

REEF ENCOUNTER

The news magazine of the International Coral Reef Society



REEF PERSPECTIVES

Michael J Risk: The blind men, the elephant & the cliff

REEF CURRENTS

Samuel E Kahng: Coral geometry & growth

RUTH GATES GRANT REPORTS

Coral heat tolerance across thermal regimes in Palau

Caribbean coral conservation goals

Conservation plan for Maui's resilient corals

REEF DEPARTURES

Charles Sheppard

Helmut Schuhmacher

Carleton Ray

REEF EDGE

Use of degraded coral heads by reef fishes

The landscape of fear and coral restoration



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Coordinating Editor

Rupert Ormond (rupert.ormond.mci@gmail.com)

Deputy Editor

Caroline Rogers (caroline_rogers@usgs.gov)

Editorial Panel

Beatriz Casareto (becasar@shizuoka.ac.jp)

Douglas Fenner (douglasfennertassi@gmail.com)

Deborah Gochfeld (gochfeld@olemiss.edu)

Edwin Hernandez-Delgado (coral_giac@yahoo.com)

Dennis Hubbard (dennis.hubbard@oberlin.edu)

Nicolas Pascal (nppacific@gmail.com)

William Precht (william.precht@gmail.com)

Silas Principe (silasprincipe@yahoo.com.br)

Sue Wells (suewells1212@gmail.com)

INTERNATIONAL CORAL REEF SOCIETY

The International Coral Reef Society was founded (as the International Society for Reef Studies) in 1980, at a meeting in Cambridge, UK. Its mission is to promote the acquisition and dissemination of scientific knowledge to secure coral reefs for future generations.

President: Christian Voolstra (Germany) (christian.voolstra@uni-konstanz.de)

Vice President: Tracy Ainsworth (USA) (tracy.ainsworth@unsw.edu.au)

Treasurer: Anderson Mayfield (USA) (abm64@miami.edu)

Recording Secretary: Anastazia Banaszak (Mexico) (banaszak@cmarl.unam.mx)

Communicating Secretary: Mark Eakin (USA) (corals.and.climate@gmail.com)

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Tries Razak (Indonesia)

James Reimer (Japan)

Hector Reyes-Bonilla (Mexico)

Verena Schoepf (Netherlands)

Coral Restoration Consortium Chapter

Tom Moore (tom.moore@noaa.gov)

Scott Winters (Scott@coralrestoration.org)

Tali Vardi (tali.vardi@noaa.gov)

European Chapter (chair)

Get Woerheide (woerheide@lmu.de)

Mexican Chapter (chair)

Rafael Cabral Tena (rafacabraltena@gmail.com)

Mid-East Chapter (chair)

John Burt (john.burt@nyu.edu)

Student Chapter (co-chairs)

Jenny Mallon (jmallon967@gmail.com)

Morgan Short (ms4341@mynsu.nova.edu)

Conservation Committee (co-chairs)

Simon Harding (simon.harding@usp.ac.fj)

Raquel Peixoto (raquel.peixoto@kaust.edu.sa)

CORAL REEFS - THE JOURNAL

The International Coral Reef Society also publishes through Springer its premier scientific journal entitled "CORAL REEFS". The Journal publishes high quality scientific papers concerning the broad range of fields relevant to both modern and ancient reefs. For further details, including the list of editors [see here](#).

Editor in Chief

Morgan Pratchett (morgan.pratchett@jcu.edu.au)

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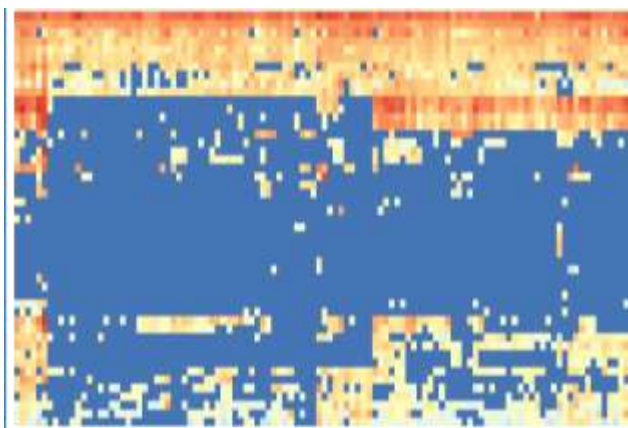
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ABOUT THE COVER | Corals, seagrasses, sponges and reef fishes among mangroves on St. John, US Virgin Islands. (Photo by Caroline Rogers)

EDITORIAL & OFFICERS' REPORTS



PRESIDENT'S MESSAGE

Christian R Woolstra, ICRS President

Dear ICRS members,

It has been six months since the last *Reef Encounter*, and since then we have seen the official declaration by NOAA and ICRI, on April 15, 2024, of the **4th Global Coral Bleaching Event** (<https://icriforum.org/4gbe/>). This was not unexpected, given the 2023 heatwave in Florida and the wider Caribbean, to which we all stood witness, and which started earlier, lasted longer, and was more severe than any previous event in that region.

What is new is that it didn't take the peak of a very strong El Niño to drive the bleaching event; rather, the relentless march of climate change triggered prevalent global bleaching upon which the El Niño is (was) superimposed. The unprecedented nature of the 4th Global Coral Bleaching Event is also exemplified by the fact that NOAA had to extend their Bleaching Alert scale to Alert Level 5 to indicate near-complete mortality ([link](#)).

When we discussed the implications of these events on the ICRS council, we decided that we wanted to write a brief perspective, since – on a personal level – the situation is becoming more depressing and frustrating by the day, and I (and many others) keep talking to coral reef researchers who are losing hope. Our thoughts are published in an Editorial in our 'house journal' *Coral Reefs* in a paper titled **The Fourth Global Coral Bleaching Event: Where do we go from here?**. The article is openly accessible at <https://doi.org/10.1007/s00338-024-02504-w>

My personal view is that this article presents some good thoughts; it was a rewarding experience to write with a group of like-minded people, which provided encouragement and resilience. First off, we have to keep doing research, but we also have to organize ourselves better and work better together to hasten insight and development of mitigating interventions. We are all in the same fight and want the same thing, and there is no room for pettiness (it's a distraction and a waste of energy and time). Second, coral reef protection must happen globally, and we should provide a strong voice to push for science, research, and implementation, irrespective of political and geographical borders. Third, we should not forget that good things are happening (albeit arguably more at a local than global scale), that strong-minded, committed people are everywhere, and that even smaller undertakings make a collective difference.

So, let's exchange any doom-laden mindset for one of a pragmatic (if hopeless) optimist. To quote the last lines of the article: "The realization that 'doing nothing changes nothing' [rather, it is poised to make things worse] can serve as inspiration to find optimism, hope, and motivation to keep fighting for a future for coral reefs."

Sincerely, Christian Woolstra



EDITORIAL

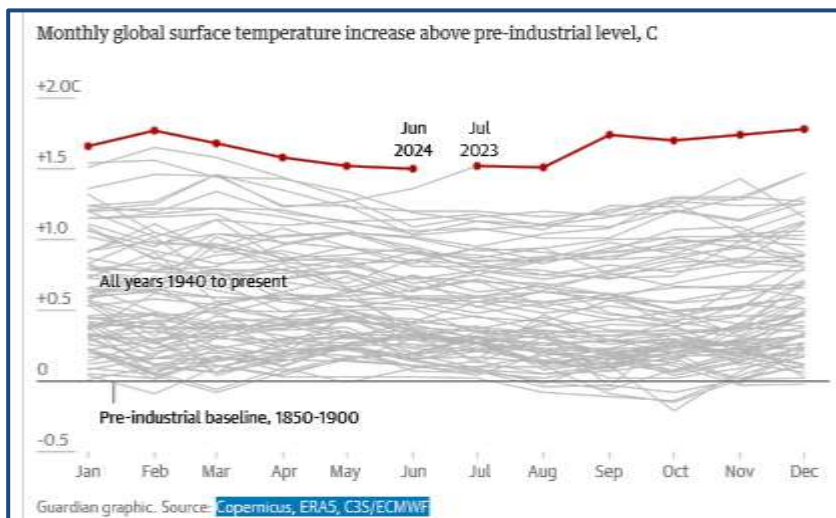
Rupert Ormond, Editor, Reef Encounter

Three related trends have been very much on my mind since our last edition. First, as discussed by Chris Voosltra on the previous page, the effects of climate change have become startlingly obvious - to those with eyes to see. Second, as documented in this issue, an increasing number of predominantly early career researchers are putting great effort into work that may enable at least some corals, perhaps even some reefs, to survive this onslaught. And third, as also witnessed in our pages, there has been a noticeable acceleration in the mortality of not only corals, but sadly also of coral scientists.

The signals that global warming is underway have never been clearer. Besides widespread mass bleaching leading to the recognition in April by NOAA of the fourth global coral bleaching event, the year up to the present month has seen the first 12 months in which global mean temperature in each month has been higher than in any other previous year. It has also been the first year in which, earlier than hoped, global temperatures have exceeded the 1.5°C above the pre-industrial norm that international climate change agreements have sought to prevent. This is the threshold that the Society proposed to the Paris Conference of the Parties (CoP) to the Climate Change Convention in Paris in 2015, and has since lobbied for, most recently at the CoPs in Glasgow, Sharm El Sheikh and Dubai.

On the ground, exceptional temperatures in many warmer countries (notably Saudi Arabia and India) have led to the deaths of thousands of people. And even in the southern Mediterranean (Greece and Spain) and North

America (Oregon and California) there have been dozens of deaths of hikers and others who had not appreciated the dangers of heat stroke¹. It seems that despite these events there remains a significant portion of the populations of even better educated countries who do not believe the “net zero” target to be a necessity. There remains a huge outreach challenge to explain, not just



Mean global temperatures more than 1.5°C above pre-industrial norm in every month of past year (July 2023 – June 2024). Source Guardian, 8th July 2024.

¹ A warning to field workers. In heat stroke the person affected quickly loses mental capacity rendering them incapable of sensible precautions. It may kick in without the more usual heat exhaustion symptoms becoming evident. (see e.g. <https://www.mayoclinic.org/diseases-conditions/heat-stroke/symptoms-causes/syc-20353581>).

to politicians, but to the people who vote for them, just why this target must be reached. Not just to save nature, as sceptics often complain, but to save ourselves from ourselves.

Meanwhile the need has never been greater to find ways in which we can increase the thermal tolerance of corals (by however little) and keep at least some reefs and ecosystems in operation until conditions ameliorate. As described in this issue a growing number of committed young researchers have been tackling this problem. Igor Pessoa has been considering how to preserve Maui's resilient corals and Liam Lachs studying heat tolerance in Palau (both with the support of grants in honour of our past President Ruth Gates), while Shakeel Joggee has been looking at coral heat shock proteins in Mauritius (part-funded by a Society's graduate fellowship). These topics are not just fashionable, they have become critical.

While a new generation of reef scientists is facing this challenge, an older generation is departing. In this issue we carry tributes to three reef scientists who did much to promote the protection of the marine environment. Carleton Ray was probably the first scientist to argue the need for MPAs and helped establish the first MPAs in East Africa and the Caribbean as long ago as the 1960s. Helmut Schuhmacher was well known from the 1970s through to the 1990s for his monitoring work on Red Sea reefs and subsequently became the grandfather of the reef conservation movement in Germany. And Charles Sheppard's sudden death has occurred when he was still considered a leader in coral reef work though the Middle-East and Indian Ocean.

We could have carried in this issue as many obituaries again, since during the past six months we have also lost other once high-profile members, including John Ware and David Hopley, whose memorial articles we expect to include in our next issue. Evidently, those of us who were in the first wave of scientists to take ecology underwater (albeit with old-fashioned twin hoses and Fenzy² life-vests) are getting beyond our "three score years and ten" best-by date. Many of us were incredibly fortunate to have seen coral reefs around the world at their wonderful pristine best, in a way no previous generation had been able to do - before accelerating economic development intervened. Many of us feel guilty that we were so lucky and yet could not do more to preserve this amazing resource for our grandchildren and their children. But those I have mentioned certainly did their best.



The vintage Fenzy life-vest, as used by us first generation of diving scientists. In effect the fore-runner of today's modern BCD – but so much less!

Rupert Ormond

² For more explanation see <https://www.youtube.com/watch?v=OmrDDsG41V0>



TREASURER'S REPORT (2021)

Anderson B. Mayfield, ICRS Treasurer

Dear ICRS Members,

Wow, I can't believe as I write this that it's already May; and half the year will have come to pass by the time you all are reading this. Good thing I filed an extension on our tax return. Yes, even non-profits like ICRS need to file a tax return in the United States, where we are based, and it's a laborious procedure. The good news is that we are no longer operating "in the red," especially since we now receive royalties from Springer, the publisher of ICRS' journal *Coral Reefs*. We have received royalties for the past two years, each coming out to around \$25,000USD. When you consider that we used to pay Springer several thousand to distribute the journal on our behalf, this is certainly a change for the better.

We have also received over \$10,000 in donations from our generous members, the majority of whom would like to remain anonymous. With this in mind, I have wondered whether having donation tiers based on levels of biological organization would help promote future such donations. I could see "coral polyp" donors being in the range of \$10-500USD, "coral colony" donors at \$500-5,000USD, and "coral reef" donors for those who contributed over \$5,000USD, but I am open to suggestions. I suppose we could even have "tentacle" donors for those who contribute <\$10USD. It's ideas like these that are likely why I find myself in science rather than in marketing or advertising. In all seriousness, though, I can't help but think of all those companies with corporate responsibility initiatives, not to mention philanthropists with a passion for the oceans; how do we get on their radars? If you have any ideas, please contact me at icrstreasurer@gmail.com. I always feel like coral reefs should "sell themselves" because they are so beautiful (Figure 1), but then again, I am obviously biased.

The vast majority of coral reefs are found in developing nations (e.g., Figure 2), and in many such places, even asking a student to pay \$20USD/year for ICRS



Figure 1. A coral reef near Yanbu, Saudi Arabia. Note the paling poritids.

membership (the current rate for least developed countries) is not allowing us to meet our mission of having our society's membership base truly reflect the diverse body of individuals working on these precious ecosystems. Although a credit card is unnecessary to pay for membership, the fact of the matter is that, with the exceptions of checks (which are likely an option only for Americans), non-credit card forms of paying are associated with fees that could even surpass the cost of membership itself!

For this reason, we are exploring the idea of free memberships for those unable to pay. We have not yet formalized how this would work, and we would welcome your collective thoughts on this matter. It would certainly be evaluated on a year-by-year basis, and there would very likely be a requirement that the individual is from a developing country; we might also limit this to students, at least while we "test the waters." If you are reading this, it means



Figure 2. A vibrant coral reef off East Timor's Atauro Island (Coral Triangle). Note the absence of large fish.

you likely are a paying member, and you might indeed feel annoyed that others might be given free memberships. We would also welcome your thoughts and feedback on this, as well as whether there are other ways we could attempt to increase inclusivity in our society (again, at icrstreasurer@gmail.com). Despite being an all-volunteer-based society, we do try to take all comments and (more commonly) complaints seriously, and we will do our best to ensure that decisions are made that best allow us to promote coral reef research and conservation in diverse areas across the planet.

Please let us have your thoughts!

Anderson Mayfield
ICRS Treasurer

SOCIETY ANNOUNCEMENTS

2024 ICRS Awards and Honors

The International Coral Reef Society Officers and Council recently announced the winners of this year's Society Awards. The awardees are:

- Eminence in Research Award – **Todd LaJeunesse**, USA
- Mid-Career Scientist Award – **Rebecca Vega Thurber**, USA
- Early-Career Scientist Award – **Sarah Davies**, USA
- Coral Reef Conservation Award (\$2,500) – **Francis Staub**, UK
- World Reef Award (\$2,500) – **Tries Razak**, Indonesia

The following nominees were awarded ICRS Fellow status:

- **James Reimer**, Japan
- **William Precht**, USA
- **Robert Toonen**, USA
- **Iliana Baums**, Germany
- **Michael Sweet**, UK
- **Michael Berumen**, Saudi Arabia

We are also pleased to announce the following Fellowship winners. These fellowships provide financial support for student research projects (Ruth Gates and Graduate Research Fellowships) and the development of science communication skills for a society member (Science Communications Fellowship-no applicants this year). The awardees are:

Ruth Gates Fellowship (\$5,000): • **Wyatt Million**, Australia

Graduate Research Fellowships (\$2,500)³

- **Ingrid Bunholi**, Brazil
- **Annabell Klinke**, Germany
- **Dominica Harrison**, Canada
- **Alexandra Jordan**, UK
- **Lili Vizer**, Hungary
- **Akaya Paul**, Japan
- **Sruti Jeetun**, Mauritius

Due to the high standard of applications received this year, the ICRS Awards committee would also like to provide an honorable mention of the following applicants:

- Mid-Career Scientist Award: **James Reimer** and **Iliana Baums**
- Ruth Gates Fellowship: **Maya Powell**
- Coral Reef Conservation Award: **Phanor Montoya-Maya**

Thank you to all nominees, nominators, and writers of letters of support. You all help make the ICRS a thriving Society. The ICRS supports diversity and inclusivity, and we are happy to be able to award the most diverse cohort of awardees to date, representing scientists and students from across the globe.

ICRS Awards Committee

³ ICRS typically awards six graduate fellowships per year, but due to the exceptional quality of applications received, we are awarding seven this year!

SOCIETY ANNOUNCEMENTS

Welcome to the NEW Coral-List!

This year the widely used coral reef email list-server "Coral-List" has found a new home with the Society (ICRS). It began life in 1995 at NOAA's Atlantic Oceanographic and Meteorological Laboratory (AOML), where it was guided by the NOAA Coral Reef Conservation Program's strategy for coral reef conservation. The ICRS is deeply grateful to Jim Hendee, Mike Jankulak, and the AOML's Ocean Chemistry and Ecosystems Division for establishing and managing the list until now.

The purpose of Coral-List has been and remains to provide a forum for internet discussions and announcements among coral health researchers pertaining to coral reef ecosystem research, conservation, and education. The list is primarily for use by coral reef ecosystem researchers, scientists and educators, but is open to everybody. As of June 2024, over 9,600 coral reef conservationists and concerned citizens were subscribed to the list.

Detailed information about the list can be found at:

<https://lists.coralreefs.org/mailman/listinfo/coral-list>

Using Coral-List

You subscribe to Coral-List by filling out a form (see the above webpage). You will be sent an email requesting confirmation, to prevent others from gratuitously subscribing you. Once confirmation is received, your request will be held for approval by the list moderator. You will be notified of the moderator's decision by email. The list is a hidden list, which means that the list of members is available only to the list administrator.

To post a message to all the list members, send an email to coral-list@lists.coralreefs.org. Note that, at present, Coral-List is a text-only medium. Posts with attachments, such as images, PDF documents, or even small logos included in email footers, will usually be rejected by the software.

Restrictions

There are a number of restrictions on the use of Coral-List. In Summary:

- Messages with solicitations of a commercial or political nature, inflammatory commentary and other messages not appropriate for the Coral-List venue will not be approved for posting.
- Crowd-funding: we require that any posting of a crowd-funding project contain a statement that says the entity or person making the post will not report a profit from the project to your government.
- Equity, Diversity, and Inclusion are central to the founding ethos of the International Coral Reefs Society which has aimed to build a global community of reef scientists, working together to ensure the future of coral reef ecosystems.
- The use of Coral-List to harass, threaten, embarrass, or target another person will be considered Cyberbullying. Online threats and mean, aggressive, or rude posts will not be tolerated.
- Coral-List has a zero-tolerance policy regarding the use of profanity in messages sent to our subscribers.
- Please Do Not Post Job Requests and Resumes. While Coral-List frequently carries posts about new employment positions, if you try to post a job request or a resume, it will be deleted.
- Finally it should be clear that any postings made to the Coral-List list-server are not the views of the International Coral Reef Society.

For further explanation see: <https://lists.coralreefs.org/mailman/listinfo/coral-list>

CHAPTER & COMMITTEE REPORTS

ICRS
International
Coral Reef Society
European
Chapter

ICRS European Chapter

OUR MISSION

- To pursue within Europe, and among reef scientists based in or visiting Europe, the Missions and Aims of the ICRS
- To prioritize networking and collaboration among reef scientists based in Europe, and among students studying at European Institutions

CHAPTER ACTIVITIES

- Providing financial support to ICRS European student members
- Working towards the next European Coral Reef Symposium (ECRS) in 2024

AWARDEES

Sarah Coyer
Mark Hamilton
Estradivari
Henrique Bravo
Thea Moulé
Robbert-Jan Geertsma

CHAPTER COUNCIL

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Marc Kochzius - Treasurer
Megan Clampitt - Comm. officer
Rupert Ormond - Honorary
Rosa van der Ven - ECR
Benjamin Müller - ECR
Jenny Mallon - PhD
Elsa B. Girard - PhD

Visit our website | Give us feedback

The European Chapter of the ICRS was inaugurated in late 2019, right before the COVID pandemic hit. The main aims and objectives of the chapter are three-fold: 1) to pursue the Missions and Aims of the International Coral Reef Society within Europe, and among reef scientists based in or visiting Europe; 2) to promote and support the holding of European Coral Reef Symposia at (ideally) four-year intervals; 3) to promote networking and collaboration among reef scientists based in Europe, and among students studying coral reefs at European Institutions. The chair of the European Chapter represents European interests and affairs on the ICRS council.

Chapter activities included the support of competitively selected early career researchers from Europe to cover the subscription fee for the virtual 14th International Coral Reef Symposium in 2021 (three awardees) as well as the in-person 15th International Coral Reef Symposium in 2022 (three awardees).

Since then, the chapter council has advised and encouraged the organizing committee of the upcoming European Coral Reef Symposium (ECRS) about to be held in Naples (Italy) since the proposal preparation stage. It has also supported the committee in negotiations with the ICRS council to confirm that it is an official ICRS event. Members of the chapter have been serving on the scientific committee of ECRS 2024. A chapter meeting is to be held during the ECRS 2024, during which a new chapter committee will be appointed. We therefore invite members of the Society based in Europe, who may be interested to join the committee to contact us via info@icrseurope.eu so that we can prepare a ballot for the elections.

More information on activities of the European Chapter of the ICRS can be also found on social media at: <http://icrseurope.eu>, <https://www.facebook.com/ICRSeurope/>, <https://x.com/ICRSeurope>, and <https://www.instagram.com/icrseurope/>

Gert Wörheide, Chair



ICRS-SECC

International Coral Reef Society
Student & Early Career Chapter

We are proud to be a diverse international network comprised of 58 Students & ECRs representing 25 countries! We are committed to continuing to expand the diversity of our chapter (and ICRS) through several avenues, including increasing awareness of issues surrounding equity, diversity, and inclusion, expanding our team of translators who translate our communications materials, and providing career development resources and opportunities.

This year our chapter is putting plans into action to achieve this vision. Our [Reefbites Blog](#) is updated with new pages featuring our blog posts translated into Spanish, German, Italian, Portuguese, and French. In addition, we are expanding our translated languages to include Arabic.

ICRS Student & Early Career Chapter

GOALS

- 1 Maintain a platform for students & ECRs in coral reef research and study
- 2 Provide supportive resources for career development in the coral reef sciences
- 3 Increase accessibility and diversity of resources and also participation of ECRs
- 4 Raise awareness of coral research & conservation
- 5 Support and promote ICRS activities

INDIGENOUS & LOCAL CORAL SCIENTISTS PANEL

 Ahmi Cacapit Ahmi is an Indigenous Chamorro pursuing her PhD at Scripps Institution of Oceanography.	 Shamoy Bideau Shamoy is a Creole from St. Lucia, raised Marine Biologist and a current Environmental Specialist.
 Kaiku Kaholoa'a Kaiku is a Native Hawaiian Stanford PhD student, investigating the drivers in coral thermal tolerance.	 Anela Akiona Originally from Hawaii, Anela (Anaka) is a PhD candidate at Scripps Institution of Oceanography.

The importance of cultural diversity in research, and strategies to foster collaboration & inclusivity

APRIL 23
-100 attendees

In April, our EDI and Skill & Professional Development committee organized a successful virtual event: "Indigenous and Local Coral Scientists Panel." This first webinar was held on April 23 and welcomed over approximately 100 attendees. We are so grateful to the panelists: Ahmi Cacapit, Shamoy Bideau, Kaiku Kaholoa'a, and Anela Akiona! If you missed it, the recording is available on our chapter's website.

Later this year we will host two separate online professional development workshops designed and led by a professional trainer for ECRs. These 2-day workshops will equip participants with the skills needed to craft winning grant proposals and

impactful research papers. Students and ECRs from underrepresented groups and developing countries will be especially encouraged to apply! Registration fees will be fully covered by the ICRS (space is limited).

Lastly, we are launching an **Early Career Coral Scientist and Practitioner Jobs Board (see below)**. To post available jobs or to see the list of posted positions, head to the “Resources” page on our website.

Igor Pessoa

Interested in being involved? Connect with us!

Email: icrs.students@gmail.com
Website: www.coralreefsecc.org
Twitter: [@ICRSreefstudent](https://twitter.com/ICRSreefstudent)
Instagram: [@icrs.students](https://www.instagram.com/icrs.students)
Reefbites: www.reefbites.com

The SECC Skills and Professional Development committee is excited to announce a new resource for the ICRS (and wider) community: the ICRS-SECC Job Board. Located at coralreefsecc.org/jobboard this is an international resource which employers in coral science can use to list open positions. The intention is to connect students and those in early career with coral science and practitioner related work – this includes technician jobs, internships, graduate positions and post-docs, jobs in government or the nonprofit sector, and tenure/non-tenure track scientist/professor listings. Please feel free to share widely and email us at icrs.students@gmail.com with any issues.

We hope you find this resource useful!

Sincerely,

ICRS-SECC Skill & Professional Development Committee

Mahsa Alidoostalimi
Ben Farmer
Ronen Liberman
Daniel Olivares-Zambrano
Maya Powell
Sarah Solomon

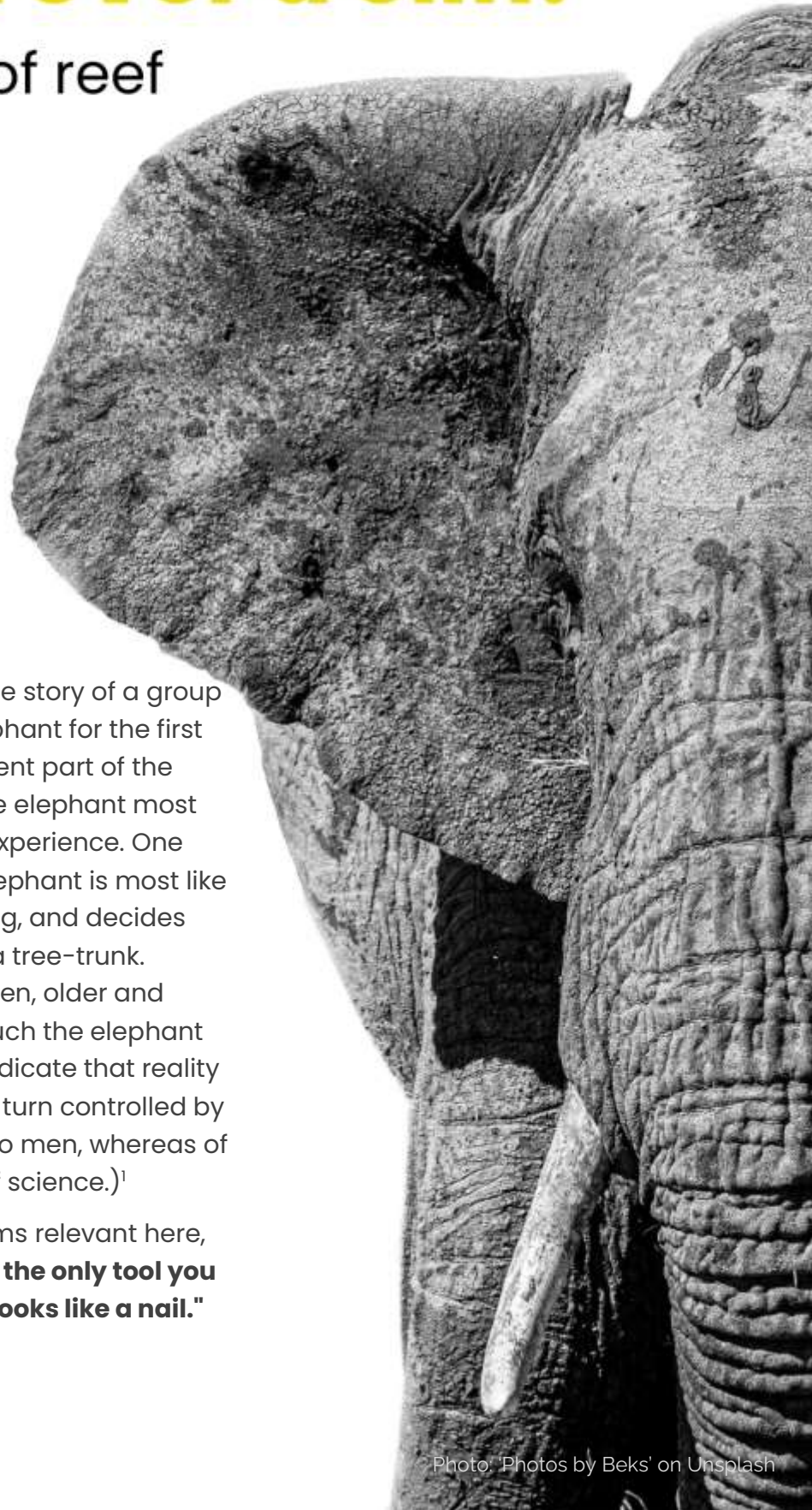
Blind men lead the elephant over a cliff: the paradoxes of reef restoration

Michael J Risk

School of Geography and Geology,
McMaster University, NOG 1R0, Canada
riskmj@mcmaster.ca

An ancient South Asian myth tells the story of a group of blind men who encounter an elephant for the first time. Each of them touches a different part of the elephant, and each decides that the elephant most resembles something in their own experience. One touches the ear, and decides the elephant is most like a fan. One touches the elephant's leg, and decides that the elephant is very much like a tree-trunk. Confusion ensues until one of the men, older and wiser than the others, decides to touch the elephant all over. Buddha uses this story to indicate that reality depends on perspective, which is in turn controlled by background. (The myth refers only to men, whereas of course both sexes contribute to reef science.)¹

There is another aphorism that seems relevant here, one usually attributed to Maslow: **"if the only tool you have is a hammer, every problem looks like a nail."**



The present situation in the scientific community regarding the coral reef crisis is very reminiscent of the parable of the blind men and the elephant. A large number of separate parts of this elephant have been touched, and conclusions have been drawn as to the nature of the beast, but a holistic vision remains elusive. As oceans warm and reefs bleach and die, there are frantic efforts under way to try to “save the reefs.”

A quarter-century ago, I wrote a paper taking the coral reef biological community (henceforth, CRBC) to task for riding madly off in all directions while reefs were dying (Risk, 2000). To summarize (although I am sure you all have read it), I postulated that the response of the CRBC to the reef crisis was lamentably slow and disorganised, compared with responses to similar largescale environmental issues.

In the cases of acid rain in the Northern Hemisphere and Great Lakes eutrophication, there was less than 10 years from identification of the problem to a generally-agreed scientific set of solutions and policy frameworks. In short, science did its job.

That neither of those two issues has been eliminated demonstrates a failure of politics, not science. In the case of coral reefs...oh boy. We knew the major drivers of coral reef decline by 1980. It's now 2024, and we are still arguing about methods, whether nutrients are important, ...yadda yadda, while reefs are in decline all over the world.

In the case of coral reefs [...] We knew the major drivers of coral reef decline by 1980. It's now 2024, and we are still arguing about methods [...] while reefs are in decline all over the world.

The reasons I suggested in 2000 for this slow, disorganized approach are just as valid now as they were then. There is a lack of competent managers - good scientists do not necessarily make good managers. There is a lot of emphasis on monitoring (and arguing about methods) without making the necessary connection that the role of monitoring is to evaluate sources of stress. The field is dominated by one discipline, biology, and interdisciplinary work is more honoured in the breach than in the observance. In short-lots of blind people wandering about feeling bits of the elephant while the poor beast staggers toward the cliff.

There is little doubt we are in the midst of a coral crisis.

Gardner et al. (2003) described the loss of 80% of corals in the Caribbean basin since the mid-1970s: the rate of loss is about 1.5% coral cover per year. Bruno and Selig (2007) note that

¹ A story, dating back to 500BC in Jain and Hindu philosophy, was popularised in the West by the 19th Century poet John Godfrey Saxe. “It was six men of Indostan, to learning much inclined, who went to see an elephant, though all of them were blind.....”



coral cover in the Indo-Pacific has declined by about half since the early 1980's, from approx. 42% to 22%; a rate of about 1% coral cover per year. Even on the Great Barrier Reef, that supposedly well-protected ecosystem is losing coral cover at the same rate. We are witnesses to the process of a global mass extinction, during which corals are dying at a rate faster than the extinction of the dinosaurs at the K/T boundary (MacLeod et al., 1997). Future paleontologists are liable to note that the world's Holocene coral reefs disappeared from one bedding plane to the next.

While it has become fashionable to talk about reef "resilience" and "adaptation", the evidence of the geologic record cannot be avoided. Reef faunas suffered several mass extinction events throughout the Phanerozoic. In some cases, the framework organisms vanished completely, such as the extinction of Paleozoic corals at the end of the Permian. Scleractinians did not arise until near the end of the Triassic, more than seven million years later (Flügel and Senowbari-Daryan, 2001). It has in fact been argued (Sheehan, 1985) that reef-building faunas take longer to recover from a mass extinction event than typical level-bottom communities. Optimistic underestimation of the scale of the present problem would not seem to be supported by the evidence: "Those who do not believe that mass extinctions are enormous catastrophes would do well to study the past" (Ward, 1995).

Dealing with this crisis, and responding to the needs of those who depend on coral reefs for their very survival, is a problem of monumental proportions that faces everyone who calls themselves a reef manager. Policy decisions have to be taken intelligently, and difficult positions may have to be maintained in the face of stubborn opposition. In order to formulate effective policy, it is important to know what went wrong. Reefs are in decline because of their response to a number of stressors, and the identification and ranking of these sources of stress is the single most important problem facing the coral reef community. This is where the elephant comes in.

There may be a hermit living in a cave somewhere in the Yukon who is as yet unaware, but by now most people will have learned of the threat posed by global warming. Media coverage has been exhaustive, and sometimes exhausting. The Economist (May 15, 2024) reports that bleaching events on the Great Barrier Reef are becoming more common, and by this Spring already 90% of the corals there had bleached. Abnormally high temperatures, usually accompanied by bleaching, have been reported from virtually every reef province, and it's been estimated that 60% of the world's corals have bleached.



Some corals can recover from a bleaching event, but repeated such events usually prove fatal. What is more, we are probably just seeing the beginning phases of the catastrophic changes in store. Future marine (and terrestrial) heat waves will be larger, more damaging, and more frequent. With the gathering evidence that the world may be witnessing the death throes of the extinction of a global biome, one might assume that the CRBC would band together and apply all their collective talent and energy to finding solutions.

The response to date has been a goat rodeo. Almost every day we see new ideas, of widely varying quality, for how to "save the reefs." Crabs will be released on Florida's reefs to eat the algae (<https://boingboing.net/2023/09/30/scientists-release-hundreds-of-thousands-of-crabs-upon-florida-to-protect-coral-reefs.html>). The urine of spiny lobsters will repel coral predators

(<https://www.theguardian.com/us-news/article/2024/may/25/spiny-lobsters-coral-reef-florida>). Biodegradable soda straws will protect young coral transplants from predators (<https://www.castanet.net/news/Around-The-Web/489531/Straws-saving-coral>). Robots will kill *Acanthaster*.

These are funny, in a very sad way. I guess the term would be

Boutique
Science-limited
application,
perhaps local
improvements,
and ultimately
pointless. Then
we get into
Maslow's
hammer-nail
framework.

It has been suggested that recovery of reefs in Maldives can be facilitated by playing back recordings, under water, of the sounds of a healthy reef (<https://metro.co.uk/2023/04/11/steve-backshall-helps-bring-the-noise-to-the-maldives-coral-reefs-18589029/>). Yes, someone working on reef bioacoustics might well think this, and it may well be true. But we have known for >30 years that the major threat to Maldivian reefs, bar climate change, is sewage discharge (Allison et al., 1991; Risk et al 1993; Risk and Sluka 2000). Surely the first principle in reef restoration is to remove the original stress first. "Folks are arguing on how to develop a better mop to wipe up the blood off the floor...rather than suturing the wound and stopping the bleeding." (Curt Storlazzi, pers comm. 2024).

There has also recently been an upsurge in the use of 3D printing, to..."save the reefs." I will cite no sources here-I have enough enemies already. Some of the 3D printing uses the well-known tendency of coral larvae to attract to specific surfaces and textures-although one such project describes this as

a new finding. Intervention techniques may very well be successful in cases where the causes of the original extirpation are known (blast fishing, for example) and recovery is planned only for a small area. To rehabilitate the world's coral reefs by 3D printing would, a back-of-the-envelope calculation suggests, require a volume of material equal to about half the global annual production of cement. Not going to happen!



The coral reef at Banda, that formed in less than 5 years. The water was clean.

Baird et al (2013) state, in one of those papers in which the title is the conclusion, "*Acanthaster planci* is a major cause of coral mortality in Indonesia." I found that curious, because in hundreds of dives over 15-odd years working all over Indonesia I don't

recall ever seeing one. Going through the many pages of reports generated over our decade-long project in that wonderful country, there is *no* mention of *Acanthaster*. Perhaps Baird et al were looking for nails. In any event, *Acanthaster* waves are just another manifestation of land-based stress (Fabricius et al., 2010).

Every reef ecologist, and everyone concerned about the decay of our favorite ecosystem, needs to keep in mind (always!!!) these basic principles:

1. Reef decline was well under way by 1970, and by 2010 we had lost most of the best of them. The same processes driving that decline will likely continue no matter what the climate does.
2. If sea-water quality is high, a reef can go from zero to hero, bare rock to 65% coral

cover, in as little as five years (Tomascik et al, 1996).

3. In every case where a reef has been monitored as the water quality improved, the reef has also improved.

If we really want to see the elephant being driven to the edge of the cliff by repeated blows of hammers, one need look no further than the myriad of reef rehabilitation projects under way. Many of these are based in Florida, including the "100 Yards of Hope" effort, when corals were outplanted to coincide with the 100th anniversary of the National Football League. Perhaps "hope" should have been spelled "hype."

For the present these efforts are all a waste of time and money. We have known for 20-odd years that the water quality in Florida is hostile to the development and survival of corals. Cover on the Florida Reef Tract has gone from approx. 60% to about 4% in 40-odd years. Porewater in the region is so toxic that coral larvae cannot survive (May et al., 2022). Yet we now see that Univ. of Miami has recently shipped a bunch of corals from Honduras up to Florida, because they seem to be thriving in Honduras so why not bring them to Florida. (<https://www.npr.org/2024/06/22/nx-s1-4995776/florida-reefs-are-in-trouble-could-the-answer-lie-in-coral-from-the-caribbean>). Presumably Florida has laws regarding cruelty to animals? In Hawaii, \$25 million dollars has been pledged to select for thermotolerant corals to be outplanted on the west coast of the Big Island (<https://news.mongabay.com/2024/06/new-approach-to-restore-coral-reefs-on-mass-scale-kicks-off-in-hawaii/>). No mention of water quality-

but the site is, after all, a long way from Kaneohe Bay, about which some papers have been written.

The sad fact is, as long as people will claim they can "save the reefs", naïve foundations and frightened politicians will shovel money out. By the time failure is apparent, the money will be all gone.

A lot of time and money has been spent on the impact of the mass death of *Diadema*, which supposedly led to the coral crash. It had been suggested (Hay, 1984; Bellwood et al., 2004) that *Diadema* had previously taken over the niche of the main fish grazers on Caribbean reefs as a result of overfishing, which made their disappearance all the more disastrous for the reefs. But this may be nonsense. First of all, if we look at the decline reported by Gardner et al, we see that the death of *Diadema* produced nary a ripple in the overall pattern. Yes, Sammarco's work (e.g. 1982) shows that the urchin was a major grazer - but its removal makes little or no change to the trend.

The sad fact is, as long as people will claim they can "save the reefs", naïve foundations and frightened politicians will shovel money out. By the time failure is apparent, the money will be all gone.

Second, *Diadema* was the major grazer in the Caribbean throughout the existence of those reefs: there was never any overfishing-driven shift in the major role of reef grazers from fish to urchins. Sammarco is one of the few who have studied grazing in both the Caribbean and the Indo-Pacific, using controlled experiments. In a series of papers (summarised in Sammarco, 1987) he has shown that benthic fauna, including corals, are subject to heavier levels of predation in the Western Indo-Pacific than in the Caribbean. There is a higher diversity of predators in the Indo-Pacific, and they are better adapted to seek out their prey. Via co-evolution, the prey are also better adapted to avoiding their predators than their Caribbean counterparts.

Given the same opportunities for settlement, through parallel experiments in the two oceans, Sammarco was able to show that coral larvae in the Caribbean are adapted *a priori* to settle on the tops of benthic surfaces. This is especially evident when grazing pressure is relaxed, revealing the default adaptation. This provides them with the best opportunities for survival and growth, yet could not be an adaptation that could survive grazing by visually-cued organisms such as fish. Indo-Pacific corals, on the other hand, will settle cryptically - even when grazing pressure is removed. The larvae are better adapted to avoid grazers and predators as newly settled spat and juveniles. They are adapted to avoid fish grazers, which use visual cues, and specialized predators (like chaetodonts).

Unless we postulate an evolutionary change in the behaviour of coral larvae that took place within the past 100 years or so, we cannot avoid the evidence of larval behaviour. Caribbean reefs have been grazed by (blind) urchins throughout the Holocene, with fish being the major grazers in the Indo-Pacific. There has been no major shift in the composition of the grazing community in the Caribbean that can be attributed to overfishing. I suggest that the *Diadema* die-off is irrelevant - a punctuation mark in the story of decline driven by land-based pollution.

Now we are faced with the imminent death of our chosen ecosystem, a terrifying realization that has spawned a plethora of responses. We need to be

hard-nosed and objective about the chances of success of these ventures, because research money is limited. I am happy to see a multi-authored Editorial in Coral Reefs (Reimer et al, 2024) calling for action, and claiming that ICRS occupies a central role in the study of coral reefs. I would be even happier had the previous membership been able to warn us 30 years ago about the impacts of land-based pollution - they had all the data they needed.

In cases where reefs have been destroyed by transient stresses such as blast-fishing, rehabilitation can indeed succeed in accelerating natural recovery (Lange et al., 2024). It may also be possible to select for thermally-tolerant coral species, by studying places where corals naturally survive high temperatures (Becking et al., 2024). Trying to selectively breed thermally-tolerant corals without understanding the genetic basis of this tolerance is not likely to succeed (Huong et al., 2024).

Above, I cite three important things that all coral rehabilitation efforts need to keep in mind. Yet I find a curious, inexplicable lacuna. I have now gone through at least 15 papers discussing reef rehabilitation, and not a single one even mentions water quality. Not one. Reasons for this are unclear - or all too clear. No one wants to challenge forces that can end careers.

It is sobering to read some of the recent work in this field. May et al. used the sea urchin embryo



toxicity technique to study porewater in Biscayne Bay. At over 80% of their sites, the porewater was so toxic that any reef growth would be impossible. All sorts of human nasties in the water: sewage, pharmaceuticals, agrichemicals. Biscayne Bay isn't the world, but it can serve as a model for any reef sitting on porous substrates, next to human influence. i.e., most of them. Li et al. (2023) studied the synergistic effects of nitrates and photosystem II herbicides, and found that this induced coral bleaching independent of water temperature. Zhou et al, 2024 show that...well, what they found is in the title. "Environmental Concentrations of Herbicide Prometryn Render Stress-Tolerant Corals Susceptible to Ocean Warming." The herbicide overwhelms the coral's photosystem repair mechanism. What's worse is that the herbicide may actively inhibit the coral's ability to recover from stress. This sort of herbicide pollution is globally widespread (Yang et al., 2024), cannot be avoided, and affects any work on coral bleaching. Huong et al. (2024) studied the metabolomics of two coral species, and concluded that a species' anti-oxidant and osmoregulatory capability was key to recovery from bleaching events. Selecting coral species for out-planting without understanding the genetic basis for resistance to thermal shock could well be futile. (Alert readers will note the nationality of authors of the latter articles. This reflects my opinion that the torch of coral reef research has passed on to the East.)

Then there are impacts from sources that simply did not exist when I was young Sunscreen pollution has been shown to affect coral larvae, and make them more susceptible to bleaching (Downs et al., 2015). The antifouling agent Irgarol 1051 affects coral larvae (Knutsen et al. 2012) and Marzoni et al (2021) found many of the herbicides used in GBR catchments may be found in nearby ocean waters, and affect coral symbionts. Microplastics seem to be an additional scourge, toxic in themselves but also carriers of herbicides, pharmaceuticals, and other modern pollutants (O'donovan et al., 2020; Pastorino, 2024).

All this excellent research simply scratches the surface of the vast arrays of chemicals that we

make and chuck into the ocean. The concept of a pristine reef, far from human habitation or impact, is no longer supportable.

Present efforts to conserve our reefs all ultimately depend on humans coming to grips with climate change, and reversing the ongoing warming in sufficient time. Ain't gonna happen! We are less than 5 years from breaching the 1.5 degree threshold (indeed we may already have reached it). Beyond that several irreversible tipping points are reached. If Hansen is right, again, multi-meter rises in sea level will occur in the next couple of decades. There is also a 10% chance that the AMOC (Atlantic Meridional Overturning Circulation) will collapse this decade (Ditlevsen and Ditlevsen, 2023). It would be churlish of me to point out that, based on coral data, we warned of this >25 years ago (Smith et al., 1997). Open-ocean pH continues to drop, such that the stability of coral skeletons is already compromised. It seems unavoidable that societies faced with economic and social collapse will have neither the resources nor the funding to support reef rehabilitation.

We have been denied the one experiment we needed to assess the future: what will be the impact of climate change on healthy reefs unaffected by humans? And for that situation, the coral reef biological community must shoulder some blame. I vividly recall the bitter Top-down vs Bottom-up arguments of years ago. Those arguing for control by grazers never had solid data to back up their position. It took decades of data produced by people with more interdisciplinary backgrounds for a better picture to emerge - but a lot of time and effort was wasted.

In short, present reef rehabilitation efforts are dispersed, scattershot, and doomed to failure as a solution to the Reef Crisis. There may be some local success stories, but these need not divert us from the unpleasant truth. We spent - YOU spent - far too long studying various parts of the elephant without noticing how close it was coming to the edge of the cliff.

After this dismal litany, what can be done? I would hate to just give up - and I would not like this rant to be a call to lose hope. I see little help coming from most senior reef researchers until a number of minds have been changed. Their recent Editorial call for action (Reimer et al., 2024) mentions neither "water quality" nor "land-based", and "pollution" occurs once, in passing.

It all depends on how much time we have before the impacts of climate change suck all the oxygen out of the room. There is hopeful talk of centuries, citation of a few decades...I am not optimistic. The vast majority of climate models and predictions have been too conservative, for things are going faster than we feared. Smith et al. (1997) showed that the transition from full-on interglacial melting to the glacial Younger Dryas took less than four years. (Yes, I keep mentioning this in the hopes that it will finally sink in). I don't think we have a century, but let's be optimistic. In that case, provided that pollution is under control, some projects may provide hope. In Fiji, Austin Bowden-Kerby and partners have a program which transplants thermotolerant corals out into cooler (less hot!) regions, where they can survive

(<https://oceandecade.org/news/launching-fijis-bula-reef/>).

We can admire the courage and dedication of those trying to save their little corners of the world's reef, while at the same time recognising that their efforts will, in all likelihood, be futile.

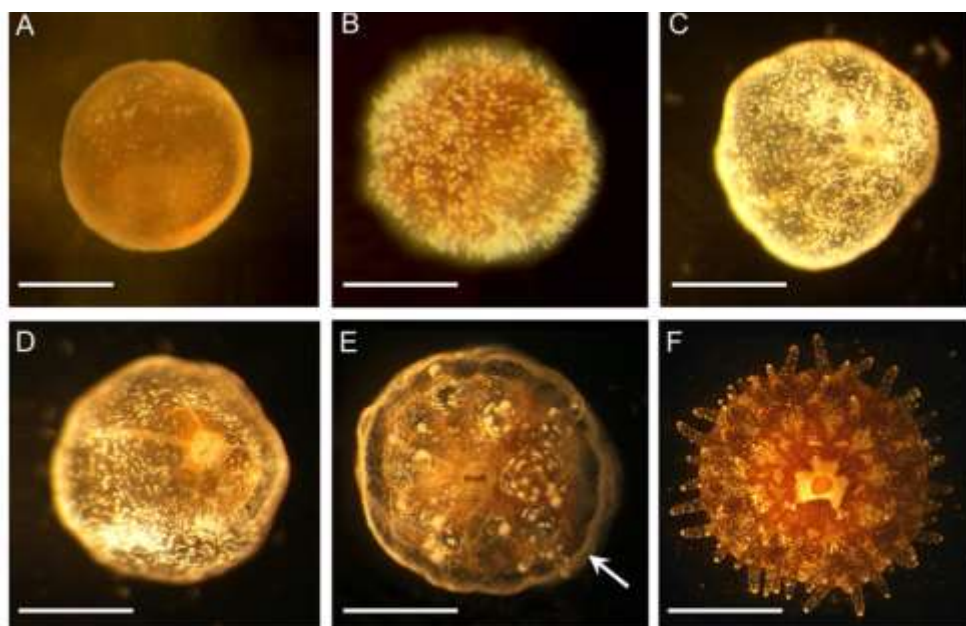
It might be possible to "migrate" small areas of reef polewards as the oceans warm and rise. Natural migration won't be fast enough to keep pace - recall that it took a thousand years for corals to colonize the areas flooded by the Holocene Transgression - and the water was clean, back then.

There will need to be an overseeing agency, able to protect their funding for decades in the face of increasing demands from other deserving agencies. Local patches may survive for a while, if the water is clean and heat-tolerant species selected. If we take the long view, however, the future is not rosy. We need something like a Norwegian Seed Bank for corals (AND hundreds of associated species) capable of enduring for centuries, if not longer.

But wait. It turns out that just such a program became available more than a decade ago, yet in a fashion by now familiar to us all, the opportunity was lost.

In 2008/9 scientists at Tel Aviv University developed a novel method for culturing corals, by which tissue spheroids were produced from a parent colony (Vizel et al., 2011). These little spheroids could then be induced to form new colonies. This work continued into cryopreservation, and more than a dozen species were frozen and regenerated. The Zoological Society, Oxford University and Haereticus formed the Global Coral Repository, which would be a way for corals to be cryopreserved for better times. This group took this "Plan B" idea to COP15 in Copenhagen, where,

The little tissue blebs pictured above can be frozen and regenerated. This may be the future of reefs.

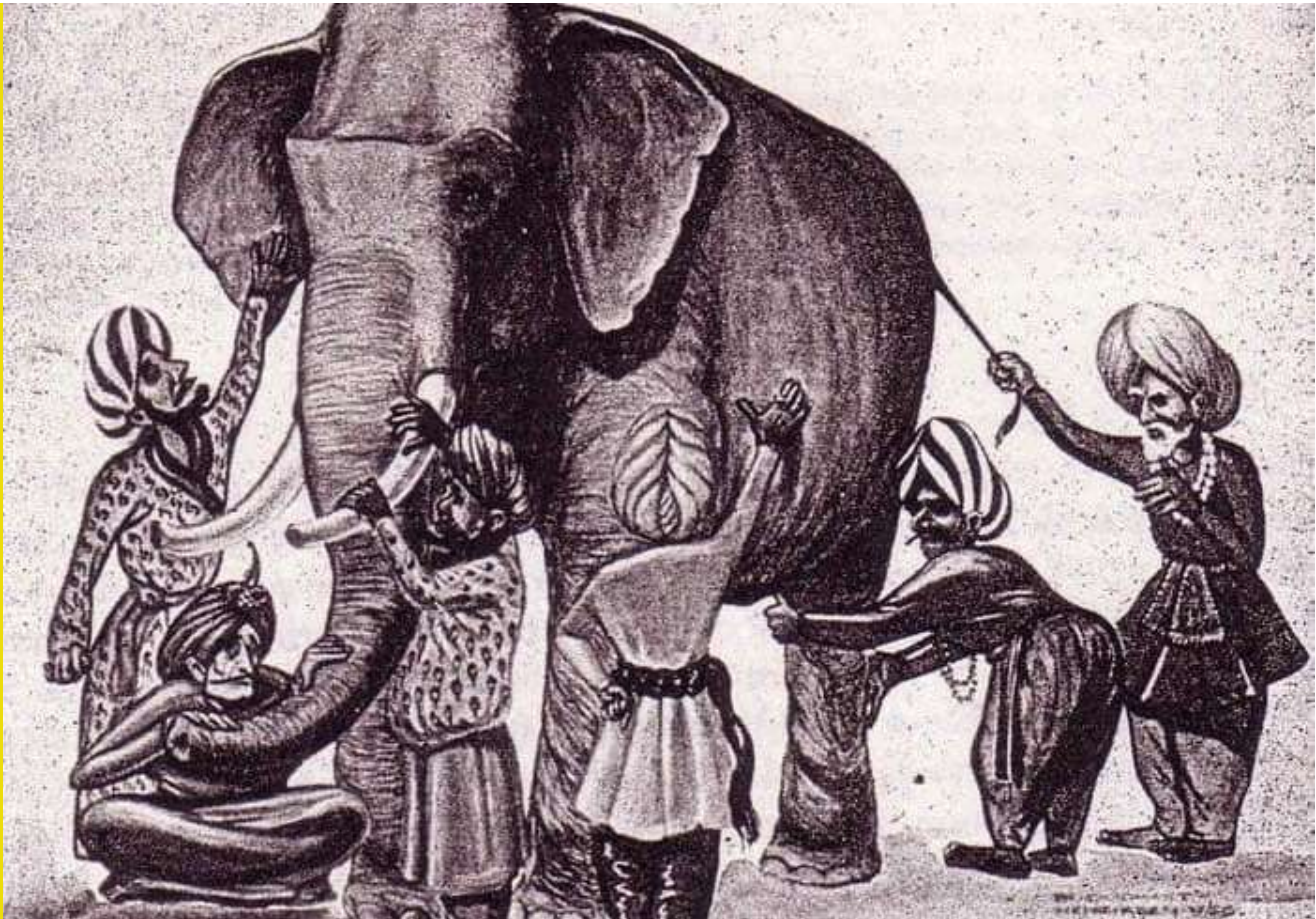


Regeneration of *Fungia granulosa* tissue explant into mature polyp. Tissue can be frozen and thawed and regenerate into polyp. Used with permission from Vizel M., Loya L., Downs CA., Kramarsky-Winter E. (2010) A novel method for coral explant culture and micropropagation. *Marine Biotechnology*. doi:10.1007/s10126-010-9313-z

however, it met strong resistance from activists and policy managers.

Looking back, it seems inconceivable that an opportunity like that was lost...but then I remind myself - I am not a cynic, I am a realist. For any of the coral-involved NGO's or government resource management agencies to adopt this idea, they would have to admit that what they were doing was doomed to failure. Funding would dry up. Ain't gonna happen.

At least the techniques are still out there. We have to hope that we have time, and that, in at least some small areas of the ocean, we can control pollution and move corals around so that they can survive into better times. But I am not optimistic. ►



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I am especially grateful to: Tom Tomascik, who rooted through his old slides to find pictures of that Banda reef; he has posted a recount, along with some video, of the development of that reef at https://www.researchgate.net/publication/374842827_Video_Rebirth_of_a_coral_reef_Banda_Api_1992-1994. I also thank Craig Downs for the picture of the coral nubbins and for shattering my spheroids during the writing. I would also like to thank the many coastal people I have met in my work, all of whom have been helpful and interested. I am saddened beyond words by what we have done, and will do, to their lives. Any biologists offended by my remarks, recall that I am one of you. Individually, reef biologists can be wonderful people, and I count many friends among their ranks. Collectively, I don't think the goats would let them in the rodeo.

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REEF CURRENTS

Coral geometry and implications for growth

Samuel E Kahng

Department of Oceanography, University of Hawaii at Manoa
kahng@hawaii.edu

Coral colony morphology varies widely between and within species and has many physiological implications associated with adaptation to environmental factors such as light, hydrodynamic regime, sedimentation, and subaerial exposure (Jackson 1979, Chappell 1980). While many coral species exhibit morphological plasticity in response to their environment, their general colony shape can be characteristic of the species and can be conserved across time in the absence of space constraints and partial mortality (Veron 2000, Todd 2008, Zawada et al. 2019). Morphology can dictate a colony's susceptibility to breakage and toppling (Denny and Gaylord 2010), exchange of nutrients and metabolites with the water (e.g., Hossain & Staples 2019, 2020), and exposure to neighboring organisms (Meeters et al. 1997).

The general morphology of a coral colony has also been associated with growth rates (i.e., linear extension) which have traditionally been assumed to be characteristics of a species and independent of size (e.g., Buddemeier & Kinzie 1976, Hughes & Jackson 1985, Kinzie & Sarmiento 1986, Pratchett et al. 2015). This growth rate assumption underlies their use as a foundation of the census-based approach to calculate calcium carbonate reef budgets (e.g., Perry et al. 2018, 2019, Molina-Hernandez et al. 2020) and as a potential indicator of environmental conditions (Carricart-Ganivet et al. 2011). However, the geometric shape of a colony dictates the inherent mathematical relationships between the different growth dimensions (i.e., length, area, volume, and mass) and can determine whether these relationships are independent of size or change with size (e.g., Porter 1976, Kahng et al. 2023). These geometry-dependent relationships have a special significance for calcifying organisms. For all calcifying organisms, there are two distinct components of growth/production: (1) organic or tissue biomass and (2) inorganic or calcium

carbonate skeleton. Each aspect of growth requires their own set of elemental resources which can have characteristically different levels of availability depending on the habitat.

For reef building corals, their biomass consists of a thin layer of tissue covering the surface area of the colony. If the average tissue layer thickness and composition are relatively constant across time, biomass production is proportional to growth in surface area (Anthony et al. 2002). Calcification or growth in skeleton mass is related to volume via density. If the average density across time is relatively constant, then calcification is directly proportional to growth in volume. A constant calcification rate (per unit area) leads to constant volume growth rate per unit surface area. The relationship between these two aspects of growth is dictated by the surface area to volume ratio ($V=M/\rho$, where V is volume, M is mass, and ρ is avg density) which in turn is dictated by coral geometry. When this ratio has extreme values (either high or low), the coral geometry may cause one aspect of growth to “geometrically” constrain the other, thereby having important implications for life history strategy.

While several physical and biotic environmental factors exert a primary influence on coral growth rate (e.g., light, temperature, disturbance regime, predation, disease, space competition, etc.) (Barnes 1973, Edmunds 2006, Pratchett et al. 2015), inherent geometric relationships between growth parameters must be clarified to be able to quantitatively reconcile the different metrics of coral growth. In recent publications, Kahng et al. (2023, 2024) used simple geometric shapes to illustrate contrasting effects of coral geometry. To illustrate how geometry can dictate surface area to volume ratios and linear extension rates (i.e., whether they are size dependent or not), three simple, but contrasting geometric shapes, mimicking the morphology of several common coral species, are discussed below.

Massive hemispheroidal corals

A circular hemisphere can be used model the shape of dome-shaped corals (e.g., massive *Porites*, *Montastraea*, etc.). While eccentricity and surface roughness of massive corals can vary, the



fundamental relations between dimensions of radius (r), surface area (function of r²) and volume (function of r³) remain characteristically the same. To isolate and illustrate the effects of geometry, a

A hemi-spheroidal coral – in this case *Favia favus*.

constant calcification rate (G) and density (ρ) can be applied to standard geometric equations for area ($S = 2\pi r^2$) and volume ($V = \frac{2}{3}\pi r^3$) to determine the *surface area to volume ratio* ($\frac{S}{V} = \frac{3}{r}$) which is size-dependent and decreases rapidly with increasing size/radius. Therefore, the relationships between the growth rates parameters for radius, surface area, and volume are not constant but characteristically change with colony size.

Using the relationship between calcification rate and volume growth rate ($G = \frac{\Delta V \rho}{S_t}$), the relationship between calcification and radial/linear extension rate ($C_t = r_{t+1} - r_t$) can be solved: $G = \frac{\rho(3C_t r_t^2 + 3C_t^2 r_t + C_t^3)}{3r_t^2}$.

As the colony reaches a larger size ($r_t \rightarrow \infty$), $G \rightarrow \rho C_t$ and the *linear extension rate increases rapidly asymptotically towards a maximum value of $C_t \rightarrow \frac{G}{\rho}$* . For large colonies, a constant calcification rate results in a constant linear extension rate. However, for small colonies linear extension rate will be slower (given the same calcification rate).

The higher surface area to volume ratio during early growth, underlies the success of microfragmentation used to accelerate restoration of coral cover for massive coral species. Given a constant calcification rate, their maximum rate of surface area growth occurs when they are small. The surface area growth rate per unit surface area (i.e., surface area productivity) declines rapidly as the colony grows towards an asymptote of zero: $\left(\frac{S_{t+1} - S_t}{S_t}\right) =$

$\frac{\left(\frac{3Gr_t^2 + r_t^3}{\rho}\right)^{2/3}}{r_t^2} - 1$. For hemispheroids with prolate or oblate shapes (i.e., nonzero eccentricity), the mathematical relationships differ slightly but the fundamental relationships between parameters and how they change with size are characteristically similar to a circular hemispheroid.

Branching corals with constant branch thickness

A cylinder can be used to model the shape of branching corals with a constant average branch radius (r). Since each new branch base covers the side of its parent branch, there is no net increase in surface area from each new branch tip, except for the area of the very first branch tip. As the colony grows, the sum of all branch lengths or total branch length (h_t) can be used to calculate skeletal volume ($V_t = h_t \pi r^2$), independent of the number of branches (β_t), average branch length (h_t / β_t), or branch spacing. The colony surface area ($S_t = 2\pi r h_t + \pi r^2$) can be calculated from the side of the cylinder using total branch length. The *surface area to volume ratio* ($\frac{S_t}{V_t} = \frac{2}{r} + \frac{1}{h_t}$) rapidly approaches a constant ($\frac{S_t}{V_t} \rightarrow \frac{2}{r}$) as the total branch length increases ($h_t \gg 1$). For all but the smallest colonies, the growth rates for total branch length, surface area, and volume are all directly proportional to one another (all are a function of h_t), and these relationships do not change with colony size.

To what extent do these model relationships reflect reality? Using photogrammetry, Million et al. (2021) measured volume, total branch length (i.e., total linear extension) and surface area for replicates



A branching coral with constant branch thickness– in this case *Acropora ?formosa*.

(n=156) of *Acropora cervicornis* to measure growth of each parameters after six months and one year. Their raw data (from supplemental materials) shows very high linear correlations ($R^2 = 0.77-0.92$) between these three growth parameters after one year of growth inclusive of incidents of breakage. This empirical validation demonstrates the stable nature of these relationships for some branching coral species. Using the relationship between calcification rate and volume growth rate, the relationship between calcification and linear extension rate ($C_t = h_{t+1} - h_t$) can be solved: $\frac{C_t}{\beta_t} = \frac{2G}{\rho r} \frac{h_t}{\beta_t} + \frac{G}{\rho \beta_t}$, where $\frac{C_t}{\beta_t}$ is average branch extension rate and $\frac{h_t}{\beta_t}$ is average branch length. *If average branch length is a conserved features for a colony, average branch extension rate approaching a constant ($\frac{C_t}{\beta_t} \rightarrow \frac{2G}{\rho r} \frac{h_t}{\beta_t}$), as the colony grows more branches ($\rho \beta_t \gg G$). For large colonies, a constant calcification rate results in a constant average branch extension rate. Given a constant calcification rate, the rate of surface area growth is constant and independent of size:*

$$\left(\frac{S_{t+1}-S_t}{S_t}\right) = \frac{2G}{\rho r}.$$

Flat plate-like corals with constant thickness

Some corals (e.g., deep-water *Leptoseris* spp.) form flat disc-like coral colonies that grown radially outward and do not accrete vertically (Kahng et al. 2020, 2023). Their *surface area to volume ratio is constant regardless of colony size* and depends only on thickness ($\frac{S_t}{V_t} = \frac{\pi r^2}{h \pi r^2} = \frac{1}{h}$), where r is radius and h is thickness. For disc shaped corals with a constant thickness, the growth rates for both surface area and volume are a function of r^2 , and these relationships do not change with colony size.

Using the relationship between calcification rate and volume growth rate, the relationship between calcification and linear extension rate ($C_t = r_{t+1} - r_t$) can be solved: $C_t = r_t \left(\sqrt{\frac{G}{\rho h} + 1} - 1 \right)$. Given a constant calcification rate, *radial extension rate increases linearly with colony size and exponentially across time* as the colony surface area (function of r^2) fuels growth along the outer perimeter (function of r) (Kahng et al. 2023). The rate of surface area growth (per unit area) is constant and independent of size: $\left(\frac{S_{t+1}-S_t}{S_t}\right) = \frac{G}{\rho h}$.



A flat plate-like coral, albeit one that is also branched – probably *Acropora cytherea*.

Biomass production vs calcification: which limits growth?

The geometry of a coral species is a strategic component of its life history strategy. Co-occurring species have S:V ratios across the full range of values from high to low with their associated metabolic effects, benefits, risks, and the inherent tradeoffs between them. At one extreme, thin diameter branching corals (high S:V ratio) can maximize growth in surface area and associated resource acquisition potential. However, this geometry requires high biomass production to cover the fast growth in surface area. When macronutrients (e.g., bioavailable nitrogen or soluble reactive phosphorus) are limited, biomass production may constrain calcification in these species. Similarly, these fast-growing species may have lower biomass reserves (e.g., of amino acids and phospholipids) to sustain them during periods of stress by virtue of their growth strategy.

At the other extreme, growth in large, hemispheroidal corals (low S:V ratio) is likely constrained by calcification (vs. biomass production) because these corals grow surface area very slowly. This slow growth in biomass suggests a potential surplus capacity for biomass production which can be allocated towards other anabolic processes (e.g., fecundity, biomass reserves, etc.). For these corals, slow growth in surface area translates into slow growth in resource acquisition potential which would be particularly disadvantageous during early growth due to size-dependent mortality (Hughes and Connel 1987). However, their S:V ratio changes ontogenetically and are an order of magnitude higher during initial growth and become low only after reaching moderate size.

	Size metric	Surface Area (SA)	Volume (V)	SA:V ratio	Ontogenetic change with increasing size			
					SA:V ratio	Linear extension rate	Surface area productivity (SAP)	
Hemispheroid (constant eccentricity)	equatorial radius (r)	function of r^2	function of r^3	function of r^{-1}	↘	↗	↘	very low for large colonies
Cylindrical branching coral (constant branch diameter)	total branch length (h)	function of h	function of h	~constant *	constant	~constant **	constant	high for thin branches
Disc (constant thickness)	radius (r)	function of r^2	function of r^2	constant	constant	↑	constant	very high for thin colonies

Table 1. An illustration of how mathematical relationships between dimensions and growth parameters are dictated by colony geometry for three contrasting shapes. Slanted arrows (↗, ↘) indicate asymptotically increasing/decreasing with increasing size. Notes: *when total branch length is large; **average branch extension rate when total number of branches is large.

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Note: Photos and tentative identifications of corals in Seychelles by the editor.

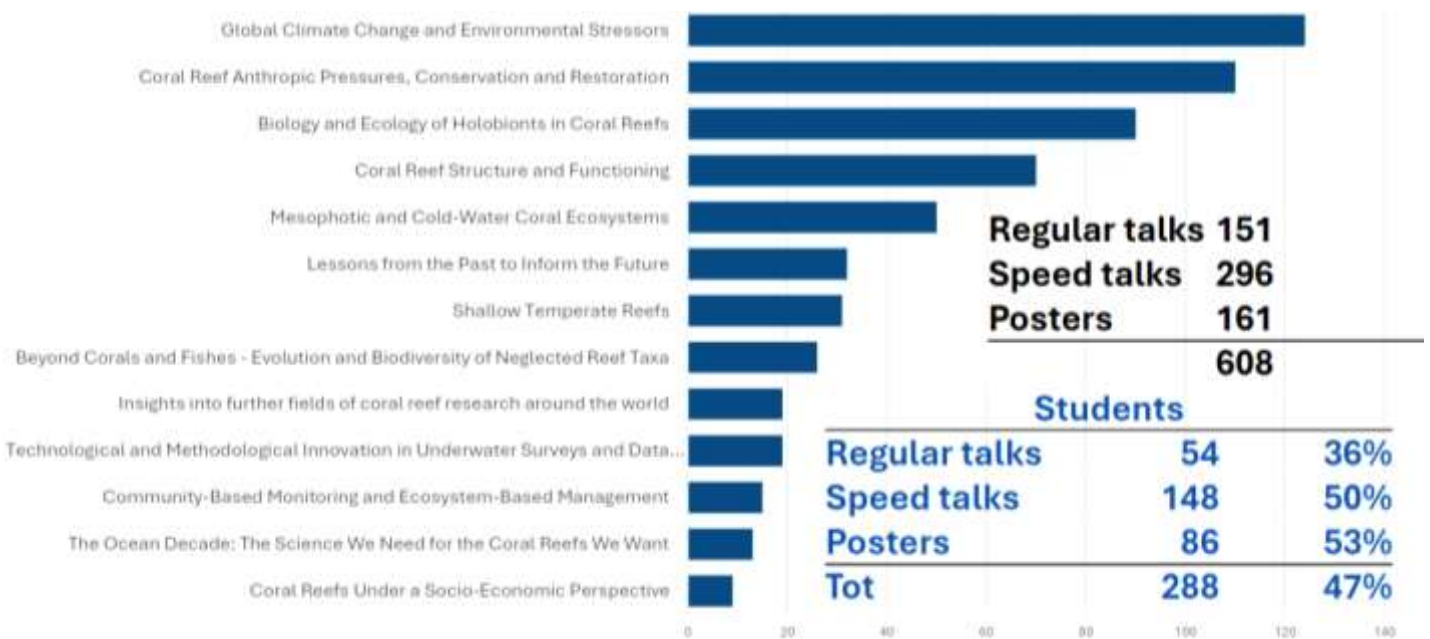
WORKSHOP AND CONFERENCE REPORTS

The European Coral Reef Symposium

Naples, Italy - 2nd-5th July 2024



The European Coral Reef Symposium (ECRS) 2024 was held from 2nd – 5th July in Naples, Italy. It proved even more successful than hoped and was attended by 741 participants (see above) from 55 countries (three in the top ten countries actually being outside Europe). A total of 447 were given over thirteen subject areas as shown below.



We anticipate carrying a full conference report in our December issue

Mainstreaming Coral Reef Conservation

Capacities:

Lessons from the CORDAP Coral Conservation and Restoration Workshop

Mombasa, Kenya, 12th-15th March 2024

To bolster the capacity for effective coral conservation and restoration efforts in the Global South, CORDAP (Coral Research & Development accelerator platform) organized a four-day workshop in the bustling port city of Mombasa, Kenya, from March 12th to 15th, 2024. The workshop brought together representatives from academia, industry, conservation, restoration, and government from 19 Global South countries.

The workshop shed light on the pivotal importance of capacity development in propelling forward coral conservation and restoration endeavors. Conservationists face numerous challenges in many mid and low-income nations, where coral reefs are often abundant and essential for local communities' well-being. Amidst the array of participating countries, common challenges surfaced regarding access to research resources and conservation infrastructure, underscoring the urgent need to invest in human capital alongside technological innovation. Furthermore, despite the availability of international grants to fund coral conservation initiatives, projects originating from the Global North often receive a disproportionate share of funding compared to those from the Global South—where the need is most acute. This discrepancy arises due to language barriers, lack of grants for baseline research and monitoring, and because many grant evaluations prioritize factors such as existing facilities and access to

innovation, which are frequently limited in less economically developed nations, thus exacerbating disparities in resource allocation.

Over four intensive days, participants worked to identify the most pressing challenges impeding capacity development in coral reef conservation and restoration in the Global South and devise actionable strategies to surmount these obstacles. The workshop facilitated multiple exchanges, predominantly focused on group brainstorming and discussion, amplifying the voices and perspectives of a diverse, gender-balanced group of participants from the Global South working in different sectors within the research and conservation fields and spanning the full spectrum of career stages.

Day one of the workshop was dedicated to identifying barriers, revealing a remarkable consensus among participants. These barriers were categorized into six overarching themes: 1)



Participants working in groups to brainstorm solutions to the main problems faced by researchers from the Global South

Collaborations (international, cross-sector, scientists + policymakers, community engagement), 2) Project Management, 3) Capacity Development, 4) Funding, 5) Facility, Tools, Research, and Innovation, and 6) Policy and Governance. Through a collaborative voting process, participants pinpointed the most pressing challenges within each category, laying the groundwork for targeted interventions and solutions. Some of the key challenges identified were the lack of technical capacity of the local community, insufficient infrastructure to conduct the project and capacity to continue the project after the funding cycle is done.

Expanding on this groundwork, days two and three were dedicated to crafting solution-oriented strategies. Participants engaged in group sessions to craft potential solutions for each identified challenge. Some solutions concentrated on enhancing grant processes. For example, participants proposed mechanisms to enhance communication with funding agencies to pinpoint funding gaps (including infrastructure and long-term funding mechanisms), eliminate language barriers in proposals (such as accepting proposals in languages other than English), and organize webinars to elucidate the grant process and requirements. Other participants suggested implementing fellowships aimed at supporting emerging leaders from the Global South, providing them opportunities for leadership, communication and grantsmanship training and fostering international collaboration. Other suggestions were directed towards establishing an online platform to serve as a global network of active coral restoration centers, facilitating knowledge exchange, collaboration, and standardization of restoration methods.

Central to the workshop's objectives was translating discussions and action plans into tangible outcomes. Day four focused on crafting strategies to amplify the visibility of these action plans and other outputs derived from the group discussions, ensuring that the momentum generated within the workshop would translate into real-world impact. Suggestions included summarizing the discussions in a scientific publication and developing a roadmap that could inform CORDAP and other funding agencies, who hopefully will implement some of these suggestions.

As the inaugural event for what CORDAP and its partners envision as a long-term program, the CORDAP Capacity Development in the Global South workshop in Mombasa serves as a beacon of hope and progress in the global effort to conserve coral reefs. Recognizing that investing in the people conducting the work is as crucial as investing in conservation actions themselves, the workshop emphasized the importance of empowering communities with the resources needed for success. We hope that the bonds forged, and insights gleaned during this event will continue to reverberate, catalyzing sustained action and innovation in coral reef conservation worldwide.

Mariana Rocha de Souza

With (full list of Authors/Attendees) Amir H, Amri AY, Babu I, Bhagooli R, Dempsey AC, Djakiman C, Faruk O, Gamage I, Geneid Y, Golbuu Y, Gube D, Hutahaeen A, Karisa J, Kaullysing D, Knoester E, Licuanan WY, Lourenço C.R., Mana R, Matairakula U, Mayfield AB, Mbutia K, Mendoza-Quiroz S, Montoya-Maya P, Mwasangu D, Nassongole B, Nduati C, Ochoa GM, Ogega N, Osuka E K, Perera P, Ramachandran R, Roch C, Tuda A, Wambugu J, Yranzo Duque, A.



Forum on Coral Bleaching in the Red Sea

In June 2024 the General Organization for the Conservation of Coral Reefs and Turtles in the Red Sea (SHAMS) held the First Saudi National Forum on Coral Bleaching in the Red Sea.

Alarming levels of bleaching-level heat stress across the globe were reported worldwide in 2023 (NOAA Coral Reef Watch). In April 2024 the ongoing bleaching event was confirmed as the fourth global coral bleaching incident (after 1998, 2010, and 2014-2017; Hughes et al. 2018, Eakin et al. 2019, Skirving et al. 2019), predictions indicating it could be of unprecedented severity.

Recognizing the urgency of the situation, the General Organization for the Conservation of Coral Reefs and Turtles in the Red Sea (SHAMS), as the national Saudi Arabian advocate for the conservation of coral reefs in the Red Sea, made coral bleaching a top priority, rallying stakeholders to address collectively the challenge, emphasizing the need for immediate action to preserve the beauty and biodiversity of the Kingdom's Red Sea reefs. SHAMS called on all stakeholders, from giga projects to universities and national entities, to attend in June the First Saudi National Forum on Coral Bleaching in the Red Sea at SHAMS

headquarters in Jeddah, , to discuss and commit to a standardized methodology to reporting and monitoring bleaching along the 1800 km of the Saudi Red Sea coastline.

The Red Sea has frequently been praised for its highly thermal tolerant corals and has long been thought to be largely spared from mass-bleaching (Grimsditch & Salm 2006, Berumen et al. 2013, Furby et al. 2013). However, as temperatures became progressively more anomalous (Raitsos et al., 2011), monitoring activities in the Saudi Arabian Red Sea reported more and more sightings of coral bleaching (Furby et al. 2013, Lozano-Cortes et al. 2016; Monroe et al. 2018, Genevier et al. 2019), alarming stakeholders into taking action and questioning the fate of the so far thriving corals of these thermally extreme, under-explored, and relatively pristine Red Sea ecosystems.

Through the recent establishment in 2023 of SHAMS as the national entity for the conservation of coral reefs in the Saudi Arabian Red Sea, the Kingdom committed to protecting, conserving, and restoring its blue economy. Its vision is to have globally distinguished, nationally iconic, and thriving coral reefs, achieving excellence in

conservation through planning, implementing effective programs, promoting community engagement, and driving research, innovation, strategic partnerships, in effective coordination with all relevant stakeholders. With a strategy approved in December 2023, SHAMS has officially took over leadership in responding to the Kingdom's rapidly changing coral reef ecosystems and sent out its first teams to conduct rapid surveys of bleaching in the



Figure 1. Bleached *Acropora* spp. off the coast of Al-Lith, Saudi Arabia (19 °N). Picture taken in December 2023. Photo credits to V. Robitzsch.



Figure 2. Bleached mid-shelf reef off the coast of Al-Lith, Saudi Arabia (19 °N). Picture taken in December 2023. Photo credits to V. Robitzch.

central and southern Red Sea (24 °N to 19 °N), where bleaching is more frequently reported, starting in October 2023, after Red Sea sea-surface temperatures had peaked (Robitzch & Berumen, 2020). From these rapid surveys it appears that inshore reefs were more severely bleached than offshore reefs (similar to reports by Furby et al., 2013), with fringing reefs showing up to 90 % of colonies bleached and high levels of dead corals, likely a result of previous disturbances (see Figs 1, 2, and 3). Damage seemed more severe in reefs located to the south (around 19 °N) compared to those to the north (around 24 °N). Also remarkable were the high sea-water temperatures, sometimes reaching 31°C at 30 m depth well into December, and the presence of fluorescent corals in December and even in January.

These results demanded urgent action and, during the First Saudi National Forum on Coral Bleaching in the Red Sea at SHAMS, all Red Sea stakeholders agreed to follow a standardized methodology for the rapid assessment of coral bleaching on coral

reefs along the entire Saudi Arabian Red Sea coast. Based on these data, SHAMS will lead and publish the first national report on Red Sea coral bleaching for the Kingdom of Saudi Arabia. This report will be crucial for ongoing conservation and restoration efforts and for informing the general national and global public about the state of this extremely valuable natural asset – the Red Sea’s coral reefs.

Vanessa Robitzch

The General Organization for the Conservation of Coral Reefs and Sea Turtles in the Red Sea (SHAMS)
21442 Al Wurood Dist., Jeddah, Saudi Arabia
email: Vanessa.Robitzch@shams.gov.sa

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Figure 3. Bleached soft coral (picture on left) and sea anemone (picture on right) off the coast of Al-Lith, Saudi Arabia (19 °N). Picture taken in December 2023. Photo credits to V. Robitzch.

Exploring Caribbean coral conservation goals:

Revisiting the Coral Reef Assessment Framework



Aliyah Griffith

Department of Earth Marine and Environmental Science, University of North Carolina, Chapel Hill, North Carolina

aliyahg@live.unc.edu; www.aliyahgriffith.com

Over the past several decades, significant progress has been made in coral benthic assessment methodologies. However, the utilization of more advanced methods across the Caribbean, as observed in various outcomes and reports (Bayley & Mogg, 2019), highlights the need for adequate funding and novel partnerships to maximize the benefits of these assessments. The need for more collaboration with academic researchers, local governments, and communities in the Caribbean often faces challenges, leading to pronounced gaps in collective analytical endeavors and overall progress (Gill et al. 2023). Notably, the Caribbean ranks last in many collective analysis studies, especially when comparisons of Marine Protected Areas (MPAs) are included (Chollett et al., 2022). Most assessments weigh a country's success on the method used rather than the context in which it was selected (Obura et al. 2019, Uribe et al. 2021). Here, we explore the decisions involved in the selection of assessment methodologies and the perceived goals associated with their use, particularly in relation to their relevance within the current literature. We first determine (1) what are the main focus areas in the literature for coral benthic assessments, (2) what are the main techniques employed and their financial realities, and (3) how the chosen method impacts the needs and the overall goal of the assessment. This framework is applied to Caribbean countries to determine what goals are being achieved and if each country is moving toward its optimal targets. By understanding the perceived goal, it can be compared to a country's final results following a complete report card review that considers community dynamics and socio-economic realities.

Research Undertaken

Text Mining

A systematic review using *Scopus* was conducted in October 2023 based on the latest PRISMA guidelines (Page et al. 2021) (Fig. 1). The abstracts and keywords of papers from 2021-2023 were analyzed. A text mining assessment using the R package *Wordcloud* and *SnowballC* revealed key terms used in all studies, identifying prominent terms used and the frequency at which the word appears in the literature. A final filter was applied, eliminating thematic words associated with 'marine biology' or 'essay,' such as 'marine,' 'sea,' 'ocean,' 'coral,' 'reef,' 'as,' 'and' 'if,' etc. This was done to maintain focus, relevance, consistency, and efficiency in the systematic review process, to ensure the inclusion of only directly pertinent terms, and to reduce noise. Two size-based frequency word clouds were created from text mining. A final frequency plot was generated depicting the top 30 words most frequently used in the abstract and keywords.

Method Comparison Breakdown

The creation of categories for different benthic composition assessment methods stems from identifying key themes in benthic assessment needs. Each was analyzed for methodological parameters such as cost, difficulty, time, etc. Method and comparison papers such as Urbina-Barreto et al. (2021) were used to estimate appropriate ranges for each approach and discern commonalities. These studies, marked by thoroughness, encompass on-site testing, allowing us to pinpoint prevalent methods within the field that effectively address key needs already identified. The main methods found were then employed by the

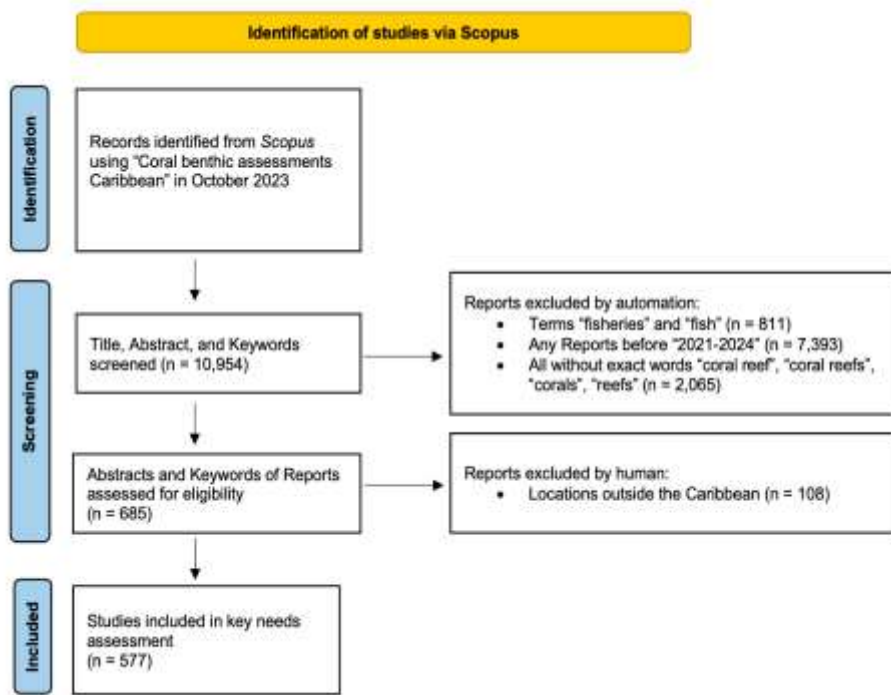


Figure 1. PRISMA flowchart of the systematic screening process of review papers for determining coral reef benthic assessment needs in the Caribbean.

author to address the methodological parameters of implementation. Methodological parameters were grouped by analysis type (AI is artificial intelligence and NI is natural intelligence), the estimated initial cost of materials (US\$50 < \$50-100 < \$100+), estimated time of application (30 min - 180 min), and difficulty (based on external costs/expectations and administration).

Monitoring Assessment Structure

The needs of benthic assessments and methods are evaluated to determine the overall goal of a study. The main goals are based on the World Coral Conservatory (WCC) coral survival approach (Zoccola et al., 2020). This determined the optimal structure of how to enhance coral survivorship through 4 categories: protect, repair, adapt, and mitigate. Multiple practices and approaches then fall under each of the 4 categories, which were correlated to our benthic assessment methods. Analyzing whether a region intends to protect, repair, adapt, or mitigate environmental challenges delineates a framework to categorize how effectively their current strategies promote coral survival. With these goals identified, we can understand where academic and local disconnect might be or how their approaches could shape their outcome.

Summary of Results

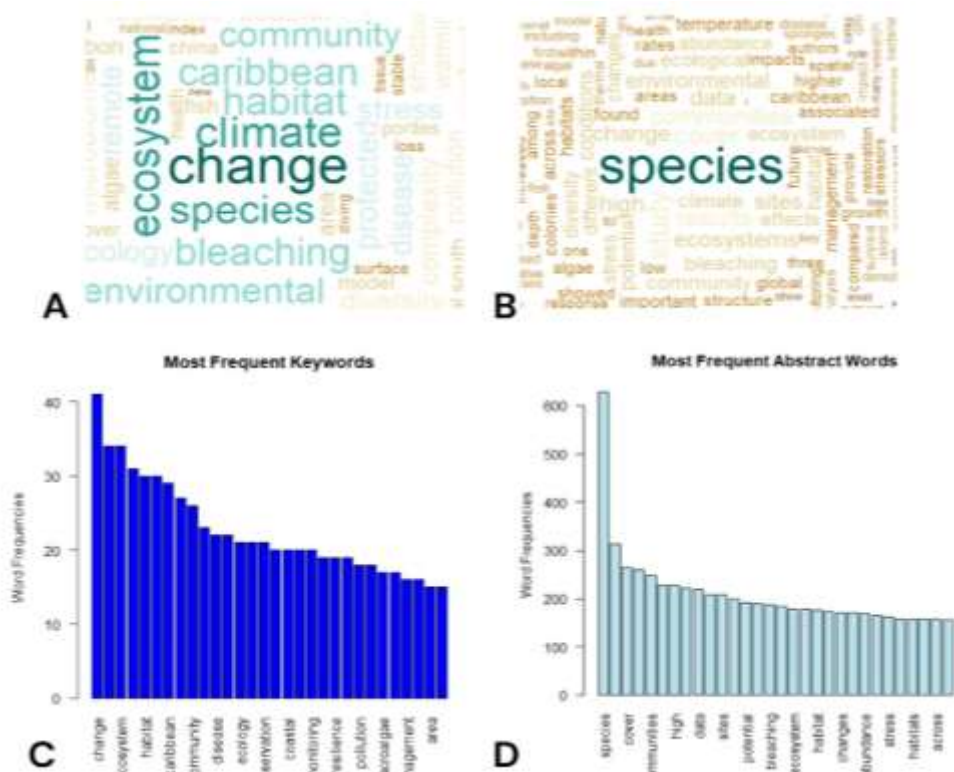
Text Mining

The text mining resulted in 30 words identified for both abstracts and keywords (Fig. 2). Both addressed the following terms: community, habitat, ecosystem, and change. The most frequent keywords are change, ecosystem, habitat, Caribbean, community, disease, ecology, conservation, coastal, monitoring, resilience, pollution, macroalgae, management, and area. The most frequent abstract words are the following: species, cover, communities, high, data, sites, potential, bleaching, ecosystem, habitat, changes, abundance, stress, habitats, and across. These describe the primary needs for a benthic assessment in the Caribbean (Fig. 2).

Method Comparison

Following the review, various benthic composition assessment methods were selected and summarized, addressing the identified needs, each offering different levels of data retrieval capability. These methods were chosen to represent a spectrum of approaches in the field, encompassing both traditional and more recent techniques. The primary method groups are line/chain transects (LCT, also known as LIT), photo quadrats (PQ), and remote-operated vehicles (ROV). The processing of these three methods can then influence time and add another level of differentiation. Currently, standard assessments use three (3) main steps: data collection, analysis, and processing (Fig. 3). Row 1: Field tools identify the data collection or tools used to administer collection. Row 2 identifies the type of analysis used to find answers in the

Figure 2: Most frequent keywords (A and C). Most frequent Abstract words (B and D).



assessment. In this row, the major difference between the analysis is depicted through administration and analysis (i.e., from human inspection or with the help of artificial intelligence.) Row 3 was determined by average costs but also confirmed when the author purchased each. ROV has the highest initial cost at \$3000 USD. The full cost of a quadrat used in surveying varies based on the size preferred. A 1m x 1m quadrat, made of PVC pipes, did not exceed \$60 USD. Line transects appear to be the most cost-efficient at about \$20 USD, but chain or leaded lines are preferred to reduce movement. All costs are based on a 60m transect assessment, though cost estimates will vary by country. Lastly, Rows 4 and 5 determine the processing step, which is determined by time and again the way the tools and analysis are administered. ROV takes the longest time to learn but is the shortest in relation to preparation and administration time. PQs are the most common and moderately easy to use, depending on the magnitude of the project, specifically when integrating AI. Although LCTs are the most time-consuming in relation to preparation and administration, it is the easiest method to learn and are often used with citizen science groups.

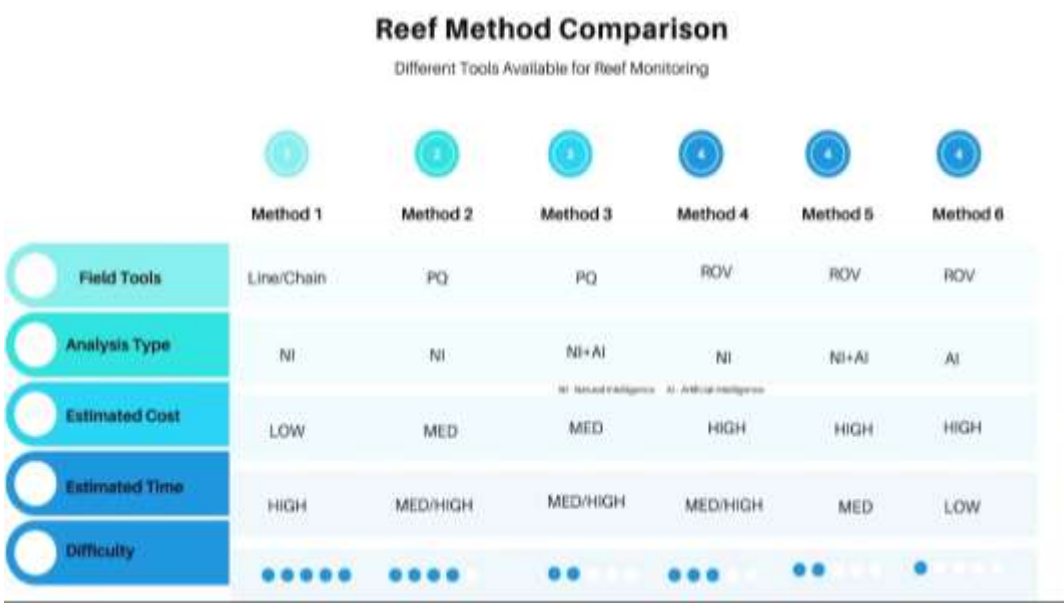


Figure 3. Standardized comparison of survey methods, assessing them as low, medium, and high range, based on time, cost, and overall skill requirement. (Analysis Type: AI is artificial intelligence, and NI is natural intelligence; Cost \$50-\$100+; Time: 30-180min; Difficulty: preparation/administration)

Key Needs and Method Relevance

The needs of the latest coral benthic assessment methodologies rely on scale-dependent factors (i.e., the ecological levels being addressed from individual scale up to an ecosystem) as well as more location-dependent impacts, such as disease and pollution. The commonalities between the abstract and keywords were then combined to determine connectivity in relation to each method: LCT, PQ, and ROV (Fig 4). The ROV is the most versatile and can address all needs and scales in benthic assessment, subject to limitations imposed by the length of the ROV cable, current strength, etc. The PQ has a time limitation and, therefore, is not listed for use in large-scale assessments unless a month or more of in-situ assessments can be performed. A similar dynamic is also seen with LCTs, where infinite time is not generally available to achieve large-scale assessments. Goals, based on Zoccola et al, 2020, that coincided with each method were then overlapped to depict how each method and needs were quantified/measured/assessed in relation to coral survival (Fig. 5).

Concluding Remarks

Surprisingly, “species richness,” a common ecological term, was not found, but a combination of the terms could reveal more about this concept. Overall, terminology could be among the first divides between local and academic approaches. We categorized each field tool method to the best of our ability to cover key practices and concerns. However, individual implementations may vary because we couldn't test every possible variation of each tool. Certain nuances can be applied to alter efficiencies, but for those presented, ROV seems to be the most versatile but the least accessible financially. The make and model and comfort with technological use can also impact these observations.

Figure 5 visualizes the potential limitations a chosen method can have with large-scale testing goals, especially if financial constraints are present. If an organization is willing to make a larger immediate investment, then more data can be collected on a larger scale and in a shorter amount of time. As the field becomes more and more aware of the local and academic divide, key principles and approaches can indicate how to conserve corals rise and fall under the Zoccola et al (2020) guide

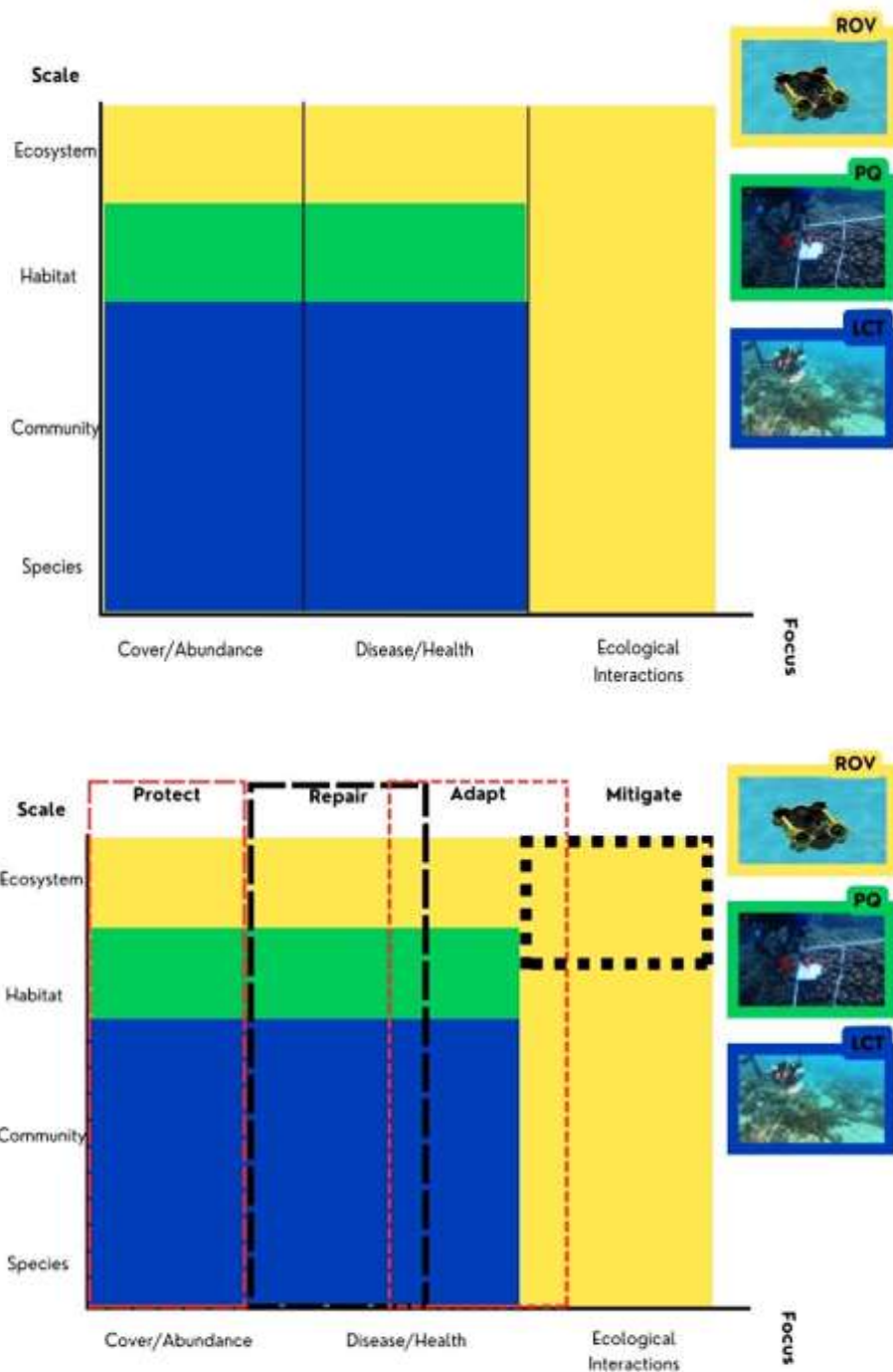


Figure 4 (above) Benthic Assessment Needs Based on Scale and Method. **Figure 5** (below) Goal Determination Based on Benthic Assessment Needs and Method Approach (goals adapted from Zoccola et al. 2020)

(Quigley et al., 2022). As there have already been pushes for scale and cost-effectiveness across restoration practices (Vardi et al., 2021), it is now more apparent than ever for this concept to be applied across all methods. The next steps are to process coral reef reports for different countries for goal identification. This assessment will be applied to available government reports. Using open-source reports to understand regional support will provide enough foundational information to analyze the monitoring variables of interest. When reviewing reports, we will focus on identifying the organization type, purpose, funding sources, established practices and tools, local impacts, and defined success (i.e., coral status). Rather than using a ranking system, model cases will showcase the highest level of quality, characteristic, or attribute within a group or set of groups. An example is labeling the countries for best practices based on their cost efficiency, data collection, time saved, local impact resilience, etc. A comprehensive review of each country's report will determine the method of interaction with coral sustainability/retention. This can aid in identifying trends in management techniques, reef monitoring, and socio-economic dynamics behind all interactions.

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Developing a conservation plan for Maui's resilient corals



Igor Pessoa

University of California Santa Cruz, California, USA

ipessoa@ucsc.edu; <https://paytanlab.ucsc.edu/people/igor-pessoa/>

The coral reefs of Maui (Hawai'i) are suffering from coral biodiversity loss as a result of climate change and local threats, such as agricultural and urban runoff (Maynard et al. 2019). Hawai'i experienced its first back-to-back mass-bleaching events in 2014-2015, and its second major bleaching event in 2019 (Rodgers et al. 2017; Winston et al. 2020). As if that was not enough, the increase in wildfires on Maui over the past decade has contributed to an increase in sedimentation and pollutant runoff (County of Maui 2021). Given the importance of understanding the effects of multiple stressors on corals, I proposed to study coral resilience and adaptation to climate and human impacts on the nearshore reefs of Maui. To that end, reef surveys were conducted throughout shallow, nearshore waters at 11 sites along the central, south, and west Maui coasts (Fig. 1).

The goal of this study is to identify and map corals with above average stress tolerance in sites that are already experiencing a decline in coral biodiversity due to bleaching and human impacts. Study sites were selected as follows: shallow reefs experiencing ongoing land-based impacts (1, 4-8, 10, 11); reefs without significant human impacts (2, 3, 9); and shallow reef pools with restricted water circulation on the south coast of Maui, in the Ahihi Kīna'u Reserve (9).

Hawaiian corals are susceptible to bleaching when seawater temperatures rise above 28°C. However, resistant corals are likely found in extreme habitats such as the shallow, nearshore reef pools located in the Ahihi Kīna'u Natural Area Reserve on the southern shore of Maui. The corals living in these small semi-enclosed nearshore pools are expected to



Figure 1: Map of Maui showing the location of the study sites: 1) Honolua Bay; 2) Kapalua Bay; 3) Napili Beach; 4) Ma'alaea Harbor; 5) Kamaole Beach; 6) Charley Young Beach; 7) Wailea Beach; 8) Kihei boat ramp; 9) Ahihi Reserve; 10) Kahului Harbor; and 11) Kanaha.

be more resistant to various environmental conditions (e.g., nutrient and temperature fluctuations, and changes in pH) and may tolerate higher levels of thermal stress. It is likely that they possess adaptive mechanisms that improve their resilience to extreme adverse conditions, thus enhancing their ability to recover from exposure to higher temperatures. However, these same resilient corals live at the upper limits of thermal tolerance for corals. They certainly cannot survive severely high temperatures, which may occur more often in these restricted-flow environments during extreme bleaching events.

Similarly, urbanized reefs harbor stress-resistant populations of corals (Rubin et al. 2021). Urbanized areas experience a suite of intense stressors that can cause shifts in the coral microbiome and outbreaks of coral disease. However, these corals may also become increasingly vulnerable to mortality as future conditions surpass the tolerance limits for corals within these stressful environments.

Initial surveys were conducted between September and October 2023 to investigate coral cover and species diversity. Data were collected during snorkeling surveys up to 3 m depth, with a major effort invested in identifying stress-resistant corals. Baseline assessments of the sites were done using georeferenced photo-quadrats with a Garmin GPS, and a bleaching color chart (Hawaiian Ko'a card) was used to assess degree of coral bleaching (Fig. 2). *In-situ* seawater temperature measured at each site by a dive computer was compared to sea surface temperature data from NOAA Coral Reef Watch. To account for historical and local variations, time series data from high-resolution satellite images from the Allen Coral Atlas and Sentinel-3 will be used to observe climatological ranges, sea surface temperature, chlorophyll-*a*, and bleaching patterns. The Allen Coral Atlas was also utilized to identify the precise locations of the stress-tolerant corals in this study, and to monitor site degradation and track changes in coral cover over time.

A total of 35 field surveys were completed at depths ranging from 0 to 3 m between 15 September and 28 October 2023. Coral surveys covered an area of approximately 900 m², encompassing primarily rocky shores (both exposed to and sheltered from wave action). Surveys were done throughout nearshore waters next to land-based sources of pollution, harbor areas, watershed sites, and agricultural and urban runoffs, as well as in shallow reef pools. *Montipora capitata*, *Montipora flabellata*, *Pocillopora meandrina*, *Porites compressa*, and *Porites lobata* were commonly observed throughout the study sites. Mean coral cover for each site was relatively low (<5%) except for Honolulu Bay and Ahihi Kīnaʻu Reserve (>20%).

Reef surveys revealed signs of coral diseases at some sites. Ten colonies of *M. capitata* and three of *Porites lobata* exhibited white syndrome. Near the Kihei boat ramp, a large *P. lobata* colony exceeding 4 m² was infected with white spot disease. Additionally, 13 *P. lobata* colonies across the study sites showed signs of *Porites trematodiasis*. Growth anomalies were also observed in both *Porites* and *Montipora* throughout the study sites. These observations suggest a potential link between chronic environmental stressors and coral health. Coral diseases often arise from a complex interplay of factors. Sediment runoff and wastewater pollution from septic tanks and cesspools are common on Maui. Prolonged exposure to such stressors could weaken coral immune systems (Mydlarz et al. 2016), making them more susceptible to the diseases observed across the study sites.

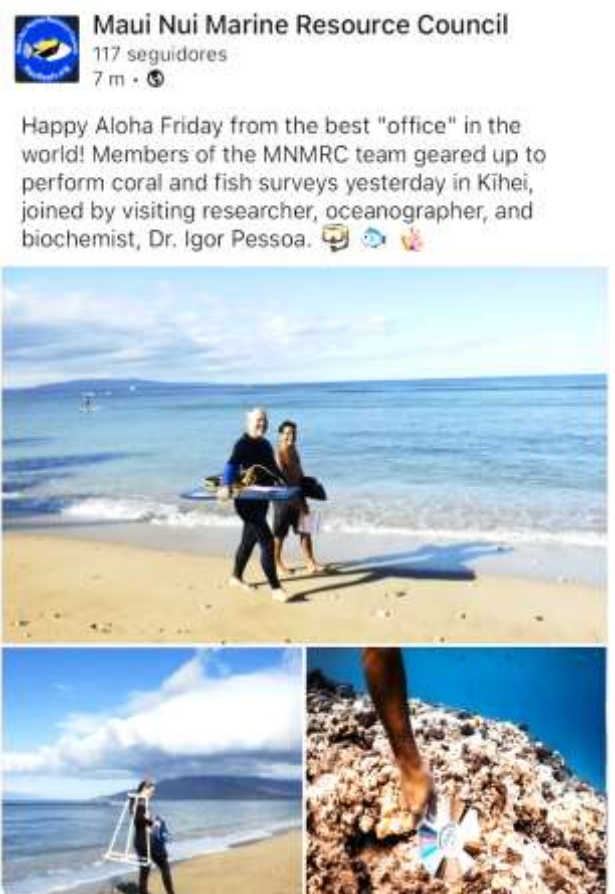


Figure 2. First fieldwork period, Sept-Oct 2022.



Figure 3. Candidate bleaching-tolerant corals observed in a shallow, nearshore reef pool.

Surveys revealed minimal or no coral bleaching at most sites. However, some adult and juvenile colonies of *Montipora capitata* and *Pocillopora* spp. showed signs of bleaching stress. Although *in-situ* data collections on Maui indicated that the bleaching threshold was not exceeded at the time of surveys, seawater temperature data from Kāneʻohe Bay, Oahu (<https://aqualink.org/sites/1042>), showed that temperatures surpassed 28°C during that period. Bleaching was observed inside the Maʻālea Harbor. At this site, surveys encompassed the entire extension of the rock breakwaters as well as the sandy bottom near the rock wall. The most abundant species in the surveyed area was *M. capitata*. Although total colony bleaching was not observed, 18.5% of the 65 *M. capitata* colonies surveyed showed some level of bleaching stress. The semi-enclosed nature of the harbor's water might explain this localized coral bleaching. Coastal current and wind patterns likely play a crucial role in the harbor's local hydrodynamics. Semi-enclosed water bodies, like the harbor, have lower water renewal rates and longer residence times, resulting in greater fluctuations in temperature compared to open coastal areas. Consequently, during summer, elevated seawater temperature in harbors can cause localized coral bleaching.

Bleaching was observed on *Pocillopora* spp. colonies at some sites. Two groups of adult *Pocillopora* spp. were tracked in this study. The first consisted of colonies < 10 cm diam (n = 104), and the second included colonies > 10 cm diam (n = 43). Overall, 15.7% of 147 colonies of *Pocillopora* spp. exhibited some degree of bleaching stress (12 white branch tips, nine light branch tips, and two totally bleached). It is possible that this represents an underestimate of bleaching within this population due to the dates of the surveys.

The shallow reef pools in the Ahihi Kīnaʻu Reserve represent a unique natural environment for investigating coral thermal tolerance mechanisms. These shallow, small reef pools, less than 2 m deep at low tide and with restricted water flow, likely experience regular exposure to hot water during the summer. If the corals in these pools survive and withstand bleaching events at higher temperatures, they are presumably heat-adapted corals. Figure 3 shows a shallow reef pool, approximately 25 m², that is semi-enclosed depending on tides and wave action. A total of 14 coral colonies were documented within a

shallow reef pool (Table 1), all of which were in good health with no signs of bleaching or disease. Coral colonies were uniformly distributed around the edge of the pool.

Coral Species	Number of Colonies	Size Class (<10cm)	Size Class (>10cm)
<i>Porites lobata</i>	4	1	3
<i>Pocillopora</i> spp.	9	6	3
<i>Montipora capitata</i>	1	0	1

Table 1. Potential heat-resistant coral species identified within the reef pool.

A total of 147 vulnerable and candidate stress-tolerant corals of *Pocillopora* spp. have been documented and georeferenced in this study. Digital images were taken for comparison with future surveys. These colonies will be monitored during the warm season for the next two years to document bleaching and survivorship to confirm whether these corals are resilient to thermal stress or not. The next fieldwork will be conducted in Sept/Oct 2024 and Sept/Oct 2025 to assess changes in coral biodiversity, identify site-specific stressors impeding coral recovery, and document coral cover loss. Of particular importance is understanding the effects of multiple stressors on these corals and developing solutions to mitigate coral biodiversity loss. This includes continuous monitoring to identify areas with high risk to vulnerable corals. This risk assessment will inform decision-makers about the impact of multiple threats to these areas, so that they can improve management strategies needed to conserve resilient coral genotypes.

As climate change and human impacts increasingly threaten coral reef biodiversity worldwide, it is likely that despite possessing adaptive mechanisms for thermal resistance, these corals may still become locally extinct. Understanding localized risks and ensuring coral resilience in the face of climate change are key to developing conservation strategies. Management decisions need to recognize the vulnerability of these corals and incorporate biodiversity loss into specific management plans to avoid potentially irreversible loss of resilient coral genotypes. If conserved, these stress-resistant coral genotypes and their associated photosymbionts have the potential to serve as genetic reservoirs for restoration efforts. This work is time-sensitive, as temperatures continue to rise and corals approach their upper thermal tolerance limit. Given future projections of ocean warming, it is critically important to develop new conservation strategies and intervene to protect heat-adapted corals.

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High within-population variability of coral heat tolerance across thermal regimes in Palau



Liam Lachs

School of Natural and Environmental Sciences, Newcastle University, Newcastle, UK
liamlachs@gmail.com; <https://www.coralassistlab.org/liam-lachs>

Background

Marine heatwaves are increasing in both frequency and intensity due to climate change (Oliver et al. 2018), leading to widespread mass coral bleaching and mortality events (Virgen-Urcelay & Donner 2023), even in remote areas without other anthropogenic disturbances. To persist corals must adapt to ever warmer ocean temperatures, which new research suggests may already be happening (Lachs et al. 2023a). As such, the ability of corals to survive marine heatwaves—herein referred to as heat tolerance—will continue to be under strong selection pressure over the coming decades. However, many unresolved questions still need to be answered in order to produce robust predictions of both natural adaptation and the feasibility of novel interventions like assisted evolution, an approach aimed at boosting the adaptive capacity of coral populations, for instance, through out-planting of corals selectively bred for high heat tolerance. We now know that considerable variability in heat tolerance can exist on individual reefs (Humanes et al. 2022), but how does this trait variability differ among reefs within the same population (*i.e.*, groups of reefs linked through high gene flow)? Which reefs are the best sources of heat tolerant corals for natural or assisted evolution? How is coral heat tolerance influenced by the local thermal history of specific habitat types (*e.g.*, outer reefs)? Can historic satellite-derived measurements of sea surface

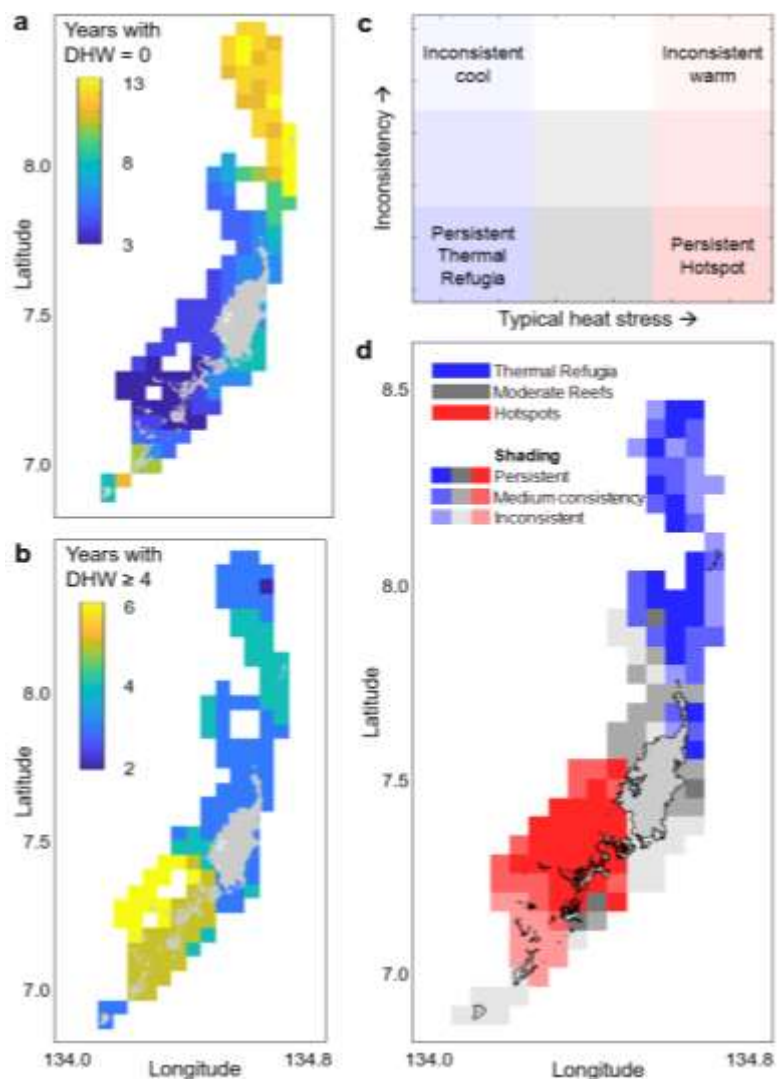


Figure 1. Thermal history of Palauan reef grid cells based on 5km CoralTemp v3.1 (1985–2020), with northern reefs having frequently avoided heat stress (a) and southwestern reefs with frequent heat stress exposure (b). (c–d) Persistent hotspots and thermal refugia can be determined by tracking the typical heat stress reefs receive relative to their consistency (standard deviation).

temperature help to identify reefs that are likely to harbour high heat tolerant corals, if so, this would be informative for coral reef managers?

Theory and evidence suggest that over large geographical scales (*i.e.*, multiple coral populations), coral thermal tolerance largely tracks historic thermal conditions (*e.g.*, the maximum of monthly means climatology: the typical temperature of the warmest month from a baseline period) (Evensen et al. 2022, Marzoni et al. 2023). Thermal refugia and hotspots, reefs that consistently avoid or are consistently exposed to heat stress, can influence coral thermal stress resistance over such large spatial scales, for example across the Great Barrier Reef (Cheung et al. 2021), Red Sea (Osman et al. 2018), or Caribbean Sea (Muñiz-Castillo et al. 2019). However, many biological mechanisms that play a role in coral adaptation play out within populations over much smaller spatial scales (<1–10s km), for example, fertilisation (Dubé et al. 2020) and larval dispersal (Hock et al. 2017).

Research Undertaken

Here, we used historic satellite-derived data on accumulated heat stress (measured as annual maximum degree heating weeks – DHW) to identify persistent thermal regimes across the coral reefs of Palau, a remote Pacific Island nation (Fig. 1). After finding persistent hotspots and thermal refugia, even over such a small spatial scale (<150km), we conducted a long-term marine heatwave experiment on the common shallow-water reef-building coral *Acropora digitifera* from replicate reefs in hotspots and thermal refugia. The patterns of heat tolerance from this experiment can be used to understand the drivers of heat tolerance variability in Palau.

Results Summary

The long-term marine heatwave experiment conducted at the Palau International Coral Reef Center took place over 5-6 weeks. The heat stress exposure reached a final DHW heat stress of ~16 °C-weeks and led to bleaching and mortality in all coral fragments. Notably, even by 4-8 °C-weeks there was considerable bleaching and mortality (Fig. 2).

One possibility was that heat tolerance may be higher at hotspot reefs because of conditions more conducive to directional selection and acclimatisation. However, our results show the opposite, with higher levels of heat tolerance on average at thermal refugia reefs (Fig. 3), despite less historic exposure to heat stress (Fig. 1). This trend was present across various metrics of heat tolerance, including the mean bleaching survival index (per colony), overall sigmoidal dose-response curves, and the lethal dosage (Fig. 3, mean lethal DHW dosage across all replicate nubbins per coral colony). Notably, the variability in heat tolerance within regions far exceeds the variability between regions (Fig. 3).

Concluding Remarks

Evolutionary theory has shown that selective pressure drives adaptation through natural selection, with evidence of this in corals across broad geographic and environmental gradients (Evensen et al. 2022,



Figure 2. The study species *Acropora digitifera* (a, b). There was substantial variability of coral heat tolerance within this population, showing the progression of bleaching responses during a long-term marine heatwave emulation experiment (c) that also led to mortality for each coral fragment (not shown).

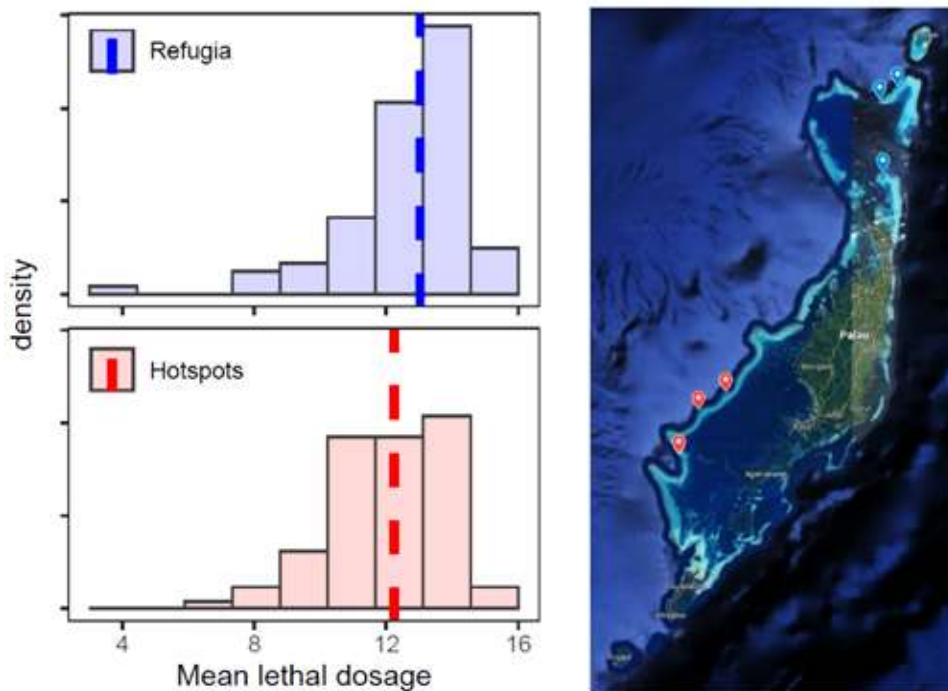


Figure 3. Three replicate collection sites in persistent thermal refugia (blue, north) and persistent hotspot reefs (red, southwest). A mean lethal DHW dosage was computed across replicate fragments for each coral in the experiment. The distribution of individual mean lethal dosages (histograms) and the median show slightly higher heat tolerance at thermal refugia (against expectations) but considerably high within-population variability of heat tolerance.

Marzonie et al. 2023). However, our study has shown that at local within-population spatial scales, and amid high trait variability, heat tolerance was in fact higher at thermal refugia. Lower tolerance at hotspots may relate to the influence of other biotic or abiotic drivers of this trait (*e.g.*, past heat stress exposure being overwhelmed by the effects of water quality or wave exposure) and potential trade-offs between heat tolerance and other fitness-related traits (*e.g.*, calcification, disease resistance), despite recent work showing no apparent trade-offs associated with heat tolerance for the study species (Lachs et al. 2023b). Our study provides information that could be

used to guide novel management actions such as climate-smart marine protected area networks or assisted evolution using assisted gene flow (Baums et al. 2019) or selective breeding (Humanes et al. 2021). Our study shows that coral colonies with high heat tolerance may not need to be sourced from distant reefs with contrasting thermal regimes, but rather could be sourced from any local reef. For this to work, effort is required to quantify colony heat tolerance at the individual level. Notably, this advice is based on *A. digitifera* in Palau, and therefore may only be applicable to cases where there are limited latitudinal or thermal gradients (*e.g.*, unlike the Great Barrier Reef), and sufficient genetic diversity remaining on individual reefs (*e.g.*, unlike some Caribbean *Acropora palmata* populations). Despite expectations, hotspots in Palau’s barrier reef systems do not necessarily harbour corals with higher heat tolerance than thermal refugia, suggesting a potential influence of drivers other than temperature on coral heat tolerance.



Figure 4. Left to right: James Guest, Liam Lachs, Adriana Humanes, Leah Bukurou, Ruben de la Torre Cerro, Alex Ward, Eveline van der Steeg, Elizabeth Beauchamp, Helios Martinez.

Acknowledgements

This work was made possible through a Ruth Gates Fellowship from the International Coral Reef Society and from the combined efforts of numerous wonderful colleagues. Thanks to my primary supervisor James Guest and Yimnang Golbuu former CEO of the Palau International Coral Reef Center for supporting this work, to PICRC staff Arius Merep for help with aquarium tank construction and Geory Mereb for guiding us across the remote reefs of Palau, to the big team of researchers who helped with the experiments: Adriana Humanes, John Bythell, Elizabeth Beauchamp, Leah Bukurou, Daisy Buzzoni, Ruben de la Torre Cerro, Helios M. Martinez, Eveline van der Steeg, Alex Ward, and for the guidance from Peter Mumby, Alasdair Edwards, Simon Donner and Holly East.

About Liam Lachs

I am a postdoctoral research associate in the Coralassist Lab interested in the potential for corals and coral reef ecosystems to adapt to ocean warming and marine heatwaves, with a focus on improving current and future predictions of mass coral bleaching.

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Website: <https://www.coralassistlab.org/liam-lachs>

Twitter: <https://twitter.com/LiamLachs>

Bluesky: <https://bsky.app/profile/liamlachs.bsky.social>

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REEF EDGE

Feary et al.

Density dependent use of highly degraded coral heads by live coral associate fish communities

David A Feary^{1*}, Mohamed Sobhy Negm¹, Mahmoud Serageldin¹, Agnes Le Port¹, Chico Birrell¹, Daniele D'Agostino¹

¹General Organization for Conservation of Coral Reefs and Sea Turtles in the Red Sea

*corresponding author email: david.feary@Shams.gov.sa

Introduction

Determining the factors that may enhance the success of coral reef fish communities under continuing habitat loss has been a central tenet of coral reef fish ecology assessments (Jones et al. 2004, Wilson et al. 2008, Pratchett et al. 2016). Species' ability to adapt to change has been highlighted (Feary 2007, Feary et al. 2007, Nakamura et al. 2013, Feary et al. 2018), though the long-term effects of such adaptation on the structure of communities have been little examined. Here we provide observations, from work carried out in April 2024, that the two live coral-associated reef fish species *Dascyllus abudafur* (previously known as *Dascyllus aruanus*, Borsa et al., 2014) and *Chromis viridis*, presumed to only shelter within live coral habitats (Feary et al. 2007, Bonin 2012), will shelter within both dead (Fig. 1) and heavily algal-covered (Fig. 2) coral reef heads.

Changes in the availability of live coral habitat is expected to have density-dependent effects on the habitat selection of coral reef species, with most work predicting higher intraspecific competition for more sparsely available live habitats (Feary et



Figure 1. *Dascyllus abudafur* in a dead coral head



Figure 2. *Chromis viridis* (above) and *Dascyllus abudafur* (below) in algal covered coral heads

al. 2007, Wilson et al. 2008). Despite this, the utilization of highly degraded habitats (Wismer et al. 2019a, 2019b), or habitats lacking in 3-dimensional live coral structure (Streit et al. 2021), by supposedly live coral associated fishes is now being increasingly identified. However, these studies are associated with recent reductions in coral cover following disturbance events, with little understanding of the long-term effects of such habitat changes. Overall, the current literature would predict that such coral-associated species are more likely to experience population declines and face extinction on heavily degraded reefs rather than persist (Booth & Beretta 2002).

The pocilloporid coral heads pictured are situated in the central Saudi Arabian Red Sea (Al Lith: 19.9801800°, 040.1372300°), within reefs that have been historically impacted by a range of anthropogenic factors. Widespread climate-induced bleaching has been identified on these reefs in the



Figure 3. Recruits of *Dascyllus abudafur* in a live coral head

summer months of 2023 (D. Suggett pers comm), while the presence of *Drupella* spp, crown-of-thorn starfish, and coral disease were all identified by the authors within these reefs. Notably, live pocilloporid coral heads within these reefs show minimal coverage (less than 1% total abundance), with reef communities dominated by sparse dead, algal-covered coral heads interspersed with patches of sand or coral rubble (authors pers obs). Therefore, such habitat use by both species may be associated with individuals being stranded on degraded coral after a reef-wide reduction in live coral availability (e.g., post-bleaching event), unable then to move to a living coral head.

Our observations also show that recruitment by both coral reef fish species may not be associated with degraded coral heads. Communities of both *D. abudafur* and *C. viridis* on degraded habitats were comprised solely of juvenile and adult-sized individuals, with no use of such habitats by new recruits of both species. Recruits of both species were only found on the sparsely available live coral heads (Fig. 3). However, as live coral decreases in proportion within the degraded landscapes, the likelihood that new recruits utilize degraded habitats may increase.

Ecological surprises denote patterns that defy conventional expectations yet occur and may likely become the norm amidst a changing climate. Our observations of two presumably coral-associated reef fish species, sheltering in bleached and algal-covered coral heads, may show the ability of such species to cope with a changing environment. However, this behavioral pattern may also illustrate the last vestiges of habitat use for both coral reef fish species in a heavily degraded reef landscape. In this, suitable live coral habitat is

exceptionally sparse, recruitment is still structured by use of a dwindling number of live coral heads, with density-dependent habitat use structuring juvenile and adult coral reef fish community structure.

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Can variation in fish predator density and the “Landscape of Fear” facilitate coral restoration success?

Peter J. Auster^{1,2*} and Mari E. Cullerton¹

¹Mystic Aquarium, Mystic, CT USA; ²University of Connecticut, Department of Marine Sciences, Groton, CT USA

*corresponding author email: peter.auster@uconn.edu

The restoration of coral reefs and reef function via coral transplant programs has been hindered by a multitude of problems, including coral bleaching, disease, and the loss of herbivores. These challenges have led directly and indirectly to coral mortality and recruitment failure in the Florida Keys region of the United States (Ware et al. 2020). Coral mortality is also affected by coralivorous fish and algal gardeners (Precht et al. 2010, Schopmeyer & Lirman 2015, Noonan & Childress 2020, Koval et al. 2020). Survivorship, movement, and behavior of corallivores and algal gardeners can be influenced

by the presence of piscivores and their perceived risk of predation within a “landscape of fear” (Mitchell & Harborne 2020, Seraphim et al. 2020, Palmer et al. 2022). Thus, higher trophic level predators may enhance the survival of coral transplants by limiting numbers (via direct predation) and limiting area of feeding behavior (via fear response) of corallivores and algal gardeners (Fig 1).

Here we posit that understanding the distribution of piscivores across the Florida coral reef ecosystem can identify mesoscale patterns of variability in

predation pressure and risk to corallivores and algal gardeners. This understanding could inform an approach for planning management-scale experiments with coral transplants that include treatments based on the effects of piscivores. In this study, we used a geographically comprehensive data set from the National Coral Reef Monitoring Program's "Assessment of Coral Reef Fish Communities in the Florida Reef Tract" (NOAA SEFSC & NCCOS 2018) to identify changes in spatial patterns of piscivorous fishes based on their observed density. Point count data for select predators (Table 1; based on Sponaugle et al. 2012) in years 2014, 2016, and 2018 were gridded over the main Florida Reef and Dry Tortugas and density was computed for each grid cell (Figs 2 & 3). We used the top quintile of total predator density to indicate predator hotspots for each survey period and indicated grid cells that were identified in one, two, or all three years. Grid size (8 x 8 km for the main Florida Reef and 4 x 4 km for Dy Tortugas) was selected to maximize spatial geospatial resolution while ensuring continuity of data

Table 1. Piscivore species and number of occurrences from point count surveys (see text). Initial observation values in the data set are based on the mean of each diver pair conducting surveys at a location and below the totals of all surveys by year for each species.

Scientific Name	Common Name	Number of Observations		
		2014	2016	2018
<i>Aulostomus maculatus</i>	Atlantic trumpetfish	98.69	31	60.66
<i>Caranx hippos</i>	Creville jack	12.5	109	1
<i>Caranx ruber</i>	Bar jack	8910.37	8963	5071.34
<i>Carcharhinus leucas</i>	Bull shark	0.5	0	0
<i>Carcharhinus perezii</i>	Reef shark	5	0	5.5
<i>Centropomus undecimalis</i>	Common snook	0.5	0	0.5
<i>Cephalopholis cruentata</i>	Graysby	534.24	406	375.95
<i>Cephalopholis fulva</i>	Coney	12.24	3	2
<i>Epinephelus itajara</i>	Goliath grouper	3	0	1
<i>Ginglymostoma cirratum</i>	Nurse shark	13.5	2	16.5
<i>Heteropriacanthus cruentatus</i>	Glasseye snapper	19.22	1	61.46
<i>Lutjanus apodus</i>	Schoolmaster	828.1	829	894.72
<i>Lutjanus griseus</i>	Gray snapper	3157.57	2143	4358.07
<i>Lutjanus jocu</i>	Dog snapper	13.74	1	13
<i>Lutjanus mahogoni</i>	Mahogany snapper	137.18	73	95.47
<i>Lutjanus synagris</i>	Lane snapper	521.37	739	1309.83
<i>Mycteroperca bonaci</i>	Black grouper	63.07	24	101.33
<i>Ocyurus chrysurus</i>	Yellowtail snapper	16061.86	12011	13150.53
<i>Serranus tigrinus</i>	Harlequin bass	333.53	272	410.29
Shark species		0.5	0	0
<i>Sphyrna barracuda</i>	Great barracuda	133.18	73	105.3



Figure 1. Examples of corallivores in patches of staghorn coral *Acropora cervicornis* transplants: (A) banded butterflyfish *Chaetodon striatus*, (B) four-eye butterflyfish *Chaetodon capistratus*. Examples of proximate occurrences of piscivores in patches of coral transplants: (C) Caribbean reef shark *Carcharhinus perezii*, (D) bar jack *Caranx ruber*.

between cells (i.e., a smaller grid size would result in many cells with no data).

The Florida Reef Tract was composed of 63 grid cells, 20 of which were identified in at least one year as a piscivore hotspot (Fig. 2). Of these cells, four were consistently identified over the three survey periods, while seven were identified twice and nine once. The Dry Tortuga region, with a total of 41 cells, had 15 cells that were identified as hotspots. Only one of these cells was identified as a hotspot across the survey years, while seven cells were identified twice, and an additional seven were identified once. Notably, 66 percent of the grid cells were never identified as a hotspot. Only 14 percent of the hotspots were consistent across all three survey years while 40 percent were in the top quintile twice. These results can be considered indicative of coarse scale gradients in piscivore pressure.

The patterns in piscivore distribution identified here can serve as a framework to consider inclusion of piscivore interactions to aid regional coral transplant programs. That is, including the hot spot status of cells as a spatial treatment, compared to those not identified as hotspots, can facilitate statistical contrasts of transplant success to evaluate the effects piscivore interactions. Of

course, there needs to be concomitant assessments of predator attributes at local-spatial scales. Downscaling from coarse to fine scales can enable a trait-mediated approach to identify sites that optimize direct predation and fear responses on corallivores and algal gardeners. For example, coarse-scale piscivore data can be used to locate sites within select grids where fine-scale maps are available or can be produced (e.g., photomosaics or high-resolution bathymetry). This in conjunction with behavioral metrics from fish surveys (e.g., rates of piscivore occurrence and response of coral associated fishes) can define “predator threat” treatments (Auster et al. 2021, Helder et al. 2022) to assess patterns in coral transplant success. The presence of piscivore hotspots along the length of the Florida Reef indicates that integrating predation treatments into other transplant program design factors (environmental gradients, fishing pressure) could be feasible.

There is a pressing need to address the conservation and restoration of coral reefs -- the Florida Reef in particular. But to do this, we must consider the full range of drivers when developing ecosystem-scale adaptive management experiments and learn as much as possible as quickly as possible (Kaufman et al. 2023). Time is not on our side.

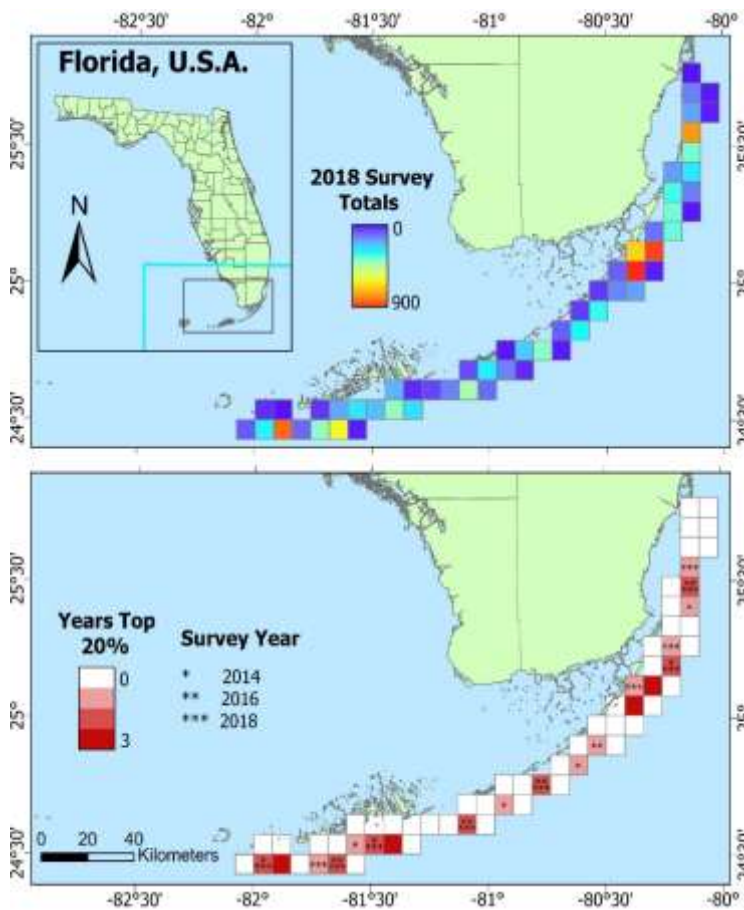


Figure 2. Distribution of aggregate piscivores from Table 1 based on density across the main Florida Reef Tract (A) and location of hotspots in different years based on top quintiles of density (B). The inset map indicates the location of the Florida Reef Tract. See text for further explanation.

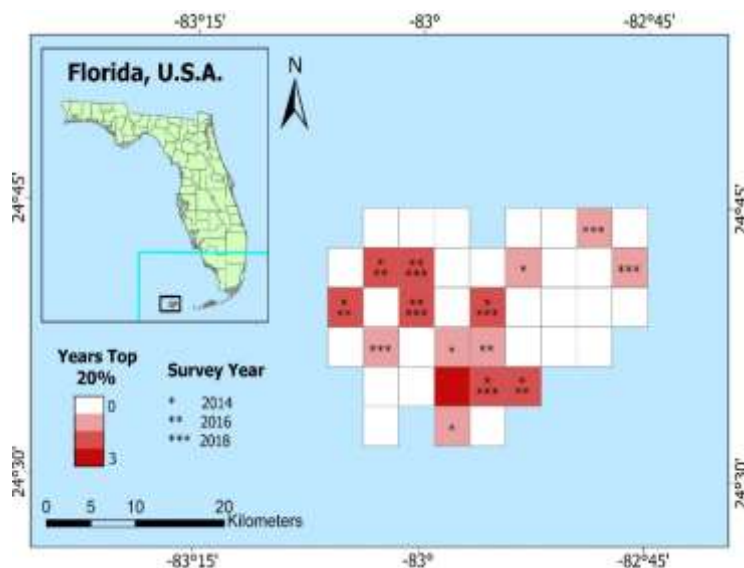


Figure 3. Location of hotspots in different years based on top quintiles of piscivores from Table 1 across Dry Tortugas. The inset map indicates the area's location west of Florida Reef Tract. See text for further explanation.

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REEF RECRUITS

Cryptic corals: Investigating causes of ecological specialization in the Great Star Coral (*Montastraea cavernosa*) to maximize restoration efforts

Dominique Gallery

Department of Integrative Biology, University of
Texas at Austin, Texas, USA
email: dgallery@utexas.edu

Introduction

Anthropogenic stressors continue to decimate coral reefs, resulting in reductions of genetic diversity within populations (Carpenter et al. 2008). Loss of genetic diversity inhibits populations' ability to adapt to changing environmental variables (e.g., warming ocean temperatures, pathogens, increased ocean acidification, etc.), leading to further losses of individuals within populations. This positive feedback loop is further complicated in nominal species with subpopulations that have limited introgression between them. Within corals, there is increasing evidence that many nominal species have subpopulations identified primarily via genetic differences (Knowlton 1993; Hays et al. 2021; Rippe et al. 2021; Black et al. 2022), known as cryptic genetic structure. Limited introgression between these subpopulations exacerbates genetic diversity loss due to restricted gene flow (Bálint et al. 2011). This results in subpopulations with strong

genetic divergence with limited interbreeding in close geographic proximity (Sanford and Kelly 2011).

Historically, to counter the loss of genetic diversity in coral reefs, restoration organizations have aimed to preserve and/or generate genetic diversity by protecting particular reefs or habitats and cultivating diverse genotypes in coral nurseries for restoration. However, the recent discovery of cryptic genetic lineages within certain species, such as *Montastraea cavernosa*, challenges these efforts by subdividing populations. To successfully ensure that restoration managers are cultivating enough genetic diversity to overcome these challenges, scientists have begun to focus research efforts on identifying species with cryptic genetic lineages and understanding the environmental variables that drive their genetic divergence.

Montastraea cavernosa (the Great Star Coral) is a ubiquitous, reef-building Caribbean coral in the Florida Keys reef tract. Recent studies (Rippe et al. 2021; Gallery et al. 2023) showed four cryptic lineages and three potential hybrid lineages of *M.*

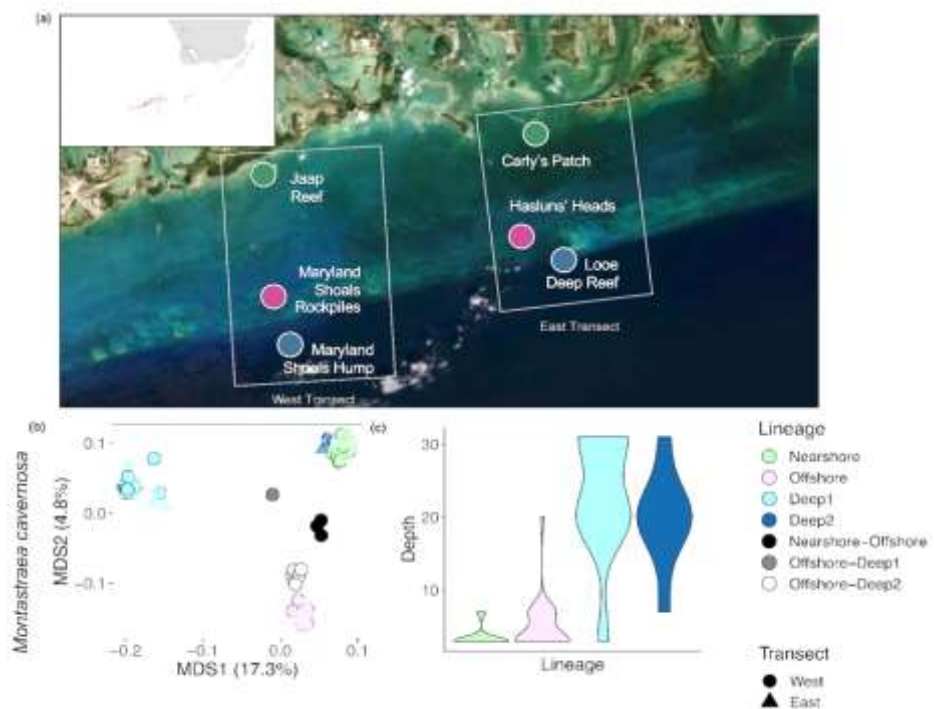


Figure 1. (a) *M. cavernosa* samples were collected from two transects in the Florida Keys in 2014 (east transect) and 2018 (west transect). (b) Principal coordinate analysis shows the genetic separation of different lineages. (c) Violin plots show each lineage's relative abundance with depth in meters for non-hybrid individuals in both transects.

cavernosa found in six locations in the Florida Keys (Fig. 1a). These lineages, identified by genetic separation of unique genotypes (Fig. 1b), are correlated with depth (Fig. 1c). In these experiments, we aimed to evaluate which environmental parameters associated with depth are correlated with lineage-specific adaptations. To examine these genotype-environment associations between lineages of *M. cavernosa*, I proposed undertaking reciprocal transplant and common garden experiments at Mote Marine Laboratory, where restoration efforts for this species are already underway. A reciprocal transplant experiment, where individuals are switched from their native environment to another environment, can identify if local adaptation is occurring by measuring the fitness of a coral in its native environment versus its non-native environment (Svensson et al. 2018). A common garden experiment, which involves placing individuals from various genetic and environmental backgrounds into the same environmental conditions, can elucidate effects from origin environments (de Villemereuil et al. 2016). Combining phenotypic and genomic traits of an organism with common garden and reciprocal experiments can indicate if local adaptations are occurring within lineages of this species. I hypothesized that the amount of light is the primary driver of differentiation between the shallow and deep lineages and within the shallow lineages, individuals have increased fitness when in their native environment compared to their non-native environment.

Table 1. Treatment groups for reciprocal transplant experiment.

Treatment Group	Number of individuals	Lineage	Habitat of Origin
1	15	Nearshore	Carly's Patch
2	15	Nearshore	Hasluns Heads
3	15	Offshore	Carly's Patch
4	15	Offshore	Hasluns Heads

Research Activities

In December 2022, I sampled and tagged 160 colonies of *M. cavernosa* from the east transect (Fig. 1a). Samples were genotyped using 2bRAD sequencing and assigned to a cryptic genetic lineage using the methods outlined in Rippe et al. (2021) and Gallery et al. (2024). After lineages were determined, I selected 60 unique genotypes for the reciprocal transplant experiment with the parameters outlined in Table 1. Samples were

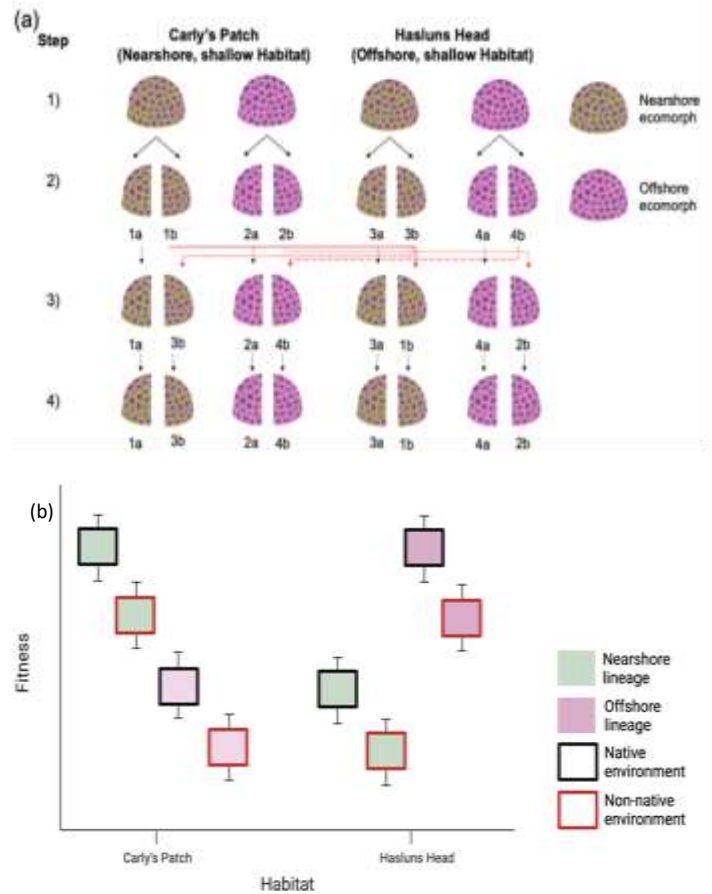


Figure 2. (a) Experimental design for the reciprocal transplant. (b) Expected results. I expect that within a lineage, a nubbin deployed to its native habitat will outperform a nubbin deployed to its non-native habitat. Between lineages, I expect nubbins deployed to the habitat matching their lineage's ideal environment to outperform nubbins in their mismatched environment.

collected from the reefs, split into two clonal fragments, and allowed to acclimate in a common tank for 1 week. At the end of the acclimatization period, a single polyp was collected from each fragment for initial gene expression and chemical analysis, buoyant weight was measured, and fragments were assigned to be deployed at either Carly's Patch or Haslun's Heads for the duration of the experiment (Fig. 2a). The experiment was initially designed for deployment to last six months; however, due to the unprecedented heat wave that impacted the Florida Keys this summer, fragments were pulled from the reef after 10 weeks, when the final buoyant weight was measured. A single polyp was collected for gene expression and chemical analysis as fitness proxies (Winters et al. 2009; Kenkel et al. 2015; Dixon et al. 2018). These proxies will be used to test my hypothesis that individuals experience increased fitness in their native environment versus their non-native environment (Fig. 2b). I further predict that due to the specialization of these lineages to a particular

environment, a non-native individual deployed into its lineage’s specialized environment will have higher fitness when compared to a native individual in its lineage’s non-specialized environment (Fig. 2b).

For the common garden experiment, I selected 15 individuals of the “Nearshore” lineage from Carly’s Patch, 15 individuals of the “Offshore” lineage from Haslun’s Heads, and 15 individuals of the “Deep 1” lineage at Looe Key Deep. The “Deep 1” lineage was chosen due to its higher abundance relative to the “Deep 2” lineage. The 45 fragments selected for this experiment were split into four nubbins and acclimatized for four weeks in a common raceway tank. After the acclimatization period, I measured the initial buoyant weight and collected a single polyp for gene expression and chemical analyses. Two nubbins from each colony were placed into the experimental tanks: high light (mimicking the light in the shallow reef) and low light (mimicking the light in the deep reef). After eight weeks, I measured the total coral growth for each nubbin and sampled each for zooxanthellae density, metabolite content, and gene expression as fitness proxies (Winters et al. 2009; Kenkel et al. 2015; Dixon et al. 2018). These proxies will be used for testing my hypothesis that shallow-lineage individuals and deep-lineage individuals fulfill different ecological niches based on the amount of light available. I predict that “Deep 1” lineage individuals will outperform “Offshore” lineage individuals in the low light tank, and “Offshore” lineage individuals will outperform “Deep 1” individuals in the high light tank.

Preliminary results

For both experiments, gene expression measurements are in the process of being sequenced. Following sequencing, gene expression analyses will be completed using methods similar to those presented in Gallery et al. (2024). Preliminary analyses of the buoyant weight of the common garden experiment, suggest that amount of light is correlated with the fitness of lineages

(Fig. 3). To analyze the buoyant weights, we calculated the difference between the initial and final weights, then used a linear model to calculate the residuals. These residuals were then processed in the R package “lmerTest” using the following

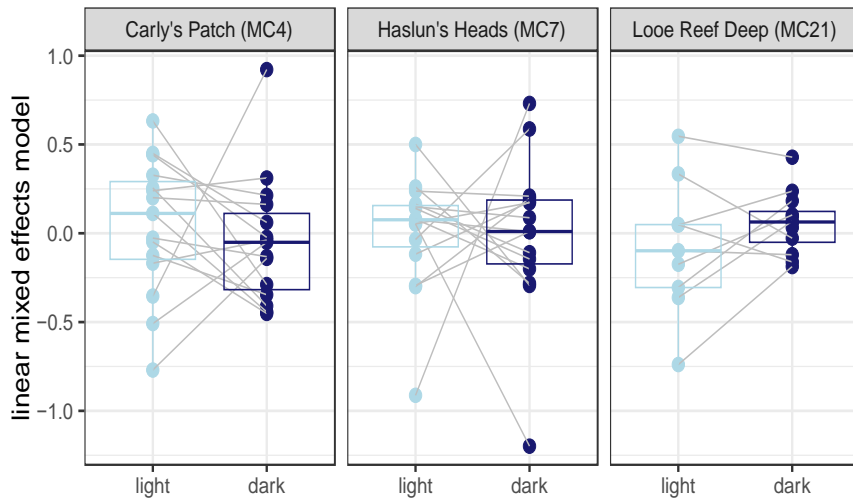


Figure 3. Preliminary results from buoyant weight fitness proxy in the common garden experiment. Panel 1: Light treatment has higher fitness than dark treatment. Panel 2: No difference in treatments. Panel 3: Dark treatment has higher fitness than light treatment.

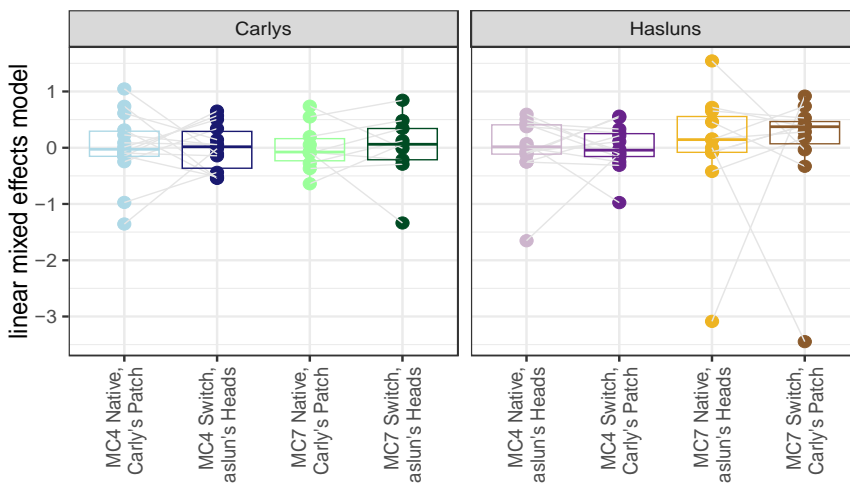


Figure 4. Preliminary results from buoyant weight fitness proxy in the reciprocal transplant experiment. Panels are the site the fragments were transplanted; site on the x-axis is the origin site of the fragments.

formula: resid ~Treatment +Habitat+(1|OG_colonyID). We calculated p-values from the linear mixed model using the function emmeans from the R package “emmeans.” We find the general trend that individuals in the “Nearshore” lineage from Carly’s Patch in the light treatment had increased fitness relative to their genetic counterparts in the dark treatment (p < 0.05). Inversely, the “Deep 1” lineage from Looe Key Deep had increased fitness in the dark treatment compared to the light treatment (p < 0.05). Finally, the intermediate depth samples from Haslun’s

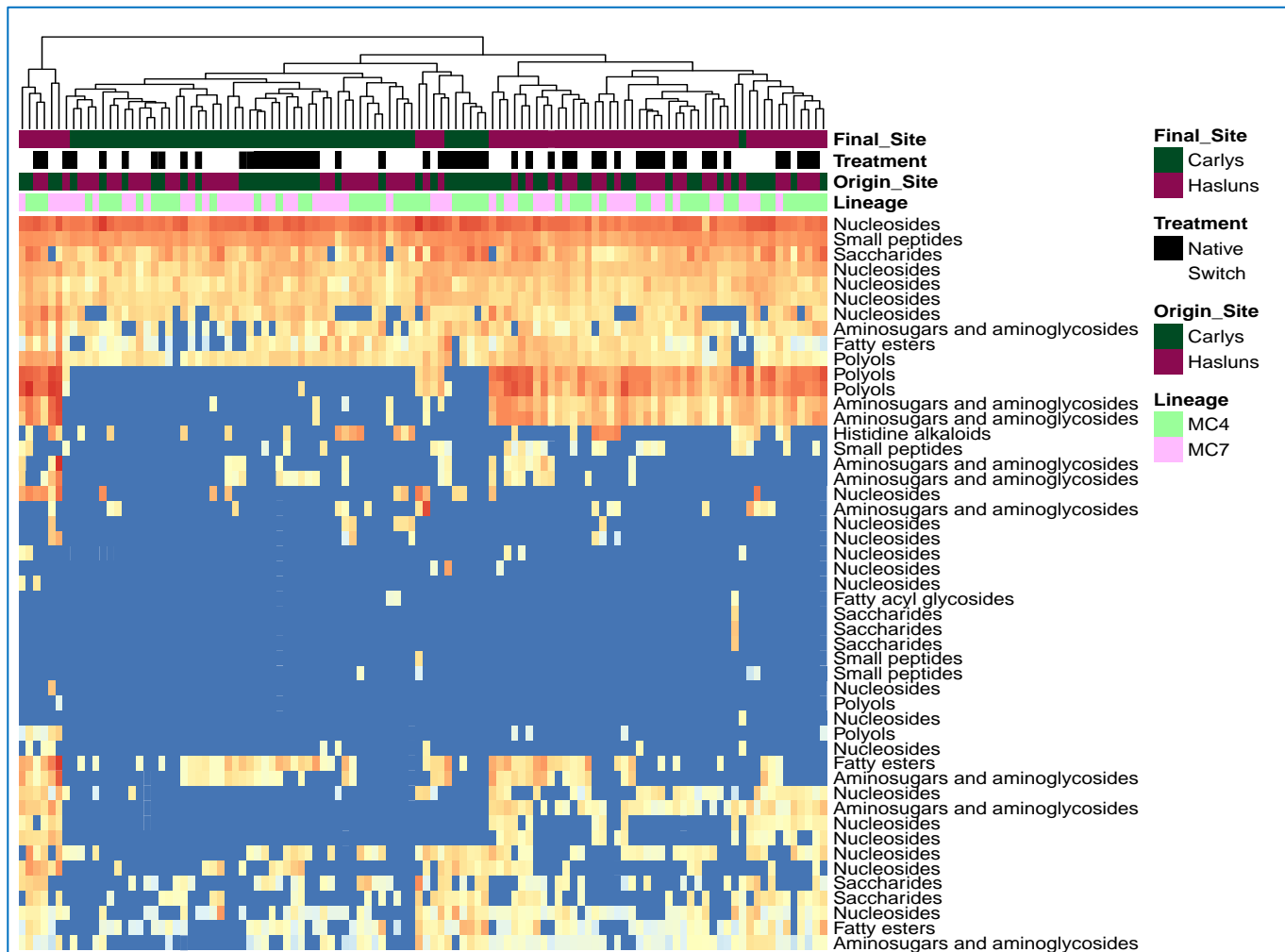


Figure 5. Preliminary results from metabolite analyses from the reciprocal transplant experiment. Samples are along the x-axis; chemical superclass is along the y-axis.

Heads had no significant difference between treatments ($p > 0.05$).

For the reciprocal transplant experiment, we found only one pairwise comparison with a significant difference. “Nearshore” lineage, native to Carly’s Patch and native to Haslun’s Heads that were transplanted to Carly’s Patch had significant, albeit slight, differences between fitness, with the non-native individuals having slightly higher fitness (Fig. 4). These results counter our predictions and require further analyses and examination. Metabolomic results from the reciprocal transplant indicate that transplant site is the primary driver of clustering differences, especially in the carbohydrates pathway chemicals (Fig. 5). This indicates a strong plasticity in secondary metabolites in *M. cavernosa*.

Conclusion

Understanding the causes of depth-driven cryptic lineages remains a vital question to be answered in the coral community, especially for *M. cavernosa*

which is an important reef-building coral in the Florida Keys and wider-Caribbean. Here we attempted to determine if light is a driving factor in the lineages with a common garden experiment. Preliminary results suggest there is an effect of light on the fitness of corals in the common garden experiment. These results suggest that when selecting depths for restoration, it may be important to consider matching the coral’s lineage to their outplanted depth. We also attempted to determine the importance of site within the shallow lineages and shallow sites. Our preliminary results from a reciprocal transplant experiment indicate that there are minimal fitness effects between sites, which is promising for restoration efforts. This may suggest that within the shallow habitats and shallow-preferring lineages, there is some flexibility for outplanting. Overall, it may be more important to match transplanted individuals to their lineage’s preferred depth range than a specific habitat. However, further studies should be conducted in this area.



Dominique
Gallery

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Effects of submarine groundwater discharge (SGD) on coral calcification

Hannah Merges

California State University Northridge, Northridge, California, USA

Email: hannah.merges.839@my.csun.edu

Background

SGD is a geological and physical process that occurs naturally in many coastal, nearshore environments, yet the effects of SGD on coral reefs differ due to local biogeochemical parameters, geography, and watershed management (Taniguchi et al. 2002; Burnett et al. 2006, Lubarsky et al. 2018; Nelson et al. 2015; Richardson et al. 2017; Silbiger et al. 2020). Fluxes of groundwater are highest when water levels are low, typically during low tide (Taniguchi et al. 2007), leading to highly variable physicochemical environments for organisms living near SGD seeps. Relative to the surrounding ambient seawater, SGD is lower in temperature, pH, and salinity, and is higher in nitrate and phosphate (Burnett et al. 2006; Silbiger et al. 2020). Total alkalinity (TA) levels vary depending on the local geology of the groundwater source (Cyronak et al. 2013). TA represents the ability of a solution to absorb H⁺ ions without a subsequent reduction in pH, suggesting that increased TA levels may be able to buffer against the lower pH in SGD (Cyronak et al. 2013). Coral respiration, calcification, and photosynthesis may all be affected by the distinct biogeochemistry of SGD (Lubarsky et al. 2018; Silbiger et al. 2020). Because SGD fluxes are changing as a result of climate change (McKenzie et al. 2021), assessing the effects of SGD on corals is necessary to predict how these changes may affect reefs in the future.

There have been a few *in situ* studies investigating the effects of SGD on coral calcification, productivity, and reef metabolism (Lubarsky et al. 2018; Silbiger et al. 2020). However, there has never been a manipulative lab experiment that tests the direct response of varying levels of SGD on coral metabolic rates. Previous *in situ* studies have shown a modal response of coral metabolism in response to SGD and have suggested that corals may be able to thrive in SGD conditions if isolated

from other stressors (Lubarsky et al. 2018). Therefore, I hypothesized that short-term exposure to SGD across a dilution gradient would result in a non-linear physiological response, with photosynthesis peaking at lower SGD (0.05% by volume) and then declining and shifting to a net respiratory state at higher SGD (4% by volume). I predict that there will be a linear relationship for calcification, with a shift towards a net dissolving state at higher SGD (4% by volume).

Activities/Research Undertaken

My research was conducted in Mo'orea, French Polynesia, at sites with over three years of spatiotemporal data on SGD fluxes and biogeochemistry. Our lab has previously characterized the biogeochemistry of two sites along the Western shore, Varari and Cabral. Varari has unidirectional flow of SGD with a predictable nutrient source and augmented nitrates and TA levels compared to ambient seawater. Cabral has a lower flow rate compared to Varari, with most of its nutrient source coming from the SGD seep and possibly mixing with organic matter from a nearby sandy pit. Contrary to Varari, the SGD from Cabral is highly depleted in TA. The differences in biogeochemistry between the sites allows for a direct comparison in how different sources of SGD may affect coral metabolism.

Colonies (n=8) of *Pocillopora acuta* were collected from ambient seawater and fragmented at the Richard B. Gump South Pacific Research Station. Coral fragments (n=9 per colony) were randomly assigned to an SGD treatment (n=9 dilutions, ranging from 0-4% SGD by volume), with one fragment per dilution from each of the eight colonies. Fragments were soaked in their respective treatments for 12 hours. To create these dilutions, groundwater was collected from both sites and filtered. Water samples were taken to measure TA, nutrients, and fluorescent dissolved organic matter (fDOM) for each dilution. Salinity was recorded with a YSI Conductivity/Temp Handheld Meter. Temperature was measured with a Traceable® digital thermometer (Control Company 5-077-8, accuracy=0.05°C, resolution=0.001°C, Webster, TX, USA). pH and millivolts were measured using a Thermo Scientific Orion Star™ A222 Conductivity Portable Meter. After soaking, each of the fragments was placed into one of nine individual, closed-system acrylic respiration chambers (650 ml) (designed by Australian Institute of Marine Science) containing the same water from the groundwater

mixture in which they were soaking. The chambers had rotating stir bars (200 rpm) and were used to measure net photosynthesis (NP) and net ecosystem calcification (NEC) in the light, and respiration (R) in the dark. Oxygen concentrations ($\mu\text{mol l}^{-1}$) and temperature ($^{\circ}\text{C}$) were recorded using a PreSens Oxygen Meter [OXY-10 SMA (G2)] system (Regensburg, Germany). NP and R rates were then calculated based on oxygen production and consumption rates ($\mu\text{mol/cm}^2/\text{hr}$). For all rates, fragments were normalized to their surface area using the wax dipping technique (Veal et al., 2010).

Summary Results

To understand how physiological rates such as photosynthesis, respiration, and calcification were impacted by different concentrations of groundwater, I used mixed model regressions to analyze physiological rate against groundwater parameters. I ran model selection for both polynomial and linear regressions using pH, salinity, and the SGD dilutions to determine which parameter had the strongest relationship with physiological rates of P, R, and NEC.

For both Varari and Cabral, I found no significant effect of SGD dilution, salinity, or pH on respiration or net photosynthesis. However, there was a significant difference between sites for calcification rates across SGD dilutions. There was a significant decrease in calcification across the dilutions at Varari (Figure 1), whereas there was no significant effect of the dilutions at Cabral. I am currently running additional models to include environmental parameters such as nutrients and fDOM to assess which parameters most strongly drive the changes in calcification, photosynthesis, and respiration.

Discussion and Concluding Remarks

These results were unexpected, given Cabral's lower TA levels, suggesting a decreased ability to buffer against the low pH associated with SGD. However, nutrients have been shown to reduce coral calcification (Silbiger et al. 2018), and given the higher levels of nutrients at Varari, this could be a likely explanation for the decreased calcification rates at that site. SGD is a ubiquitous process, and it is necessary to understand how this disturbance may be affecting the metabolism and productivity of coral reefs. Many coastal communities around the world rely on the resources provided by coral reefs. Particularly in Mo'orea, many people rely on the shallow reef for

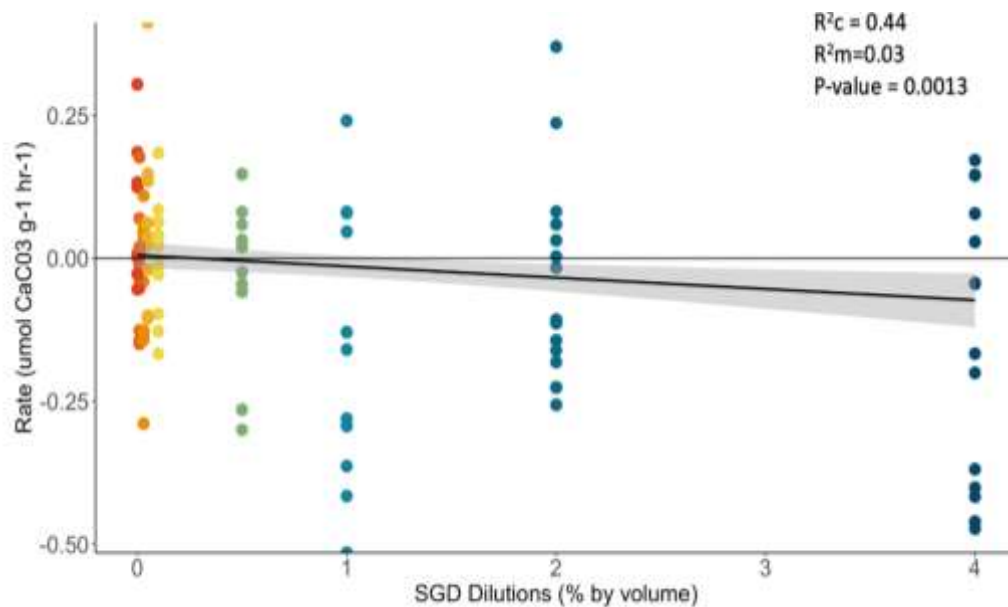


Figure 1. Net ecosystem calcification (NEC) rates plotted against submarine groundwater discharge (SGD) dilutions. NEC rates at Varari decreased significantly and transitioned to a net dissolution state as SGD concentration increased. Points are colored by the SGD dilutions.

subsistence fishing. Therefore, it is imperative that we understand how reefs respond to pulse disturbances such as SGD. There is still much to learn about the impacts that SGD can have on coral colonies and on reef ecosystems more broadly. Thus, I will be continuing this research in 2024 to assess the direct effect of SGD on *P. acuta* larval settlement. I hypothesize that the complex makeup of SGD will result in a decreased ability to settle under higher levels of SGD.

I'd like to thank the International Coral Reef Society Graduate Fellowship for providing funding to support this research. This research was in collaboration with the National Science Foundation funded Moorea Coral Reef Long Term Ecological Research Site which has nearly 20 years of time-series data at various sites around the island. I'd also like to acknowledge the support of my lab-mates, Maya Zeff and Kiran Reed, and two students, Haiata Phr and Timeri Lo, from Université de la Polynésie Française for their contributions to this research.



Hannah
Merges

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Investigating the heat shock protein response to growth anomalies in the scleractinian coral *Acropora muricata*

Shakeel Yavan Jogee

Department of Biosciences and Ocean Studies,
Faculty of Science, University of Mauritius
email: shakeeljogee96@gmail.com

Background

Heat shock proteins (HSPs) are crucial in sustaining protein homeostasis by aiding in proper protein structure folding and translocation, inhibiting the agglomeration of proteins damaged by environmental stress and helping in targeting, refolding and the subsequent degradation of damaged proteins through specific destructive pathways (Bozaykut et al. 2014, Balchin et al. 2016). Under normal non-stressful environmental conditions, a basal level of HSP is needed for normal protein folding, maintenance of signal transduction and normal development (Chen et al. 2018), but as a protective mechanism, corals stressed by environmental disturbances generally increase their level of HSPs (Seveso et al. 2014, Rosic et al. 2011). In particular, the induction of the

chaperonine 60-kDa heat shock protein (Hsp60) has been well studied in response to several environmental stressors, such as coral disease (Seveso et al. 2012), thermal bleaching (Choresch et al. 2001) and light stress (Downs et al. 2000).

Coral diseases are an example of a biotic stressor that can induce biochemical alterations in corals (Wong et al. 2021, Domart-Coulon et al. 2006, Seveso et al. 2012). Skeletal growth anomalies (SGAs), like many other coral diseases are a prominent stressor in coral reef ecosystems. SGAs are morphologically characterized by protruding skeletal growths, pale appearance, and loss of polyp and coenosarc structure (Burns et al. 2011 Domart-Coulon et al. 2006). SGAs have been found to impair essential biological processes in corals, such as feeding, reproduction, defense and energy budget (Work et al. 2008, Burns et al. 2011). Work et al. (2008) has systematically classified SGAs on *Acropora* corals into seven morphological groups: exophytic, bosselated, crateriform, nodular, vermiform, fimbriated, and annular. In addition to their gross morphologies, differences were also observed in cellular morphologies, such as the hyperplasia of cells of the polyps' basal body walls, reduced numbers or absence of zooxanthellae and mild to severe necrosis of mesenterial filaments.

SGAs on branching *Acropora* spp. have been previously reported in two lagoons of Mauritius (Bhagooli et al. 2017). We have recently found three types of growth anomalies in *Acropora muricata* at Belle Mare, Mauritius (Jogee & Bhagooli,

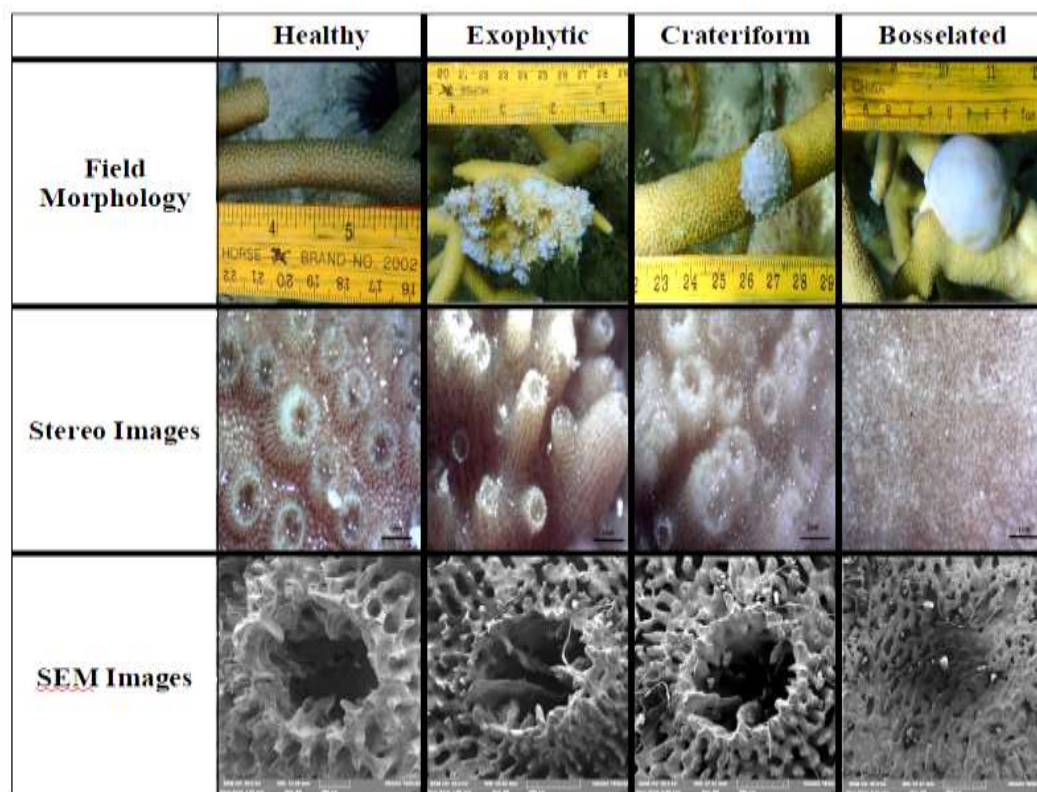


Figure 1. Three types of skeletal growth anomalies (exophytic, crateriform, bosselated) in *Acropora muricata* at Belle Mare, Mauritius (Jogee and Bhagooli, unpublished data). Preliminary collections have been done in collaboration with the University of Mauritius.

unpublished data). The types are morphologically very different in terms of the presence/absence and structure of the corallites, as confirmed by light and scanning microscopy (Fig. 1). Preliminary measurements of quantum yield of photosystem II using a pulse-amplitude modulation (Diving-PAM) fluorometer have indicated variable photosynthetic activities between healthy-looking and SGA-affected tissues of *A. muricata*. The proposed study further investigates photosynthesis in SGAs with a newly acquired Imaging-PAM fluorometer at the University of Mauritius.

Studies on the regulation of HSPs in response to SGAs have been conducted on *Platygyra canosa*, and the up-regulation of Hsp90 protein has been reported in SGA-affected areas compared to the healthy region of the coral (Wong et al. 2021). Domart-Coulon et al. (2006) made a similar observation in *Porites compressa*, in which up-regulation of Hsp90a1 was recorded in the SGA-affected areas compared to the non-affected areas of the coral. However, despite all the critical cellular alterations that occur in *Acropora* SGAs, no attempt has been made to investigate the biochemical changes through HSP expression and modulation, putative biomarkers for cellular stress, in these different types of *Acropora* SGAs. This study, thus, aimed to assess the expression patterns of Hsp60 in *Acropora muricata* in response to the different SGA morphotypes.

Research Undertaken

To date, the research undertaken at the University of Mauritius involved a 3-hour thermal stress experiment and photo-physiological assessment of SGAs under control (28°C) and thermal stress (30, 32°C) conditions. Three tanks filled with seawater were used for each temperature treatment. Triplicate samples of each SGA type and of healthy-looking *A. muricata* were placed in each tank. An Imaging-PAM fluorometer was used to assess chlorophyll fluorescence and associated parameters, such as the quantum yield of photosystem II (Φ_{PSII}), mean maximum relative electron transport rate (rETRmax), and maximal non-photochemical quenching (NPQmax). Measurements were taken in both the SGAs and the healthy-looking *A. muricata* before the temperature treatments and after 3 hours of thermal stress.

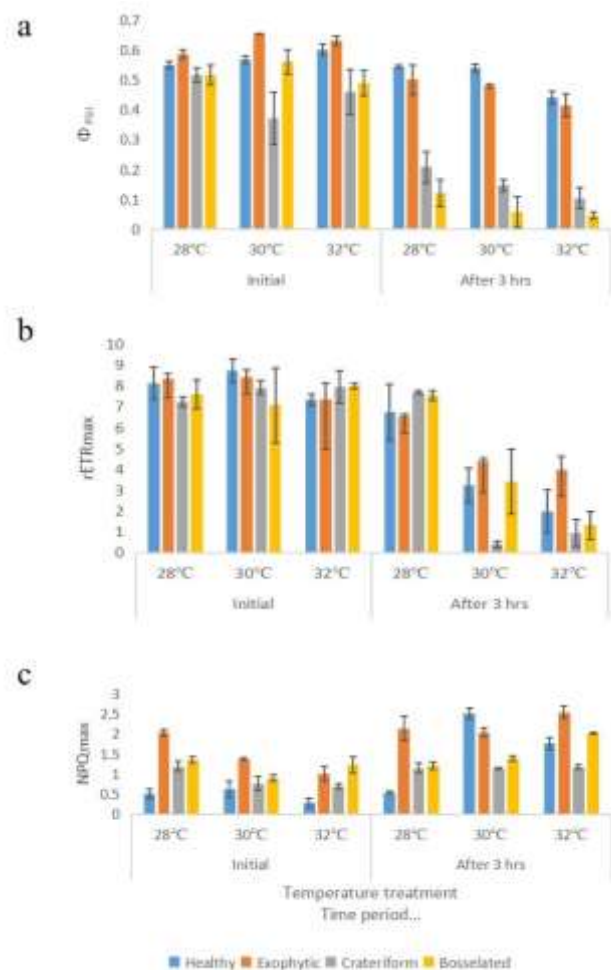


Figure 2. (a) Φ_{PSII} , (b) rETRmax and (c) NPQmax of the healthy-looking tissues and SGAs on *A. muricata* initially and after 3 hours of thermal stress.

The research undertaken at the University of Milano-Bicocca under the fellowship involved the HSP quantification in the SGAs after exposure to thermal stress conditions. Western-blotting was used to assess the Hsp60 levels in the healthy-looking tissues and SGAs in *A. muricata*.

Preliminary Results

a. Photo-physiological performance

A slight reduction in Φ_{PSII} , rETRmax and NPQmax for the crateriform and bosselated types of SGAs was observed compared to the healthy-looking *A. muricata* tissues. A reduction in Φ_{PSII} and rETRmax was observed in all morphotypes of SGAs after 3 hours of thermal stress at 30 and 32°C (Fig. 2a & b). NPQmax increased in all SGAs after 3 hours in the 30 and 32°C treatments compared to the 28°C controls (Fig. 2c).



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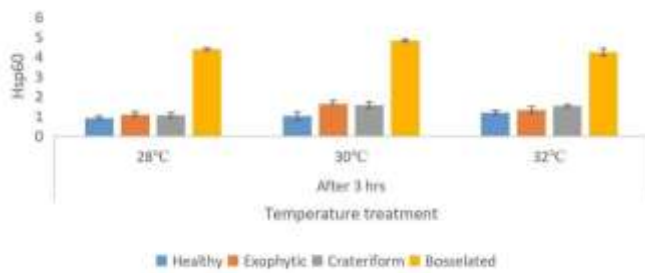


Figure 3. Hsp60 expression patterns of healthy-looking *A. muricata* tissues and exophytic, crateriform and bosselated SGAs after 3 hours of thermal stress at 30 and 32°C.

b. Hsp60 Expression

Hsp60 levels under control conditions appeared to be very slightly up-regulated in the exophytic and crateriform SGAs compared to the healthy-looking tissues of *A. muricata* (Fig. 3). Hsp60 levels under control conditions were highly up-regulated in the bosselated type SGA compared to the other SGAs. Compared to the control conditions, Hsp60 levels increased slightly in the healthy-looking tissues and SGAs following the thermal stress at 30 and 32°C (Fig. 3).

Concluding Remarks

The results obtained so far clearly show contrasting photo-physiological characteristics of the SGAs compared to healthy-looking *A. muricata*. The findings of this study also revealed differential responses of the three SGA morphotypes and healthy-looking samples under thermal stress. However, the photo-physiology and HSP characterization are not enough to adequately understand the innate physiology of the SGAs and their responses to thermal stress. Additional types of photo-physiological analyses, such as zooxanthellae density, chlorophyll concentration and zooxanthellae genotyping will improve our understanding of SGAs on *Acropora* and their and their likelihood of proliferating under global warming scenarios.

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Light is critical for the distribution and trophic ecology of the temperate coral *Astrangia poculata*

Taylor Lindsay with Willow Dunster, Kelton McMahon and Carlos Prada
University of Rhode Island, Kingston, Rhode Island, USA
email: taylor_lindsay@uri.edu

Background & Introduction

The temperate coral *Astrangia poculata* is an ideal system to study coral symbiosis due to its ability to use facultative symbiosis. White, aposymbiotic colonies (hereafter ‘apo’) survive almost entirely on heterotrophy, while brown, symbiotic colonies (hereafter ‘sym’) use both heterotrophy and photosynthesis via endosymbionts (also known as mixotrophy) (Dimond and Carrington 2008). Having healthy apo and sym colonies provides a unique system in which heterotrophy is naturally isolated from photosynthesis, without the physiological imbalance associated with stress-induced coral bleaching, providing a unique system to study trophic ecology in corals.

Despite being a model species, the ecological drivers of *A. poculata* abundance and distribution of morphotypes remain unclear. Previous studies have documented *A. poculata* distribution in shallow waters but have not explored its deeper range. Grace (2004) showed that *A. poculata* density increases from 2m to 7m associated with an inverse relationship with algal cover. Sharp (2017) quantified apo, sym, and mixed colonies along a depth gradient from 3-14m and found no significant differences in abundance. However, their results suggest a shift from a mixed assemblage of symbiont states in 3-12.5m to mainly apo colonies deeper than 12.5m. Our work expands on both studies by investigating the factors that affect the distribution of apo and sym colonies along a broader depth gradient from 0 to 25 meters.

Light availability is critical for mixotrophic tropical corals, but its effects on the trophic ecology of temperate corals has not yet been explored. In temperate waters like Narragansett Bay, Rhode Island, high turbidity limits the growth of photosynthetic organisms beyond a shallow photic layer. *Astrangia poculata* employs multiple strategies to cope with extreme light and temperature in temperate environments, including altering symbiotic state (Dimond and Carrington 2008), colony morphology (Grace, 2004), immunity (Changsut et al. 2022), behavior (especially in winter) (Grace, 2017), and microbiome community (Sharp et al. 2017). While much is known about the role of light availability on the trophic ecology, survival and distribution of tropical corals, the trophic plasticity and physiological response of temperate corals to changes in light availability remain unclear. Historically, bulk stable isotope analysis (SIA) has been used as a proxy for heterotrophy versus photosynthesis in corals. SIA has previously been used in *A. poculata* to examine seasonality of trophic ecology (Trumbauer et al. 2021) and to assess carbon sources for calcification (Cummings and McCarty 1982). However, it has become increasingly clear that macronutrient sharing between symbiont and

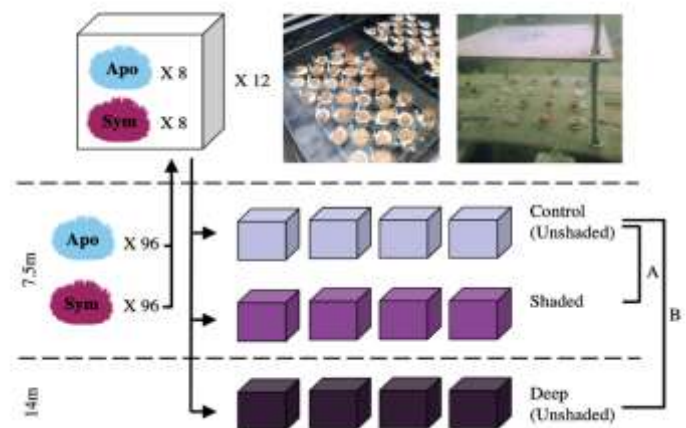


Figure 1. Experimental design and photographs of light exclusion experiment. 96 colonies of aposymbiotic and symbiotic *A. poculata* were collected from 7.6m below MLLW. Colonies were attached to plugs and deployed in open cages in one of three environmental conditions: control (unshaded, 7.5m), shaded (shaded, 7.5m) and deep (unshaded, cold, 14m). This experimental design allows us to use planned comparisons to evaluate the isolated effects of light limitation (A) and the cumulative effects of depth (B).

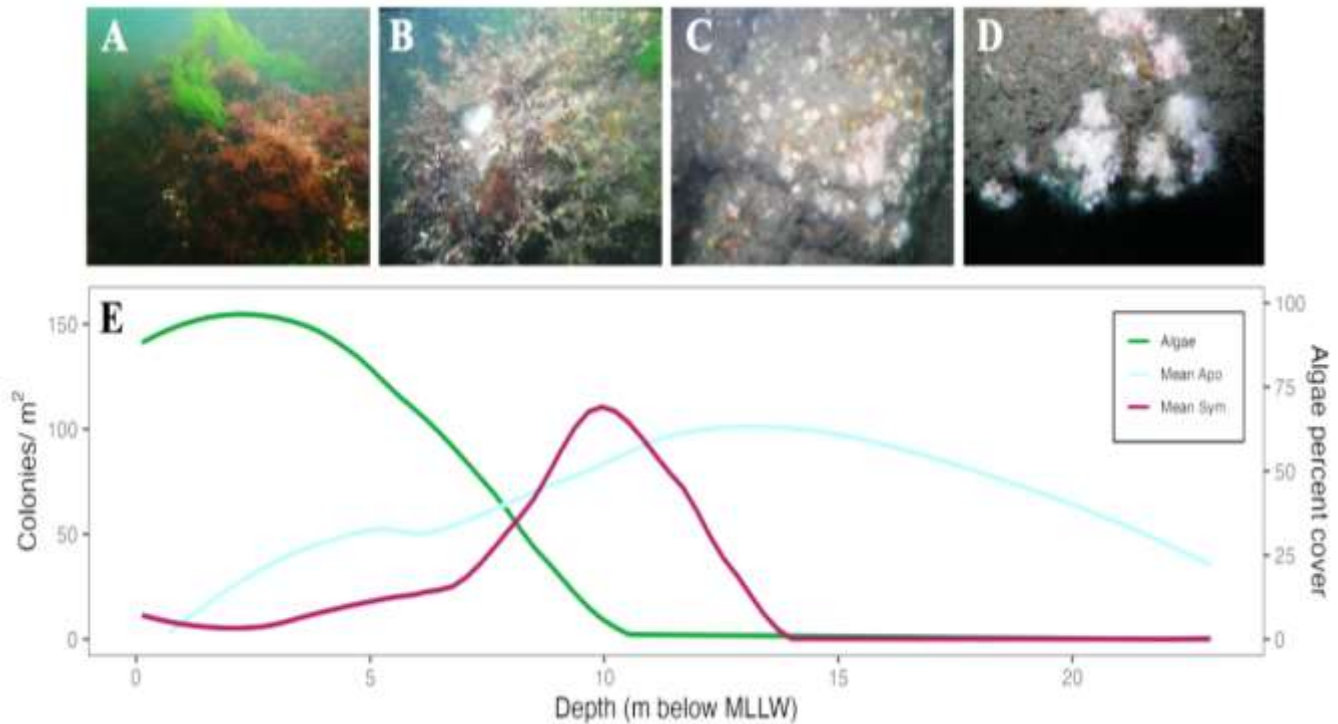


Figure 2. Changes in benthic cover and *A. poculata* abundance across a depth gradient. Photographs show the shift from algal dominance to sparse coral cover across depths: A) 2m: Macroalgae dominates the substratum, B) 8m: Algae is shorter and less dense and apo and sym *A. poculata* colonies are visible without pulling back the canopy, C) 11m: No algae present, *A. poculata* is the main cover species and the assemblage is mixed apo and sym colonies, D) 18m: No algae or sym colonies present, apo colonies become less abundant, E) Patterns of symbiotic (pink) and aposymbiotic (blue) colony abundance across a depth gradient. The second axis shows the percent cover of macroalgae (green).

host, nutrient recycling, and de novo synthesis of amino acids makes SIA unreliable in mixotrophic corals (Ferrier-Pagès and Leal 2019). Compound-specific stable isotope analysis of amino acids (CSIA-AA), when coupled with physiological responses to light availability, provides a powerful suite of tools to disentangle these processes and better understand trophic plasticity within the coral holobiont. For example, CSIA-AA allows researchers to identify the organism's trophic level (a metric of reliance on heterotrophy vs symbiotic autotrophy) as well as the relative contribution of primary producer sources within the food web (e.g., endosymbionts vs water column eukaryotic microalgae), with more confidence than conventional SIA methods (McMahon et al. 2016; Lesser et al. 2022).

Here, we conducted an ecological survey of *Astrangia poculata* and a light-exclusion experiment to 1) Discover the ecological drivers shaping the distribution of *A. poculata*

along a depth gradient; 2) Quantify the effect of light availability on the plasticity of *A. poculata* symbiosis and physiology; and 3) Determine how symbiotic and aposymbiotic corals sequester, store, and allocate energy resources using CSIA-AA methodology.

Research Undertaken

Distribution sampling

To quantify the distribution of apo and sym *Astrangia poculata* along a depth gradient in Narragansett Bay, RI, we conducted quadrat sampling by randomly placing 0.25m quadrats from 0 – 24.5m below mean low low water (MLLW). Quadrats were only placed on rocky substrate with <45° angle, to ensure that all quantified habitats received sunlight. An a priori study was used to confirm that visual identification could correctly identify symbiont state (n = 12, p = 0.007). The two morphs were counted by divers in duplicate and final values are an average of these counts. For each quadrat, we also estimated the mean algal

canopy cover, and duplicate Onset hobo loggers attached to the quadrat measured ambient light levels.

Light limitation experiment

To investigate the effect of light on *A. poculata* symbiosis, physiology, and energy dynamics, we conducted a shading experiment at Fort Wetherill State Park in Rhode Island. Colonies were collected from 7.5m below MLLW and separated by color into sym and apo groups. Colonies were attached to plugs and deployed in replicate cages in three different conditions: unshaded at 7.5m (control), shaded at 7.5m, or unshaded at 14m (darker and colder than shaded treatment), following the experimental design shown in Figure 1. Light and temperature were recorded in each of the experimental conditions using Onset hobo loggers. For the four-month duration of the experiment, we tracked survival and cleaned the cages once per week.

At the conclusion of the field experiment (November 2023), corals were collected, and immediately snap-frozen to -80°C . In the lab, we airbrushed samples and used the wax-dipping technique to measure surface area. To assess immune response associated with stress, we quantified antioxidant concentration. We quantified chlorophyll and symbiont density to determine symbiotic state of the coral. To elucidate energy storage, we have quantified protein concentrations, and plan to add assays for carbohydrates, lipids, and total biomass in future work. Finally, we have begun lab work for CSIA-AA to identify the energy sources and trophic plasticity of the corals. All statistics reported here follow planned-comparisons testing between the control and individual treatments using Wilcoxon's tests, unless otherwise stated.

Preliminary Results & Discussion

Distribution

Our surveys showed that both apo and sym colonies had low abundance in shallow water (0-7m), reached a maximum abundance at mid-depth (sym: 7-12m, apo: 7-18m) and then

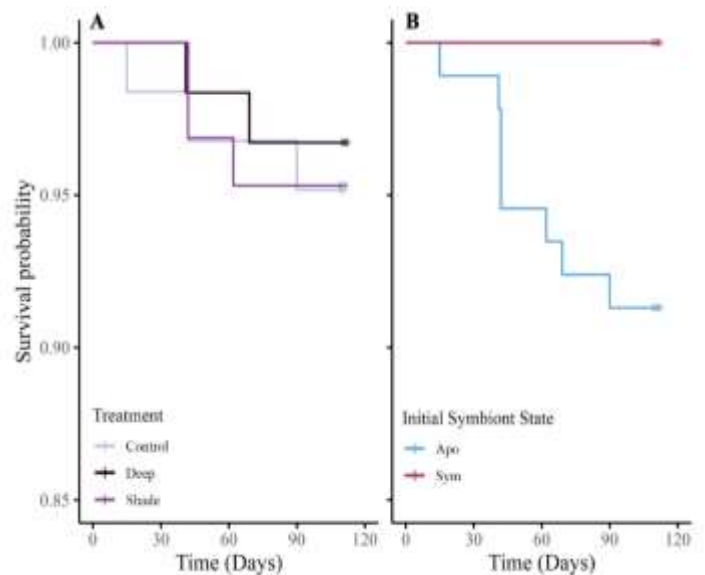


Figure 3. *Astrangia poculata* survival over four months under shading experiment. A) There was no significant difference in mortality between control and treatments (Kaplan-Meier, $p = 0.9$). B) Colonies that were symbiotic at the start of the experiment had 100% survival, significantly higher than those that started as aposymbiotic (Kaplan-Meier, $p = 0.0039$).

decreased with depth (Fig. 2). Two main factors likely affected the distribution of apo and sym colonies. First, competition with algae for light or space limited coral growth in shallow areas, supporting previous work by Grace (2004). A linear regression between algal percent cover and total *A. poculata* abundance (examining only the depths algae is present, 0-11m below MLLW) showed a strong negative relationship ($R^2 = -0.74$, $p < 0.0001$). This pattern may also be exacerbated by algal abrasion on coral colonies leading to wounding or retracted polyps, therefore limiting heterotrophy (Coyer et al., 1993; Grace, 2004). Second, symbiotic colony presence abruptly stopped at a maximum depth of 12.6m, while apo continued deeper than our max quadrat depth of 24.5m. This indicates that light limitation controls the vertical distribution of sym *A. poculata*.

Light limitation experiment

Over the course of the light-limitation experiment, few individual corals died with no difference in mortality across the three experimental conditions (Kaplan-Meier, $p = 0.9$), reinforcing existing knowledge that *A. poculata* is a very robust species (Fig. 3).

However, mortality differed between morphotypes: apo colonies had a significantly higher mortality rate ($n=8$) than sym colonies ($n=0$) (Kaplan-Meier, $p = 0.0039$). This suggests that mixotrophic individuals may have a competitive advantage over exclusively heterotrophic individuals, even in light-limited conditions. Our future work will test if mixotrophic colonies store more energy-rich metabolites (lipids, carbohydrates), allowing them to survive longer under stressful conditions.

Preliminary results suggest that light limitation initially caused sym colonies to lose their symbionts. In the field, divers observed that previously brown colonies turned white by the end of the experiment in the shaded and deep experimental conditions. Control treatments had significantly higher concentrations of chlorophyll than either shaded ($p < 0.0001$) or deep ($p < 0.0001$) treatments (Fig. 4). We are working to quantify symbiont density and expect deep colonies to experience more drastic differences in sym density.

Colonies in deep habitats (low light and cold) experienced higher concentrations of proteins ($p < 0.0001$) and lower antioxidants ($p = 0.024$) than colonies in the control (Fig. 4), while shaded colonies did not differ from the control for either metric. The increase in protein concentration may be associated with the shift from photosynthesis to heterotrophy at low light and therefore different protein sources, or a higher proclivity to store more metabolites in less productive environments. We aim to disentangle these possibilities using CSIA-AA methodology. The decrease in antioxidant concentration was unexpected, as antioxidant activity typically combats the production of reactive oxygen species (ROS) produced by bleaching or disease. Corals transplanted to deep environments did not appear to experience ROS caused by bleaching stress, despite most colonies experiencing a shift from sym to apo. This provides evidence that symbiont loss in temperate corals is a fundamentally different process from thermal bleaching in tropical corals.

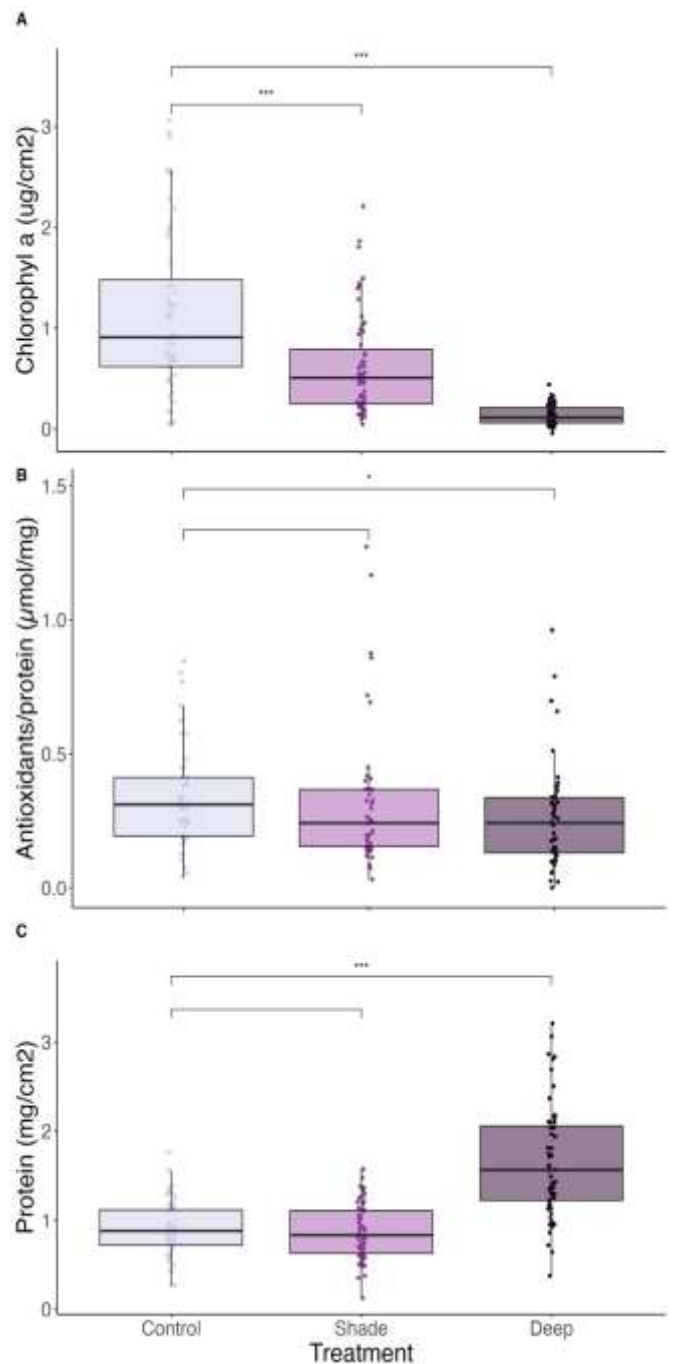


Figure 4. *A. poculata* physiology changed between treatments. A) Chlorophyll a concentration was significantly lower in the shade ($p = 4.15e-5$) and deep ($p = 7.84e-16$) treatments than the control. B) Deep colonies had significant lower concentrations of antioxidants per protein than the control ($p = 0.024$), the shade treatment did not differ ($p = 0.15$), C) Deep colonies had significantly higher concentrations of protein than the control ($p = 1.21e-11$), while shaded colonies did not differ from controls ($p = 0.57$).

Concluding Remarks

The distribution of mixotrophic and heterotrophic *A. poculata* in Narragansett Bay, RI, is largely driven by light availability and competition with macroalgae for space and light. Here, we document the effects of light-limitation on survival, symbiont state and the associated physiology in facultatively symbiotic corals. Preliminary results indicate that a history of mixotrophy appears to enhance survival, but the exact mechanisms remain unclear. The additive effects of being introduced to lower temperature and light limitation at depth appears to induce physiological changes in cold-water corals. Future work will leverage CSIA-AA methodology to unravel the effects of light availability on the trophic ecology of temperate corals. Like tropical corals, light is a critical factor for temperate corals in driving their distribution, physiology and trophic ecology and an important consideration for any study of the biology or ecology of these corals.



Taylor
Lindsay

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REEF SHELF

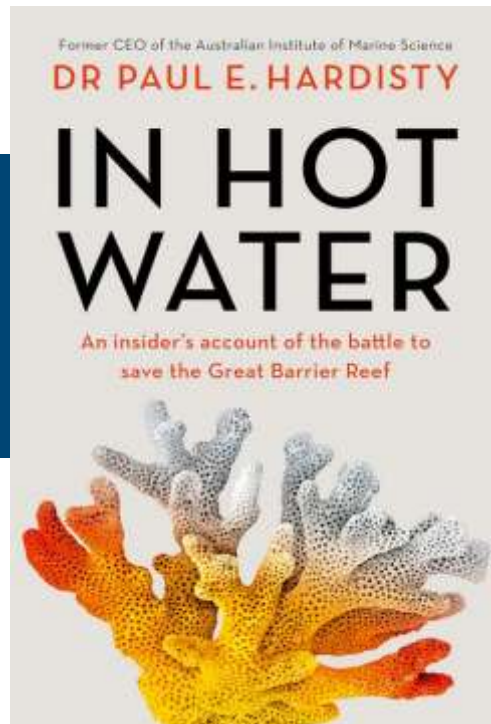
In hot water: Inside the battle to save the Great Barrier Reef

Paul E Hardisty (2024)
Melbourne, Affirm Press, 276 pp.
ISBN 9781923022386

There are two sorts of books about the global environmental crisis – let's call it the Anthropocene crisis. One sort is from the head, the other from the heart. The best of these are from both. Coral reef science is graced by two such books from our own community: Peter Sale's (2011) *Our dying planet: An ecologist's view of the crisis we face*, and Callum Roberts' (2012) *Ocean of life: How our seas are changing*. Each of these books combines vast scholarship and deep understanding borne of years of fieldwork together with a deep love for the ocean.

This book is not like that. It is part memoir and part *cri de coeur*. The memoir dimension is perhaps the least interesting because it, in fact, covers a very short period of 'the battle to save the Great Barrier Reef': the author was parachuted as CEO into the Australian Institute of Marine Science in 2017 and left abruptly in unexplained circumstances in 2023. A curious appointment given his background – Hardisty is an environmental engineer concerned broadly with groundwater remediation and protection – and even more curious sudden departure.

Now I take a strong view about the directors of the world's great marine science institutes – our patrimony. They should be – and many have been – marine scientists of the first rank. Think of Otto Kinne of the Biologische Anstalt Helgoland in Hamburg or Roger Revelle of Scripps in La Jolla. Such individuals spoke with an authority built on a solid foundation of fundamental research. This inspired their colleagues, and also allowed them to speak truth to power as well as to the general public. Revelle, for example, testified to Congress about the potential of global warming in 1957 – the first use of that term.



Hardisty is, unfortunately, not of this tradition. One will search in vain to find a corpus of relevant scientific research in which he has been involved. So his narrative is padded out with anecdotes of earlier skirmishes in the ongoing battle – the author's discovery, for instance, of the letters of Sir Maurice Yonge. And his reporting of current battles is not much better. He comes across as a naïf, sketching the protagonists as caricatures, and the policy and political issues in play as simple choices between good and bad. Nowhere does he show an understanding of the geopolitical and economic forces involved in the Anthropocene crisis – a point I'll return to below.

The other dimension of the book is his *cri de coeur*. He does indeed speak from the heart, as do we all who have been smitten by coral reefs. He says, in his *Introduction*, 'The fate of the Great Barrier Reef is now inextricably linked to the fate of the planet, as ours is to both. The reef is a symbol of our struggle to rise above narrow self-interest and act for the common good. If we can safeguard the reef, we can save the rest.' No idealistic undergraduate could have put it better. In fact, I can hear myself saying it fifty years ago. But fine words butter no parsnips.

The Anthropocene crisis – really, the transition, now underway, to a new state of the Earth system – is driven by global forces. Those forces manifest as economic forces of growth and consumption, especially of energy and natural resources. But they are geopolitical in origin – to first order, the drive

by countries to grow and raise their living standards in competition with others. Even as the West slowly reduces its emissions, the Rest are more than taking up the slack. Global emissions are accelerating. The post-war international rules-based order, underwritten by the United States, is unravelling, and the international institutions it spawned are increasingly irrelevant. Any book that wishes to deal with the Anthropocene crisis –

whether from the head, the heart, or both – needs to confront this reality.

This is not such a book.

Roger Bradbury
Australian National University
(roger.bradbury@mac.com)

The Chagos Archipelago: a Biological Biography

Charles Sheppard (photos by Anne Sheppard)
CRC Press (Taylor & Francis). 138 pp.
ISBN 9781032713380

Sometimes it is best when reviewing an author's work, to quote their own words when they said it best. "This book is mainly a biological account of the archipelago told from a personal view by someone who has visited and worked in the place over a period of nearly half a century." "The archipelago's natural history has never made it into the stories being told about it. This book fills that gap." "The story of Chagos with its immense natural riches, its completing claims, and the desire of some commercial opportunists to exploit it, is thus the story of our planet in miniature." "It contains it all: displaced people, old and derelict industry (coconut in this case), the military, politics, rich ecosystems that some want to exploit, ruined habitats on land, climate change, and territorial claims." Chagos is "the largest unexploited marine system left in the tropical world." "The ultimate question, I believe, is not whether mankind can afford to leave a few places on our planet in near-natural conditions. Rather, can we afford not to?"

Chagos has "a mere 6 km² of land." "...about half of it is in the atoll Diego Garcia with its military base. That leaves half the land area for all the rest, and that land is split up into about 55 tiny islands..." "Most of the islands, including all the larger ones, were ecologically ravaged in plantation days. Only the smallest islands, in contrast to the larger ones, were too small or difficult to convert into coconut plantations and avoided the attentions of the planters. So today they survive in magnificent



THE CHAGOS ARCHIPELAGO A BIOLOGICAL BIOGRAPHY

CHARLES SHEPPARD
PHOTOS BY ANNE SHEPPARD



splendor." "The reefs, in contrast, were mostly left alone and as a result, their marine life remained glorious." The islands that were inhabited are monocultures of coconut palms that seabirds can't nest in, and they are infested with rats and swarms of mosquitoes.

About half of the book is about the islands. Humans on islands eat any seabirds there, they are easy to catch. They also plant coconut palms, lots of them, to sell the coconut copra. Seabirds that nest in trees can't nest in coconut palms; other species need open spaces. Dense coconut forests produce huge numbers of fronds on the forest floor, that keep native trees from sprouting. Rats come with people, and they eat any bird eggs and chicks they can find. If you try to eradicate the rats but there are still coconut trees, some will be up in the trees and survive, you may have to remove all the coconut trees to get rid of the rats. To get native hardwood trees growing again, you need to plant them. If there are donkeys, they will eat the newly planted trees. But if the native trees grow, the seabird colonies will return. Atolls produce almost

no nutrient runoff and are in very low-nutrient water. Usually, we think about nutrients being too much and being harmful to reefs. But the guano from seabirds increases runoff, and islands on atolls that have seabirds have more fish and corals near them. The nutrients in the water are so low that a slight increase in nutrients is actually helpful. The book has references for the latter, which are based on Chagos.

The book is well-written and easy to read, it presumes no specialized scientific knowledge to understand, but it gives us an overview of the archipelago, on land as well as underwater. There is a good reason for the scientific attention Chagos has received from over a hundred scientists, mostly invited on expeditions by the author. It is one of the few remaining coral reef wildernesses left on the planet. Luckily, baseline information was taken before the 1998 mass coral bleaching devastated the corals there. Also, luckily, many of the coral species largely recovered. But they were damaged again by more recent bleaching. Now we wait with crossed fingers, holding our breath that the corals will recover again. But heat waves are coming more often, and the corals won't have enough time to recover if global warming continues, and all signs are that it will continue.

The book has a table that shows that the lagoons of 9 atolls in Chagos, Indian Ocean, have an average mean depth of 27 m (range 8-50 m) and an average maximum depth of 42 m (range 17-84 m). A very few atolls have very shallow lagoons, like Wake Atoll, where the lagoon is about 1 m deep. Surprisingly, much of the floor of some atoll lagoons in Chagos were almost completely covered with coral interspersed with sand patches, and another had coral patches alternating with sand and one was almost completely covered in coral.

The book provides much information about what happened as a result of mass bleaching events. Interestingly, he says that not only can bleached corals die of starvation due to the loss of zooxanthellae, but can die much faster if the water is hot enough. The best coral survival was near passes between the lagoon and outside, which have rapid water motion with changing tides. There was no bloom of macroalgae, but then there was no heavy nutrient runoff from humans and the reefs weren't overfished, so herbivores kept macroalgae in check. The standing dead coral skeletons were soon riddled with holes from bioeroders and when

they collapsed there were smooth rubble fields. Reef surfaces by then were often about a meter lower than when the corals were alive. Many invertebrates disappeared, but fish did not. After a few years, dead table corals had loads of coral recruits on them. Most of the new recruits were broadcast spawning corals, not brooders. In time, the reefs had lots of big table corals, which are broadcast spawners and are called "weedy" for their fast growth and high sensitivity to mortality events. There were no expeditions right after the 1983 and 1987 El Nino events, so we will never know how much damage they did. To understand why reefs are what they are now, we need to know not only the gradual changes on reefs, but the effects of disturbances, so re-surveying after disturbances is important.

There are many nuggets of information. Sadly, Chagos has had two major poaching activities. First, huge numbers of sea cucumbers were removed. In the more recent period, reef sharks were poached. They used to be common, now there are only a few. That has happened almost everywhere there are people on the planet, and now we consider it normal to have few or no reef sharks. One I found striking is that with the annual sea level rise in Chagos of 6 mm a year, a few high tides have been so high that there are pictures of young sharks swimming over grass (not sea grass, land grass), and rays have been seen swimming in a parking lot. Yes. I can imagine a conversation: "Where's your car parked?" "Oh, over there just beyond the stingray." The cost of bringing in hard rocks to harden shorelines on Diego Garcia to stop the erosion of seashores is now several million dollars a year and will only get worse. In time, perhaps 20 years or so, Diego Garcia will have to be abandoned due to rising sea levels.

We are very lucky that Professor Sheppard happened to finish this book before he suddenly, unexpectedly, and tragically passed away. We are all better for having it in existence. We would be wise to learn the lessons in it.

Douglas Fenner
Lynker Technologies / Coral Reef Consulting
(douglasfennertassi@gmail.com)

St. John: Sea and Sky: Celebrating the nature of a small tropical island

Caroline S Rogers (2024)

Published by Caroline S Rogers. 339 pp

ISBN 978-8-218-24919-9

This charming book is truly a labour of love, a love of St. John, the smallest of the three main US Virgin Islands, where the author, Caroline Rogers, spent most of her working career, and still lives. For those unsure, the US Virgin Islands are tucked away at the north-east corner of the Caribbean, and were only acquired by the US in 1917, when they were bought from Denmark. Despite being less than 10 miles in length and only some 20 square miles in extent, this single island harbours, as Caroline demonstrates through hundreds of wonderful photographs (see issue covers), a truly surprising array of wildlife, both terrestrial and marine. The subtitle of her book – Sea and Sky – refers to the fact that the first section covers the island's diverse bird life. One suspects that Caroline, like many reef scientists, was first a bird-watcher and then drawn beneath the waves by the opportunity that reef fish effectively offered for underwater bird-watching! But a high proportion of the birds she illustrates do play a role in the marine ecosystem, such as the little blue heron seen foraging along the shore among intertidal algae and the brown pelicans whose feeding behaviour she captures so nicely.

St. John: Sea and Sky is not intended as a guidebook, let alone a text book, but given that every one of 330 pages feature one or more quality photographs of the different species in characteristic pose, residents and visitors to the region will find that it complements well any standard guidebook with artists' illustrations, since the latter do not always show what an animal is like in real life.

In addition, the images are accompanied by brief notes and anecdotes, which highlight key features of the ecology and behaviour of the different species – such as the confusing differences between initial and terminal phase parrotfishes. Among the more amusing revelations is the explanation for how in St. John numbers of juvenile porcupine fish may be found on the roof tops of houses and indeed in residents' freshwater swimming pools.

Apparently in some years the porcupine fish breed so successfully that large schools of juveniles form offshore, attracting the attention of foraging frigate birds. These however may find their spiny prey too



hot to handle and disgorge them when back over the island!

The images also reveal lesser known aspects of some species' behaviour, for example that juvenile angel fish are such prolific cleaners of other fishes. I especially appreciated an image of two spotted trunkfishes (*Lactophrys bicaudalis*) feeding on a cushion seastar (*Oreaster reticulatus*) (see below), since my and colleagues account in the 1970s of the related pufferfish (*Arothron hispidus*) in the Red Sea as a significant predator of crown-of-thorns starfish¹. (*Acanthaster planci*) seemed little believed at the time.



Caroline's photographic record of St. John's marine and bird life will be of value not only to local and visiting naturalists, but as a record of the island's biodiversity until now. As she relates in her introduction, sadly, as in so many regions, the reef community is in decline, under the impact primarily of coral disease and coral bleaching. It began with white-band disease in the 1980s wiping out most of the elkhorn coral (*Acropora palmata*), and has continued most recently with the arrival in 2019-20 of the stony coral tissue loss disease (SCTLD) that has been killing more than half the 40 species that occur on the island. As a result corals are noticeably sparser than when she first became familiar with the island. Thankfully the elkhorn coral, which appears immune to SCTLD, has made a limited return. Let us hope this lovingly crafted record of the islands ecological richness will inspire those that can do so to work more urgently to safeguard places such as this.

Rupert Ormond
MCI and Heriot-Watt University, Edinburgh

¹ Ormond RFG et al. (1973). Formation and breakdown of aggregations of *Acanthaster planci* in the Sudanese Red Sea.

REEF DEPARTURES

Tributes to recently departed members and reef scientists

Charles Sheppard OBE 1949-2024



On 10th April, 2024, one of us (AP) received a copy of Charles Sheppard's latest book, *The Chagos Archipelago: A Biological Biography* to do a review for The Linnean Society. Unhappily, that same day Charles had a massive stroke. Two weeks

later, our colleague and good friend died. Hence, Charles' latest book sadly was also the last of more than a dozen on the ecology and conservation of coral reefs and on the world's oceans, Chagos and the Middle East.

Until the age of twelve, Charles was brought up in Singapore, which may have partly fired up his love for the tropics. After boarding school in Sussex, UK, he studied Pharmacology at Hatfield before undertaking a PhD at Durham University in the early/mid 1970s. His research examined fauna within the holdfasts (the sampling unit) of *Laminaria* kelp in different environmental conditions. UK botanist and successful TV presenter, Professor David Bellamy, was Charles' supervisor. While a postgraduate, along with David Bellamy, Charles participated in his first research expedition to the Chagos Archipelago. During a series of expeditions led by Charles over subsequent decades, he introduced over one hundred scientists to the region. Research progressively revealed that Chagos contained (almost certainly) the best quality reefs in the entire Indian Ocean. Charles' work in Chagos helped launch his career as a leading authority on corals and reefs and several tropical regions, most notably Chagos and the wider Indian Ocean. He published prolifically (some 250 research articles) on coral community structure, systematics, behavioural ecology (including coral aggression) and conservation science, including climatic impacts on

marine ecosystems. For a decade (2003-2013), Charles was the Conservation Officer for the administration of Chagos (British Indian Ocean Territory/BIOT). Moreover, he led in the creation of Chagos as an MPA in 2010, at the time the largest in the world. Principally for recognition of Charles' work in Chagos, he received an OBE from the Queen in 2014. He was also a Zoology Society of London (ZSL) Conservation Fellow and awarded the ZSL Award for Outstanding Contributions to Conservation in 2016.

Special mention should be given to Charles' global reviews of the world's oceans. He was editor of Elsevier's *Seas at the Millennium* (2000) and later *World Seas*. However, Charles's expertise extended beyond ecology and conservation. Over a period of 30 years beginning in the 1990s, he was editor of the journal, *Marine Pollution Bulletin*. During this period, *MPB* became one of Elsevier's highest-ranking and most successful environmental journals. For the last few years Charles was editor of *Advances in Marine Biology*.

On completion of his PhD and with seminal publications on the reefs of Chagos, Charles took up a post-doctoral position at the Australian Institute of Marine Science (AIMS) until the early 1980s. Charles then took up an environmental position in



Charles during one of his more recent trips to the Chagos Archipelago in the Indian Ocean. He was instrumental in its achieving Marine Protected Area status.



Typical Charles, keeping everyone amused during the 1980s survey of the southern Red Sea coast of Saudi Arabia. (photo Callum Roberts)

Yanbu on Saudi Arabia's Red Sea coast and then worked as an independent consultant for IUCN, UN agencies and other international organisations. It was in Saudi Arabia that one of us (CR), as a PhD student, had the pleasure of joining Charles on an expedition to map little known coastal ecosystems of the Southern Red Sea. Charles' irrepressible good humour turned several baking summer months under harsh field conditions into a hugely enjoyable trip full of indelible lifetime memories. On one long, empty drive across the desert, we blew the fanbelt on the Land Rover. After diagnosing the problem, Charles looked up from the cooked engine to his three grimy, male, shorts-wearing companions and asked -"Anyone got a pair of tights?"

In 1990 Charles became a lecturer at the University of Newcastle and in 1993 he moved to Warwick University, where he became a professor. He made major contributions to the newly created MSc, Ecosystems Analysis and Governance, as well as to undergraduate modules. His lectures were always very popular and, as supervisor to many PhD students over the years, Charles was a great mentor and inspiration to a new generation of marine biologists and environmental scientists. Charles' research and consultancy invariably involved teamwork, ideally with his wife, Anne (also a marine biologist and photographer). Together, they produced a widely accessible, free online tool to identify Indian Ocean corals <http://chagosinformationportal.org/corals>. It's a resource that has been enormously helpful across the region to professional and aspiring marine scientists.

In both the field and back at the office, Charles' keen intellect and sharp mind always shone



Charles, still in good humour, on board ship with wife Anne

through. On top of that he loved his work and, with his wicked sense of humour was always great fun to be around. As a passionate environmental scientist, Charles long held the view that many of the world's environmental problems stem from high and rising human populations; he also felt it was an issue largely being ignored. Charles understood that the magnificent and (relatively) healthy reefs of Chagos reflected the absence of a human population, except on the main atoll/island of Diego Garcia. During the 1960s all the islanders were unlawfully evicted to make way for a joint US/UK military facility. To date, permission for the Chagossians to return has been denied, an issue which continues to be highly controversial and challenged in international courts.

Besides family life, outside of work, Charles held a private pilot's license and loved sailing - in UK, the Mediterranean, the Caribbean and further afield. Over the past ten years one of us (AP) and family spent many happy times cruising in company with Charles and Anne along Scotland's magnificent west coast.



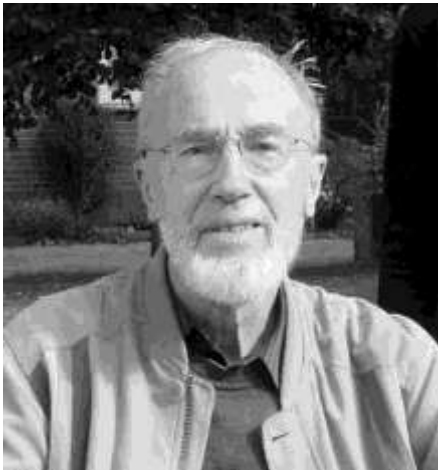
Charles, doing what he liked best, surveying reefs

Charles is survived by Anne, their two children Andrew and Kirsten, his sister Diana and granddaughter, Wren. His loss to family and friends is slow to sink in and immeasurable, but his presence is still very much felt and will endure.

Andrew Price, University of Warwick (a.r.price@warwick.ac.uk), with contributions from Callum Roberts, John Turner, Rupert Ormond, Sue Wells and Anne Sheppard

Helmut Schuhmacher 1941-2023

Professor Helmut Schuhmacher of Heidelberg (Germany) succumbed to his progressing illness and passed away close to his family in Dannenberg on the river Elbe on Tuesday November 21, 2023



Professor Helmut Schuhmacher, born 1941, was an old and well-tryed hand at reef science. Among the founding fathers of the International Society for Reef Studies, he was certainly the

Nestor⁴ of German reef science. The cover illustration of the first volume of the Society's journal "Coral Reefs" is a photo taken by him on the reefs of Aqaba. His seminal studies of long-term reef dynamics began in the Red Sea in the early 1970s. Unlike today, when well-organized marine labs exist along its shoreline, the Red Sea region was then still mostly untouched, and its now major cities had only just begun to develop or were still in the planning phase. After his dissertation on a freshwater streams subject in 1969, Helmut turned to the world's coral reefs and began his studies in the Gulf of Aqaba (Red Sea). The result of this dedication was a long sequence of meticulously accurate publications that are still of great value today, as some of the most solid baseline studies available. Given the difficulties, he must have had an abundance of affection for his study object.

As a PhD student in the late 1980s, one of us (Götz Reinicke) first met Helmut Schuhmacher at the University of Duisburg-Essen. After establishing his chair in Hydrobiology and Urban Stream Ecology,

he diverted part of his attention towards coral reefs again and assembled a team of young enthusiasts to study coral reefs in the Red Sea. At his side, we had our first reef encounters on the Aqaba Marine Science Station reef. We pursued his research interests in long-term community dynamics (as studied in the "U7" in Aqaba, Jordan, and in the test squares "TQ 1-4" on Sanganeb Atoll, in Sudan), I myself focusing on the soft octocorals. Several successors continued these studies for a total of over 40 years from the sites' establishment with Hans Mergner, in 1976 and 1980 respectively, including a 2019 revisiting of the Sanganeb TQs. The results document stagnant reef growth in the Sudanese Red Sea, with continuity and ongoing change in the coral communities over four decades (<https://doi.org/10.3390/d16070379>).

Starting out as a teacher in higher education, Helmut Schuhmacher became a dedicated academic and public teacher in aquatic ecology. He was known for his vast public outreach giving numerous talks for a general audience. At the age of almost 80, his messages, sometimes whispered, still grabbed the attention of large lecture halls when addressing "Corals Reefs in the Era of Climate Change". There is probably not a single German-speaking reef biologist or carbonate sedimentologist who has not read his wonderful textbook "Korallenriffe", published by BLV in 1976, and translated into both French and Spanish. His latest book "Korallen" (BLV, 2010) is a visually stunning, and scientifically accurate celebration of the wonderworld found on coral reefs. Intended for the non-specialist, it nonetheless offers a fascinating and informative read for both specialist and amateur alike – it makes for a great

⁴ i.e. an influential, wise and elderly colleague, after the Ancient Greek hero of this name, celebrated for these characteristics.

undergraduate textbook. Leafing through the book is a bit like a field trip, with instructor Schuhmacher taking one first diving and then to the lab to have a closer look at this or that fascinating item. Not many have researched so many different aspects of reef biology and geology to allow them to give such a broad, even-handed, and engaging overview. His students at Essen University sometimes raised their eyebrows when he occasionally enlivened lectures on marine biology by revealing his thrill in stunning details at the evolutionary tricks and fascinating adaptations of organisms, while they themselves struggled to extract and understand the general principles of marine ecology.

Helmut's pioneering research concentrated on habitat mapping of coral reefs and the detailed study of the long-term dynamics of coral communities in the Red Sea. These studies are unique, since they started already in the 1970s when these reefs there were almost untouched. Based on these investigations, a first model of reef growth as the balance of construction and erosion was developed, taking community dynamics, carbonate production and sea level changes into account. Further research focused on how fungiids (mushroom corals) and other coral species deal with sedimentation, and on the skeletal strength (rigidity) in of stony and soft corals and of *Ceratoporella* (Porifera) using methods applied from material testing and engineering technology.

He also studied the use of electrochemically produced lime substrates in mariculture for the settlement of stony corals to form artificial reefs, including their use in the rehabilitation of degraded coral reefs.

The broad scope of Helmut Schuhmacher's scientific interest embraced coral taxonomy and systematic issues, morphological details of skeletal structures in both hard and soft corals, as well as other contributors to and eroders of



the reef framework. His vast collection of coral specimens brought back from the Indo-Pacific as well as the Caribbean is now kept in the archives of the Ocean Museum Germany in Stralsund. His understanding of reef development always took account of the complex interaction of the diversity of reef dwellers, were they sessile or motile, protozoans, algae or animals. And his thinking took in the fourth dimension of time in the understanding of reef structures and development. During a German research focus project on “Evolution of reefs in earth history” (1990-1996), he promoted research on recent tropical coral reefs to serve as reference systems for comparison with various fossil environments in the earth's history.

Helmut's network of international connections extending back to the beginning of the ICRS were a regular source of scientific correspondence, argument and inspiration. Frequent visits of guest lectures to Essen stimulated discussions and the exchange of experiences. His mind was wideset, looking beyond immediate events and always keeping the big picture in view. Based on his studies of skeletal structures he early realized the problems of ocean acidification for coral reefs and increased his lecturing to public audiences accordingly. He engaged in three German campaigns as part of the IYORs (International Year of the Reef) in 1997, 2008 and 2018 and lectured during an outreach workshop day for scientific journalists in preparation of ICRS2022 in Bremen. The imminent destiny of the world's coral reefs

long worried him so that he was determined to make his voice heard. As a front man for coral reef research in Germany, one who had connected with reef science worldwide over five decades, he took great joy in and was proud of being awarded the Eminence in Research Award of the International Society of Reef Studies in 2022. Coral reefs had in him a tireless and effective advocate, who understood how to use his excellent science to speak for the conservation of his favorite marine ecosystems. Helmut Schuhmacher's



personal perspective on and his passion for the world's coral reefs live on in his many scholars, colleagues and friends. Many of us owe him much, and in him we have now lost a dedicated proponent for the awareness of man's responsibility for the well-being of the most diverse and fascinating ecosystems of the oceans.

The river of life flows into the sea of eternity.

Götz B. Reinicke and Christian Dullo,
Ocean Museum Germany, Stralsund, and
GEOMAR Helmholtz Centre for Ocean Research, Kiel

Photo credits: (1,2) Family archive (3) Götz B. Reinicke

G. Carleton Ray 1928–2023

Carleton Ray began promoting coral reef conservation two decades ahead of other scientists. "We must avoid the careless and tragic exploitation of the sea which we have not avoided in the case of the land...Some of the richest areas should be set aside...The taking of any marine life, animal or plant, by any means, should be prohibited. The areas should be distributed widely so that they could act as reproductive centers from which non-protected areas would be replenished with life."

(G. Carleton Ray, 1954)



Carleton began his career in 1954, exploring the flora and fauna of the Bahama Islands and championing marine conservation over the next seven

decades. He must have been supremely happy with how marine conservation soared and the number of people practising it burgeoned around the world.

In 1954, Carleton interrupted his doctoral studies at Columbia University, to explore the coral reefs of the Bahamas and co-author a book on underwater life with Elgin Ciampi, a student who inspired him to scuba-dive. The Bahamas Development Board supported their room costs. While spearfished for food, favouring the approachable and tasty Nassau Grouper, they recognised the need for conservation stating in the introduction to their book that: "*We must avoid the careless and tragic exploitation of the sea which we have not avoided in the case of the land...Some of the richest areas should be set aside...The taking of any marine life, animal or plant, by any means, should be prohibited. The areas should be distributed widely so that they*

could act as reproductive centers from which non-protected areas would be replenished with life."

This last principle provided the foundation for protected area networks across species' life stages and at seascape scale and to which Carleton devoted his life's work. I vividly recall him explaining to me how large marine mammals transported nutrients across oceans between their feeding grounds in high latitudes to the tropics where they calved. Carleton was decades ahead of the times. Today we pursue his concepts repackaged in different terminology.

It is difficult to say whether Carleton was first and foremost a scientist or a conservation practitioner. He blended the two to become a leader in both marine conservation science and its applications in practice.

Carleton also accomplished many other notable pioneering feats. In 1963 he was the first person to dive through holes in the ice in Antarctica where he filmed and recorded Weddell seals and was likely the first person to dive inside both polar circles. He developed the first sub-ice observation chamber that he used in McMurdo Sound. It remained in use for more than 50 years. In recognition of his pioneering marine research in Antarctica, Carleton had Mount Ray in the Prince Olaf Mountain Range named after him. The adventure, excitement and scientific opportunity of those pursuits would have been what motivated him. I know from later discussions with him that being the first would not have concerned him at all.



Carlton diving with Weddell seals below the ice. His interests extended from tropical to temperate and

Carleton was instrumental in establishing the Exuma Cays Land and Sea Park in 1958 in the Bahamas, the first marine park and protected area. Carleton advocated for the creation of inshore marine conservation areas at the first World Conference on National Parks, Seattle, 1962, where his paper was the only one addressing the marine environment. In 1972, at the Second World Conference on National Parks, Carleton called for a different approach for marine parks and reserves. He argued that to achieve sustainability of species and their ecosystems, marine conservation must be extended beyond areas confined by boundaries and introduced the concept of an ecosystem approach to marine parks and reserves.

Carleton's leadership in marine parks attracted invitations in the 1960s to consider the establishment of marine parks in Kenya and in Africa and the Turks and Caicos Islands in the Caribbean Sea. He continued a long and enduring relationship with the Bahamas National Trust for terrestrial and marine wildlife protection. While advocating for marine conservation at high levels of international and national agencies, Carleton remained acutely aware of the need to recruit support for the cause at multiple levels. He carried his love of sea life to children, writing for Ranger Rick, National Geographic, and publishing "*Wonders of the Living Sea*" in 1963 to inspire their interest in the ocean world.

I first met Carleton in 1975, at the world's first regional meeting on Marine Protected Areas in Tehran over pre-dinner drinks and verses of the Rubaiyat of Omar Khayyam. Carleton attended as IUCN consultant on critical marine habitats. He was appointed chair of the meeting because of his pioneering work on marine protected areas. Later that year we met again at the world's first International Conference on Marine Parks and Reserves where Carleton's keynote paper on critical marine habitats provided a focus for the meeting.

Indeed, Carleton's early papers on critical marine habitats remain as relevant today as they were in the early and mid-1970s.

Carleton's expansive vision of ocean conservation and experience from the arctic to Antarctica, including temperate and tropical seas between, led him to be brought in by IUCN as adviser to their nascent marine program. He went on to help develop IUCN's Marine Steering Committee that he chaired. This pulled us together as I was IUCN's only field project at the time. Our union was fortunate for me as Carleton was a consummate field scientist who understood the exigencies of working on and underwater in different countries. He quickly smoothed the difficulties I had working with IUCN that, in 1975, had no in-house marine expertise to ease the challenges of working alone along the coasts of Sri Lanka, India and Pakistan.

Through Carleton's efforts and inspiration IUCN embraced marine conservation and has built a solid global program on the foundation he laid. Many of the old-guard IUCNers will remember him and his contributions. Younger marine conservation scientists know of him too and many have benefitted from his teaching and individual mentoring.

Carleton was an inspiration to me, and many others, and he opened the door to a long and rewarding career in marine conservation for me. We need all the advocates we can motivate to support marine conservation at seascape scale (Carleton's vision) and his tireless efforts will be greatly missed. Carleton died at 95 years old



Carlton with his wife, Jerry McCormick-Ray.

working to the end on the revision of his book on marine conservation science with Geraldine "Jerry" McCormick-Ray, his wife of 46 years.

With deep appreciation

Rodney V Salm
resilientreefs@gmail.org



ICRS Membership

ICRS membership is open to anyone interested in any aspect of the science of coral reefs. While the Society's membership consists principally of researchers, managers and students involved with coral reefs and associated ecosystems, and other people with genuine interests in or concern for reefs, of any type, are welcome. The benefits of membership include:

- ❖ Receipt of the Society's scientific journal *Coral Reefs* (on-line)
- ❖ Free (on-line) access to all past issues of *Coral Reefs*
- ❖ Receipt of the Society's newsletter/magazine *Reef Encounter* (by email or on-line)
- ❖ Eligibility for the graduate fellowships, students travel grants and communications fellowships offered by the Society
- ❖ Eligibility for the multiple honors and awards given by the Society, including mid- and early-career and conservation awards
- ❖ Access to the Society's on-line membership services, including the on-line Membership Directory
- ❖ Reduced registration fees for the International Coral Reef Symposium and other meetings sponsored by the Society.

Full / Individual Member

Membership includes all the benefits listed above, but rates vary depending on the mean income level of the member's country.

Student Membership

The benefits are the same as for a Full / Individual Member, and include on-line access to *Coral Reefs* at a much reduced rate.

Family Membership

Family memberships are available for partners who live at the same address. Each receives the same benefits as Full/Individual Members, but only one hard copy of any material is supplied.

Sustaining Membership

Sustaining Membership is for those members who would like to contribute extra to support the work of the Society. They receive additional minor benefits and their support is acknowledged in Society publications.

Honorary Membership

Honorary Membership has been conferred on a small number of members who have rendered special service to the Society or otherwise distinguished themselves in the field of reef science.

Membership services are now operated by Schneider Group which provides such services to academic societies. They may be contacted at:

ICRS Member Services

**5400 Bosque Blvd, Suite 680
Waco, Texas 76710-4446 USA**

Phone: 254-399-9636

Fax: 254-776-3767

email: icrs@sgmeet.com

The membership subscription varies considerably depending on the type of membership selected and the primary country of residence of the member. Very generous membership rates are available for students and residents of developing countries.

For low to low-middle income countries, full membership costs only \$40 (US) per year, and student membership only \$20 (US) per year.

For details of current rates and to complete the on-line membership form or download a hard copy please go to the Society's membership portal at: <https://icrs.memberclicks.net/>

NOTES FOR REEF ENCOUNTER CONTRIBUTORS

Reef Encounter welcomes in particular, (1) general overview articles (3-5 pages) on particular reef science topics in which the author(s) has a special interest, (2) short communications / scientific letters (1-2 pages) reporting recent observations, and (3) general interest articles describing personal views and experiences. It also carries Announcements, Conference Reports, Book and Product Reviews, and Obituaries.

Authors are encouraged to include colour pictures or other illustrations (normally 2-4 per article). There are no specifications regarding the format of articles for submission to the editors, but we particularly ask that references should be cited and listed using the style of the ICRS academic journal CORAL REEFS, see: <http://www.springer.com/life+sciences/ecology/journal/338>. Articles from non-ICRS members are welcome, but those from members are generally given priority. Items should be submitted by email to the senior editor (rupert.ormond.mci@gmail.com) or a relevant member of the editorial panel (see page 2).



Terminal phase of the spotlight parrotfish (*Sparisoma viride*), St. John, US Virgin Islands
(photo Caroline Rogers)



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