrations. Concentration of chlorophyll a (μg cm⁻²) and total carotenoids (μg cm⁻²) in *Pachyseris speciosa* (N = 5–6 nubbins/treatment) and *Acropora millepora* (N = 16 nubbins/treatment) under high DLI (white), low DLI (black), and variable DLI (VL1, light gray, and VL2, dark gray) treatments at the end of the 20-days experiment. Tukey HSD posthoc results from one-way ANOVA comparison superimposed. Error bars represent standard error. https://doi.org/10.1371/journal.pone.0203882.g002

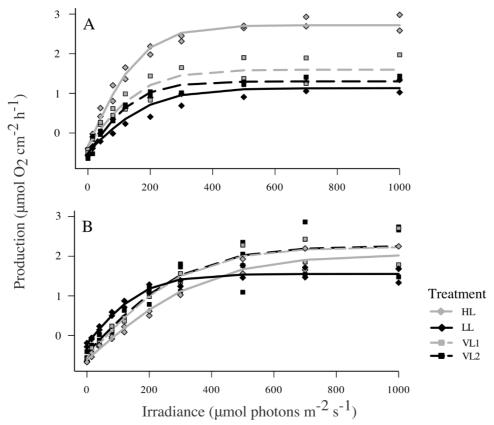


Figure 5: Photosynthesis-irradiance curves describing the contrasting photosynthetic features of the study species. Mean light-dependent oxygen production or consumption (μmol O₂ cm⁻² h⁻¹) for *Pachyseris speciosa* (A) and Acropora millepora (B) at the end of the 20-day experiment in the high DLI (HL, solid grey), low DLI (LL, solid black), and variable DLI (VL1, dashed light gray, and VL2, dashed dark gray) treatments. N = 2–3 colonies/treatment/species. https://doi.org/10.1371/journal.pone.0203882.g003

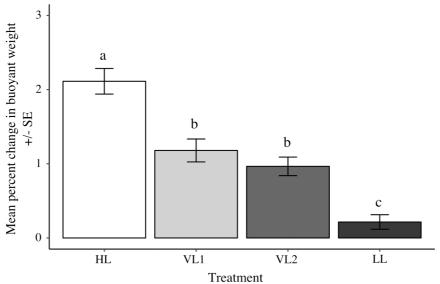


Figure 6: Relative growth of *Acropora millepora* between constant and variable DLI treatments. Mean percent change of *Acropora millepora* buoyant weight in the high DLI (HL, white), low DLI (LL, black), and two variable DLI treatments (VL1, light grey & VL2, dark grey) after 12 days. Tukey HSD post-hoc results from one-way ANOVA comparisons superimposed. Error bars represent standard error, n = 16 per treatment. https://doi.org/10.1371/journal.pone.0203882.g005

2.3 Effects of variable light and elevated pCO₂ on the growth and physiology of two juvenile and adult *Acropora* corals

While experiment 1 (DiPerna et al., 2018) established the relationship between light and growth rates of mature coral, to understand the full ecological implications of reduced light for coral reefs, it is necessary to also understand the effects of light on coral recruitment, as well as the potential for adult coral to adapt to low-light conditions. Experiment 2 addresses these concerns. This experiment has not yet been published as a peer-reviewed journal article, so it is described here in a little more detail.

Objective

To investigate the ability of two different *Acropora* reef corals (their juveniles and adults) to acclimatise to low and variable light environments, as encountered in areas of high day-to-day light variability driven by turbidity resuspension. Furthermore, to predict how these light thresholds and limits to acclimatisation change under increasing carbon dioxide levels.

Methods

All experiments were conducted within the National Sea Simulator (SeaSim) at the Australian Institute of Marine Science (AIMS), Townsville Australia (Figure 7).



Figure 7: Experimental room to assess the effects of low, variable, medium and high daily light integrals on coral recruits and adults.

In January 2017, 990 aragonite coral-frag plugs, preconditioned and covered in crustose coralline algae (CCA) and other biofilms, were haphazardly distributed across six 52 L aquaria for bulk larval settlement. Each tank was illuminated with LED lights (hydra HD, Aquaillumination USA) with a 12 hour light/dark cycle, including four hours linear intensity ramp up and down, and four hours of noon max intensity at 120 µmol photon m⁻² s⁻¹ (DLI of 2.59 mol photon m⁻²), measured with a calibrated underwater PAR sensor (LI-140, Licor, USA). Water temperature was maintained at 27 °C with a water exchange rate of 200 mL min⁻¹ of 0.04 µm ultra-filtered seawater. Each tank had ~1,500 one month old larvae added of either *Acropora tenuis* or *A. hyacinthus* (from five *A. tenuis* and three *A. hyacinthus* adult colonies). Larvae were allowed 24 hrs to settle before a cocktail of Symbiodinium, obtained

from AIMS's symbiont culture facility, comprised of even parts C1, D, D1, A3 and A3c types, was added at a concentration of ~1000 Symbiodinium mL⁻¹. Larval recruitment and Symbiodinium inoculation was assessed visually after three weeks, and the plugs with the most recruits (n = 226 for *A. tenuis* and n = 288 for *A. hyacinthus*), were evenly divided into 24 aquaria with the same light, temperature, pCO₂ and salinity conditions as the settlement aquaria. These 24 aquaria would ultimately end up as two pCO₂ treatments, fully crossed with four light treatments, with three replicate tanks per treatment. Water mixing was provided by individual pumps in each tank and water exchange rates were set at 600 mL min⁻¹ of ultrafiltered seawater, as well as 100 mL min⁻¹ of untreated raw water. The raw water was added as a food supply for the coral juveniles, as unquantified observations within the SeaSim suggest this improves juvenile coral growth and survival. Temperature in the tanks was monitored with temperature probes and remained constant throughout the experiment.

Half of the aquaria were maintained in ambient pCO_2 conditions of ~400 ppm, while the pCO_2 in the other half was ramped to 900 ppm over four days. The pCO_2 was manipulated via a feedback control system, where pCO_2 was continually monitored in one tank per pCO_2 treatment (telair pCO_2 analyser), and the CO_2 required to attain the treatment was supplied to the incoming seawater of all the tanks per treatment via a membrane control contactor. duraFET pH sensors (CPS471D isFET, Endress and Hauser) were distributed across the 24 aquaria (eight per pCO_2 treatment) to ensure the pCO_2 in all aquaria did not differ from the one being used in the feedback control. To ensure the ambient treatment was maintained at 400 ppm, seawater for this treatment was first stripped of CO_2 with soda lime, and then dosed as per the elevated treatment.

Samples were taken weekly from the raw and filtered incoming seawater (n = 9 each), prior to CO_2 manipulation, for salinity and dissolved nutrients. Dissolved nutrients included ammonium (NH₄), nitrate (NO₃), nitrite (NO₂), phosphate (PO₄), and silica dioxide (SiO₂). Salinity samples were made with a hand-held conductivity meter (HQ30d, Hach USA), while nutrients were analysed by after filtration to 0.04 μ m by the analytical services department of AIMS. A further set of samples were taken throughout the experiment (n = 5) for total alkalinity (A_T) and dissolved inorganic carbon (C_T) analyses (Marianda VINDTA 3C, Germany). Water quality parameters within the aquaria were calculated based on the different supply rates of raw (600 mL min⁻¹) and filtered (600 mL min⁻¹) seawater.

The four light treatments used in the experiment (low, medium, high and variable) each had 12 hrs of light and a five hr ramp, but at different intensities. The high light treatment had a noon max of 500 µmol photon m⁻² s⁻¹ and a DLI of 12.6 mol photon m⁻², the medium treatment had a noon max of 300 µmol photon m⁻² s⁻¹ and a DLI of 7.56 mol photon m⁻², while the low light treatment had a noon max of 100 µmol photon m⁻² s⁻¹ and a DLI of 2.52 mol photon m⁻². The variable treatment oscillated on a five day cycle, with four days at the low treatment intensity, a ramp day at the medium, then four days at the high treatment intensity. The mean DLI of the variable treatment was therefore the same as medium treatment. The light treatments were evenly ramped from the initially low conditions to their respective treatments over three days and the variable treatment began on a high light phase. Light treatments were alternated around the aquaria room, while pCO₂ treatments were blocked on each side due to design constraints within the room design.

Photographs of the juveniles were taken weekly, and the survivorship (alive vs dead) and growth (number of corallites) was visually assessed by a single observer (Figure 8). Filamentous algal overgrowth was minimised by hand tweezing each plug twice per week throughout the duration of the experiment. Juvenile corals were under experimental conditions for 63 days before final photographs were taken.

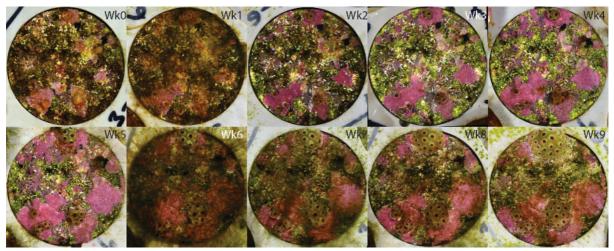


Figure 8: Effects of constant and variable daily light integrals on the growth of two species of Acropora recruits over a 9-weeks period.

Four adult colonies of A. tenuis and A. hyacinthus were collected from ~3 m depth at Davies reef and brought to the Seasim two weeks after the juveniles had been introduced to the experimental aquaria. Each colony was cut into 12 nubbins of ~5cm, superglued to aragonite plugs, given two days to heal before their buoyant weights were recorded (Shimatzu) and two per species were placed into each of the 24 aquaria. Hatched Artemia nauplii were added to the aguaria daily at densities of 0.35 nauplii mL-1 to feed the corals. The adults remained under the experimental conditions for 51 days before the experiment ended, and mortality was limited to a single nubbin in a low light + 900 ppm pCO2 tank. The adult corals were allowed to acclimate to experimental conditions for 41 days before daily measurements of noon time effective photosystem II quantum yield (Y(II): (Fm'-F)/Fm'), as well as maximal photosystem II quantum yield (Fv/Fm) were taken with a pulse amplitude modulated fluorometer (Diving PAM, Waltz, Germany). PAM settings were: measuring intensity 2, saturating intensity 8, saturating width 0.8 s, gain 2 and damping 2. Noon time Y(II) measurements were taken after at least one hour of noon irradiance, lights were then turned off for at least one hour before Fv/Fm measurements were taken. Relative electron transport rates (rETR: φ_{PSII} x PAR), as an index of instantaneous photosynthetic activity, were calculated and used in analyses instead of electron transport rates (ETR), as the necessary coefficients for ETR calculations (PSII: PSI ratio and the absorption coefficient) are variable and poorly defined in corals. Photosystem II excitation pressure $(Q_m: 1 - (\phi_{PSII}) / (F_v/F_m)$, where values close to zero indicate light limitation at maximum irradiance, while values close to 1 indicate photoinhibition, were also compared. PAM measurements of the variable treatment nubbins were made daily during the final 10 days of the experiment to capture a complete cycle through this light treatment, while all other treatments were recorded three times within this period (days 2, 6 and 9 of the final 10 days). Three measurements were taken per nubbin and averaged prior to analysis. Buoyant weights were recorded again at the end of the experiment (49 days from initial measurements), and buoyant weight increases relative to the initial weight of each nubbin (i.e. weight gain / initial

weight) were compared between the two experimental treatments and parental colony identification. A small branch was also taken from each nubbin at the end of the experiment, frozen in liquid nitrogen and stored for later analyses in -80°C.

The frozen nubbins were processed at AIMS for total protein and pigment (chlorophylls a and c_2 , and total carotenoids) content following standard procedures. Briefly, each nubbin was water-picked in 10 mL of ultra-filtered seawater (0.04 μ m) to remove coral tissue. This tissue slurry was then homogenised and centrifuged to separate coral and symbiont components. Total coral protein content was quantified from the coral tissue supernatant with the DC protein assay kit (Bio-Rad Laboratories, Australia), while *Symbiodinium* pigments in the pellet were determined spectrophotometrically. Protein and pigment contents were standardised to nubbin surface area, estimated with the single wax-dipping technique.

Generalised linear models (GLMs) were used to analyse the effects of the experimental treatments on adult coral growth, protein and pigment content, as well as to compare photophyiological parameters at individual time points. Light and pCO₂ treatments, and parental colony identification, were included in the GLMs as fixed factors, while experimental aquaria identification was removed from final models due to statistical insignificance. Changes in photophysiology in corals from the variable light treatment, over the final ten days of the experiment, were analysed using generalised additive mixed models (GAMMS). In these GAMMs, light, CO₂, parental colony identification (all fixed factors), and experimental aquaria (random) were included as factors, while date was included as the smooth-term.

Results for juvenile growth and survival are still being analysed and only the adult data is presented below.

Results

Weekly water quality parameters of the seawater supplied to the experimental aquaria averaged 34.8 \pm 0.36 SE ppt salinity, 0.39 \pm 0.05 μ mol L⁻¹ NH₄, 1.55 \pm 0.07 μ mol L⁻¹ NO₃, 0.24 \pm 0.03 μ mol L⁻¹ NO₂, 0.15 \pm 0.01 μ mol L⁻¹ PO₄, 7.82 \pm 0.65 μ mol L⁻¹ SiO₂, and 2301.93 \pm 4.33 μ mol kg⁻¹ A_T. The manipulated pCO₂ and pH treatment levels in the experimental aquaria were maintained at their set values for the duration of the experiment (Figure 9). The pCO₂ ranged between 390 – 430 ppm and 852 – 992 ppm in the control and elevated treatment tanks, and the two treatments never overlapped.

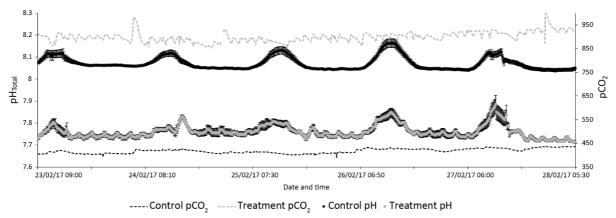


Figure 9: Representative seawater pHT and pCO₂ in the experimental aquaria over a five day period. Values of pHT are averaged between aquaria (n = 8 per treatment), and error bars are standard errors.

Growth rates of both species were significantly affected by light, but not pCO₂ or the interaction between these two treatments. For both species, growth rates increased linearly with accumulated DLI, from low to high light, and did not differ between the medium- and variable-light treatments with the same DLI. For *A. tenuis*, light reductions of 80%, between the high and low light treatments, resulted in growth rates decreasing 63% (0.35 \pm 0.05 SE% d⁻¹ to 0.11 \pm 0.01% d⁻¹). Similarly, high light growth rates of 0.19 \pm 0.2% d⁻¹ in *A. hyacinthus* decreased 72% to 0.05 \pm 0.01% d⁻¹ in the low light treatment (Figure 10). Growth rates also differed between parental colonies in both species, however the effects of the light treatment were stronger.

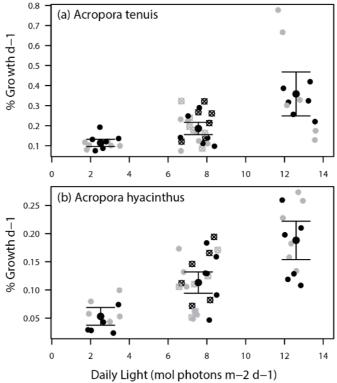


Figure 10: Effects of constant (solid points) and variable (open crossed points) daily light integrals on the growth of adult *Acropora tenuis* (a) and *A. hyacinthus* colonies after 49 days of experimental exposure. Grey points represent the 900 ppm pCO2 treatment, while black points are the 400 ppm treatment.

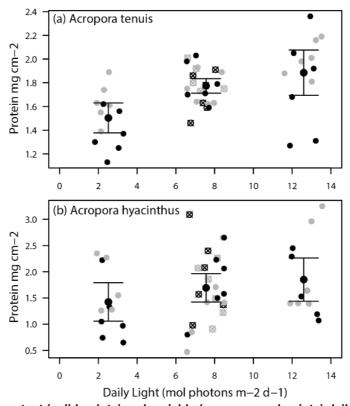


Figure 11: Effects of constant (solid points) and variable (open crossed points) daily light integrals on the protein content of adult *Acropora tenuis* (a) and *A. hyacinthus* colonies after 49 days of experimental exposure. Grey points represent the 900 ppm pCO2 treatment, while black points are the 400 ppm treatment

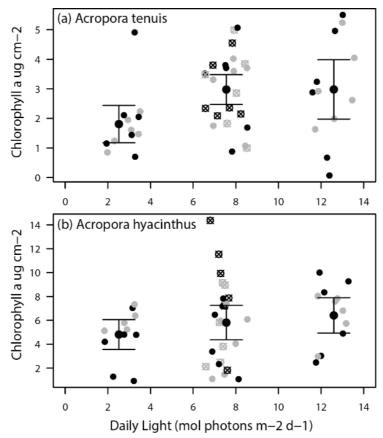


Figure 12: Effects of constant (solid points) and variable (open crossed points) daily light integrals on the chlorophyll a content of adult *Acropora tenuis* (a) and *A. hyacinthus* colonies after 49 days of experimental exposure. Grey points represent the 900 ppm pCO₂ treatment, while black points are the 400 ppm treatment.

Tissue protein content in both species was also positively affected by increasing DLI, and there were again no differences between the medium and variable light treatments (Figure 11). In *A. tenuis*, protein content also significantly increased under elevated pCO₂ compared to present day levels. *A. tenuis* protein content was reduced by ~10% in the low light treatment compared to the other light treatments, and was also 10% lower in the 400 ppm pCO₂ treatment compared to 900 ppm. However, in combination protein content in the low light + 400ppm treatment was 68% lower than the high light + 900 ppm treatment (1.37 \pm 0.08 vs 2.01 \pm 0.06 mg cm⁻¹), suggesting effects can be more than additive. *A. hyacinthus* protein content was reduced by 12 - 24% in the low light treatment compared to the other light treatments, and significant differences were seen between parental colonies (Figure 11).

The response of pigment analyses differed between coral taxa. In *A. tenuis*, there was a 39% decline in chlorophyll a content per coral surface area from the high to low light treatments $(2.98 \pm 0.5 \, \mu g \, cm^{-2} \, to \, 1.81 \pm 0.32 \, \mu g \, cm^{-2}$: Figure 12), as well as a 57% decline in total carotenoid content cm⁻¹ $(2.14 \pm 0.36 \, \mu g \, cm^{-2} \, to \, 0.91 \pm 0.27 \, \mu g \, cm^{-2})$. However, these were marginally significant, and differences between light treatment levels were not significantly different in *post-hoc* examination. Instead there were considerable differences in *A. tenuis* chlorophyll a and total carotenoids cm⁻² between parental colonies. *A. tenuis* chlorophyll c_2 cm⁻² was unaffected by the light and CO₂ treatments, and only differed between parental colonies. For *A. hyacinthus*, chlorophyll a cm⁻² was affected by light but not CO₂ treatments. Concentrations were elevated and equal in the high and variable light treatments, while the

medium and low light levels were equal and \sim 50% reduced (i.e. chlorophyll a in (HL = VL) > (ML = LL)). No consistent patterns were detected in response to the light or CO₂ treatments for any of the other pigments, which only differed between parental colonies.

Both coral species in the variable light treatment were seen to continually photoacclimate through the changing light cycle (Figure 13 and Figure 14). The GAMMs showed that changes in all parameters measured (ϕ_{PSII} , F_v/F_m , Q_m and rETR) were primarily accounted for by the changing light cycle, rather than time, pCO₂, or the interaction between light and pCO₂. This indicates that the photosynthetic apparatuses of these corals were adjusting accordingly to their light regime on a daily basis. The Q_m in *A. tenuis* was also affected by time, suggesting a lag in acclimation to the changing light.

The variable treatment ϕ_{PSII} , in both species, was lowest under high light, and increased during the low light part of the cycle (Figure 12). In *A. tenuis* there was a ~5% increase in the variable light treatment ϕ_{PSII} between high light values of 0.60 ± 0.01SE to low light values of 0.66 ± 0.01. *A. hyacinthus* ϕ_{PSII} values in the variable light treatment were 10% increased from high light values of 0.55 ± 0.02 to low light values of 0.63 ± 0.02. This shows that during periods of low light, more centres of photo-activity were open to capture more available light. During the high light period, more of these photo-centres closed to prevent photodamage. Interestingly, in the constant light treatments values of ϕ_{PSII} between high and low light did not differ in both species. *A. tenuis* recorded a mean ϕ_{PSII} value of 0.61 ± 0.01 under high constant light, and 0.63 ± 0.01 in the low constant light (Figure 13). Similarly ϕ_{PSII} in *A. hyacinthus* was 0.58 ± 0.01 under high constant light, and 0.59 ± 0.01 under low constant light. This indicates that after 49 days of exposure these corals had acclimated to their respective light treatments and were all using approximately 60% of available light for photosynthesis.

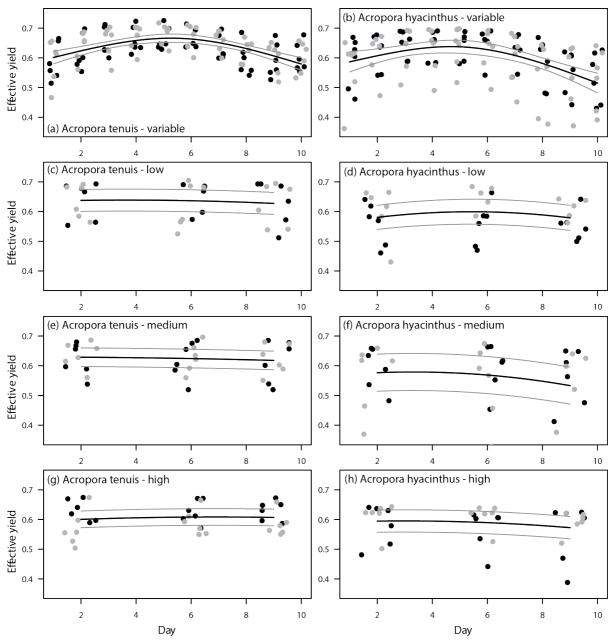


Figure 13: The effective quantum yield (ϕ_{PSII}) of photosystem II in *Acropora tenuis* (a, c, e and g) *and A. hyacinthus* (b, d, f and h) in the variable (a and b), low (c and d), constant medium (e anf f) and high (g and h) light intensity treatments over the final ten days of the 49 day experiment. This time period covered a complete light-cycle in the variable treatment. Grey points represent the 900 ppm pCO₂ treatment, while black points are the 400 ppm treatment. The black lines represent the modelled means, while the grey lines are confidence intervals. The ϕ_{PSII} shows the proportion of available light that is being used for photosynthesis (i.e. a value of 0.6 indicates 60% of light is being photosynthesised).

The eETR values, as an index of photosynthesis, differed drastically between light treatments in both coral species (Figure 14). Values increased approximately six-fold in high light, compared to low light. Both species were using approximately 60% of available light for photosynthesis (ϕ_{PSII} results above), but were receiving different amounts of light in each light treatment. This drove changes in rETR, indicating that the more light these corals received within the range tested, the higher their rates of photosynthesis.

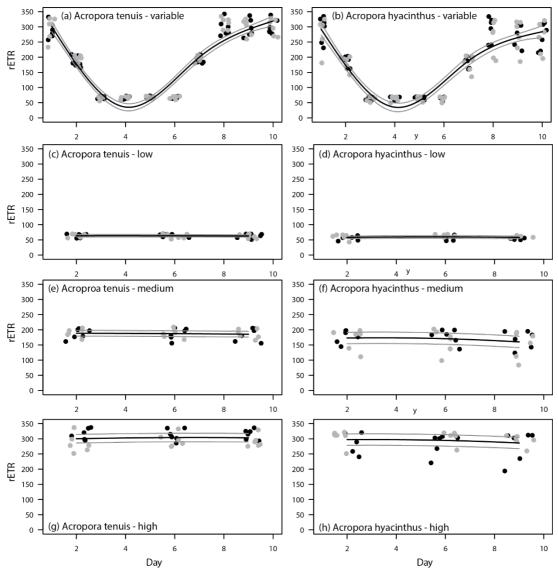


Figure 14: The relative electron transport rate (rETR) in *Acropora tenuis* (a, c, e and g) and *A. hyacinthus* (b, d, f and h) in the variable (a and b), low (c and d), constant medium (e anf f) and high (g and h) light intensity treatments over the final ten days of the 49 day experiment. This time period covered a complete light-cycle in the variable treatment. Grey points represent the 900 ppm pCO₂ treatment, while black points are the 400 ppm treatment. The black lines represent the modelled means, while the grey lines are confidence intervals. rETRs give an estimate of photosynthetic rates.

Conclusions

Results from this experiment show conclusively that for these two coral species it is the cumulative amount of light they receive, regardless of how variable the delivery, which affects their physiology. Coral growth rates increased linearly with DLI, and did not differ between variable and constant light treatments with the DLI. This pattern was also reflected in the amount of proteins the coral tissue contained. Photophysiological investigations indicated that corals under low light treatment were unable to acclimate (i.e by increasing ϕ_{PSII} or photopigments) to increase rates of photosynthesis to make up for the lower light levels. The positive effect increasing DLI has would certainly have an upper limit, where light levels become photoinhibiting, however these were not reached in this experiment. Interestingly pCO₂ was seen to have relatively little effect on the physiology of these corals (including growth rates), despite many other studies finding that this is the case.

This means that even short-term reductions in light over coral reefs can affect growth rates and recovery from disturbance.

2.4 Responses of the coral *Acropora tenuis* to moderate and strong Light limitation in coastal waters

This work was conducted in collaboration with scientists at the Helmholtz-Institute for Functional Marine Biodiversity at the University of Oldenburg with funding from Australian Government's Super Science Initiative (Grant FS110200034), the Australian Government's National Environmental Research Program and National Environmental Science Program – Tropical Ecosystems Hub, the PADI Grant Foundation, the ARC Centre of Excellence for Coral Reef Studies (Grant No. CEO561435 (2012-2013) and CE140100020 (2014-2016)), and the Australian Institute of Marine Science.

It has been submitted for publication as "Contrasting responses of the coral *Acropora tenuis* to moderate and strong light limitation in coastal waters", by Julia Strahl, Melissa M. Rocker and Katharina Fabricius. An abstract of the work is presented here.

Abstract

Coastal water quality and light attenuation can detrimentally affect coral health, although greater food availability in nutrient-rich waters might also increase the resilience of some corals to environmental stress. This study investigated the effects of light limitation and water quality on the physiological performance of the coral Acropora tenuis. Branches of individual colonies were collected in 2 m water depth at six inshore reefs at increasing distances from major river sources in the Great Barrier Reef, along a strong water quality gradient in the Burdekin and a weak gradient in the Whitsunday regions. Rates of net photosynthesis, dark respiration, and light and dark calcification were determined at daily light integrals (DLI) of moderate (13.86-16.38 mol photons $m^{-2} d^{-1}$), low (7.92-34 9.36 mol photons $m^{-2} d^{-1}$) and no light, in both the dry season (October 2013, June 2014) and the wet season (February 2014). Along the strong but not the weak water quality gradient, rates of net photosynthesis, dark respiration and light calcification increased towards the river mouth both in the dry and the wet seasons. Additionally, a ~ 50% light reduction (from moderate to low light), as often found in shallow turbid waters in the Burdekin region, reduced rates of net photosynthesis and light calcification by up to 70% and 50%. The data show the acclimation potential in A. tenuis to river-derived nutrients and sediments at moderate DLI (i.e., in very shallow water). However, prolonged and frequent periods of low DLI (i.e., in deeper water, especially after high river sediment discharges) will affect the corals' energy balance, and may represent a major factor limiting the depth distribution of these corals in turbid coastal reefs.

Conclusions

This work complements the laboratory-based experiments described above, providing evidence that these relationships also hold true in the field. Both photosynthesis by coral symbionts and coral calcification are very substantially reduced in the field at bPAR < 10 mol photons $m^{-2} d^{-1}$.

2.5 Summary of findings: PAR thresholds and responses

Key points from the experimental work and review of literature described in this section will be taken forward for development of a bPAR WQI. These include:

- Growth of both corals and seagrasses can be impacted by even short periods of low light. Recruitment of corals can also be impacted by short periods of low light.
- Coral (Acropora tenuis and A. hyacinthus) growth responds to daily integrated PAR, regardless of PAR variability on shorter time-scales. Variability during the day (e.g. due to cloud cover or tidal resuspension) has the effect of reducing daily integrated light relative to uninterrupted clear-sky and clear-water conditions.
- Strong coral (*Acropora spp.*) growth is observed in both the laboratory and in the field bPAR in the 12 to 16 mol photons m⁻² d⁻¹ range. Above this range, there is relatively little increase in growth.
- Photoinhibition (reduced growth) can occur at very high PAR (e.g. 32 mol photons m⁻² d⁻¹), but coral species that grow in the shallow environments that receive very high bPAR are generally adapted to these conditions.
- Both photosynthesis by coral symbionts and coral calcification (*Acropora spp.*) are very substantially reduced in the field at bPAR < 10 mol photons m⁻² d⁻¹ and further reduced at lower bPAR.
- Seagrasses are generally at risk of light limitation when bPAR falls below 5 or 6 mol m⁻² d⁻¹.
- Seagrass (*Halophila* species) growing in deep water (>10 m) have lower light requirements, and are impacted if light falls below 3.2 mol m⁻² d⁻¹.

3.0 DEVELOPMENT OF A REMOTE SENSING ALGORITHM FOR BENTHIC LIGHT (BPAR) IN THE GREAT BARRIER REEF

This work is being prepared for publication as "Model for deriving benthic irradiance in the Great Barrier Reef from MODIS satellite imagery", by Marites M. Magno-Canto, Lachlan I. W. McKinna, Katharina E. Fabricius, Barbara J. Robson and Yvette Everingham.

An abstract and key figures are provided here.

Abstract

We developed a simple but spectrally-resolved ocean color model to derive benthic photosynthetically active radiation (bPAR) for waters of the Great Barrier Reef (GBR). Australia for the first time. For coastal marine environments and coral reefs, the underwater light field is critical to ecosystem health, but bPAR data rarely exist at ecologically-relevant spatiotemporal scales, despite the wealth of publicly-available remotely sensed datasets. While a number of ocean color satellite processing algorithms have been developed for monitoring optically complex waters of the GBR, none have focused on deriving benthic light availability. The bPAR model presented here is a simple implementation of Beer-Lambert's Law that uses: (i) surface values of the downwelling solar irradiance, $E_s(\lambda)$, (ii) high-resolution bathymetry data, and (iii) the diffuse attenuation coefficient, $K_d(\lambda)$, calculated from derived GBR-specific spectral inherent optical properties (IOPs) to derive instantaneous estimates of bPAR at the bottom of the water column. Assuming clear skies, these values were then used to obtain daily integrated benthic PAR values for each day when concurrent satellite imagery and in situ data were available. Matchups between concurrent satellite-derived bPAR and in situ values recorded at four test sites within the GBR of varying optical properties and depths showed strong agreement, small bias and acceptable model performance within 24-25% accuracy (mean absolute error, MAE = 1.24, 1.25). Overall matchup results suggest that our benthic irradiance model was not limited by the spatial variation in optical properties that may be typical of a complex and shallow coastal waters such as that found within the GBR lagoon. We further applied this model to data from a small region in the central GBR, revealing patterns of strong temporal variability. Our model will provide the critical dataset that will allow future assessment of changes in bPAR in response to external drivers, and may form the basis for a future water quality index for the GBR that is based on light availability. Lastly, despite having some limitations, this model will also be applicable to other coastal waters for which spectral IOP and high resolution bathymetry datasets exist.

Key figures

Locations of PAR loggers deployed to provide validation data for algorithm development are shown in Figure 15, and match-ups between observed and remote sensing PAR at each of these sites are shown in Figure 16. The algorithm developed here has been applied to produce daily integrated benthic light maps for the Great Barrier Reef. The algorithm has also been applied to produce satellite-derived daily integrated PAR maps at depths of 8 m, 30 m and the bottom of the water column (i.e. bPAR). An example daily integrated bPAR map is given as

Figure 17. Daily integrated bPAR maps for every day from December 2002 through to March 2017 are being made available through eAtlas.

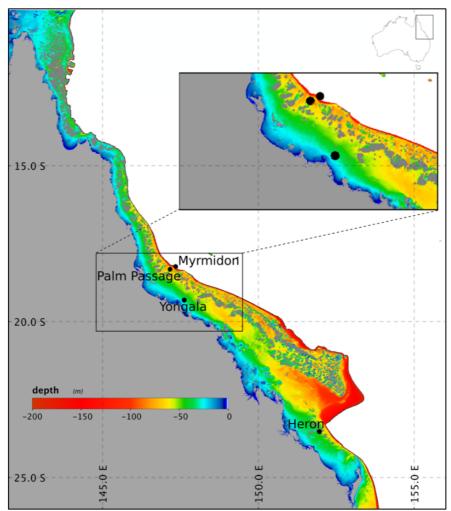


Figure 15: Location map of the four validation sites within the GBR region along the north eastern coast of Australia (inset map). The colour indicates depth contours within the shelf. The rectangle indicates the boundary of the small regional box, Burdekin region, used for temporal evaluation of the model (as detailed in section 3.5) with the corresponding subset bathymetry showing the complex topographic features in the model region. Gray masked regions indicate land and coral reefs.

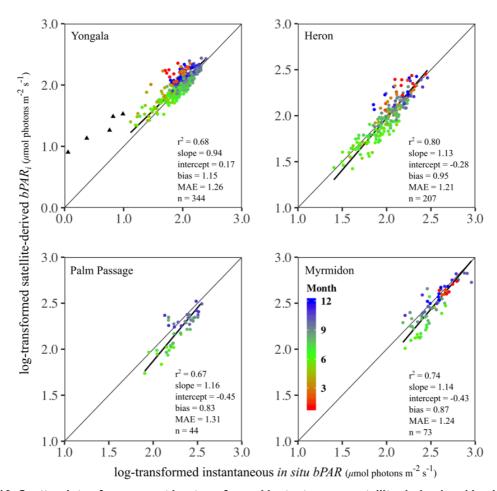


Figure 16: Scatterplots of concurrent log-transformed instantaneous satellite-derived and in situ bPAR for the four test regions of varying optical properties. The colour gradient of the data points correspond to the month of the concurrent observations. The thin and thick black solid lines indicate the 1:1 line and the reduced major axis regression slope, respectively.

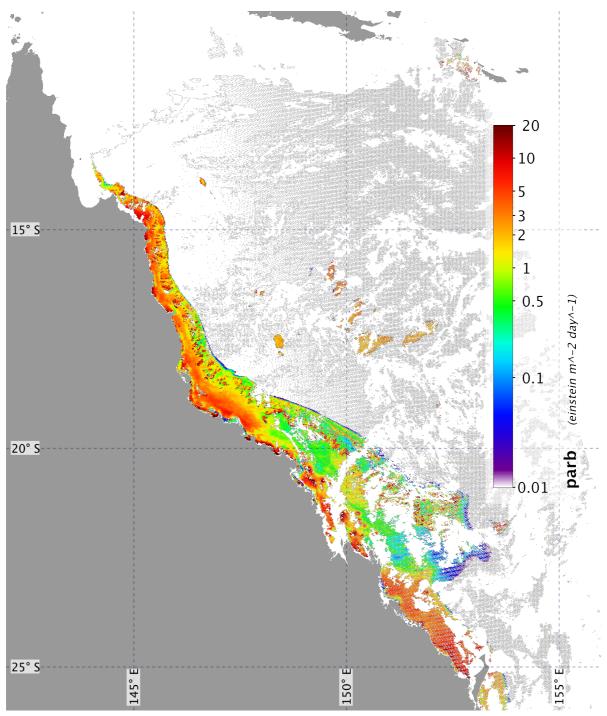


Figure 17: Example bPAR (benthic light) map showing the amount of light reaching the bottom of the water column on 1 January 2004, using data derived from NASA's MODIS satellite and an inherent optical property-based algorithm developed during the course of this project.

Conclusions

The bPAR algorithm developed in this project provides a cost-effective, readily-automated means to assess light reaching benthic habitats throughout the Great Barrier Reef on a daily, seasonal or annual basis. The algorithm developed here will be incorporated into the main NASA data visualisation software (SeaDAS) so that it becomes routinely available. This provides the necessary data source for development of a bPAR WQI to better monitor fluctuations and changes in the ecosystem health of the GBR.

4.0 DEVELOPMENT OF A BENTHIC-LIGHT BASED WATER QUALITY INDEX (WQI)

Water depth varies across the Great Barrier Reef Marine Park and Coral Sea from 0 to more than 4,000 m. Most corals are associated with shallow waters, though mesophotic reef communities are found at depths of 30 to 150 m (Englebert et al., 2017; Muir, Wallace, Bridge, & Bongaerts, 2015), and seagrasses have been observed at depths of up to 61 m (Coles, McKenzie, De'ath, Roelofs, & Long, 2009). A map showing depth variations in areas up to 61 m deep is provided as Figure 18.

In developing a WQI, it is not sufficient to simply consider mean annual bPAR in a region, as high light intensity during some of the year may effectively mask short periods of reduced bPAR that will be sufficient to hinder coral and seagrass growth (see Sections 0 and 0). Considering the need to relate changes in bPAR to ecological outcomes in a way that allows progress and variations in water quality to be tracked from one year to the next, we present the following recommended approach:

- 1) Assign a raw index from 0 to 1 for each spatial cell in the satellite data across the GBR domain for each day in the record, where 0 = 0 mol photons m⁻²d⁻¹ (representing no light) and 1 indicates a daily light integral (DLI) of 14 mol photons m⁻²d⁻¹ or more, representing high-light conditions above which additional improvements in growth rates are unlikely (see Section 0).
- 2) Calculate the mean raw index value for each cell over each month. This step avoids biasing the index towards values from months with clear skies.
- 3) Calculate an annual mean value for each cell for each water year (defined as 1 October of one calendar year through to 30 September of the year following) from the monthly mean values.
- 4) Map the regions over which the annual-mean raw index value is greater than or equal to 0.3 (corresponding to a DLI of at least 4 mol photons m⁻²d⁻¹, likely sufficient to support seagrasses see Section 0) and regions over which the annual-mean raw index value is equal to or greater than 0.7 (corresponding to a DLI of at least 10 mol photons m⁻²d⁻¹ and likely sufficient to support sustained growth of common coral species see Sections 0 and 0). Figure 19 compares areas mapped for the 2002-2003 wet season with areas of known or previously-predicted seagrass and reef cover.
- 5) Calculate the total area of potentially optimal bPAR benthic habitat (raw index >= 0.7) in each region for each water year and divide this by the maximum observed area of potentially suitable habitat in that region in any season between 2002 and 2018. This adjustment ensures that regions with more deep water are not unduly penalised relative to shallow regions, and nearshore regions are not compared with a completely unachievable standard.
- 6) Divide by 0.8 to produce values varying between 0 and 1. (This scaling factor may need to be revisited as a longer time series becomes available).

An argument could be made for the use of lower thresholds as seagrasses and mesophotic corals exist in areas of lower DLI. However, testing of several possible combinations showed that the application of a 14 mol photons m⁻²d⁻¹ cap with a 0.7 threshold for

"potentially suitable habitat area" produces a WQI that is responsive to regional and interannual variations and adequately reflects observed benthic habitat distributions.

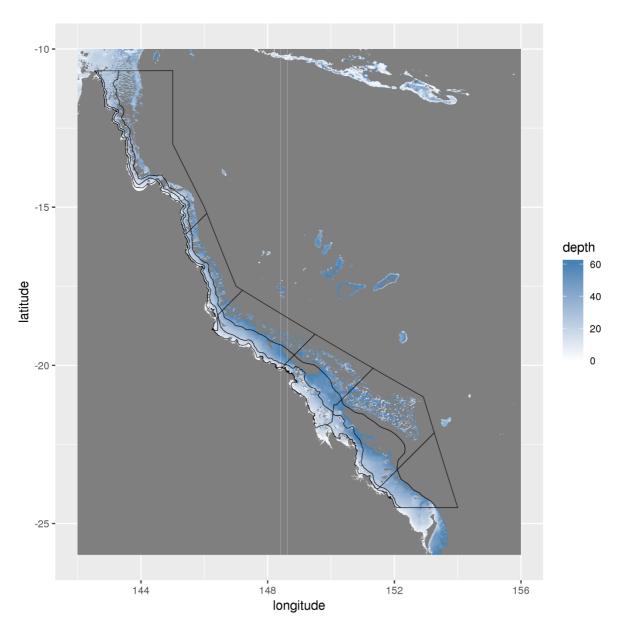


Figure 18: Bathymetry map showing areas where depth is less than 61m, the depth to which sparse seagrass beds have been observed in the Great Barrier Reef (Coles et al., 2009). Boundaries of regions are shown as black outlines.

Figure 19 compares locations of coral reefs in GBRMPA maps and observed and previously-predicted locations of seagrass beds (right) with areas potentially suitable for coral and seagrass growth in 2002-2003 according to the benthic light WQI described above. Other factors, including direct impacts of sedimentation, freshwater and pesticide exposure, impacts of past flood plumes, and impacts of cyclones, crown of thorns starfish, diseases and bleaching events will modify actual distributions of these habitats.

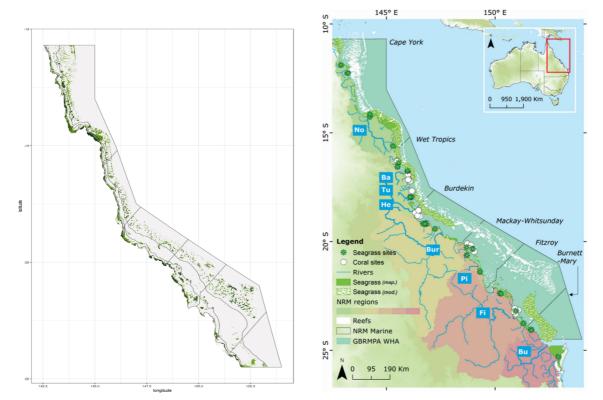


Figure 19: Left: Map showing areas where our WQI suggests that bPAR could support strong growth of seagrass (pale green) and coral (dark green) in 2003-2004. Right: Figure copied from Petus et al. (2016) under Creative Commons by Attribution (CC-BY) license (http://creativecommons.org/licenses/by/4.0/. The GBR (Great Barrier Reef) World Heritage Area, Natural Resource Management (NRM) regions and marine portions, and major rivers (Normanby: No, Barron: Ba, Tully: Tu, Herbert: He, Burdekin: Bur, Pioneer: Pi, Fitzroy: Fi and Burnett: Bu). Key marine ecosystems: coral reefs and seagrass meadows. Coral reef outlines used are per the GBR Marine Park Authority Spatial Data Centre official reefs spatial data layer 2013. Seagrass areas show where meadows boundaries have been mapped (map: composite of surveyed data as at November, 1984–June, 2010) and the modelled (mod.) probability (50%–100%, pixel size 2 km2) of deepwater seagrass habitat [17]. The seagrass and coral reef sites monitored though the Great Barrier Reef Marine Monitoring Program are indicated with green asterisks and white dots, respectively.

Benthic light WQI time series for each region are shown as Figure 20. Index values are assigned letter grades (A-E) following the system recently established in previous NESP TWQ work (Robillot et al., 2018). bPAR WQI values and grades are consistently high in Cape York regions but relatively low and temporally variable in the Fitzroy and Burnett-Mary regions. The impacts of major flood events such as a strong 2008 wet season in the Fitzroy Catchment and the larger and more widespread flooding associated with cyclone Yasi in 2011 are clearly evident in the time-series, especially in coastal regions. Offshore scores are less reactive, but still show year-to-year variability. The indicator is thus sensitive to both regional variations and year-to-year variations in water quality.

GBR-scale maps of area of potentially favourable habitat (in terms of benthic light) for each water year from 2002-2003 to 2019 (the last year is an incomplete water year) are provided as Figure 21. Detailed maps of bPAR and raw index values for each region in each water year are also available as outputs of this project.

Figure 22 and Figure 23 show alternative visualisations of the bPAR WQI scores for each region, highlighting north-to-south and east-to-west patterns in the distribution and variability of scores.

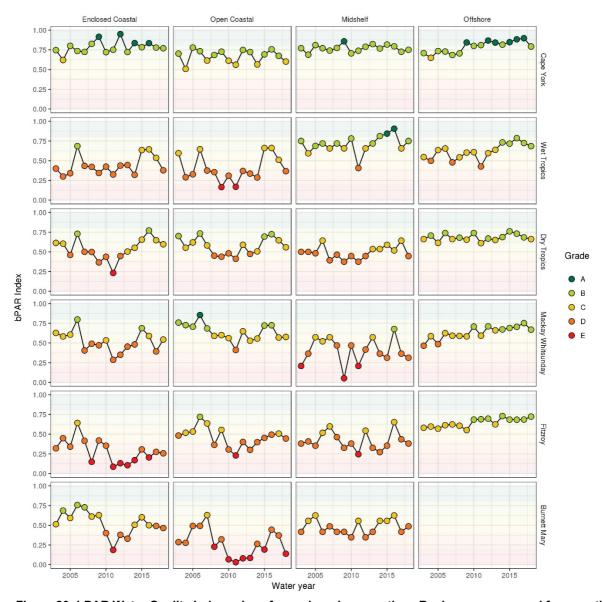


Figure 20: bPAR Water Quality Index values for each region over time. Regions are arranged from north to south (top to bottom) and from nearshore to offshore (left to right). Results are not shown for the Offshore Burnett Mary as the depth of water in this region precludes the occurrence of photosynthetic benthic habitats at the 1 km grid scale of this analysis.

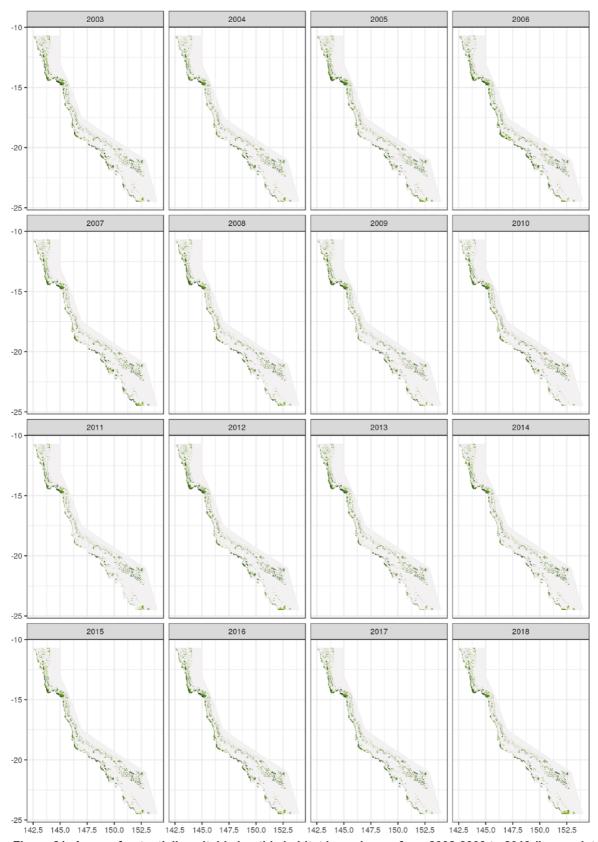


Figure 21: Areas of potentially suitable benthic habitat in each year from 2002-2003 to 2019 (incomplete year). Light green areas are those for which the mean annual raw bPAR index is greater than 0.4 (potentially suitable for sparse seagrass growth if other factors are also favourable). Dark green areas are those for which the raw bPAR index is greater than 0.7 (potentially supporting reliable coral growth if other factors are also favourable).

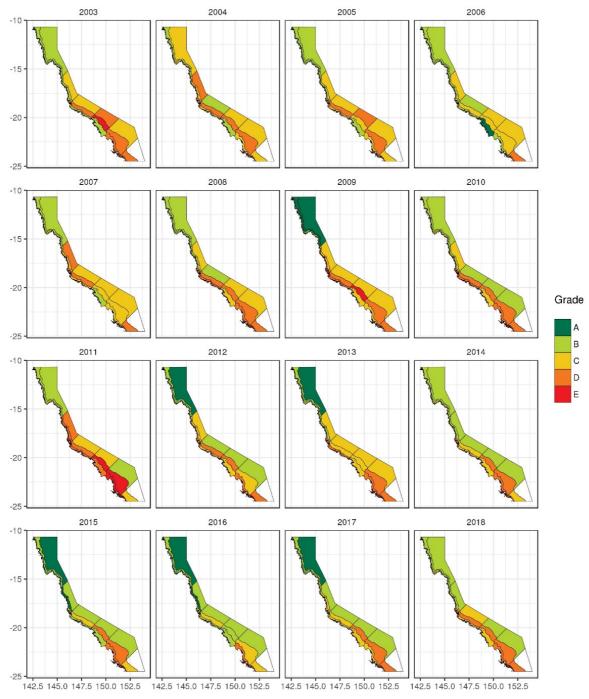


Figure 22: Alternative visualisation of WQI letter grades, highlighting spatial distribution of scores.

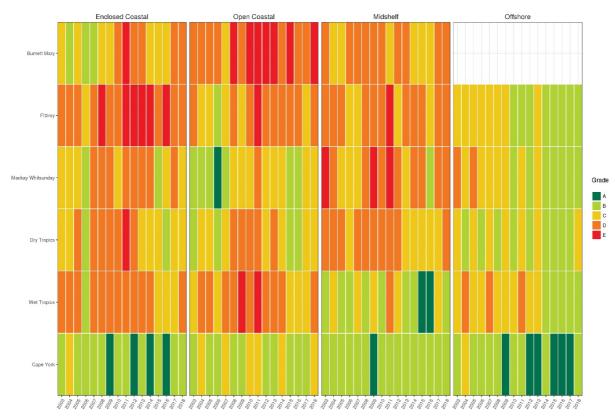


Figure 23: An alternative visualisation of the bPAR WQI scores, highlighting the general trend of improving water quality when moving from south to north (top to bottom) and from nearshore to offshore (left to right).

5.0 CONCLUSIONS AND FUTURE WORK

Combining experimental studies and analysis of existing MMP data, we have determined threshold bPAR values for ecological health in the Great Barrier Reef and used these together with a new remote sensing algorithm that allows regional-scale mapping of bPAR, we have been able to produce a new benthic irradiance water quality index that is cost-effective, easily communicated, responsive to human activities and year-to-year variations in runoff, and of direct ecological relevance.

The new water quality index has been used to map habitat suitability for coral and seagrass health and biodiversity in terms of benthic irradiance in each year from 2002-03 to 2016-17. Year-to-year variations in the area of potential benthic habitat can thus be assessed. The results show that years following major flood events are associated with reduced potential benthic productivity and habitat area, not only in coastal regions but also in midshelf regions. Year to year variations in offshore benthic light are smaller.

The WQI developed in this project can be automated and could be incorporated into Reef Plan report cards. It can also feed indirectly into Reef Plan through application in reporting of changes in seagrass distribution and abundance in the Marine Monitoring Program. In additional WQI maps will provide a new data layer to be facilitate assessment of cumulative risks and coral recovery potential in the aftermath of coral bleaching events and Crown of Thorns Starfish outbreaks. Work will continue through NESP TWQ Hub Project 5.3 to ensure that these outcomes are achieved.

This project is to be continued as NESP TWQ Hub Project 5.3. During the extension, we will:

- Further develop the remote sensing algorithm to improve its accuracy by accounting
 for regional and seasonal variations in cloud cover. This is important because wetseason benthic light will tend to be lower (and thus more limiting of potential habitat)
 in nearshore regions, but bPAR cannot be calculated for areas covered by clouds,
 which will affect annual results when cloud cover varies regionally.
- Work with key stakeholders to embed the bPAR Water quality index into their workflows.
- Evaluate GeoScience Australia's DataCube as an additional means of distribution and automation of the bPAR and WQI products.

and:

• Develop and compare the utility of an additional bPAR product based on eReefs model output, which will allow the WQI to be used in evaluation of future land-management and climate change scenarios.

DATA AVAILABILITY

Data and associated metadata arising from this project will be made available through eAtlas (https://eatlas.org.au). This includes:

- Benthic photosynthetically Available Radiation logged at four Great Barrier Reef sites, Yongala, Myrmidon, Palm Passage and Heron Island South, April 2016 to November 2017.
- Daily integrated bPAR maps for the Great Barrier Reef.
- Data from SeaSim experiment "Photophysiology of Acropora millepora and Pachyseris speciosa in response to variability in daily light integrals"
- Data from SeaSIM experiment, Light variability and CO₂ effects on adults and juveniles
 of two coral species.
- Wet season and dry season mean daily integrated light, from the 2002-2003 wet season through to the 2016-2017 wet season.
- Marine Water quality index maps for the Great Barrier Reef for each year from 2002-2003 to the 2016-2017.

REFERENCES

- Albright, R., Anthony, K. R. N., Baird, M., Beeden, R., Byrne, M., Collier, C., . . . Abal, E. (2016). Ocean acidification: Linking science to management solutions using the Great Barrier Reef as a case study. *Journal of Environmental Management, 182*, 641-650.
- Baird, M. E., Adams, M. P., Andrewartha, J., Cherukuru, N., Gustafsson, M., Hadley, S., . . . Mongin, M. (2017). CSIRO environmental modelling suite: scientific description of the optical, carbon chemistry and biogeochemical models (BGC1p0).
- Brando, V. E., Dekker, A. G., Park, Y. J., & Schroeder, T. (2012). Adaptive semianalytical inversion of ocean color radiometry in optically complex waters. *Applied Optics*, *51*(15), 2808-2833.
- Brodie, J., Baird, M., Waterhouse, J., Warne, M., Skerratt, J., Smith, R., . . . Mongin, M. (2017). Development of basin-specific ecologically relevant water quality targets for the Great Barrier Reef: Australian Centre for Tropical Water and Aquatic Ecosystem Research.
- Chartrand, K. M., Bryant, C. V., Carter, A. B., Ralph, P. J., & Rasheed, M. A. (2016). Light Thresholds to Prevent Dredging Impacts on the Great Barrier Reef Seagrass, Zostera muelleri ssp. capricorni. *Frontiers in Marine Science*, 3.
- Chartrand, K. M., Szabo, M., Sinutok, S., Rasheed, M. A., & Ralph, P. J. (2018). Living at the margins The response of deep-water seagrasses to light and temperature renders them susceptible to acute impacts. *Marine Environmental Research*, *136*, 126-138.
- Cherukuru, N., Brando, V. E., Blondeau-Patissier, D., Ford, P. W., Clementson, L. A., & Robson, B. J. (2017). Impact of wet season river flood discharge on phytoplankton absorption properties in the southern Great Barrier Reef region coastal waters. *Estuarine, Coastal and Shelf Science, 196*, 379-386.
- Coles, R., McKenzie, L., De'ath, G., Roelofs, A., & Long, W. L. (2009). Spatial distribution of deepwater seagrass in the inter-reef lagoon of the Great Barrier Reef World Heritage Area. *Marine Ecology Progress Series*, 392, 57-68.
- Collier, C., Adams, M., Langlois, L., Waycott, M., O'Brien, K., Maxwell, P., & McKenzie, L. (2016). Thresholds for morphological response to light reduction for four tropical seagrass species. *Ecological indicators*, *67*, 358-366.
- Collier, C., Chartrand, K., Honchin, C., Fletcher, A., & Rasheed, M. (2016). Light thresholds for seagrasses of the GBR: a synthesis and guiding document. Including knowledge gaps and future priorities.
- Collier, C., & Waycott, M. (2009). *Drivers of change to seagrass distributions and communities on the Great Barrier Reef: Literature review and gaps analysis*: Reef and Rainforest Research Centre.
- Collier, C. J., Ow, Y. X., Langlois, L., Uthicke, S., Johansson, C. L., O'Brien, K. R., . . . Adams, M. P. (2017). Optimum temperatures for net primary productivity of three tropical seagrass species. *Frontiers in plant science*, *8*, 1446.
- Collier, C. J., Waycott, M., & McKenzie, L. J. (2012). Light thresholds derived from seagrass loss in the coastal zone of the northern Great Barrier Reef, Australia. *Ecological indicators*, 23, 211-219.
- Dennison, W. C., Orth, R. J., Moore, K. A., Stevenson, J. C., Carter, V., Kollar, S., . . . Batiuk, R. A. (1993). Assessing water quality with submersed aquatic vegetation: habitat requirements as barometers of Chesapeake Bay health. *BioScience*, *43*(2), 86-94.
- Devlin, M. J., Petus, C., Da Silva, E., Tracey, D., Wolff, N. H., Waterhouse, J., & Brodie, J. (2015). Water quality and river plume monitoring in the Great Barrier Reef: an overview

- of methods based on ocean colour satellite data. Remote Sensing, 7(10), 12909-12941.
- DiPerna, S., Hoogenboom, M., Noonan, S., & Fabricius, K. (2018). Effects of variability in daily light integrals on the photophysiology of the corals Pachyseris speciosa and Acropora millepora. *PLoS One*, *13*(9). doi:ARTN e0203882 10.1371/journal.pone.0203882
- Englebert, N., Bongaerts, P., Muir, P. R., Hay, K. B., Pichon, M., & Hoegh-Guldberg, O. (2017). Lower Mesophotic Coral Communities (60-125mDepth) of the Northern Great Barrier Reef and Coral Sea. *PLoS One*, *12*(2).
- Fabricius, K. E., Logan, M., Weeks, S., & Brodie, J. (2014). The effects of river run-off on water clarity across the central Great Barrier Reef. *Marine pollution bulletin*, *84*(1-2), 191-200. doi:10.1016/j.marpolbul.2014.05.012
- Fabricius, K. E., Logan, M., Weeks, S. J., Lewis, S. E., & Brodie, J. (2016). Changes in water clarity in response to river discharges on the Great Barrier Reef continental shelf: 2002-2013. *Estuarine Coastal and Shelf Science,* 173, A1-A15. doi:10.1016/j.ecss.2016.03.001
- Jones, E. M., Baird, M. E., Mongin, M., Parslow, J., Skerratt, J., Lovell, J., . . . Taylor, J. (2016). Use of remote-sensing reflectance to constrain a data assimilating marine biogeochemical model of the Great Barrier Reef. *Biogeosciences*, 13(23), 6441-6469.
- Kilminster, K., McMahon, K., Waycott, M., Kendrick, G. A., Scanes, P., McKenzie, L., . . . Udy, J. (2015). Unravelling complexity in seagrass systems for management: Australia as a microcosm. *Science of the Total Environment, 534*, 97-109.
- Logan, M., Fabricius, K., Weeks, S., Canto, M., Noonan, S., Wolanski, E., & Brodie, J. (2013). The relationship between Burdekin River discharges and photic depth in the central Great Barrier Reef: Reef and Rainforest Research Centre Limited.
- Maxwell, P. S., Pitt, K. A., Burfeind, D. D., Olds, A. D., Babcock, R. C., & Connolly, R. M. (2014). Phenotypic plasticity promotes persistence following severe events: physiological and morphological responses of seagrass to flooding. *Journal of Ecology*, 102(1), 54-64.
- McKenzie, L. J., Collier, C. J., Langlois, L. A., Yoshida, R. L., Smith, N., Waycott, M., & TropWater. (2018). *Marine Monitoring Program: Annual report for inshore seagrass monitoring 2016-2017*. Townsville: Great Barrier Reef Marine Park Authority.
- Muir, P., Wallace, C., Bridge, T. C. L., & Bongaerts, P. (2015). Diverse Staghorn Coral Fauna on the Mesophotic Reefs of North-East Australia. *PLoS One*, *10*(2).
- Negri, A. P., Flores, F., Mercurio, P., Mueller, J. F., & Collier, C. J. (2015). Lethal and sublethal chronic effects of the herbicide diuron on seagrass. *Aquatic Toxicology*, *165*, 73-83.
- O'Brien, K. R., Waycott, M., Maxwell, P., Kendrick, G. A., Udy, J. W., Ferguson, A. J., . . . McMahon, K. (2018). Seagrass ecosystem trajectory depends on the relative timescales of resistance, recovery and disturbance. *Marine pollution bulletin*, 134, 166-176.
- Petus, C., Devlin, M., Thompson, A., McKenzie, L., da Silva, E. T., Collier, C., . . . Martin, K. (2016). Estimating the Exposure of Coral Reefs and Seagrass Meadows to Land-Sourced Contaminants in River Flood Plumes of the Great Barrier Reef: Validating a Simple Satellite Risk Framework with Environmental Data. *Remote Sensing*, 8(3).
- Ralph, P. J., Durako, M. J., Enriquez, S., Collier, C. J., & Doblin, M. A. (2007). Impact of light limitation on seagrasses. *Journal of Experimental Marine Biology and Ecology, 350*(1-2), 176-193.

- Rasheed, M. A., McKenna, S. A., Carter, A. B., & Coles, R. G. (2014). Contrasting recovery of shallow and deep water seagrass communities following climate associated losses in tropical north Queensland, Australia. *Marine pollution bulletin, 83*(2), 491-499.
- Reef Water Quality Protection Plan Secretariat. (2013). *Reef Water Quality Protection Plan 2013*. Retrieved from Brisbane, Queensland:
- Robillot, C., Logan, M., Baird, M., Waterhouse, J., Martin, K., & Schaffelke, B. (2018). *Testing and implementation of an improved water quality index for the 2016 and 2017 Great Barrier Reef Report Cards: Summary Report* Retrieved from Townsville, Queensland:
- Skerratt, J. H., Mongin, M., Wild-Allen, K. A., Baird, M. E., Robson, B. J., Schaffelke, B., . . . Steven, A. D. L. (2018). Plankton and nutrient dynamics on the Great Barrier Reef: Skill assessment and analysis of the eReefs biogeochemical model. *Journal of Marine Systems*.
- State of Queensland. (2018). *Reef 2050 Water Quality Improvement Plan 2017-2022*. Retrieved from Brisbane, Queensland:
- Waterhouse, J., Lønborg, C., Logan, M., Petus, C., Tracey, D., Lewis, S., . . . Skuza, M. (2018). *Marine Monitoring Program: Annual report for inshore water quality monitoring 2016-2017.* (ISSN: 2208-4096). Townsville: Great Barrier Reef Marine Park Authority.
- Waterhouse, J., Shchaffelke, B., Bartley, R., Eberhard, R., Brodie, J., Star, M., . . . Kroon, F. (2017). 2017 Scientific Consensus Statement LAND USE IMPACTS ON GREAT BARRIER REEF WATER QUALITY AND ECOSYSTEM CONDITION. Retrieved from Queensland, Australia:
- Weeks, S., Werdell, P., Schaffelke, B., Canto, M., Lee, Z., Wilding, J., & Feldman, G. (2012). Satellite-derived photic depth on the Great Barrier Reef: spatio-temporal patterns of water clarity. *Remote Sensing*, *4*(12), 3781-3795.

