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PERSPECTIVE

Coral reef ecology in the Anthropocene

Gareth J. Williams\textsuperscript{1*}, Nicholas A.J. Graham\textsuperscript{2}, Jean-Baptiste Jouffray\textsuperscript{3,4}, Albert V. Norström\textsuperscript{3}, Magnus Nyström\textsuperscript{3}, Jamison M. Gove\textsuperscript{5}, Adel Heenan\textsuperscript{1}, Lisa M. Wedding\textsuperscript{6}

\textsuperscript{1}School of Ocean Sciences, Bangor University, Anglesey, UK
\textsuperscript{2}Lancaster Environment Centre, Lancaster University, UK
\textsuperscript{3}Stockholm Resilience Centre, Stockholm University, Stockholm, Sweden
\textsuperscript{4}Global Economic Dynamics and the Biosphere Academy Programme, Royal Swedish Academy of Sciences, Stockholm, Sweden
\textsuperscript{5}NOAA Pacific Islands Fisheries Science Center, Honolulu, HI, USA
\textsuperscript{6}Center for Ocean Solutions, Stanford University, Stanford, CA, USA

*Correspondence author. E-mail: g.j.williams@bangor.ac.uk

Summary

1. We are in the Anthropocene – an epoch where humans are the dominant force of planetary change. Ecosystems increasingly reflect rapid human-induced, socioeconomic and cultural selection rather than being a product of their surrounding natural biophysical setting. This poses the intriguing question: to what extent do existing ecological paradigms capture and explain the current ecological patterns and processes we observe?
2. We argue that, although biophysical drivers still influence ecosystem structure and function at particular scales, their ability to offer predictive capacity over coupled social-ecological systems is increasingly compromised as we move further into the Anthropocene.

3. Traditionally, the dynamics of coral reefs have been studied in response to their proximate drivers of change rather than their underlying socioeconomic and cultural drivers. We hypothesise this is limiting our ability to accurately predict spatial and temporal changes in coral reef ecosystem structure and function.

4. We propose ‘social-ecological macroecology’ as a novel approach to a) identify the interactive effects of biophysical and socioeconomic and cultural drivers of coral reef ecosystems across spatial and temporal scales, b) test the robustness of existing coral reef paradigms, c) explore whether existing paradigms can be adapted to capture the dynamics of contemporary coral reefs, and d) if they cannot, develop novel coral reef social-ecological paradigms, where human dynamics are part of the paradigms rather than the drivers of them.

5. Human socioeconomic and cultural processes must become embedded in coral reef ecological theory and practice as much as biophysical processes are today if we are to predict and manage these systems successfully in this era of rapid change. This necessary shift in our approach to coral reef science will be challenging and will require truly interdisciplinary collaborations between the natural and social sciences.

Key-words: Anthropocene, coral reef, ecology, macroecology, prediction, scale, social-ecological macroecology, social-ecological systems
Introduction

Natural biophysical gradients such as wave energy, primary production, and seawater temperature drive coral reef ecosystem structure and function across multiple scales and trophic levels, from microbes (Kelly et al. 2014) and plankton (Gove et al. 2016), to corals (Gove et al. 2015) and fish assemblages (Heenan et al. 2016). However, human impacts such as fishing (Edwards et al. 2014), nearshore nutrient enrichment (D’Angelo & Wiedenmann 2014), sedimentation (Wolanski, Martinez & Richmond 2009), and the warming and acidifying of our oceans (Albright et al. 2016; Hughes et al. 2018a) are pushing the environmental boundary conditions defined by natural biophysical drivers on many coral reefs globally. Furthermore, the distal socioeconomic and cultural drivers underlying these proximate impacts, such as trade, consumer demands, human migration, and carbon dioxide emissions, are all predicted to increase (Norström et al. 2016; Hughes et al. 2017). This presents a new reality where the majority of coral reefs will increasingly reflect human-induced, socioeconomic and cultural drivers rather than being a product of their long-term natural biophysical setting. How we study and describe reef ecology must include this paradigm shift in thinking if we are to predict and manage their dynamics effectively.

We propose an approach that will identify how key biophysical, socioeconomic and cultural drivers of reefs interact across scales to drive coral reef ecosystem patterns and processes. In doing so, this approach will arm us with the predictive capacity required to manage coral reef dynamics in this era of rapid change. We start by reviewing how natural biophysical drivers influence reefs, from dictating the dominance, behaviour, and trophic ecology of individual reef organisms, through to governing the spatial ecology of reef communities across the seascape. We then highlight how human socioeconomic and cultural drivers have become an important structuring force of contemporary coral reefs at particular scales. In doing so, we underline our lack of understanding regarding the degree biophysical,
or human socioeconomic and cultural drivers dominate depending on the scale of
observation, suggesting macroecological approaches as a potential solution. Finally, we
question whether traditional coral reef paradigms capture this new interwoven reality and
stress the need for a ‘socio-ecological macroecology’ approach to develop paradigms for
coral reefs in the Anthropocene.

Biophysical drivers: setting natural bounds on coral reef ecosystems

By studying coral reefs in remote locations with limited direct human influence, we
have learnt how coral reefs respond to, and are shaped by gradients in biophysical drivers
such as wave energy, primary production, and seawater temperature (Fig. 1). High wave
energy environments, for instance, can promote the dominance of low-lying benthic
organisms such as turf algae, crustose coralline algae, and encrusting corals that are less
vulnerable to physical dislodgement (Geister 1977; Gove et al. 2015). In contrast, lower
wave energy environments tend to favour more structurally complex benthic communities,
dominated by three-dimensional calcifying corals and upright macroalgae (Williams et al.
2013; Aston et al. 2018). Such increases in substrate complexity are often positively related
to reef fish density and biomass (Graham & Nash 2012) due to increased refuge from
predation (Rogers, Blanchard & Mumby 2014), and as such waves can indirectly mediate
predator-prey dynamics on reefs. Across the Pacific Ocean, for example, the biomass of
grazing herbivorous fishes peaks at islands with moderate wave exposure where the largest
edible algal mass for these fishes tends to occur (Heenan et al. 2016). Wave energy can also
influence reef fish community structure through interactions with fin morphology and
swimming performance (Fulton, Bellwood & Wainwright 2005), with high wave energy
environments capable of impacting the feeding success of some fishes and thus key
ecosystem functions like herbivory (Bejarano et al. 2017).
Natural gradients in nutrient concentrations and primary production have predictable effects on coral reef ecosystems (Gove et al. 2016). For example, tropical islands located in more productive regions of the Pacific Ocean support a greater number of microbes with nutrient-related metabolisms (e.g., nitrate and nitrite ammonification) (Kelly et al. 2014), an increased cover of calcifying benthic organisms (Williams et al. 2015a), and a greater biomass of grazing herbivorous, planktivorous, and top-predatory fishes (Nadon et al. 2012; Williams et al. 2015b; Heenan et al. 2016). Gradients in nutrients and primary production also exist at smaller scales around individual islands. For example, when deep subsurface waves interact with bathymetry around islands they break and can pump water up through the thermocline. These so-called ‘internal waves’ can raise nutrient concentrations in the shallows (Leichter, Stewart & Miller 2003; Wang, Dai & Chen 2007; Aston et al. 2018), which in turn can promote heterotrophic feeding and growth rates in corals (Leichter & Salvatore 2006; Fox et al. 2018; Williams et al. 2018), and ultimately drive broad spatial transitions in benthic functional group dominance around islands (Aston et al. 2018). Coral reefs are also hydrodynamically connected by additional physical processes such as lagoonal outflow and surface downwelling that can move allochthonous nutrient sources between reef habitats (Williams et al. 2018) and, in the absence of confounding local human impacts, enhance reef productivity and function (Graham et al. 2018).

Seawater temperature is another key determinant of coral reef persistence and function. Most coral reef ecosystems occur in waters with a seasonal minimum sea-surface temperature of 18°C (Kleypas, McManus & Menez 1999). Marginal reef communities can form in waters below 22°C, and this can be explained by the interacting effect of temperature with light, nutrients, and aragonite saturation (Couce, Ridgwell & Hendy 2012). Bounded within these temperature limits, gradients in seawater temperature influence the dominance and life history of individual reef organisms. For example, hard coral cover
decreases at lower temperatures, while macroalgae become more prevalent with latitudinal and cyclical seasonal drops in temperature (Glenn, Smith & Doty 1990; Fulton et al. 2014; Williams et al. 2015a). Browsing herbivorous fishes become more dominant in cooler waters, while warmer waters support an increased biomass of detritivorous fishes (Floeter et al. 2005; Hoey, Pratchett & Cvitanovic 2011; Heenan et al. 2016). Fish body size also varies predictably with temperature. Body size is inversely related to temperature due to the increased growth rate, earlier maturation, and shorter life span of individuals at higher temperatures (Atkinson 1994; Trip et al. 2008; Taylor, Trip & Choat 2018).

These natural constraints on a reef’s biophysical and functional form do not act in isolation and appear predictable in the absence of confounding local human impacts (Williams et al. 2015a). However, anthropogenic activities have become a dominant driver of coral reef ecosystems across a broad range of socioeconomic and cultural contexts, increasing the complexity of drivers and their interactions that govern ecosystem state (Fig. 2).

**Socioeconomic and cultural drivers: a new reality for coral reefs**

The footprint of human activity is evident on coral reefs at all trophic levels. Fishing has dramatically reduced overall fish biomass on coral reefs (Williams et al. 2011; MacNeil et al. 2015; Graham et al. 2017), with an emphasised loss of herbivores (Edwards et al. 2014) and top predators (Sandin et al. 2008; Valdivia, Cox & Bruno 2017; Cinner et al. 2018) and thus the key ecosystem functions they perform. Fishing can also disrupt the basic physiology and behavior of target species, including the sex change dynamics (Taylor 2014) and flight responses of reef fishes (Januchowski-Hartley et al. 2012), both of which have the potential to affect overall reef ecosystem function (Madin et al. 2010).

Land-use change alters sedimentation regimes and nutrient input to reefs (Wolanski, Martinez & Richmond 2009). In conjunction with fishing (McClanahan et al. 2003), these...
effects can favour the competitive superiority of fleshy algae (Barott et al. 2012) to ultimately promote their overall dominance (Smith, Hunter & Smith 2010; Smith et al. 2016). Dredging and plastic pollution are increasing coral disease prevalence on reefs (Pollock et al. 2014; Lamb et al. 2018), which in turn contributes to a loss of live coral cover and reduced reef calcification rates. Humans are also re-structuring coral reef microbial communities (Kelly et al. 2014), and promoting the abundance of disease-causing bacteria and viruses (Dinsdale et al. 2008). Remarkably, human-introduced invasive rats can lower fish growth rates and levels of herbivory on reefs by predating on seabirds that would otherwise deliver offshore nutrient subsidies to shallow waters bordering the islands (Graham et al. 2018).

Globally, human-induced warming of the ocean is resulting in increasingly frequent mass coral bleaching events (Hughes et al. 2018a) that are transforming coral assemblages (Hughes et al. 2018b) and in some cases causing regime shifts to fleshy macroalgae (Graham et al. 2015). In combination with human-induced ocean acidification (Albright et al. 2016), these shifts in benthic composition have broader ecosystem effects, from compromising the growth of reef structures (Perry et al. 2013; Perry et al. 2018) to changing the diversity, abundance, and behaviour of other reef-associated organisms (Keith et al. 2018; Richardson et al. 2018; Stuart-Smith et al. 2018). Hence, myriad interconnected human drivers are rapidly changing the structure and function of reefs (Pendleton et al. 2016).

The proximate human impacts to reefs described above are, themselves, ultimately dictated by underlying distal socioeconomic and cultural drivers, such as global trade, markets and finance, as well as the movement and behavioral choices of people and their associated demands on coastal resources (Kittinger et al. 2012; Hicks et al. 2016a; Norström et al. 2016) (Fig.2). While the coral reef research community has made significant advances in measuring the response (decline) of coral reef ecosystems to these distal socioeconomic and cultural drivers, we have not done so intentionally in an *a priori* manner. Instead, we
have indirectly measured their effect by studying their emergent proximate impacts, such as commercial and recreational fisheries (Fig. 2). We hypothesise this is limiting our ability to accurately predict spatiotemporal changes of contemporary reef ecosystems. We further suggest that these human socioeconomic and cultural drivers can combine to become such a dominating structuring force of reef ecosystem state that they overwhelm any influence of a reefs’ surrounding natural biophysical setting. Williams et al. (2015a) tested this hypothesis by quantifying the relationship between coral reef benthic communities and gradients in biophysical drivers across Pacific islands that spanned a gradient of human density. At island-mean scales, they demonstrated that biophysical drivers were able to strongly predict coral reef ecosystem state when human density was low, but that these relationships were lost or fundamentally altered when human population density increased. We propose that this loss of predictive power over reef ecosystem state will be regained when human socioeconomic and cultural variables are instead fully integrated into analyses and used as predictors in the modeling framework. Further, we argue that implementing a multi-scaled macroecology approach will provide a more nuanced understanding of how biophysical, socioeconomic, and cultural drivers interact across spatial and temporal scales to influence coral reef patterns and processes.

Work has begun to address the crucial data and knowledge gaps linking the structure and function of natural ecosystems to the distal socioeconomic and cultural drivers that underpin their proximate drivers of change. Examples include the socioeconomic drivers of biodiversity loss and societal response capacities of hyperdiverse tropical ecosystems (Barlow et al. 2018), quantitative data on land grabbing and the international trade of coral reef resources (Norström et al. 2016), and the increasing amount of social science quantitative indicators people can use in social-ecological systems research and sustainability science (Hicks et al. 2016b). These types of data can improve our ability to predict the
dynamics of natural ecosystems (Hicks et al. 2016a), including coral reefs. For example, distance to markets is a better predictor of the condition of reef fisheries than local human population densities in the vicinity of the reefs (Cinner et al. 2013). Further, combining travel times to reefs, as a measure of their accessibility (Maire et al. 2016), with human population sizes within a given distance, produces a metric known as ‘gravity’, which is a stronger predictor of fisheries exploitation on any given reef than human population density alone (Cinner et al. 2016; Cinner et al. 2018). When reef fisheries are quantified as either doing better (bright spots) or worse (dark spots) than expected given their natural biophysical bounds, it is human socioeconomic and cultural data such as customary taboos, marine tenure, and levels of local engagement in management, that are able to better predict the two outcomes (Cinner et al. 2016). We highly advocate these recent approaches and anticipate that unless we start to more routinely monitor, decipher, and account for socioecological links across scales we will become unable to predict spatiotemporal changes to coral reef ecosystem dynamics. We need to move to a point where we are integrating this thinking in to new ecological theories and paradigms that explicitly insert humans in to the equation across scales. As such, we require a new multi-scaled macroecological approach to coral reef ecology that is aligned with our current time, i.e., the Anthropocene.

Looking to the future: coral reef ecology in the Anthropocene

The past century has seen an evolution in ecological thinking, with theories and frameworks continuously updated and refined based on our ever-increasing understanding of natural systems. Coral reef science is no exception. Early theories and descriptions of the origins, structure, and distribution of coral reefs (Darwin 1842) were extended to encompass a more mechanistic, ecological, and process-based understanding of these diverse ecosystems (Odum & Odum 1955). Concurrently, the broad field of ecology was evolving across
multiple terrestrial and aquatic systems. The longstanding Clementsian view of unidirectional ecological succession (Clements 1936) gave way to an appreciation of more complex interacting processes governing ecosystem dynamics and non-equilibrium theory (Odum 1969; Whittaker 1970). Concepts of ecological resilience then developed (Holling 1973) and were later directly applied to non-equilibrium systems like coral reefs (Connell 1978; Nyström, Folke & Moberg 2000). More recently, resilience theory has expanded to embrace a social-ecological systems framework that explicitly treats humans as internal rather than external to the system (Berkes & Folke 1998; Biggs et al. 2012). These works have given rise to a range of ecological paradigms that have formed our views on what defines coral reef ecosystems, what shapes them, and how they function.

What is now unequivocal is that human imprints can be observed at all biophysical scales, across all levels of biological organisation, and in the processes upon which ecological theories rest, such as species dispersal, colonisation, invasion, extinction, isolation, tolerance, and competition (Ellis 2015). Acknowledging that humans have emerged as a significant force in nature, “natural” biophysical processes that previously determined the assembly, dynamics, structure and functional ecology of ecological communities, may now be overwhelmed by anthropogenic activities (Fig. 2). This new situation poses an intriguing question: to what extent do traditional ecological paradigms capture and explain the ecological patterns and processes we observe in the Anthropocene?

The unprecedented breakdown of isolation by human migration and trade has caused dramatic changes to the dispersion and diversity of species globally (Meyerson & Mooney 2007; Westphal et al. 2008; Banks et al. 2014), with both positive and negative impacts to ecosystem services (Charles & Dukes 2007; Pejchar & Mooney 2009; Schlaepfer, Sax & Olden 2011). This loss of isolation is potentially compromising the explanatory and predictive power of traditional ecological models. For example, when Helmus et al. (2014)
investigated the species–isolation relationship for anole lizards among Caribbean islands. They found that anole biogeography reflects anthropogenic processes, such as economic isolation of human populations, rather than geographic processes postulated in traditional island biogeography theory. Similar perturbations to the effectiveness and relevance of traditional ecological models and paradigms are likely occurring in the ocean.

In the marine environment, humans have influenced species biogeography by the unintentional and intentional introduction of species through transport and trade. Examples include ballast water release from cargo ships, aquaculture, and the aquarium industry (Padilla & Williams 2004). Moreover, we have created artificial ‘islands’ that are no longer static stepping-stones, but instead, float and move. Human-derived flotsam is providing a dispersal mechanism for tropical Atlantic fishes to cross the deep-water Mid-Atlantic Barrier (Luiz et al. 2012) and is facilitating alien species invasions (Gregory 2009). Floating plastic waste harbours distinct microbial assemblages, the so-called ‘Plastisphere’ (Zettler, Mincer & Amaral-Zettler 2013), with this unique biotope providing a mechanism by which disease-causing pathogens of reef corals spread in the Anthropocene (Lamb et al. 2018). Recent biophysical dispersal models have even offered the provocative suggestion that human infrastructure, such as oil and gas installations across the North Sea, can form a highly interconnected regional network of coral ecosystems capable of supplying larvae to natural populations downstream (Henry et al. 2018). In these instances, to fully understand and be able to predict the observed ecological dynamics at play requires a new strategy. The human socioeconomic and cultural processes governing such modifications to species dispersal and diversity must become an integral part of ecological theory and practice as much as biological and geophysical processes are today (Ellis 2015; Österblom et al. 2017).

The pervasive global influence of humans in governing the spatial dynamics of ecological systems requires new theoretical advances to study, define, and sustainably...
manage them (Herrick & Sarukhán 2007; Mumby & Steneck 2008; Hulme-Beaman et al. 2016; Rose et al. 2016; Cadotte et al. 2017). Coral reefs are no exception; they face a new reality with their dynamics governed by cross-scale interacting biophysical and human socioeconomic and cultural drivers (Norström et al. 2016; Hughes et al. 2017) (Fig. 2) and we question whether traditional coral reef paradigms accurately capture this complexity.

Moving forward, humans (and their activities) must become an integral part of coral reefs and their dynamics. For this purpose, we propose ‘social-ecological macroecology’ as a novel concept for studying coral reefs in the 21st century. This approach embeds macroecology – the study of organism-environment relationships at large spatial and temporal scales (Brown & Maurer 1989; Keith et al. 2012; Heffernan et al. 2014), within a social-ecological systems framework. In doing so, social-ecological macroecology explicitly inserts the presence, behaviour, dynamics, and ecology of the human species into the equation, and does so across spatial and temporal scales. We stress the critical role of a macroecology approach – the scale of observation directly influences the ecological finding(s), their interpretation, and their subsequent use in guiding coral reef management.

Taking a social-ecological macroecology approach to studying coral reefs will require some innovative thinking and we suggest four core pathways to this approach:

1. **Identify the interactive effects of biophysical and human socioeconomic and cultural drivers of coral reef ecosystems across spatial and temporal scales.** This will improve our predictive capacity, such that we understand how changing one parameter, either biophysical, socioeconomic or cultural, at any specific scale interacts with other drivers at other scales to alter coral reef ecosystem structure and function.
2. **Test the robustness of classic coral reef paradigms.** We need to revisit and test whether classic ecological paradigms developed, in many instances, outside of the social-ecological systems framework, are still able to capture the dynamics of Anthropocene reefs accurately.

3. **Adapt current coral reef paradigms.** If classic paradigms fail to capture the spatiotemporal dynamics of reefs today accurately, we should explore whether adapting these paradigms, by including human dynamics as drivers, substantially improve their predictive capacity.

4. **Develop novel coral reef social-ecological paradigms.** In some cases, adapting existing coral reef paradigms may not be enough; we will need to develop novel rules and theories to create ‘*social-ecological paradigms,*’ where human dynamics are part of the paradigms rather than the external drivers of them.

    We will need to continually re-visit and test the performance of any of the adapted or novel paradigms developed under this approach due to the unprecedented rate of social and ecological change in the Anthropocene. In following these guidelines, coral reef ecologists should be able to identify, at any given spatial or temporal scale of observation, which interacting predictors (biophysical, socioeconomic or cultural) offer the best predictive capacity over coral reef ecosystem structure and function.

**Conclusions**

We remain convinced that human social, cultural and economic processes must become an integral part of ecological theory and practice as much as biological, geological
and physical processes are today. This warrants a revisiting of traditional coral reef
ecological paradigms and theories and either adapting them so that they capture
contemporary dynamics of intertwined social-ecological systems, or developing novel social-
ecological theories. This will be challenging and will require truly interdisciplinary
collaborations between researchers in the natural and social sciences.

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The authors declare that they have no conflict of interest.

Author contributions

G.J.W, N.A.J.G, J-B.J, A.V.N, and M.N conceived the research idea and led its development
with all the other authors providing input. G.J.W led the writing with all authors contributing
to the discussion and editing of the paper.

Data accessibility

There are no specific data sets used in this Perspective piece.
References


Fish Assemblages between Populated and Remote Reefs Spanning Multiple Archipelagos Across the Central and Western Pacific. *Journal of Marine Biology;* Article ID 826234, 1-14.


### Figures and figure legends

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<td>Higher wave energy reefs are dominated by low-lying corals and algae less vulnerable to physical stress while lower wave energy favours more upright, structurally complex corals and algae.</td>
<td>Higher wave exposure is linked with increased grazing herbivore (G) feeding frequency.</td>
<td>Higher sea-surface temperatures support more corals while lower temperatures favour macroalgae.</td>
<td>Warmer waters support an increased biomass of detritivores (D), while cooler waters support an increased biomass of browsing herbivores (B).</td>
<td>Higher oceanic primary production supports a greater number of microbes enriched in genes involved in nutrient-related metabolisms (e.g., nitrate and nitrite ammonification).</td>
<td>Higher oceanic primary production supports high coverage of calcifying benthic organisms.</td>
<td>Higher oceanic primary production supports increased grazing herbivorous (G), planktivorous (P), and top-predatory (T) fish biomass.</td>
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**Figure 1.** Examples of the natural bounds set by gradients in biophysical drivers on coral reef ecosystem structure and function across trophic levels, from microbes to sharks.
Figure 2. Drivers of coral reef ecosystems pre- and post- Anthropocene. Before coral reefs entered the Anthropocene, their ecosystem state was heavily governed by natural biophysical drivers, even in the presence of small subsistence-based human populations (left). This is still the case for some remote, uninhabited coral reef islands and atolls that are far removed from direct human impacts. However, many coral reefs today are impacted by local human drivers, such as commercial and recreational fishing and effluent discharge from land (right). Importantly, these proximate drivers of reef ecosystem state are themselves ultimately dictated by a complex network of underlying socioeconomic and cultural drivers (right). The biophysical drivers are still present on Anthropocene reefs, but their relative influence in governing reef ecosystem state is likely greatly reduced. Because of this, we propose the need for ‘social-ecological macroecology’ which embeds macroecology – the study of organism-environment relationships at large spatial and temporal scales, within a social-ecological systems framework.