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PERSPECTIVE

From polyps to pixels: understanding coral reef resilience to local and global change across scales

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Abstract

Context Coral reef resilience is the product of multiple interacting processes that occur across various interacting scales. This complexity presents challenges for identifying solutions to the ongoing worldwide decline of coral reef ecosystems that are threatened by both local and global human stressors.

Objectives We highlight how coral reef resilience is studied at spatial, temporal, and functional scales, and explore emerging technologies that are bringing new insights to our understanding of reef resilience. We then provide a framework for integrating insights across scales by using new and existing technological and analytical tools. We also discuss the implications of scale on both the ecological processes that lead to declines of reefs, and how we study those mechanisms.

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Methods To illustrate, we present a case study from Kāne‘ohe Bay, Hawai‘i, USA, linking remotely sensed hyperspectral imagery to within-colony symbiont communities that show differential responses to stress.

Results In doing so, we transform the scale at which we can study coral resilience from a few individuals to entire ecosystems.

Conclusions Together, these perspectives guide best practices for designing management solutions that scale from individuals to ecosystems by integrating multiple levels of biological organization from cellular processes to global patterns of coral degradation and resilience.

Keywords Scaling · Cross-scale · Remote sensing · Sustainability

Introduction

Scale is fundamental to our understanding of any system, particularly given that our observations are directly affected by an integration of processes acting at multiple scales (Wiens 1989; Levin 1992) posed that the ‘central problem in ecology’ is that the scale of observations is often different than the scale of the process being studied. Multiple facets of scale need to be considered, including grain and extent (Turner et al. 2001). Grain is the size of individual units of observation, such as a coral polyp or a transect. Extent is the domain of the study, such as a cell or an archipelago. The grain and extent of a study define the limits for which scale-dependent inferences can be drawn, given that information content often correlates with both. Therefore, considering ecosystems as complex hierarchical systems, where biological organization encompasses a wide range of scales, from microbes within individuals to ecosystems connected by dispersal of organisms across thousands of kilometers, allows for a deeper understanding of ecological change and a greater ability to predict and address those changes (Allen and Starr 1982; Wiens 1989; Peterson et al. 1998).

Coral reefs are complex hierarchical systems that host a wide diversity of marine life and provide vital ecosystem services (Moberg and Folke 1999; Hoegh-Guldberg et al. 2019), but are threatened worldwide by multiple local and global stressors (Jackson et al. 2001; Pandolfi et al. 2003; Hughes et al. 2017). Critical to understanding the impact of these stressors is our ability to measure change, which can manifest on different spatial, temporal, and functional scales. Examples include shifts in the relative abundance of species and their size classes, to wholesale differences in the functioning of the ecosystem. Much of what has been observed over the past 70 years of coral reef research has focused on the relative spatial cover of corals (Hughes et al. 2010), given their foundational role as habitat generators and ecosystem engineers. However, ecological change is occurring at multiple scales of biological organization, and modern technologies are now rapidly improving our ability to assess changes on reefs across scales that range from cellular to global (Calders et al. 2020).

One property of complex systems that determines ecosystem change is resilience, which can be viewed as *ecological resilience*—the capacity of an ecosystem to withstand disturbance without changing its overall identity in terms of structure and function (Holling 1973; Gunderson 2000; Nyström et al. 2008)—or from a focus on stability, termed *engineering resilience*, which can be measured as the speed of recovery, or return to equilibrium, following a disturbance (Holling and Meffe 1996). Resilience on coral reefs can scale from the physiology of individual organisms, to the persistence of an entire reef, to the broader linked social-ecological system (Jackson 1991; Hatcher 1997; Nyström et al. 2008; Roche et al. 2018) (Fig. 1). For example, studying the regulation of proteins, enzymes, and individual genes across the coral holobiont (i.e., the coral animal, Symbiodiniaceae, and the microbiome) is needed to understand resistance to stressors (Bourne et al. 2016; Bay et al. 2017). Predicting the potential for selection can be further understood at the grain size of a population. For example, as disturbances cause differential mortality of susceptible coral colonies, resistant genotypes will persist, increasing the frequency of beneficial genes or alleles in the population. Further implications of resilience are evidenced at the scale of ecological communities, including the well-referenced example of coral to macroalgal phase shifts of reef benthic communities (Hughes 1994). Beyond the scale of a community, reefs are connected through larval dispersal by processes which interact with climate and biophysical gradients to establish the connectivity of multiple reefs within and among archipelagos.

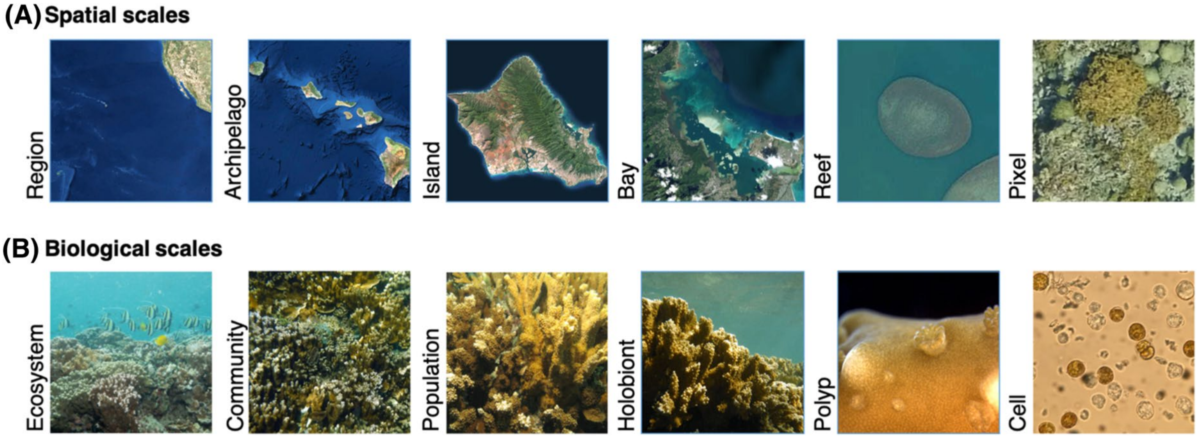

Fig. 1 Multiple spatial and biological scales used to study reef processes and dynamics that can vary in extent and grain exemplified for *Montipora capitata* in Kāne'ohe Bay, Hawai'i, USA [Image credits: (Region—Reef) ESRI basemap imagery, (Pixel) Joshua Levy, (Ecosystem, Population-Polyp) Raphael Ritson-Williams, (Community) Ingrid Knapp, (Cell)–Shayle Matsuda]

Thus, each of these scales can be explored at multiple grain sizes and extents using a variety of tools and observations designed to understand the underlying processes and interactions driving local and global change.

Here we explore how coral reef resilience could be better understood by bridging investigations across multiple levels of biological organization and scales (Fig. 1). We review how data are collected at each level, highlight recent technological advances, and discuss implications for understanding cross-scale phenomena. Additionally, we present a framework for drawing inference across multiple measures and multiple scales, ranging from polyps to pixels, using a case study in Kāne'ohe Bay, Hawai'i, USA. This perspective provides a framework for bridging between molecular studies and remote sensing to tell a more complete story that better describes coral reef resilience through the lens of cross-scale resilience theory.

Tools and advances across scales of biological organization

Cell

'Omics' tools (e.g., genomics, epigenomics, transcriptomics, proteomics and metabolomics) are at the forefront of the study of the intracellular aspects of coral. These tools have greatly increased our understanding of fine-scale population connectivity and genetic structure, adaptation and acclimatization to environmental change, symbiont community dynamics, and sublethal responses to environmental stressors, disease, and recovery (Vega Thurber et al. 2009; Barshis et al. 2013; Dixon et al. 2015; Seneca and Palumbi 2015; Voolstra et al. 2015; Kenkel and Matz 2016; Putnam et al. 2016; Forsman et al. 2020; Roach et al. 2021). For example, such approaches have been used to determine the genomic basis of coral resilience to climate change (i.e., what genes underlie thermal tolerance) and to what degree thermotolerance is driven by genetic adaptation versus physiological plasticity (Barshis et al. 2013; Palumbi et al. 2014). These advances enable the selection of thermotolerant genotypes for coral restoration and other human interventions to increase coral persistence under climate change, such as assisted gene flow or translocation (National Academies of Sciences, Engineering, and Medicine 2019a). 'Omics' tools have the advantage that only a small tissue sample or even single cells collected in the field or lab can generate an immense amount of data (e.g., millions of sequence-reads per individual). This convenience is balanced by the need for specialized expertise and equipment, high costs of lab preparation and sequencing [e.g., Restriction-site Associated DNA Sequencing (RAD-Seq) and RNAseq] along with the development of bioinformatic pipelines, and computational constraints of big data generation.

Multiple advances in cellular studies of corals are paving a path towards greater applications to conservation solutions. First, sequence data and metadata are typically deposited in freely and publicly available repositories [e.g., NCBI Sequence Read Archive (Leinonen et al. 2010)], offering potential avenues for broader research endeavors spanning across coral species and multiple stressors. Technological advances also continue to reduce costs of both sequencing and computation of sequence data. Together, these advances will lead to greater availability and application of these tools as the field continues to progress. Nonetheless, small sample sizes at this level of biological organization likely under-represent the functional and genetic diversity of corals and conditions, and thus a scale-gap occurs in making broad inferences from such localized data.

Polyp

Single polyps originating from planula larvae form the 'individual' level of biological organization for corals, and many polyps together form a coral colony. Studies at the larval and polyp scale are key to understanding fundamental biological processes in corals, such as settlement and metamorphosis, establishment and maintenance of symbiosis, and formation of calcium carbonate skeletons, which in turn govern resilience at higher levels of organization. Polyp biology has largely been informed by studying coral reproduction (Harrison 2011), where researchers typically collect coral gametes in the field and conduct laboratory experiments to understand patterns of fertilization, dispersal, settlement, and post-settlement ecology (Ritson-Williams et al. 2009). Research on coral larvae spans from behavior (Dixson et al. 2014), physiology (Gleason and Hofmann 2011), and ecology (Ritson-Williams et al. 2016) to genomics and transcriptomics (Polato et al. 2013; Kirk et al. 2018; Fuller et al. 2020), using many of the same techniques applied to the cellular processes described earlier.

Studying coral polyps and larvae has generally been limited to laboratory experiments because of their small size and the low probability of observing settlement and early post-settlement life stages in situ (but see Carlon and Olson 1993). However, hundreds to thousands of larvae can be grown and settled in the laboratory (Ritson-Williams et al. 2016), and recent technological advances are increasing the success and accessibility of spawning corals in ex situ closed mesocosms (Craggs et al. 2017), accelerating research at this scale. In situ sampling of established recruits over time for population genetic analyses, however, could enable integration over multiple time scales, allowing us to track changes in genotypic diversity if a habitat is surveyed repeatedly before and after a disturbance event. Further, there is evidence that symbionts (and by proxy, physiologic resistance to stress) can vary across microhabitats found within a single coral colony (Rowan et al. 1997), and there have been recent advances in single cell 'omic techniques that allow for measuring variation across polyps within a holobiont, so we expect that our understanding of polyp level biology as it relates to aspects of coral resilience will greatly increase in the near future.

Holobiont

The coral colony is composed of many individual polyps that, together with the microbiome and symbiotic microalgae in the family Symbiodiniaceae (LaJeunesse et al. 2018), form the coral holobiont. Individual holobionts have variable responses to stress (Barshis et al. 2013; Drury et al. 2017; Ritson-Williams and Gates 2020). This variability in stress response was classically studied using ecology and physiology (Edmunds and Gates 2008) but has recently progressed using transcriptomics (Kenkel and Matz 2016; Kirk et al. 2018), genomics (Bay and Palumbi 2014; Howells et al. 2016; Fuller et al. 2020), and microbiology (Bourne et al. 2016). Genetic techniques have greatly increased our knowledge of the diversity of coral-associated symbionts and microbes (Rowan and Powers 1992; Vega Thurber et al. 2009; Hernandez-Agreda et al. 2017; LaJeunesse et al. 2018), and many studies have demonstrated how coral holobiont performance and resilience are linked to the composition and diversity of Symbiodiniaceae (Iglesias-Prieto et al. 1992; Glynn et al. 2001; Berkelmans and Van Oppen 2006; LaJeunesse et al. 2010; Cunning et al. 2016; Hume et al. 2019), other microeukaryotes (Kwong et al. 2019), bacteria (Ziegler et al. 2017; Boilard et al. 2020), and viruses (Vega Thurber et al. 2017).

The clonal properties of corals provide an advantage for research such that genetically identical fragments of the same colony can be used as replicates in experimental manipulations. Importantly, while the identity of the coral animal may remain fixed across these replicate fragments, microbial partners may vary (Rowan et al. 1997), and can even be directly manipulated to study and/or generate specific holobiont combinations and phenotypes, including stress tolerance (Rosado et al. 2019; Cunning and Baker 2020). However, microbial manipulations can be limited in both grain and extent, and therefore may not translate well to broader scales. Advances in studying coral microbiomes, transcriptomics, and genomics will allow for increasing the extent of studies on the variability of coral holobionts, demonstrating the research potential at this organizational scale. Mathematical modeling approaches applied to coral-symbiont interactions (e.g., dynamic energy budget theory; (Muller et al. 2009; Cunning et al. 2017), may also help to mechanistically link environmental impacts on the coral holobiont to higher levels of biological organization (e.g., Martin et al. 2013).

Population

Population-level analyses of corals have improved our understanding of coral resilience through identification of cryptic species (Rose et al. 2018; Forsman et al. 2020; Burgess et al. 2021), inferred mechanisms of adaptive potential (Knowlton and Leray 2015; Bay et al. 2017), characterization of relationships among populations and dispersal patterns (Toonen et al. 2011; Drury et al. 2018; Matz et al. 2018), and attribution of key processes driving population dynamics (Madin and Connolly 2006; Roth et al. 2010; Hughes et al. 2019; Dietzel et al. 2021). Population-level molecular analyses and coral genotyping have informed predictions of future impacts of environmental change (Selkoe et al. 2016; Bay et al. 2017; Underwood et al. 2018; Fuller et al. 2020), and resistance to disease (Vollmer and Kline 2008). Population dynamic studies of corals have revealed the importance of variation in recruitment (Hughes and Tanner 2000; Edmunds et al. 2010) and overall size structure (Bak and Meesters 1999; Dietzel et al. 2020, 2021) in determining resistance and recovery from disturbance.

Despite early calls for coral demography to be the center of coral population studies (Connell 1973; Hughes 1984), the need to move beyond measures of percent cover for corals and include coral demography are still being echoed today (Edmunds and Riegl 2020). Further, measures of vital rates (e.g., growth, survival, fecundity), and their incorporation in modeling the future trajectory of corals is understudied. One challenge to demographic studies is the complex life history of corals that involve a variety of reproductive strategies and complex growth, but also fission, fusion, and shrinkage (Edmunds and Riegl 2020). Advances in photogrammetry and 3-dimensional modeling of coral reef systems are providing new pathways for studying coral population dynamics (Burns et al. 2015) (Fig. 2), and in particular coral size frequency (Burns et al. 2016; Hernández-Landa et al. 2020). This emerging method can enable us to better estimate the complex 3-dimensional structures made by corals without the need for in situ observations, expanding how we estimate coral resilience in a changing world.

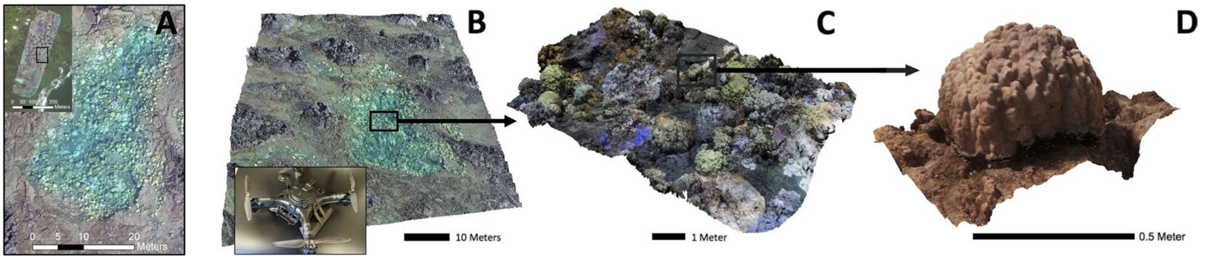

Fig. 2 3D modeling of a coral reef system across multiple spatial scales. **A** Close-up of an area within the Wai'ōpae coastline on Hawai'i island showing individual coral colonies with inset map showing spatial coverage of the survey area reconstructed in 3D using aerial images. **B** Oblique view of the 3D model of the same location (m-resolution), with IVAN multirotor aerial Unmanned Aircraft Vehicle (UAV) platform shown in inset photo. **C** Oblique view of a 3D model of coral colonies (mm-resolution) and **D** a 3D model of an individual colony (mm-resolution) reconstructed from this same location, both generated with underwater Structure from Motion (SfM) photogrammetry techniques (Image credit: Burns and Perroy, UH Hilo)

Community

Community-level studies of corals reefs have increased our understanding of how biotic interactions, diversity, and the role of corals as habitat engineers relate to reef resilience. Biotic interactions can play a major role in driving coral community composition through competition (e.g., among corals and algae), predation, and ecological feedbacks such as herbivory effects. The role of interactions between corals, algae, and herbivores in shaping reef resilience in particular has received considerable attention (Nyström and Folke 2001; Bellwood et al. 2004; Mumby et al. 2007; Hughes et al. 2010; Steneck et al. 2018), as herbivory has been identified as a key process determining whether reefs might rapidly transition from coral dominated to algae dominated reefs (Hughes et al. 2007; Mumby et al. 2007; Burkepile and Hay 2008; Steneck et al. 2019). Community-level studies also include the implications of diversity (Warwick and Clarke 1990; Paulay 1997), and coral community structure (Loya et al. 2001; Hughes et al. 2018) on resilience. Studies on coral assemblage effects on the broader reef community have also been critical for understanding reef resilience, such as the ecological effects of coral declines on fish assemblages (Pratchett et al. 2008; Fukunaga et al. 2020), and how reduced structural complexity leads to broad scale community change (Alvarez-Filip et al. 2009).

Compared to other levels of biological organization on coral reefs, studying benthic communities can be done relatively inexpensively with simple equipment and methods. Basic metrics such as percent cover of coral can be obtained relatively rapidly and across large geographic scales by researchers and community (formally termed "citizen") scientists alike (Aronson et al. 1994; Hodgson 1999; Stuart-Smith et al. 2017). However, the simplicity of the tools needed belies the importance of an in-depth knowledge of the natural history of the focal community, often integrating an understanding of each of the other levels of biological organization discussed here. Similarly, given the lack of standardized methodologies through the relatively long history of monitoring coral communities, comparing data sets across spatial and temporal scales can be challenging (Jackson et al. 2014). Our understanding of coral communities is advancing through new approaches including in situ and low altitude aerial photogrammetry (Burns et al. 2015; Levy et al. 2018), and aerial imagery (Asner et al. 2020) that provide repeatable, unbiased, high-resolution data at broader spatial extents than previously possible. Data acquisition from these emerging imaging capabilities are also being made possible from innovation in automated image analysis tools, such as CoralNet (Beijbom et al. 2015; Williams et al. 2019).

Ecosystem

Studies of corals at the ecosystem level involve examining spatial variation and temporal trends across extents and/or grain sizes at or larger than individual coral communities (Fig. 1). These broad scale data can assess resiliency of a system to pulse events such a marine heatwaves and cyclones (Stuart-Smith et al. 2018), as well as press disturbances like habitat degradation from land-based pollution (Palandro et al. 2008). Ecosystem-scale data are particularly important for understanding context, and for extrapolating finer resolution biotic responses discovered in 'omic, holobiont, population, and community studies for understanding resiliency at management-relevant spatial scales. Remotely sensed data sources (e.g., multispectral and hyperspectral imagery, LiDAR, SONAR) have emerged as a key source of data for ecosystem-level observations that include the ability to measure depth (Salameh et al. 2019), habitat complexity (Lepczyk et al. 2021), environmental drivers like sea surface temperature and turbidity (El Mahrad et al. 2020), and more recently live coral cover at broad extents (Asner et al. 2020). While live coral cover mapping is currently limited to aircraft-based imaging spectrometers, forthcoming spaceborne spectrometers from NASA, the European Space Agency, and the private sector will make this capability globally accessible. Until then, space-based observation of broad benthic and geomorphic reef compositions from multispectral satellites will continue (Hedley et al. 2016; Li et al. 2020).

Resolution and extent of remotely sensed data are inversely correlated given the logistical costs of data collection, which limits the scope of what can be investigated for any individual mapping effort. Further, gaps in the satellite record for different types of data can be troublesome especially for analyses over time. For example, sea temperature datasets only date back to the 1980s [e.g., the Coral Reef Temperature

Anomaly Database (CoRTAD) (Saha et al. 2018)], which presents uncertainty in retrospective analyses of heatwaves. Despite these challenges, uptake of remotely sensed data in coral research is rapidly growing as both spectral and radiometric resolution improves from both satellite and aerial sensors. Further, use of high quality, reliable ecosystem-level information for coral management is increasing as data becomes more available through efforts such as the Allen Coral Atlas (https://allencoralatlas.org) that are making information on coral reef habitat composition, bleaching, and other products available for the entire globe (Li et al. 2020, 2021).

Human and physical drivers of reefs across scales

Coral reefs are affected by multiple physical and anthropogenic drivers, such as pollution, overfishing, and climate change (Jackson et al. 2001; Fabricius 2005; Hughes et al. 2017). These drivers often do not occur in isolation and can therefore result in additive, synergistic, or antagonistic responses across multiple scales (Côté et al. 2016). For example, variable bleaching responses to increased temperature can occur within a single colony (Rowan et al. 1997), among colonies of the same species within a population (Jones 2008; Williams et al. 2010; Ritson-Williams and Gates 2020), or across different species within a community (van Woesik et al. 2011). At the ecosystem level, biophysical influences on benthic cover can vary at the scale of islands (Williams et al. 2015) and within small islands; for example, wave forcing and geomorphology can predict benthic regimes at the scale of 100 s of meters (Gove et al. 2015; Aston et al. 2019).

When examining how drivers interact and influence biological outcomes on coral reefs, the implication of scale must be considered (Turner et al. 2001). Yet, biological response and driver data are not necessarily measured at the same scale. For example, there is often a disconnect between fine scale (spatial or temporal) temperature variation, measured with in situ loggers (<1 m/every 20 min), verses global satellite derived temperature (4 km/twice weekly) and global climate model outputs (100 km^2/monthly) (Safaie et al. 2018). Human influences on coral reefs are also manifested at a variety of spatial and temporal scales, and these multi-stressor relationships can be masked if studied at differing grain or extent sizes than those at which the processes occur. For example, Jouffray et al. (2019) uncovered important biophysical and human influences on coral reefs in Hawaiʻi, and did not detect any differences in their results after repeating analyses at multiple grain sizes. In particular, the study did not uncover effects of land-based pollution despite well understood connections between pollution and reef condition (Fabricius 2005), which was hypothesized to be a result of the grain size of the pollution data not matching the highly localized scale at which pollution affects reefs. Development and use of unmanned systems (Obura et al. 2019), sensor networks (Trevathan et al. 2012), and low-cost cameras (Greene et al. 2020) are attempting to bridge the gap between observable biological responses and environmental driver data at scales relevant for improving our understanding of these complex systems.

One limitation to linking drivers and observations at appropriate scales is a lack of evidence for the scale at which the processes are occurring. For example, there is some evidence that scaling patterns are common for coral communities in relation to biophysical gradients that may allow for a common scaling law for coral reef benthic communities on island seascapes (Gove et al. 2015; Aston et al. 2019). However, the evidence for scaling in benthic reef communities comes from remote Pacific islands with relatively low human impacts, and relationships may break down when human influences disrupt natural processes. For example, Williams et al. (2015) found that across the Pacific homogenized reefs with low diversity and a high abundance of 'weedy' species common on populated islands were not coupled with background environmental regimes compared to strong biophysical coupling observed on unpopulated islands. Indeed, physical and human influences on coral reef systems can be evident in different contexts (Cinner et al. 2018; Jouffray et al. 2019); therefore, interactions among human and physical drivers need to be better understood in order to define boundaries for conservation and restoration. Difficulty uncovering appropriate scales for inquiry is further compounded by the potential for cross-scale phenomena, where processes could be occurring across and within scales (Peters et al. 2007). Cross-scale redundancy has been shown to be an indicator of resilience, where better recovery after disturbance was observed for reefs with herbivory operating across multiple scales (Nash et al. 2016). Multiscale problems also may require potentially arbitrary delineations of discrete scales (Levin 1992), potentially masking the underlying processes. Thus, future research needs to explicitly incorporate scale in order to understand how human and biophysical drivers interact to influence reef status and trends.

Linking observations across scales

Given the range of tools used to gain insight into reef resilience, and the scales of stressors on corals, it is critical to link our understanding of processes that allow for coral resilience across scales so that we may better predict how corals will respond to changing environmental conditions. For example, much of what we know about bleaching resistance of corals comes from molecular studies and manipulative tank experiments, both of which are logistically limited in size and breadth. But understanding how bleaching resistance is manifested in populations, communities, and ecosystems is fundamental to both informing future predictions and designing effective management for corals.

For example, symbiont communities of corals are an important factor relating to many biological and ecological outcomes on coral reefs (Baker et al. 2008). Different genera of symbionts influence the thermal tolerance of the host coral, so the composition and relative abundance of symbiont taxa is particularly important for the long-term persistence of coral reef ecosystems (Berkelmans and Van Oppen 2006; Logan et al. 2021). Various molecular biology techniques can resolve these patterns, but time, cost, and accessibility limit the availability of these data to relatively few well-studied ecosystems. Here, we provide an example of how the differential responses to heat stress by individual corals with different symbionts can be predicted via remotely-sensed hyperspectral imagery. We show that symbiont community can be linked to hyperspectral imagery through color morphs in *Montipora capitata*, effectively transforming the scale at which we examine symbiosis ecology from the within polyp-scale to the whole reef-scale (Fig. 3).

Previous molecular genetic studies of *M. capitata* holobionts in Kāne‘ohe Bay, O‘ahu, Hawai‘i, revealed two color morphs, brown and orange, which were associated with *Cladocopium* and *Durusdinium* symbionts, respectively. The color morph and symbiont were correlated with differential responses to a major bleaching event (Cunning et al. 2016; Innis et al. 2018), with orange, *Durusdinium*-dominated colonies showing much greater bleaching resistance. When combining this observation with high-fidelity imaging spectroscopy collected by aircraft through the Global Airborne Observatory (Asner et al. 2012), we were able to successfully distinguish between individual corals of the two color morphs at a scale of an entire patch reef (Fig. 3). By connecting the biology

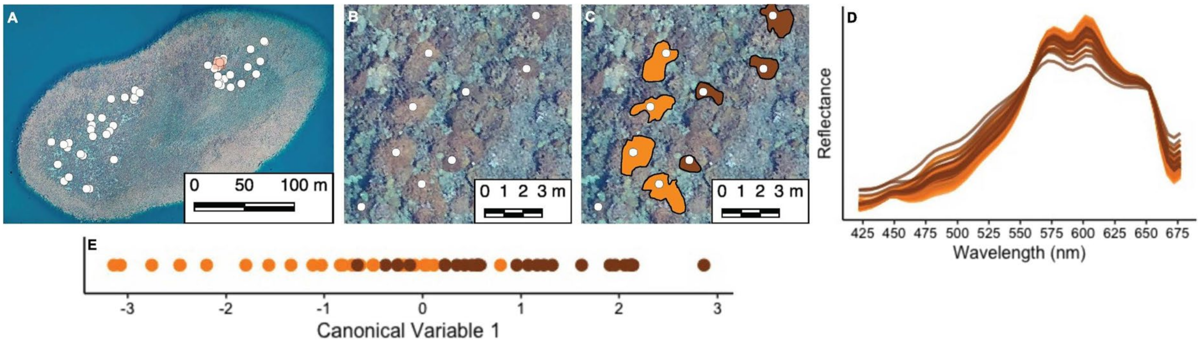

Fig. 3 Spectral analysis of *Montipora capitata* color morphs in Kāne‘ohe Bay. **A** Sampling points at Reef 44 where benthic reflectance was retrieved from brown (n = 25) and orange (n = 25) color morphs. **B** Illustrative region with neighboring orange and brown color morphs which were **C** defined as each color based on high resolution Global Airborne Observatory imagery. **D** The brightness normalized spectra of brown and orange color morphs show different reflectance at various wavelengths which can be used in discriminant analysis, **E** correctly classifying 64% of samples (Image credit: G. Asner and J. Heckler, Global Airborne Observatory). For details on methods see Supplemental Material

of individual corals studied in situ using ‘Omics techniques with remotely sensed data at broad scales, we link coral physiology at the scale of individuals and the scale of seascapes, showing that differential responses to stress at a physiological level can be predicted at a seascape scale. Thus, we provide an example of how cross-scale study could revolutionize our understanding and management of coral reefs given that these inferences can be scaled up to entire islands or archipelagos to provide actionable science on how the potential resilience of coral populations to climate-driven disturbances can vary spatially. For example, using remotely sensed data to identify thermotolerant individuals can be used for locating heat tolerant genotypes for use in restoration (Drury et al. 2022). Further, transcriptomic and physiological measurements are being used around the world to rapidly identify thermally resilient coral colonies in situ (Cunning et al. 2021; Naugle et al. 2021; Savary et al. 2021). Combining these data with 3D photogrammetry or remotely sensed data over multiple years encompassing thermal disturbance events, when fine-scale physiological or ‘omics sampling may not feasible, could help in understanding the long-term fate of these thermally “tough” colonies over ecologically and management relevant spatial and temporal scales (Little et al. 2021).

In addition to emerging technologies transforming the way we study coral resilience, advances in how data from multiple scales can be brought together for new inferences is possible through the increasing use of hierarchical modeling in ecology and conservation (Bolker et al. 2009; MacNeil and Connolly 2015). Hierarchical models allow for explicitly incorporating hypotheses and data at multiple scales in an integrated form, due to the ability to formulate flexible nested model structures. Thus, finer scale patterns and processes can be understood in the context of broader scale phenomena. For example, data collected at a fine scale on the response of a coral to disturbance may be combined with predictors that correspond to multiple hierarchical scales and can be incorporated at the scale at which the relationship to the coral’s response is hypothesized. MacNeil et al. (2009) illustrate how this statistical framework can be used to uncover how fish abundance and habitat diversity vary in relation to site-, reef-, and atoll-scale processes using hierarchical models that considered data at each scale. Since this publication, and a subsequent call for this to become a major research avenue for reef research (Hixon 2011), these methods have yet to be adopted by coral reef scientists globally. Therefore, the use of hierarchical models in linking fine- and broad-scale ecosystem processes holds great promise for furthering our understanding of reef resilience (MacNeil et al. 2015; Cinner et al. 2016; Donovan et al. 2020).

One path forward for coral reef resilience studies is to use emerging technologies and quantitative frameworks to translate how the physiological and behavioral responses of individuals scale to the seascape, and ultimately to the benefits and services reefs provide to people. We demonstrate that this is possible via data collected across scales in Kāneʻohe Bay, Oʻahu, Hawaiʻi, USA, but that is just the beginning.

Applications for effectively managing and conserving reefs

Given that the resilience of coral reefs is manifested across multiple scales of biological organization, and that feedbacks can exist among those scales, it is critical to link ideas and insights from the cellular-to-polyps-to-ecosystem-levels in order to effectively manage and conserve coral reefs in the face of local and global change.

Matches and mismatches exist between the scale at which we measure coral reef resilience (Fig. 4A), and the scales at which resilience is manifested, thereby posing serious challenges to coral reef conservation and management. These challenges exist because the varying spatial and temporal scales at which human impacts affect coral reefs (Fig. 4B) are often misaligned with the scales of management policy and action (Fig. 4C) (Cumming et al. 2006; Bellwood et al. 2019). To address the challenges from this scale-dependent mismatch, resilience-based management has emerged (Mcleod et al. 2019), including broad strategies that are adaptive and flexible and employ both interventionist and restoration-based tactics. Importantly, resilience-based management acknowledges upfront that systems are scale-dependent, and an understanding of scale needs to be incorporated into solutions (Mcleod et al. 2019).

Despite the emergence of resilience-based management strategies, global climate change only exacerbates the scale-dependent mismatches between

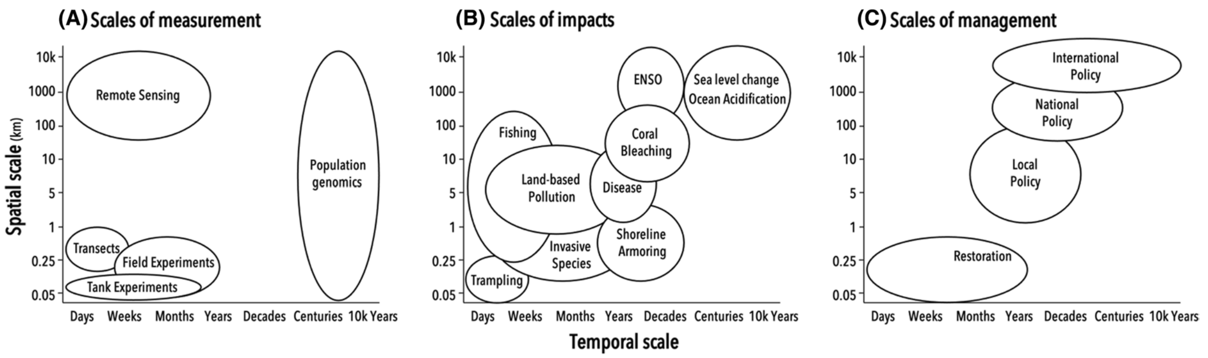

Fig. 4 Matches and mismatches between the scales of measurement (**A**), human impacts (**B**) and management (**C**) for coral reef resilience

coral reef resilience management and human impacts. Coral reef management is most often local in scale and limited to jurisdictions in which reefs occur; thus, addressing global scale stressors is often beyond the purview of those that are most affected. One path forward includes regional international partnerships between countries that share coral reef habitats, providing a platform for federal governments and conservation agencies to work together to meet coral reef resilience goals. The MAR Fund (https://marfund.org/) is an example of such a partnership that provides support for the countries bordering the Mesoamerican Barrier Reef in the Caribbean: Mexico, Belize, Guatemala and Honduras. Potential improvements in reef futures are possible by building off of these local and regional initiatives to bolster reef resilience alongside concerted efforts to curb global climate change. There is growing evidence that mitigating local stressors such as fishing and pollution can increase the potential for corals to withstand climate effects (Gilmour et al. 2013; Claar et al. 2020; Donovan et al. 2020, 2021). For example, nutrient pollution and overfishing of herbivores can both lead to increases in macroalgae, which causes greater mortality of corals following heatwaves (Donovan et al. 2021).

Coral restoration and human interventions provide another path forward for reef futures (Bay et al. 2019; National Academies of Sciences, Engineering, and Medicine 2019b). There have been advancements in managed selection (Van Oppen et al. 2015), such as propagating or translocating heat tolerant corals (Barott et al. 2021; Drury and Lirman 2021), assisted symbiont shuffling (e.g., promoting symbiosis with heat tolerant symbionts) (Buerger et al. 2020), genetic manipulation (Cleves et al. 2020), and altering coral microbiomes (e.g., treating corals with probiotics) (Rosado et al. 2019). Applications of these methods are being adopted by coral restoration projects, which often focus on rearing fragments of corals in nurseries and out-planting to select reef sites to encourage population-level recovery. However, the ability of these methods to scale to ecosystem level restoration is unclear (Boström-Einarsson et al. 2020; Hein et al. 2020) and more work is needed to integrate out-planting with existing ecological and physical bounds of the system (Ladd et al. 2019). Examples using synoptic-scale observations to enhance coral restoration projects includes linking coral outplanting successes and failures to remotely sensed drivers on a global scale (Foo and Asner 2021), and using live coral and algal mapping for restoration site selection (Schill et al. 2021).

A path forward

Due to the wide variety of local and regional stressors to coral reefs, and the mismatch that often occurs between these impacts and management efforts, we propose that future coral reef science activities consider the multi-scale dynamics of coral reef systems, and embrace emerging technologies and methods to address reef science for conservation and management. One way to approach this challenge may be to (i) aggregate mechanistic biological principles from finer scales (e.g., intra-holobiont organismic or chemical interactions) into (ii) species-level performance principles and models at coral population levels, and then to (iii) integrate those populations at community levels through competitive models for space, and then (iv) use the emerging high-resolution remote sensing to constrain the patterns of changing communities in space and time. While most of these individual undertakings are currently limited to research and development that precludes full utilization of an interlinked approach, setting an agenda now for achieving these linkages is fundamental to the longer-term goals and milestones required to scale up coral biology to the ecosystem level at which management interventions are sought.

There have been substantial advances in how we study coral resilience and what has been learned at both the finest grains (i.e., molecular and physiology) and at the broadest (i.e., remote sensing). Thus, the future of coral reef science lies at the intersection. Here, we have provided one such example of how within-individual bleaching resistance was transformed to a seascape scale (Fig. 3). Integration across scales of coral biology and ecology is the future of reef science, and in order for this to be possible, ideas and data must flow across and within disciplines making new and bigger discoveries possible.

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