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Water column contributions to coral reef productivity: overcoming challenges of context dependence

Anjali W. Shakya* and Jacob E. Allgeier*

Department of Ecology and Evolutionary Biology, University of Michigan, 1105 N University Ave, Ann Arbor, MI 48109, USA

ABSTRACT

Coral reefs are declining at an unprecedented rate. Effective management and conservation initiatives necessitate improved understanding of the drivers of production because the high rates found in these ecosystems are the foundation of the many services they provide. The water column is the nexus of coral reef ecosystem dynamics, and functions as the interface through which essentially all energy and nutrients are transferred to fuel both new and recycled production. Substantial research has described many aspects of water column dynamics, often focusing on specific components because water column dynamics are highly spatially and temporally context dependent. Although necessary, a cost of this approach is that these dynamics are often not well linked to the broader ecosystem or across systems. To help overcome the challenge of context dependence, we provide a comprehensive review of this literature, and synthesise it through the perspective of ecosystem ecology. Specifically, we provide a framework to organise the drivers of temporal and spatial variation in production dynamics, structured around five primary state factors. These state factors are used to deconstruct the environmental contexts in which three water column sub-food webs mediate 'new' and 'recycled' production. We then highlight critical pathways by which global change drivers are altering coral reefs *via* the water column. We end by discussing four key knowledge gaps hindering understanding of the role of the water column for mediating coral reef production, and how overcoming these could improve conservation and management strategies. Throughout, we identify areas of extensive research and those where studies remain lacking and provide a database of 84 published studies. Improved integration of water column dynamics into models of coral reef ecosystem function is imperative to achieve the understanding of ecosystem production necessary to develop effective conservation and management strategies needed to stem global coral loss.

Key words: carbon, ecosystem function, fisheries, food web, global change, management, nutrients, phytoplankton, plankton, zooplankton.

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* Authors for correspondence: A.W. Shakya (E-mail: ashakya@umich.edu) and J.E. Allgeier (Tel.: +734 764 6797; E-mail: jeallg@umich.edu).

I. INTRODUCTION

Tropical coral reef ecosystems are among the most productive ecosystems on Earth despite paradoxically existing in nutrient-poor conditions. Observations of this paradox date back to Darwin (1842), and have been largely based on one of the most visually arresting features of coral reefs – extreme abundance and diversity of benthic organisms existing in crystal clear (and seemingly depauperate) waters. A long-standing tenet in coral reef ecology is that the high rates of production are sustained by high rates of endogenous (internal) cycling (Sargent & Austin, 1949; Pomeroy, 1970; Johannes *et al.*, 1972; Hatcher, 1988, 1990). However, coral reefs are open systems and thus are consistently bathed in water containing oceanic or terrestrial inputs. There has been a substantial amount of research focused on water column dynamics, but much of this work has considered specific components of the water column without necessarily linking them to the broader ecosystem or across systems. A primary reason is the high number of temporal and spatial contexts that exist across photic reef ecosystems – making both investigations of, and generalisations about the water column challenging. Due to these challenges, the role of the water column for the whole reef ecosystem remains largely obscure to researchers, particularly in the context of how water column dynamics mediate ecosystem production.

Odum & Odum (1955) published a seminal study of the coral reefs surrounding Eniwetok Atoll that was among the earliest to quantify ecosystem-level production at the entire-reef scale. This study was among the first to embrace an ecosystem ecology perspective, conceptually reconstructing energy flow through a coral reef ecosystem by identifying where biomass was stored to determine the components of the ecosystem that were most important for driving production. In doing so, they logically focused efforts on the benthic organisms (i.e. corals, algae) that dominated ecosystem biomass. Contributions of larger plankton were observed by the authors, who nonetheless concluded, 'it seems that the reef is indeed energetically self-sustaining and deriving no net gain of larger planktonic material from the in-flowing water' (Odum & Odum, 1955, p. 313). This work set an important precedent for the development of the emerging field of coral reef ecology in that it was one of the earliest studies to highlight the high rates of production within these ecosystems.

Decades later, we now know that in aquatic ecosystems, large amounts of biomass are not needed to support high rates of production, as is typically the case in terrestrial ecosystems where production and biomass are typically correlated (Fig. 1). Because aquatic producers do not invest substantially in supportive structures (e.g. the carbon contained within a tree trunk), nutrients and energy can be reallocated to increase rates of biomass turnover [production (g m^{-2} $time^{-1}$)/biomass (g m^{-2}); Fig. 1], and thus increased production per unit mass (Chapin, Matson & Vitousek, 2011). Although this was not fully evident at the time of Odum & Odum's (1955) study, the idea that biomass does not predict production is now a principal concept of ecosystem ecology (Chapin *et al.*, 2011). Thus while ecosystem ecology was formative for the early development of coral reef ecology as a field (Grigg, Polovina & Atkinson, 1984; Atkinson, 1987; Hatcher, 1988, 1990), an updated and more nuanced ecosystem ecology perspective could benefit the field, particularly if improved understanding of ecosystem production and thus resolving the paradox of production is an ultimate goal.

The water column is the nexus of coral reef ecosystem dynamics, and functions as the interface through which essentially all nutrients (and a large amount of energy) are transferred to fuel both new and recycled production. Thus, while benthic primary production is likely where most production is generated, the water column mediates much of this production, and consequently generates production as well. Improved understanding of the drivers of production in coral reefs has important consequences for society, particularly in this era of rapid global change. The high rates of productivity found in these systems are the basis for many ecological services including: the maintenance of biodiversity, storm protection, carbon sequestration, and fisheries, all of which are at increasing risk from multiple anthropogenic stressors (Micheli *et al.*, 2014; Grafeld *et al.*, 2017; Woodhead *et al.*, 2019). Although a substantial amount of research has been conducted on the water column, the resulting findings are inadequately integrated into perspectives of coral reef functioning and by proxy, conservation and management strategies to stem coral loss.

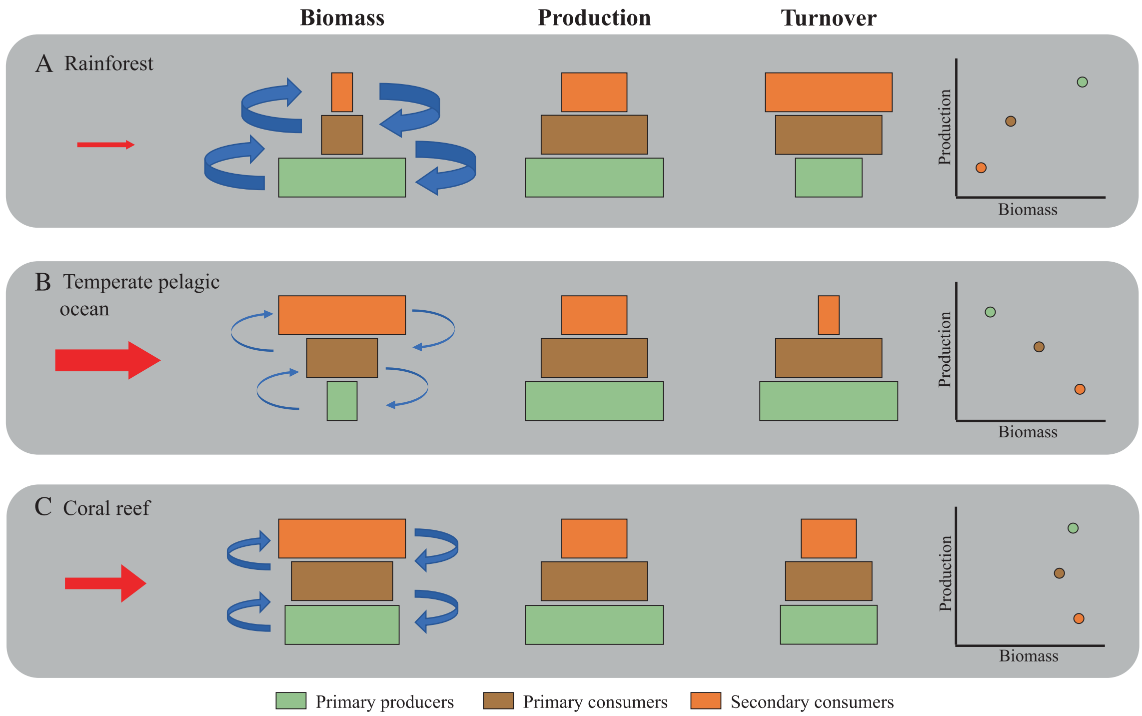

Fig. 1. Conceptualisation of tri-trophic biomass and production pyramids in three ecosystem types: (A) rainforests, (B) temperate pelagic ocean, and (C) coral reefs. Arrow sizes indicate the relative reliance on exogenous inputs (red) and endogenous cycling (blue). Production is held equivalent across systems to facilitate comparison. Turnover, a measure of time calculated as the ratio of production/biomass, is a useful indicator of how rapidly energy is transferred across trophic levels.

(1) Coral reefs from an ecosystem ecology perspective

A common perception in coral reef ecology is that the high rates of productivity within these systems are supported by high levels of endogenous recycling among reef constituents (e.g. coral, macroalgae, invertebrates, fishes) (Sargent & Austin, 1949; Odum & Odum, 1955; Hatcher, 1988, 1990; O'Neil & Capone, 2008). In this way, reefs have long been likened to 'rainforests of the sea' (Pomeroy, 1970, 1974; DeAngelis *et al.*, 1989). This notion is rooted in the idea that reefs, like rainforests, have a large amount of biomass that acts as a reservoir for nutrients that in turn govern productivity rates, i.e. they have high 'nutrient capacity' (DeAngelis *et al.*, 1989; Allgeier *et al.*, 2016). However, rainforests, like most terrestrial ecosystems, are relatively 'closed' systems with long residence times, meaning that the time it takes a given element to cycle through the system is relatively long (DeAngelis, 1992). Closed ecosystems rely on the cycling of endogenous nutrients to support production, here referred to as 'recycled' production (Sargent & Austin, 1949; Hatcher & Frith, 1985), and productivity should increase with faster rates of endogenous nutrient cycling (O'Neill, 1976; DeAngelis *et al.*, 1989). However, in truly closed systems, even at extremely high rates of endogenous recycling, production will ultimately become limited by the ecosystem's nutrient capacity (Smith, 1988; DeAngelis *et al.*, 1989).

By contrast, as the openness of a system increases and residence times decrease, productivity becomes less determined by the rate of endogenous recycling and extent of nutrient capacity, and instead relies increasingly on the rate at which the system can capture and generate new biomass (turnover) relative to the amount of exogenous (external) nutrients entering the system (Pomeroy, 1970; Eppley & Peterson, 1979; DeAngelis *et al.*, 1989; Huxel & McCann, 1998). Take, for example, three fundamentally different ecosystems that are all highly productive despite extreme differences in biomass, openness, and nutrient capacity: tropical rainforests, temperate pelagic oceans, and coral reefs (Fig. 1). On opposing ends of the spectrum: rainforests, which are relatively closed ecosystems with a high nutrient capacity and low exogenous inputs, have high rates of recycled production (Fig. 1A), while temperate pelagic oceans are very open systems with low nutrient capacity (particularly relative to rainforests) and extremely high exogenous nutrient inputs from upwelling that fuels substantial new production (Fig. 1B; Cushing, 1971; Serret *et al.*, 1999). In contrast to both, coral reefs are relatively open systems (Fig. 1C) – receiving much more input from exogenous sources than rainforests, but much less than the temperate pelagic oceans, and have relatively high nutrient capacity. For example, Allgeier, Speare & Burkepile (2018) estimated that at the high end, exogenous nutrient inputs to coral reefs solely in the form of larval fish can replace the nutrient capacity of the entire fish community as rapidly as every 28 days – however in rainforests the replacement time of phosphorus and nitrogen is 1–2 years (Barnes *et al.*, 1998). It is important to note that even though the waters surrounding coral reef ecosystems have small concentrations of nutrients, if this water is delivered to coral reefs at high rates, the cumulative amount of nutrients made available to that reef over time (*via* water flow) can play an important role in supporting reef production.

In coral reef ecosystems benthic processes play critical roles in fuelling recycled production (see Table 1 for definitions of key terms). This production can be augmented by both new and recycled production that is mediated through the water column (Fig. 2). Specifically, water column dynamics contribute to whole-system production *via* three primary pathways: (*i*) new production is generated from the capture of exogenous nutrients or organic matter by photosynthetic and heterotrophic plankton or fishes, respectively; (*ii*) recycled production is fuelled by the consumption of new production (or associated recycled nutrients) that enters the planktonic or benthic food webs; and (*iii*) recycled production is fuelled by production (or associated nutrients) regenerated from the planktonic or benthic food webs (see Fig. 2) (Lewis, 1977). The distinction between *b* and *c* is that recycled production generated from new production (*ii*) only occurs in an open system, whereas recycled production fuelled by regenerated production (*iii*) occurs in both open and closed systems (Hatcher, 1997*b*). Collectively, these processes are driven by three sub-food webs in the water column, herein: *traditional*, *detrital*, and *microbial* (see Section III).

Because of the high degree of context dependence on coral reefs, the relative importance of each sub-food web can vary dramatically across time and space. For example, on Caribbean reefs, endogenous detrital pathways mediated by sponge filter feeding and shedding on coral reefs have been shown to fuel recycled production that is comparable to gross primary production (Hatcher, 1990; de Goeij *et al.*, 2013). By contrast, exogenous pelagic planktonic inputs comprised >70% of the energetic basis for four predator species on reefs in the Maldives (Skinner *et al.*, 2021). In both cases, production is mediated through the water column but *via* substantially different pathways. A fundamental challenge to understanding the extent to which dynamics between microscopic components of the water column influence whole-system productivity is knowing the context during which a given productivity pathway and sub-food web is more prominent.

A substantial focus of past research on water column dynamics has, quite reasonably, been on the more conspicuous parts of the food web, particularly as they pertain to fisheries (Hobson & Chess, 1979; Hamner *et al.*, 1988). This 'traditional' perspective was largely driven by the fact that the more visible organisms, including phytoplankton, mesozooplankton (>200 μm, often referred to as 'net plankton'), and fishes, tended to have higher biomass and thus would be the primary components contributing to the production of fish. From this more traditional perspective, it is reasonable that smaller, less-conspicuous components of the water column have often been neglected. However, constituents within the water column such as bacteria and smaller size classes of plankton (<200 μm) – which are often overlooked by standard net sampling – can still represent an important pathway fuelling production in the water column and benthos. In fact, marine oceanographers have long recognised that the extremely high turnover associated with the 'microbial loop' is a primary driver of production in the oligotrophic ocean, and these microbial pathways are increasingly being studied to identify when and where they represent an important contribution to total reef production (Sargent & Austin, 1949; Sorokin, 1973; Ferrier-Pagès & Gattuso, 1998; Mumby & Steneck, 2018).

Here we use an ecosystem ecology perspective to provide an overarching framework to help generalise the complex ecological, temporal, and spatial contexts that determine the relative importance of water column dynamics for reef production. We do this by first placing water column dynamics within the framework of ecosystem state factors (Fig. 3). As originally described by Jenny (1941), state factors are a set of biotic and abiotic variables that describe external environmental conditions which in tandem control ecosystem structure and processes (Amundson & Jenny, 1997; Chapin *et al.*, 2011). Water column energy dynamics are

Table 1. Glossary of key terms.

Net ecosystem production (NEP)	The total amount of primary production remaining in an ecosystem after accounting for the respiration costs of autotrophs, heterotrophs, and decomposers; NEP = gross primary production (GPP) − ecosystem respiration (ER).
Net primary production (NPP)	The organic matter produced by autotrophs that is available for consumption by heterotrophs. Refers to the amount of primary production remaining after removing the costs of autotrophic respiration; NPP = GPP − $R_{\text{auto.}}$
New production	The generation of organic material through the use of nutrients (or energy) from outside the system.
Primary production	The formation of autotrophic biomass *via* photosynthesis (per unit area per unit time). Autotrophic organisms fix inorganic carbon to synthesise organic matter.
Recycled production	The generation of organic material through the use of nutrients (or energy) recycled among the components of an ecosystem.
Secondary production	The formation of heterotrophic biomass *via* consumption (per unit area per unit time). Consumers ingest organic matter, and the assimilated energy is converted into new consumer biomass.

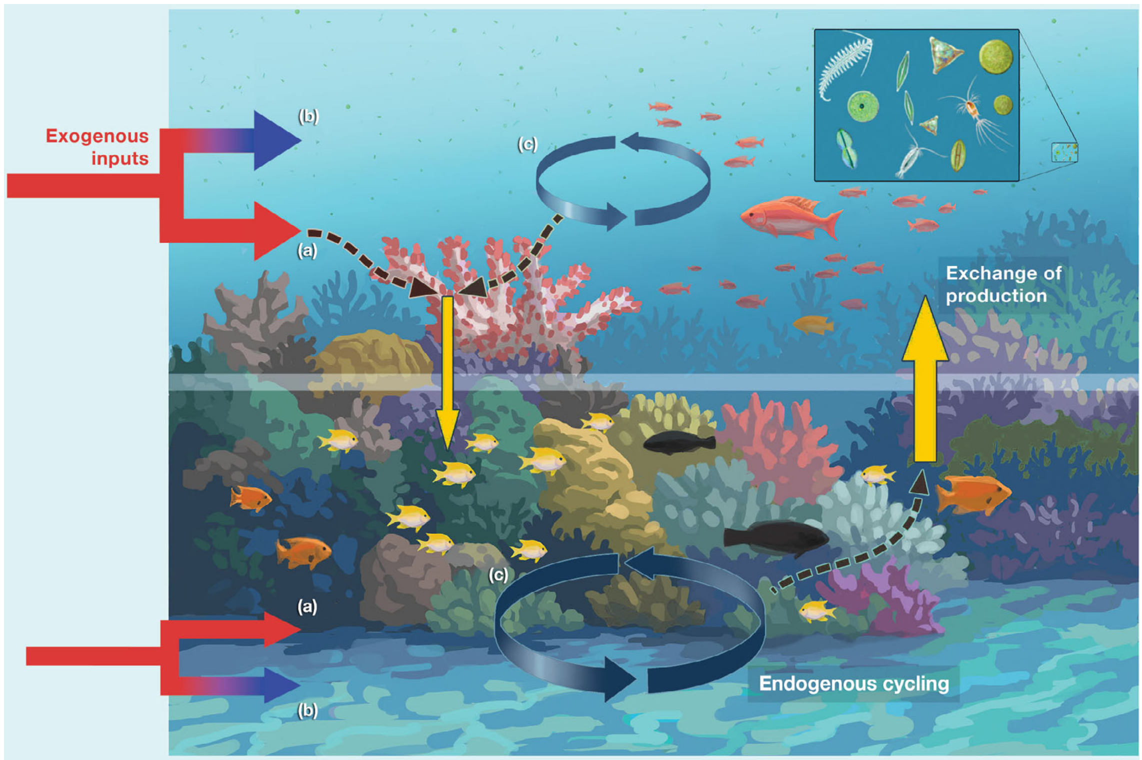

Fig. 2. A coral reef ecosystem identifying inputs that fuel water column and benthic productivity. Exogenous inputs (red arrows) fuel new production while endogenous recycling (blue arrows) fuels recycled production, both supporting total reef production. Three primary pathways describe water column energetic contributions to whole-system production: (a) new production is generated from the capture of exogenous nutrients or organic matter by photosynthetic and heterotrophic plankton or fishes respectively; (b) recycled production is fuelled by the consumption of new production (or associated recycled nutrients generated from waste products from heterotrophs, e.g. remineralization or excretion) that enters the planktonic or benthic food webs; and (c) recycled production is fuelled by production (or associated nutrients) regenerated from the planktonic or benthic food webs. Dashed lines indicate the exchange of materials from each of these pathways to facilitate production between the water column and benthos (yellow arrows). Illustration by John Megahan.

then detailed by explaining how different state factors drive the dynamics of the three sub-food webs – the traditional, microbial, and detrital. We extend this information to show how it can be applied to help improve our understanding of coral reefs of the Anthropocene, and end by detailing four overarching knowledge gaps and challenges for the future. Throughout, we identify areas of research that are currently well studied and those that represent key knowledge gaps, and provide a bibliography of relevant literature as online supporting information (see Table S1).

II. STATE FACTORS

(1) Climate

'Climate' directly governs temperature, precipitation, and light, and is the most influential factor in determining the distribution of ecosystems globally (Chapin *et al.*, 2011). Increasing water temperature is now considered one of the most important sources of coral mortality (Hoegh-Guldberg, 1999; Hughes *et al.*, 2017*a*). It has also been shown to decrease abundance (Richardson, 2008), increase growth rates (Huntley & Lopez, 1992), and alter composition of coral reef planktonic communities (McKinnon *et al.*, 2007). Additional climatic processes such as evaporation and precipitation influence salinity, water levels, and light intensity on shallow reefs (McKinnon *et al.*, 2003; Al-aidaroos *et al.*, 2017) but how these factors interact on biotic processes in the reef water column remains understudied (Coles & Jokiel, 1992; Manuel *et al.*, 2013).

Climate is relatively consistent across tropical and subtropical waters (Stevens, 2012), which results in a weak relationship between net primary production (NPP), light and temperature (Krumhardt *et al.*, 2020) – one that is otherwise strong at higher latitudes (Kleypas, Mcmanus & Meñez, 1999). In the Anthropocene, climate change-driven shifts in localised precipitation, heat, and ocean currents (among others) are playing an increasingly important role in the distribution of coral reefs – e.g. poleward shifts with the tropicalization of temperate marine systems and

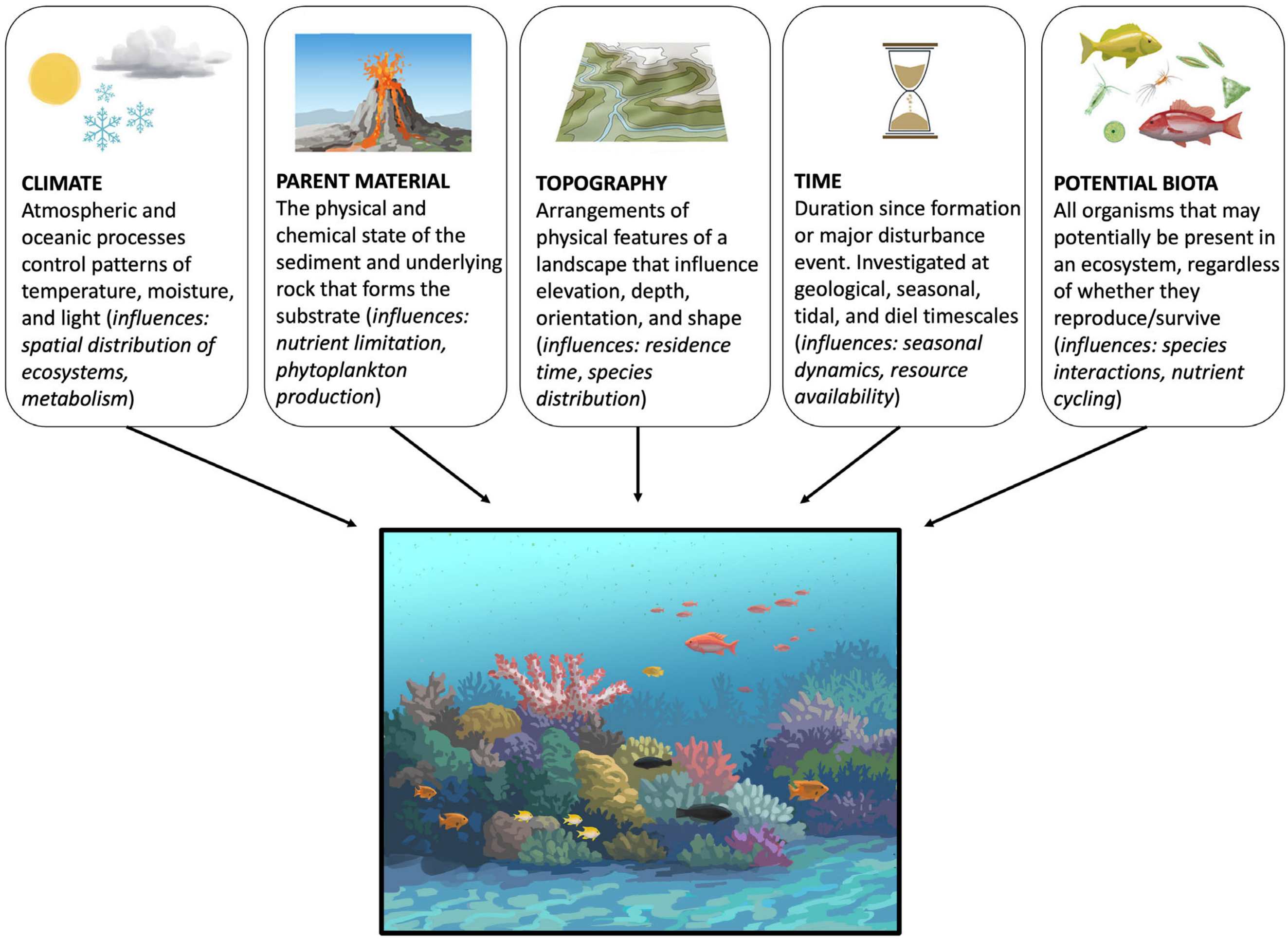

Fig. 3. State factors are a set of five biotic and abiotic variables that together govern the physical composition of an ecosystem (structure) as well as the inputs, transfers, and losses of nutrients and energy across an ecosystem (processes). Illustrations by John Megahan.

increasingly extreme conditions near the equator (Vergés *et al.*, 2014; Storlazzi, Elias & Berkowitz, 2015; Hughes *et al.*, 2017*a*). The effects of climate on coral reef water column energy dynamics are largely unknown, but climate change-associated increases in warming have been shown to increase consumer metabolism and lead to consumer-specific changes in energy use and gain, thus emphasising the extent to which they meditate food web structure and function *via* top-down mechanisms in predictable ways (O'Connor *et al.*, 2009; Lang *et al.*, 2017). Further research is needed to understand the numerous alternative pathways by which warming will alter water column dynamics on coral reefs, for example, indirect pathways such as the influence of bottom-up recycling and enrichment *via* increased metabolism.

(2) Parent material

'Parent material' refers to the physical and chemical properties of the sediment and underlying rocks that form the substrate of a system and influence the availability of nutrients that fuel production. In oligotrophic coral reef ecosystems, parent material has been implicated in driving nutrient limitation of primary production (Littler, Littler & Titlyanov, 1991; Carew *et al.*, 1997; Chapin *et al.*, 2011; Haßler *et al.*, 2019). Coral reefs formed on high volcanic islands tend to be nitrogen (N) limited because of the high phosphorus (P) content of young volcanic rock, and low-lying carbonate islands are typically P limited due to the tendency of carbonate sediments to physically adsorb P (Littler *et al.*, 1991). Such patterns of nutrient availability were found to correlate with nutrient limitation of photosynthesis in nearshore macrophyte communities across a gradient of high to low islands in the Seychelles Archipelago (Littler *et al.*, 1991). Additionally, limitations in N or P driven by parent material are reflected in the nutrient stoichiometry of fish communities (Allgeier *et al.*, 2021), underscoring the potential importance of basal limitations in nutrients for whole-system trophic dynamics and production (Atkinson, 1981). Despite this, no discernible trends in water column nutrient regimes have been found across ocean basins (see review in Dufour *et al.*, 2001). This surprising result highlights an important knowledge gap in our understanding of the mechanisms by which parent material may mediate nutrient limitation and what this might portend for water column dynamics.

Understanding the role that parent material plays in influencing nutrient limitation in coral reef water column food webs is highly relevant in the face of increasing anthropogenic change. Nutrient pollution remains one of the greatest local stressors on coral reefs and can interact with additional climate-change stressors such as bleaching (Donovan *et al.*, 2020). Research to understand the extent to which parent material can predict nutrient limitation would help hone the precision with which conservation efforts can mitigate anthropogenic nutrient enrichment, e.g. wastewater management.

(3) Topography

The 'topography' of the landscape describes the arrangement of physical features in an ecosystem. On coral reefs, the topography of a system is generally classified by the reef formation, i.e. barrier, patch, atoll, or fringing. Within these, the different zones, i.e. forereef, back reef, and lagoon, further describe topographic characteristics. Topography is one of the most significant state factors for photic reefs because, more than any other state factor, it is representative of the relative 'openness' of a system, and thus characterises the potential to which it can be subsidised with exogenous nutrients and energy (Hatcher, 1997*a*). For example, most forereefs are extremely 'open' because they are continually flushed by pelagic subsidies that support the production of water column and benthic communities (Goreau & Goreau, 1973; Heidelberg, Sebens & Purcell, 2004; Hamner, Colin & Hamner, 2007; Morais & Bellwood, 2019).

The terrestrial topography of islands can also influence water column dynamics in various ways. Following large rain events, substantial amounts of terrigenous nutrients and sediments are delivered to coastal waters as a result of a reef's proximity to riverine inputs (Alongi & McKinnon, 2005) and as precipitation runs off steep terrestrial slopes of volcanic islands (Nunn *et al.*, 2016). These impacts can be particularly pronounced following a dry season or drought, resulting in phytoplankton blooms which subsequently fuel new production (Birkeland, 1982). Importantly, the role of topography is among the best-studied state factors for water column dynamics because location on a reef can strongly determine potential influence of exogenous material, thus driving the amount of new *versus* recycled production (Hatcher, 1988; Dufour *et al.*, 2001).

(4) Time

Defined by Jenny (1941) as the duration since ecosystem formation, 'time' highlights how ecosystem creation has shaped its current state, and the potential for ecosystems to reset and recover following major disturbance events (Jenny, 1980). For example, Siqueira *et al.* (2021) showed that a key mechanism driving the biodiversity hotspot in the Indo-Australian Archipelago is its ability to provide a temporally stable habitat that has provided constant exogenous planktonic resources to support planktivores over the past 5 million years. In addition to geological timescales, three more ecologically relevant timescales: seasonal, tidal, and diel, are particularly useful for understanding reef water column dynamics and production. For instance, seasonal upwellings can import 2–6 times the ambient amount of new nutrients to outer reef systems and replace up to a third of the water volume during each intrusion event, creating a tremendous source of new nutrients to fuel reef production (Furnas & Mitchell, 1996). Importantly, such events occur during the summer months when episodic periods of calm winds can increase residence times, allowing the system sufficient time to assimilate these exogenous nutrients fully into the food web. In turn, these nutrients support high rates of new production relative to the winter months when upwelling is weaker, water residence time is lower, and recycled production contributes more to water column (and thus ecosystem) production (Furnas *et al.*, 1990). Similarly, tidal and diel cycles can alter resource availability across the reef at finer temporal scales. Temporal variation in resource supply is one of the most important factors regulating water column dynamics and heightened understanding of these dynamics would greatly improve our understanding of the capacity of the water column to influence production at the reef scale.

(5) Potential biota

The 'potential biota' includes all organisms that have the potential to be present in any given ecosystem (Amundson, 2021). In coral reef ecosystems, consumers mediate important top-down and bottom-up processes, and these processes are strongly driven by the identity of the consumer (Burkepile & Hay, 2008; Allgeier *et al.*, 2016; Brandl *et al.*, 2019). The extent to which potential biota influences water column dynamics often strongly interacts with reef topography because of the habitat preferences of certain species (e.g. Rogers, Blanchard & Mumby, 2014). For example, planktivorous fishes can be found on most reef topographies, but on the forereef where exogenous planktonic subsidies first enter the reef complex, their production can exceed that of all other functional feeding groups, despite their relatively low proportion of total biomass (Morais & Bellwood, 2019). This top-down process can also drive important bottom-up processes such as the transfer of nutrients from the water column (consumption of plankton) *via* excretion that can represent a very important mechanism that fuels new or recycled production on the benthos. For example, zooplanktivorous fishes supply high rates of P (Pinnegar & Polunin, 2006) – an important limiting nutrient for corals – at rates that are disproportionate to their biomass (Allgeier *et al.*, 2014), that in turn enhances growth rates of coral in which they shelter (Holbrook *et al.*, 2008). Importantly, while the role of fish functional groups or species in transferring energy and nutrients that mediate water column production has been relatively well studied, critical knowledge gaps remain about the role of key invertebrate species of molluscs, polychaetes, sponges (but see de Goeij *et al.*, 2013; Lesser, 2006; Mumby & Steneck, 2018), corals (Naumann *et al.*, 2009; Mayer & Wild, 2010) etc., for mediating production *via* water column pathways.

III. WATER COLUMN ENERGY DYNAMICS

State factors interact to mediate the relative temporal and spatial context in which different components of the water column food web contribute to productivity pathways. Here we review the role of the traditional, detrital, and microbial sub-food webs with respect to their relative contributions to autotrophic and heterotrophic production. The role of mesozooplankton is highlighted, as they interface directly with all three sub-food webs and represent a link of energy flow to higher trophic levels. We use state factors to help frame how each sub-food web harnesses exogenous and endogenous resources to produce new and recycled biomass. This framing enables us to identify which trends are generalizable among coral reefs and those that are context dependent.

(1) Traditional food web

The traditional food web has historically been considered the most important energetic pathway supporting fisheries because it directly links autotrophic phytoplankton production to fisheries *via* heterotrophic mesozooplankton (Fig. 4; green arrows) (Ryther, 1969; Davis & Birdsong, 1973; Hobson, 1978, 1991). Specifically, mesozooplankton (>200 μm) are a primary food resource for planktivorous fishes, which in turn support piscivores and other important fisheries species. Historically, mesozooplankton in coral reefs were thought to derive their energy from large phytoplankton (microphytoplankton, >20 μm) such as diatoms (Calbet, 2001), largely based on findings from temperate systems. However, microphytoplankton typically comprise less than 10% of phytoplankton biomass on reefs, suggesting that the smaller sizes of phytoplankton (<20 μm) must also be important in supplementing mesozooplankton energy requirements (Agawin, Duarte & Agustí, 2000; Ferrier-Pagès & Gattuso, 1998; Linley & Koop, 1986; Roman, Furnas & Mullin, 1990; Fig. 4). It is now known that on coral reefs, mesozooplankton additionally rely on resources such as bacteria and small plankton *via* the microbial food web (Agawin *et al.*, 2000; Calbet, Landry & Nunnery, 2001), and on dead organic matter *via* the detrital food web (Marshall, 1965; Gerber & Marshall, 1974; Gottfried & Roman, 1983). However, quantifications of the trophic relationships between mesozooplankton and the various size classes of phytoplankton in reef systems are relatively scarce (Pagano *et al.*, 2012; Dupuy *et al.*, 2016), limiting our ability to understand the extent to which mesozooplankton production is derived from the respective sources. It is known that resource availability is one of the most important drivers of mesozooplankton production, and thus understanding the factors that drive spatial and temporal variation in resources can elucidate the potential for mesozooplankton to support heterotrophic production, including fisheries (Gerber & Marshall, 1982; Pagano *et al.*, 2012; Nakajima *et al.*, 2017).

Nutrient availability is a key constraint on production in this sub-food web. In oligotrophic systems, phytoplankton are small because they need high surface area to volume ratios to increase their ability to take up nutrients – thus reducing their utility as food for mesozooplankton (Ferrier-Pagès & Gattuso, 1998). However, this can reverse with increased nutrient availability – including that from humans – as bigger phytoplankton are observed in areas with more nutrients. Patterns of nutrient limitation largely depend on the physical (topography) and biological (potential biota) properties of the system (Calbet *et al.*, 1996; Pagano *et al.*, 2012). For example, areas along continental shelves that are topographically steep tend to have greater upwelling, bringing exogenous nutrients that facilitate new production of phytoplankton that subsequently fuels zooplankton production (Andrews & Gentien, 1982). Reef topography can also determine residence time and therefore the biota's reliance on the use of recycled nutrients to support recycled production on the reef. Delesalle & Sournia (1992) showed that relatively open atoll lagoons with short residence times did not allow phytoplankton communities to develop due to high flushing rates, whereas increasingly closed atoll lagoons with longer residence times allowed phytoplankton to take advantage of the nutrient pool, leading to increased phytoplankton biomass. Importantly, in cases where there is longer residence time, reef plankton will be primarily fuelled by nutrients recycled from benthic pathways, e.g. excretion from fish feeding on the benthos, or exudates from coral. However, Delesalle & Sournia (1992) also suggested that extensive residence times (>50 days) may result in an overabundance of zooplankton grazing or the exhaustion of nutrients subsequently limiting phytoplankton biomass – although the mechanisms driving this outcome remain poorly understood. In such instances when the autotrophic base of the traditional sub-food web is insufficient to support higher trophic levels, detrital inputs may support total system productivity (Marshall, 1965; Gerber & Marshall, 1974, 1982; Gottfried & Roman, 1983).

(2) Detrital food web

Non-living organic matter, or detritus, is a unique energetic component of the water column in that it does not require energy for its own maintenance, yet it can supply energy to a wide range of consumers (Moore *et al.*, 2004). The detrital sub-food web consists of dead organic matter in particulate and dissolved forms that provide nutrients and energy to mesozooplankton and detritivorous fish (Fig. 4; red arrows). Furthermore, particle-associated microbes process reef detritus and represent a link between the microbial and detrital sub-food webs supporting higher trophic levels (Johannes, 1967;

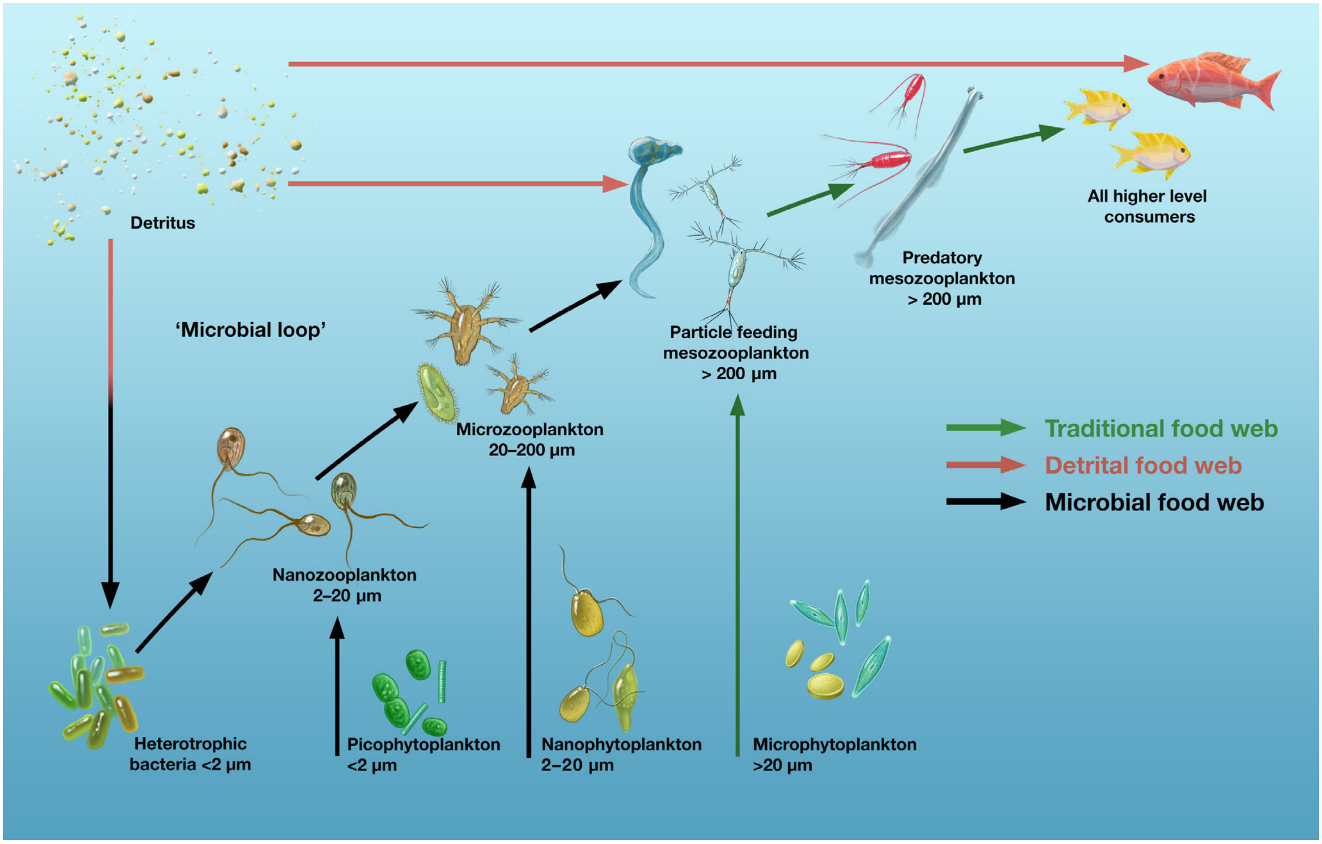

Fig. 4. Three main sub-food webs facilitate the flux of materials within the water column. Mesozooplankton play a key role in joining the traditional (green), detrital (red), and microbial (black) sub-food webs. Illustrations by John Megahan.

Robertson, 1982; Alongi, 1988). Historically, detritus has been recognised for its importance in supporting benthic productivity pathways by providing nutrition to benthic organisms such as corals and filter feeders (Riddle *et al.*, 1990; Hansen *et al.*, 1992), but the inputs and exports of reef detritus remain poorly understood and have yet to be fully quantified.

Reef detritus is an amalgamation of: (*i*) pelagic inputs, e.g. faecal pellets, dead plankton (Robertson, 1982; Hobbie & Williams, 1984; Moore *et al.*, 2004); (*ii*) benthic recycling, e.g. algal exudates, coral mucus, and sponge pseudo-faeces (Gottfried & Roman, 1983; de Goeij *et al.*, 2013); and/or (*iii*) terrestrial inputs, e.g. runoff and groundwater discharge (Alongi & McKinnon, 2005; Hu *et al.*, 2015). It tends to concentrate in areas that have high exogenous input of these resources and/or long residence time, such that detritus is not flushed from the system. For example, Gerber & Marshall (1974) found particulate organic carbon in reef zones with relatively long water residence times just inshore of the Eniwetok Atoll lagoon to be 25.75 mg C/m^3 and 20.40 mg C/m^3 in the mid-lagoon; over twice that of the average for the open surrounding ocean, ($\sim$10 mg C/m^3). Importantly, detritus does not typically have long residence time in the water column, and detrital sinking contributes directly to benthic production (Sakka *et al.*, 2002). However, processes such as hydrological turbulence or bioturbation from animals (Williamson *et al.*, 2021) can resuspend detrital particles and/or nutrients from the microbial remineralization of detrital particles, making them available to planktonic heterotrophs and autotrophs, respectively (Russell-Hunter, 1974; Ullman & Sandstrom, 1987). Gerber & Marshall (1974) found detrital algal fragments of benthic origin in the guts of planktivorous fishes and zooplankton at Eniwetok Atoll, demonstrating the importance of detritus as a basal resource for the water column food web in a semi-enclosed lagoon. This idea is supported by the fact that mesozooplankton production has been found to be supported by highly selective feeding on specific detrital particle types and phytoplankton species, additionally highlighting how the potential biota of a given reef can also determine the relative importance of the detrital sub-food web for ecosystem production.

Importantly, the detrital sub-food web is largely associated with recycled production and has been well studied with respect to the role that sponges and coral contribute to both recycled and overall reef ecosystem production (de Goeij *et al.*, 2013; Rix *et al.*, 2016). The 'sponge loop' describes a process by which sponges take in dissolved organic matter (DOM), have rapid tissue turnover, and lose biomass in the form of particulate organic matter (pseudo-faeces) which is often returned back to the water column as detritus (Richter *et al.*, 2001; de Goeij & Duyl, 2007; de Goeij *et al.*, 2013; Rix *et al.*, 2016). While DOM in the water column is also available to bacterioplankton (microbial sub-food web, see Section III.3), sponges can remove the same amount of DOM in 30 min as bacterioplankton would consume in 30 days (de Goeij *et al.*, 2013). Ambient nutrient and energy availability such as that from coral mucus also represents a critical component of the detritus that supports the 'sponge loop' and illustrates an important transfer of energy from benthic production through the water column – up to 40% of the carbon ingested and photosynthetically fixed by coral colonies is released as mucus (Crossland, Barnes & Borowitzka, 1980; Wild *et al.*, 2004; Tanaka *et al.*, 2008; Archer *et al.*, 2017). Physiological differences among species of corals (Richman, Loya & Sloboclkin, 1975; Goldman, 1984; Tanaka *et al.*, 2008) and sponges (Hansen *et al.*, 1992) can result in large differences in their relative contribution to the detrital pool. For these reasons, differences in topography and potential biota (across ocean basins in particular) can strongly influence the relative importance of the detrital sub-food web for coral reef production. For example, Wilkinson & Cheshire (1990) found that sponges on the outer shelf and oceanic reefs of Belize consumed 4–6% of the estimated gross primary productivity for an average coral reef, whereas sponges in these same areas of the Great Barrier Reef only consumed 0.1–0.5% of this primary production. Differences in the magnitude of consumption of primary production by inner shelf sponges were less striking between the two regions. Furthermore, the specific sponge microbial biota plays a role in determining the trophic niche of sponges and controls the detrital products that are ingested from and excreted back into the water column (Freeman, Easson & Baker, 2014; Morganti *et al.*, 2017). The resulting differences in detrital material and energetic pathways among species and ocean basins are not well understood, but in all coral reef systems microbes play an important role in further remineralizing detritus to produce labile resources that are more easily exploited to fuel production.

(3) Microbial food web

The microbial sub-food web contains bacteria and small size classes of plankton and consists of a relatively high number of trophic linkages (Fig. 4; black arrows). Within this sub-food web is the 'microbial loop' whereby DOM is recycled and retained among viruses, bacteria, flagellates, and microzooplankton (Azam *et al.*, 1983; Silveira *et al.*, 2017). Microbial biomass makes up only a small portion of total biomass on the reef due to the characteristically small size of bacteria, pico-, and nanophytoplankton, heteroflagellates, and microzooplankton. However, their small size and high metabolism allows for the rapid turnover of the microbial biomass pool leading to high rates of nutrient remineralization (Azam *et al.*, 1983; Armengol *et al.*, 2019) and high production (Pomeroy, 1974; Furnas *et al.*, 2005) which can fuel higher trophic levels. For example, grazing of autotrophic and heterotrophic production in the microbial food web by larger size classes of zooplankton such as mesozooplankton links the microbial sub-food web with the traditional and detrital sub-food webs (Fig. 4). Thus, while the large number of trophic transfers means that energy transfer is relatively inefficient due to energetic losses with each transfer (Lindeman, 1942), turnover rates are sufficiently high still to support substantial net energy transfer (Ferrier-Pagès & Gattuso, 1998). These small size classes, specifically picoplankton, are abundant in oligotrophic waters surrounding coral reefs and have been shown to be a major resource for reef benthic communities *via* water column pathways (Houlbreque *et al.*, 2006; Bell, 2008).

Trophic interactions between microbial biota along with their grazers and predators remain poorly resolved and likely differ across reef ecosystems due to environmental factors unique to each reef (Wyatt *et al.*, 2010). The residence time of water over the reef can determine how DOM, a basal resource, is incorporated into the microbial sub-food web by controlling its interaction time with microbes. This is seen on certain reef topographies on the Great Barrier Reef where the water column has prolonged and immediate contact with benthic reef communities, such as the reef flat, which exhibits high bacterioplankton productivity (9.3–38.5 mg C m^{-3} day^{-1}) compared to the surrounding open ocean (17.6–20.2 mg C m^{-3} day^{-1}) (Moriarty, Pollard & Hunt, 1985; Sorokin, 1995). Additionally, tidal time scales flush new sources of organic matter and bacteria from the reef flat onto adjacent reef zones, and when these areas have high residence time such as lagoons, it has been shown to increase bacterioplankton productivity further to 21.8–68.0 mg C m^{-3} day^{-1} (Sorokin, 1995). By contrast, a fringing reef in Moorea with short residence time and negligible tidal influence showed reduced bacterioplankton concentrations when compared to surrounding oceanic waters (Nelson *et al.*, 2011), further suggesting benthic reef communities are a major contributor to microbial production in the water column. Due to the critical role bacteria play in linking the detrital and microbial sub-food webs, additional research is needed to quantify bacterioplankton's reliance on endogenous *versus* exogenous forms of particulate organic matter (POM) and DOM, especially across time and space.

Insight into the production of microorganisms may become increasingly important for understanding ecosystem-level production on coral reefs of the Anthropocene as reefs undergo phase shifts with macroalgae, urchins, or sponges dominating following coral declines (Norström *et al.*, 2009). As humans remove vast amounts of fish biomass through overfishing and microbes take advantage of increased algal DOM, coral reef energy budgets are becoming less dominated by fishes and more by microbes, making microorganisms the primary movers of energy in degraded reefs (McDole *et al.*, 2012). This shift can lead to less-efficient metabolic pathways with higher turnover relative to the hyper-efficient pathways on coral-dominated reefs (Haas *et al.*, 2016). A key knowledge gap that will improve our understanding of the potential transition to microbially dominant reef production is the temporal dynamics of microorganisms in the water column, particularly those that occur on short time scales (daily, tidal, diel, etc.). Such information may provide insight into the effect of disturbances on the balance of water column–benthic coupling, as well as the availability and flow of materials up successive trophic levels in the reef system.

IV. CORAL REEFS OF THE ANTHROPOCENE

Humans are modifying all of the aforementioned state factors (with time being philosophically debated as we tend to speed up processes) with clear consequences for coral reef ecosystems (Hoegh-Guldberg *et al*., 2007; Hughes *et al*., 2017*a*,*b*). Typically, human-induced changes in coral reef systems are considered for their effects on benthic processes, particularly in light of shifts from coral- to macroalgal-dominated reefs (McManus & Polsenberg, 2004; Hughes *et al*., 2007). Overfishing, terrestrial-based pollution, and increasing storm frequency and intensity are three of the most salient anthropogenic stressors that are given particular attention for their effects on the coral reef benthos. Here we focus on these three stressors to illustrate ways in which their impacts on coral reefs are fundamentally mediated through the water column. We acknowledge that this discussion is not comprehensive and that numerous additional stressors influence whole-reef dynamics (e.g. bleaching events and disease).

Overfishing has led to the widespread removal of animal biomass from coral reefs with direct consequences for the nutrient capacity and thus nutrient and energy dynamics of coral reefs. Harvesting fish or invertebrate biomass reduces the rate at which nutrients are recycled within coral reefs *via* reduction in excretion, but also reduces the rate at which exogenous sources of nutrients and energy can be captured from the water column. For example, fishing pressure on Caribbean reefs has been shown to reduce the storage and the supply of nutrients by fishes *via* excretion by nearly half (Allgeier *et al*., 2016). Because a system that has been reduced to low biomass levels has lower internal nutrient and energy recycling, reefs that suffer massive overfishing will be more dependent on exogenous sources of nutrients and energy to rebuild fish biomass (O'Neill, 1976), i.e. reefs with less exogenous nutrients will be expected to recover much more slowly. Indeed, Cinner *et al*. (2016) show that 'Bright Spot' reefs, i.e. those that have higher fish biomass than predicted, tend to be more associated with deep water (due to their topography) – suggesting a higher likelihood of increased exogenous inputs – although these deeper reefs may also provide refugia from fishing efforts (Lindfield *et al*., 2016). These changing dynamics can be exacerbated by fishing efforts that target organisms that capture exogenous inputs from the water column. For example, overharvest of bivalves on Pacific reefs can substantially reduce water column–benthic linkages (Gaertner-Mazouni *et al*., 2012).

The traditional and microbial food webs are expected to be most affected by fishing because of the importance of nutrients supplied by consumers for fuelling recycled phytoplankton and microbial production. The detrital food web would also be altered *via* a reduction in detrital material provided by egestion and decrease in 'sloppy feeding', by the lack of resuspended material from bioturbation (Vanni, 2002; Williamson *et al*., 2021), and reduction in faeces which provide essential nutrients and can fuel microbial production (Meyer & Schultz, 1985; Rothans & Miller, 1991; Wotton & Malmqvist, 2001). As such, in the context of implementing restoration or management regimes to rebuild coral reef fisheries, the reef's potential biota should be considered whereby management should focus on efforts that promote the success of zooplanktivorous fishes that both capture nutrients from, and supply nutrients to the water column, as well as those organisms that play important roles in bioturbation and detrital resuspension, e.g. detritivorous fishes such as acanthurids. Additionally, reef topography should be a focal area of consideration because increased exogenous inputs should promote faster rebuilding of fish biomass e.g. forereef systems receiving oceanic inputs.

Terrestrial-based pollution has been among the longest-cited stressors to coral reefs (Olafson, 1978; Fabricius, 2005). Terrestrially derived nutrients and organic matter can originate from industrial, agricultural, and municipal sources and impact coral reefs through runoff, fluvial inputs, and rainfall. A recent phenomenon gaining attention is the formation of dead zones on coral reefs – areas of hypoxia resulting from microbial respiration of POM produced by algal blooms that occur in response to terrestrial nutrient input (Diaz & Rosenberg, 2008; Altieri & Diaz, 2019). Coral reef ecosystems deviate from typical conditions in which dead zones proliferate, but Altieri *et al*. (2017) found that reef topography was a key driver in the distribution of dead zones. Specifically, the nearshore habitats with high residence times and low exchange with the open ocean allow for the stratification of the water column, and prevent the vertical mixing needed to reoxygenate the benthos (Altieri & Diaz, 2019). To date, the extent to which coral reef dead zones influence water column dynamics is not fully understood, but without question, dead zone-associated microbes and organic matter have substantial implications for the detrital food web.

Dead zones can be exacerbated by climate patterns that promote water column stratification by increased rainfall and high temperatures (Diaz & Rosenberg, 2008). For example, Lecchini *et al*. (2020) observed dead zones occurring in Bora Bora following a climatic anomaly in which heavy precipitation and increased water temperatures led to the proliferation of bacteria and phytoplankton, creating hypoxic conditions and mass mortality of corals, benthic macroinvertebrates, and resident fish species. With similar climatic conditions projected to become more common across reefs, hypoxic conditions and dead zones may become common as opposed to extreme occurrences. Management practices should focus on routine monitoring of water quality across reef zones coupled with an increased understanding of nutrient limitation of the water column phytoplankton communities – all of which could be informed by improved understanding of the linkage between parent material and nutrient limitation. Additionally, the use of plant species such as seagrass (Fourqurean & Zieman, 2002) and macroalgae (Donovan *et al.*, 2020) as proxies for ambient nutrient conditions could be incorporated into monitoring efforts. Further monitoring efforts could be coupled with weather tracking whereby nutrient input restrictions would be increased when conditions are most apt to lead to dead zone formations.

The intensity of tropical storms (i.e. cyclones and hurricanes) and frequency of the most intense storms, is projected to increase within the century (Knutson *et al.*, 2010, 2020; Masson-Delmotte *et al.*, 2021). Such destructive events can destroy entire reefs, resulting in a loss of benthic biomass and causing drastic changes to the underlying topography. Reef-building corals create the three-dimensional structure of the reef, without which the available habitat for biota is reduced, also lowering the nutrient capacity of the system (Rogers, Blanchard & Mumby, 2018). Immediately following destructive storm events, terrestrial runoff and suspended benthic sediments substantially increase the amount of detritus and nutrients in the water column which can fuel water column primary production (Harmelin-Vivien, 1994). Following a large storm event in Hawaii, phytoplankton blooms led to a spike in standing zooplankton crop and nitrate levels which took a month to return to normal pre-storm levels (Jokiel *et al.*, 1993). This increase in plankton limited light from reaching corals and favoured filter-feeding benthic organisms such as bivalves and sponges, altering water column energetic pathways and benthic–pelagic coupling compared to an undisturbed reef system. Additionally, the temporal extent of stressors is known to be a critical factor of mortality for coral (e.g. Connell, Hughes & Wallace, 1997; Hughes *et al.*, 2017*b*). Management efforts should prioritise monitoring temporal water column changes (i.e. before and after) destructive storm events to inform post-storm recovery and improve management efficacy.

V. KNOWLEDGE GAPS FOR MANAGEMENT AND CONSERVATION

Ecosystem production is a process that integrates essentially all functions and services that ecosystems provide to humans. Incorporating a better understanding of the role that water column dynamics play in mediating ecosystem production could improve our ability to manage coral reef ecosystems effectively. Here we highlight four key knowledge gaps associated with coral reef water column dynamics that should be prioritised.

(1) Characterising the extent to which exogenous subsidies support reef production

A food web that is supported by large amounts of exogenous inputs should rebuild at a faster rate after losses in nutrient capacity, e.g. overfishing, than one that is not (O'Neill, 1976). This theoretical assumption, if supported, would provide a very practical basis for determining where and when conservation efforts to rebuild ecosystems should be focused. However, our understanding of the extent to which this occurs on coral reefs is limited. Recent research has shown that planktivorous fish feeding from the water column represented a disproportionate amount of reef fish production relative to their biomass, but the extent to which this production was derived from new or recycled production remains unclear (Morais & Bellwood, 2019). Recent advances in the use of compound-specific stable isotope analysis (CSIA) provide a powerful tool that can allow consumers' basal resources to be identified with high level of specificity (McMahon *et al.*, 2016). In a recent study using CSIA, Skinner *et al.* (2021) showed that ~75% of the energetic base for four coral reef predators was derived from off-shore subsidies. Applying such techniques to understand the energetic or nutrient basis of the whole community, including coral, other invertebrates, and primary producers, will vastly improve the efficacy by which conservation and management efforts can capitalise on attributes of reefs to increase their capacity to capture and incorporate exogenous materials and thus rebuild the food web more quickly.

(2) Understanding the importance of parent material for coral reef productivity

Because primary production is often limited by the availability of nutrients, understanding how nutrient availability is regulated within an ecosystem is essential for effective management of nutrient pollution (Conley *et al.*, 2009). Littler *et al.* (1991) identified parent material for regulating nutrient limitation by relating patterns of N and P limitation to benthic macroalgal production across carbonate and granitic geologies; however, how parent material influences water column productivity was not investigated. The potential detrimental impacts of nutrient pollution for coral reefs is fully evident, but the mechanisms by which this occurs remain underdeveloped and thus limit management efforts and efficacy (Szmant, 2002). Prioritising efforts to understand the relationship between parent material and water column and benthic nutrient limitation has the potential to greatly improve our ability to predict which nutrients limit primary production and thus to improve our ability to manage wastewater input into these stressed ecosystems.

(3) Improved spatial and temporal resolution of water column constituents

The rapid increase in modelling power and capacity should be leveraged to understand and predict water column and whole-system reef production. But caution is needed when robust empirical data are limited. Primary data gaps in water column dynamics are associated with a lack of spatial and temporal resolution – specifically, how the composition of water column constituents, including planktonic species and DOM, POM, and inorganic and organic nutrients, vary across space and time. For example, water column sampling historically has been dominated by net plankton tows that overlook the smaller size components within the water column, thought to be more important for driving water column production. More studies are needed across diverse locations, and importantly at higher temporal resolution, if we hope to: (*i*) identify the general, and the context-dependent factors that determine water column composition; and (*ii*) begin to establish how water composition influences water column productivity.

(4) Increase frequency and diversity in locations of ecosystem-level measurements on coral reefs

Ecosystem-scale measurements (e.g. ecosystem metabolism, CO_2 flux, O_2 production, nutrient-uptake rates) allow for a comprehensive approach to understanding ecosystem function that is inclusive of all state factors (Carpenter *et al.*, 1995). The historical precedent for ecosystem-scale experiments and observations on coral reefs (e.g. Atkinson, Falter & Hearn, 2001; Hatcher, 1990; Lewis, 1977), has been waning over the past few decades, but with increases in technological advances in water sensors, particularly an improved ability to measure eddy covariance (measuring O_2 concentrations over a three-dimensional velocity field with a high-resolution amplifiers), there has been a substantial recent increase in studies (e.g. Berg *et al.*, 2022; Long *et al.*, 2013; Mackellar & McGowan, 2010; Yamamoto *et al.*, 2015). These highly integrative measures are revolutionising our ability to take ecosystem-scale measurements on coral reefs. Increasing the diversity in location and frequency in time at which measurements are conducted will (*i*) greatly improve our understanding of emergent ecosystem properties of coral reefs, (*ii*) allow for the assessment of overall ecosystem health that could be used in management similar to an indicator or warning signal (e.g. Carpenter *et al.*, 2011), and (*iii*) be used as a basis by which to implement adaptive management strategies at local, temporal, and spatial scales that are most relevant to conservation (Cinner *et al.*, 2020). We argue that harnessing technological advances in monitoring ecosystem-level dynamics on coral reefs that is inclusive of water column dynamics is essential for making the needed advances to stem global coral reef degradation.

VI. CONCLUSIONS

(1) The water column is the nexus of coral reef ecosystem dynamics, functioning as the interface through which a substantial proportion of energy and nutrients are transferred to fuel both new and recycled production. Historically, studies have focused on specific components of the water column without linking these findings to the broader ecosystem, likely due to dynamics of the water column being heavily context dependent. While there is an increasing awareness of the importance of water column dynamics for ecosystem services like coral reef fisheries (Morais & Bellwood, 2019; Skinner *et al.*, 2021), this line of thinking remains peripheral to the typical perception of coral reefs.

(2) The past decades have seen a re-emergence of ecosystem ecology particularly with an emphasis on its application for conservation and sustainability (Liu *et al.*, 2015). This allows for a holistic approach that is inclusive of the physical, chemical, and biological variables that regulate ecosystem processes.

(3) We stress that basic ecosystem ecology principles including the simplistic state factor framework presented herein can help identify generalities about how coral reefs mediate production, and when and where these dynamics are spatially and temporally context dependent.

(4) Within the water column, the traditional, detrital, and microbial sub-food webs take in and recycle nutrients and energy, allowing for the exchange of resources and production with the benthos and outside systems. Synthesising these dynamics as they are shaped by various state factors allows for trends to be identified as generalizable and context dependent.

(5) Broadening the study of coral reefs beyond benthic dynamics to include water column dynamics is imperative to understand coral reef ecosystem production under global change scenarios. We argue that doing so will effectively enhance our ability to generate the novel management and conservation solutions needed to mitigate the rapid demise of these globally important ecosystems.

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IX. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Table S1. Details of 84 select references pertaining to water column dynamics of tropical coral reef systems.

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