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Organic carbon cycling in a Caribbean coral reef

Hidden biomass, sneezing sponges, and net heterotrophy

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Chapter

1

Introduction

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GENERAL INTRODUCTION

“People say to me ‘Are you looking for the ultimate laws of physics?’ No, I’m not. I’m just looking to find out more about the world. And if it turns out there is an ultimate law that explains everything, so be it. That would be very nice to discover. And if it turns it’s like an onion with millions of layers, and we’re just sick and tired of looking at the layers, then that’s the way it is. But whatever way it comes out, its nature is there and she’s going to come out the way she is. And therefore, when we go out to investigate it, we shouldn’t pre-decide what it is we’re trying to do except to find out more about it.”

—Richard P. Feynman

If we were to regard a coral reef as an onion, its number of ecological layers would be seemingly endless, from the biosynthesis of molecules to numerous interactions within and between holobionts to global-scale drivers of reef ecosystem dynamics. Attempts to quantify and describe the biogeochemical complexity of coral reef ecosystems and the communities found in them can be demanding. Yet, it is of utmost importance to investigate coral reefs and the natural world in general. The charismatic words of theoretical physicist Richard P. Feynman fueled my curiosity about nature and gave me a sense of purpose in light of the current coral reef crisis, the fear that coral reefs might disappear from our planet in a single lifetime (Bellwood et al. 2004). In contrast to the laws of physics, the ecology of coral reefs changes in response to alterations of their environment. In Feynman’s analogy, we are shaping the “onion” as we investigate it. The important roles of species and biogeochemical interactions that were once thought to shape coral reefs are now questioned (Mumby and Steneck 2008), whereas new processes and phenomena have been discovered as drivers of present-day reef communities (e.g., de Goeij et al. 2013). The quantification of historic and newly discovered processes that characterize resilient coral reef communities in field surveys, controlled experiments, and ecosystem models represents a promising avenue to formulate a deeper understanding of coral reefs and how they develop in the future.

Changing paradigms in coral reef ecology

Coral reefs are among the most diverse and productive ecosystems on Earth (Paulay 1997; Reaka-Kudla 1997; Roberts et al. 2002). They form biological structures large enough to be visible from space (Madin et al. 2019), in waters that contain almost no food (Muscatine and Porter 1977). The high biodiversity and abundance of organisms on coral reefs is therefore often compared to an “oasis in a marine desert” (Polovina 1984; de Goeij et al. 2017). The community that occurs in this oasis is characterized by high rates of photosynthesis-driven gross primary

productivity (GPP or P) (Kinsey 1985; Hatcher 1988) and the efficient recycling of organic matter by numerous heterotrophs (Kinsey 1983). Total rates of community respiration (R) typically match GPP, which is commonly expressed as a P:R ratio close to one. This indicates little to no excess production or imports of organic carbon and a relatively stable amount of standing biomass through time (Margalef 1974; Hatcher 1990; Crossland et al. 1991).

According to one of the earliest and most comprehensive assessments of the biomass distribution of a reef community (Odum and Odum 1955), primary producers (e.g., corals, macroalgae) accounted for the vast majority of the standing biomass, providing sufficient food to sustain relatively smaller stocks of a diverse range of heterotrophic organisms including herbivores, detritivores, carnivores and omnivores (e.g., fish, motile invertebrates). The exceptionally high diversity of taxa and their nutritional strategies was suggested to provide functional redundancy in the reef community (Lawton 1994), contributing to the continuation of critical processes (e.g., productivity and resource retention) when community composition changed due to external disturbances (e.g., hurricanes, disease outbreaks) (Elmqvist et al. 2003; Nyström 2006). For example, increased primary productivity by turf algae and macroalgae can sustain preexisting amounts of grazer biomass during a temporary reduction in coral abundance following the passing of hurricanes (Gardner et al. 2005; Davis et al. 2021). During the process of feeding, grazers create open substrate to which coral larvae from adjacent reefs can attach, enabling the recovery of local coral populations (Mumby et al. 2007). Due to functional redundancy and high productivity, coral reefs have long been regarded as highly resilient ecosystems capable of withstanding almost any environmental perturbation (Carpenter 1981; Hughes and Jackson 1985).

The paradigm of reefs being “exceptionally resilient” has changed, however, as modern reefs often no longer display the post-disturbance recovery that typified them in the past (Mumby and Steneck 2008). A continued decline of coral abundance and coral reef growth has been reported for many locations around the world in response to a variety of human activities (Gardner et al. 2003; Sweatman et al. 2011; Cornwall et al. 2021; Reverter et al. 2022). Coral reefs are particularly sensitive to ocean acidification and prolonged, unusually high seawater temperatures as a consequence of rising atmospheric CO₂ levels (Walther et al. 2002; Cornwall et al. 2021), but also lack tolerance to local disturbances, such as overfishing and various forms of seawater pollution (Nyström et al. 2000). It has become clear that all such forms of unprecedented stress on modern reefs have contributed to changes in the composition of reef communities, whereby reef-building corals and coralline algae become replaced by fleshy algae, gorgonians, and sponges, and the abundance of (pathogenic) microbes increases (Gardner et al. 2003; Jackson et al. 2014; Haas et al. 2016). This degradation of reefs can result

in the loss of important ecological services, such as coastal protection and food production, to millions of people and many associated ecosystems that directly depend on these services (Moberg and Folke 1999; Burke et al. 2011; Guannel et al. 2016; Rivera et al. 2020). Solutions to stop or reverse reef degradation align largely with current efforts to reduce greenhouse gas emissions or implement local management interventions to lower the impacts of fishing and coastal construction. Yet, the question remains how we can best manage and restore these ecosystems as long as we do not fully understand the biological processes that mediate environment-driven alterations in the composition and function of reef communities.

Structural shifts towards more opportunistic taxa have likely produced an entire new web of ecological relationships on modern reefs, whereas at the same time historically important relationships could become less important. Examples of historically important ecological processes that no longer function effectively on degraded reefs around the world include the breakdown of nutrient exchange between corals and their photosynthetic endosymbionts (Wilson et al. 2006; Knowlton and Jackson 2008) or the reduced abundance and number of herbivorous species that can no longer prevent algal overgrowth of corals (Aronson and Precht 2000; Micheli and Halpern 2005; Mouillot et al. 2014). On the contrary, increasingly relevant processes shaping modern reef communities include higher production and consumption of detritus (Wilson et al. 2003; Mumby and Steneck 2018) and increased abundances of bacterioplankton growing on macroalgal exudates (Haas et al. 2011). All these changes in reef community composition and functioning raise the question to what degree modern coral reefs are still metabolically balanced ($P:R = 1$) and whether primary producers are still able to meet the carbon demand of local heterotrophs, i.e., whether reefs are still self-sustaining (Bar-On et al. 2018; van Heuven et al. 2018; Woodson et al. 2020; Webb et al. 2021). Further, it is unclear to what extent species interactions alter the balance between GPP and R, and also the rates of resource retention on present-day and future coral reefs are largely unknown (Kennedy et al. 2013; McWilliam et al. 2020; Nagelkerken et al. 2020).

Investigating the relationship between coral reef community composition, community metabolism, and organic matter cycling would supplement the traditional views on these topics outlined earlier. Historic frameworks of reef functioning relied heavily on primary productivity and herbivory, whereas the roles of then understudied, but now more abundant reef taxa (e.g., sponges, microbes) or food sources (e.g., dissolved organic carbon, detritus) were not often considered. We now know, for example, that corals and benthic macroalgae release large proportions of their photosynthetically acquired carbon as mucus (Wild et al. 2004b; Brown and Bythell 2005) and dissolved organic matter (DOM) (Naumann

et al. 2010a; Mueller et al. 2014b). When DOM is retained in the system, it becomes available to suspension feeders and detritivores after its initial uptake by bacterioplankton (in a process called the “microbial loop”) (Azam et al. 1983; Ferrier-Pagès and Gattuso 1998; Nelson et al. 2013) and by sponges (the “sponge loop”) (de Goeij et al. 2013; Maldonado 2016; de Goeij et al. 2017; Rix et al. 2017). The extent to which e.g., the sponge loop contributes to overall reef metabolism is difficult to assess as sponges are foremost abundant in cryptic habitats (e.g., caves, crevices, overhangs) that are not considered in standard protocols for surveying benthic community composition. The cryptic surfaces within reef communities account for large areas of colonizable surface (up to 8 m² under each projected m² of reef) (Choi and Ginsburg 1983; Ginsburg 1983; Richter et al. 2001; Scheffers et al. 2004) that are predominantly occupied by sponges (Jackson and Winston 1982; Wunsch 1999; de Goeij and van Duyl 2007). The possibility that organic carbon is retained within reef communities through the sponge loop and that reef areas traditionally not surveyed might hold enormous amounts of sponge biomass further illustrate how relevant questions remain on the intrinsic metabolic behavior of reef communities. Thus, there is a need for more in-depth analyses of carbon flows on reefs considering previously neglected aspects such as cryptic reef communities and DOM cycling.

In addition to their function (e.g., DOM production and uptake), the abundance of individual taxa or species groups will determine which trophic and ecological relationships are foremost responsible for shaping coral reef communities. Abundances of benthic organisms are traditionally estimated as the percentage cover of the projected reef substrate (i.e., the covered area as seen from above) by each species or species’ group (Kohler and Gill 2006). While these 2D-photo surveys represent an easy tool to generate simple estimates of “reef health” (e.g., coral versus macroalgal cover), they do not capture the abundance of organisms in cryptic habitats (Hatcher 1990; Yahel et al. 1998; Bell 2008; Haas et al. 2011; de Goeij et al. 2013) nor the abundance (in terms of biomass) of erect reef organisms (Goatley and Bellwood 2011). Rather than using 2D projections, true estimates of the biomass of all taxa that are present within a 3-dimensional reef matrix can generate more accurate estimates of the metabolic flows within reef communities (Diaz and Rützler 2001; van Oevelen et al. 2006).

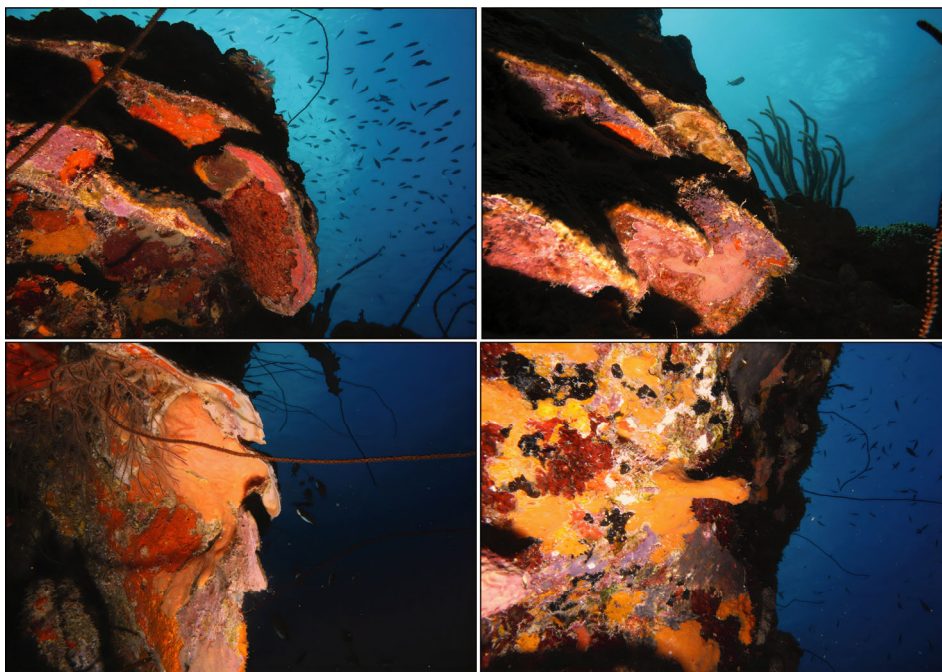


Figure 1. Examples of low-light reef surfaces colonized by cryptic communities and almost exclusively dominated by encrusting sponges.

How (much) do sponges retain organic carbon?

Marine sponges come in many morphological shapes, from bio-eroding sponges that bore into the reef substrate, to thin encrusting sponges forming mm- to cm-thick tissue layers covering the substrate (Figure 1), to massive sponges that grow upward and form balls, barrels, tubes, rope-, or vase-shaped bodies reaching up to several meters high (Wulff 2001). All sponges actively channel seawater through their bodies. Water enters via small pores (ostia) on their outer surface, moves through channels inside the sponge, and exits through outflow openings (oscula) that are much larger than the ostia. Seawater is processed as it flows through the sponge's internal canal system, leading to the depletion of plankton (Pile et al. 1996; Ribes et al. 1999) and DOM (Yahel et al. 2003; de Goeij et al. 2008b; Mueller et al. 2014a, Bart et al. 2021a). The aforementioned sponge loop describes the transformation of the consumed DOM into detritus by sponges, which thereby becomes available to other animals that cannot feed on DOM, but are capable of feeding on detritus (de Goeij et al. 2013; Bart et al. 2021b). The description of the sponge loop has greatly contributed to a better understanding of DOM cycling on coral reefs and other benthic ecosystems, but also sparked controversies as we currently do not know the extent of DOM cycling through sponges.

Only thin-encrusting sponges have been found to convert DOM into detritus (de Goeij et al. 2013; Alexander et al. 2014), thereby expelling a relatively large proportion of their biomass as detrital waste (12–39 % turnover of organic carbon daily) (Rix et al. 2016; de Goeij et al. 2017). Because of their previously unappreciated abundance in cryptic habitats (Wunsch 1999; Richter et al. 2001; Scheffers 2005; van Duyl et al. 2006), the inclusion of encrusting sponges in community-wide DOM and detritus budgets of coral reef communities seems timely. The role of sponges in the cycling of DOM and detritus on coral reefs has so far been considered in only one food web model (Silveira et al. 2015), which suggested that resource retention by sponges supports local fish populations.

In contrast to encrusting sponges, massive sponges with upward growth forms are characterized by lower production rates (Maier et al. 2020; Bart et al. 2021b) or even net uptake of detritus (McMurray et al. 2016; Hoer et al. 2018; Wooster et al. 2019), leading to the alternative hypothesis that massive sponges transfer DOM to animals that directly predate on their biomass (McMurray et al. 2018; Bart et al. 2021b). However, the exact mechanisms of detritus production by sponges are still unclear. Sponge-derived detritus is commonly assumed to be expelled with the outflowing water (Reiswig 1975; Maldonado et al. 2012) and quantified based on measurements of the concentration differences between inflowing and outflowing water (Yahel et al. 2005; Morganti et al. 2016), despite anecdotal observations that sponges can produce mucus, i.e., an alternative form of detritus (Teragawa 1986; Bell et al. 2015; Schönberg 2015; Pineda et al. 2017; Cummings et al. 2020) and that detritus in some sponge species appears to be expelled from the ostia (Storr 1976). Detritus production by massive sponges could therefore be larger than currently assumed.

Modeling food webs in coral reef communities

Theoretical models of species networks, in which individual species are interconnected by a system of differential equations, are commonly used to estimate the population dynamics of taxa interacting with each other and their environment. Population sizes are predicted from species-specific rates of GPP, R, herbivory, predation, and other fluxes that drive population abundances (e.g., Lotka 1925; Paine 1966; May 1971; Pimm et al. 1991). These models form the basis for developing and exploring many ecological concepts, including food web structure (Paine 1980; Pimm and Kitching 1988), trophic cascades (Shurin et al. 2002; Knight et al. 2005), food web complexity and stability (Huisman and Weissing 1999; Allesina et al. 2009; van Altena et al. 2016), and alternative stable states (Beisner et al. 2003). In turn, if the fluxes in these species networks are poorly known, they can be estimated from the abundances of the resident species by solving the differential equations for equilibrium in a “linear-inverse model”

(LIM) (van Oevelen et al. 2010). Inverse models in food web ecology do not estimate population sizes over time but instead assume that each resident taxon (or group of taxa) is in “steady state”, where inputs (e.g., GPP, herbivory) and outputs (e.g., R, DOM release) are balanced, such that its biomass does not change over time (Lotka 1925; Solomon 1949; Hannon 1973; Christensen and Pauly 1993). Fluxes can be initially constrained by defining minimum and maximum possible values of these fluxes based on the available data (e.g., biomass, flux measurements, isotope tracer analysis). The assumption of steady-states is a useful approach in food webs of coral reefs, where the uncertainty of fluxes is typically high (Odum and Odum 1955; Hiatt and Strasburg 1960; Opitz 1996; van Oevelen et al. 2006; Cáceres et al. 2016). However, the dynamic balances of organisms in real food webs are not necessarily at equilibrium. Coral reefs may be growing or deteriorating and the abundances of resident taxa may track seasonal cycles (e.g., climatic oscillations, periodic upwelling) or display complex non-equilibrium dynamics (Karlson and Hurd 1993; Diaz-Pulido and Garzón-Ferreira 2002; McClanahan 2008).

One way to validate the outcomes of LIMs is by comparing the predicted community-wide C fluxes against independent *in-situ* measurements and against predictions from models that assume no equilibria. To this end, experimental underwater confinements can be placed on the reef to enclose m²-sized areas of reef benthos and measure the combined metabolic fluxes of all members of the enclosed community (van Heuven et al. 2018; Roth et al. 2021). Although this approach is promising, it is yet to be used to test whether steady-state LIMs can accurately predict C fluxes in coral reef communities.

Steady-state food web models of coral reefs can be further improved by estimating organic biomasses of the species on the reef. The modeled fluxes are typically quantified in terms of wet weight (e.g., Polovina 1984; Opitz 1993; Arias-González et al. 2004), which introduces a bias due to varying contents of seawater and inorganic (i.e., skeletal) components in the tissues of different organisms. It is more ecologically meaningful to quantify biomass and the cycled organic matter in terms of ash-free dry weight (AFDW) or organic carbon (C) (Johnson et al. 1995; Niquil et al. 1998), which removes the influence of seawater content and inorganic materials on the weight estimates of animal and plant tissues (Diaz and Rützler 2001; van Oevelen et al. 2006). Further, cryptic communities are underrepresented in existing models of coral reefs (Nichols et al. 2022) and many models have focused on the top of the food web to address aspects in fisheries (e.g., Tsehaye and Nagelkerke 2008; Varkey et al. 2012; Houk et al. 2018). Incomplete representation of important functional groups or even the entire cryptic community can hamper the ability to derive accurate insights from food web models (de Jonge et al. 2019), particularly when the underestimated taxa (cryptic

sponges) produce large amounts of detritus, which has been suggested to stabilize food webs (Moore et al. 2004; Wolkovich et al. 2014).

The coral reefs on Curaçao

All field work described in this dissertation was conducted on the reefs along the leeward shore of the island of Curaçao, situated in the Southern Caribbean (12°12'N, 68°56'W). Curaçao has a core of volcanic and sedimentary limestone rocks ringed with limestone terraces formed by corals that started growing when the island was uplifted close enough to the ocean's surface sometime around the Eocene (54.8 to 33.7 million years ago) (van Buurt 2009). The principal currents and swell arrive from the east-northeast, thus the southwestern facing shores, spanning approximately 70 km, are more protected and are considered leeward shores (van Duyl 1985). The island is surrounded by a continuous fringing reef that begins within meters of the leeward shore and slopes down at an angle of 30–60° to a depth of 80 m, then continuing seaward with a series of terraced deep-water reefs.

In recent decades, the reefs of Curaçao have experienced only limited impacts of storms, marine heat waves, coral diseases, and other large-scale disturbances. Nevertheless, local reef communities have changed in response to human activities. The most pronounced changes have occurred over the last 40 years, including the island-wide die off of the sea urchin *Diadema antillarum* that, due to overfishing of herbivorous fishes, had become the main herbivore on Caribbean reef systems (Bak et al. 1984), a five- to 20-fold decline in coral recruitment (Vermeij 2006), significant losses of adult corals (van Duyl 1985; Jackson et al. 2014), increased abundance of macroalgae and benthic cyanobacterial mats (de Bakker et al. 2017), and large reductions in fish biomass due to overfishing (Estep et al. 2017; Vermeij et al. 2019). Nevertheless, in certain areas corals can still make up 30 % of the visible substrate (Bak et al. 2005; Sandin et al. 2008b; Vermeij 2012; Estep et al. 2017). Therefore, parts of the reefs under study are regarded as some of the more intact and less affected reef systems in the Caribbean, while other areas are considered severely degraded (Schutte et al. 2010; Jackson et al. 2014; Estep et al. 2017).

Aim & objectives

The overall aim of this work is to quantify and analyze the major biomass stocks and carbon flows within a Caribbean coral reef community, including cryptic reef communities and fluxes of dissolved organic matter and detritus. The aim was divided into the following research objectives:

- To estimate the standing stocks of benthic organisms, including cryptic taxa, in shallow reef communities occurring along the leeward reef slope of Curaçao.
- To quantify and characterize the detritus production by massive sponges.
- To quantify the metabolic rates and organic carbon fluxes in Curaçao's leeward reef community using a linear-inverse model.
- To compare and evaluate the community-wide carbon fluxes predicted by the model against *in-situ* measurements of the same fluxes.

Outline of the thesis

We begin by estimating the standing biomass stocks of various functional groups of benthic organisms (scleractinian corals, gorgonians, calcifying algae, non-calcifying phototrophs, massive and encrusting sponges) residing on exposed and cryptic reef surfaces along the leeward reef slope of Curaçao between 9 and 14 m depth (**Chapter 2**). To achieve this, 3D models of the reef benthos—including cavities, crevices, and overhangs—were generated using photogrammetry, which allowed us to estimate the surface area underneath traditional quadrats. Surface areas were combined with additional measurements (e.g., substrate cover, algal canopy height, organic carbon contents in biological tissues) to determine the biomass (AFDW and organic C) of reef organisms. In this newly developed census method, biomass stocks within the surveyed areas were contrasted against traditional abundance estimates expressed as percentage cover, producing a completely different picture of the relative abundances of functional groups within reef communities. For example, cryptic species covered only a small fraction of the visible reef area but are major contributors to the total community biomass on the surveyed reef.

In **Chapter 3**, we quantify the production of detritus by the common Caribbean tube sponge *Aplysina archeri*, and visually highlight a novel mechanism of waste removal in this sponge and an Indo-Pacific ball-shaped sponge of the genus *Chelonaplysilla*. Release of waste was documented (using time-lapse videography under 7-fold magnification) and measured in a flow-through aquarium. Sponge surfaces were also “time-lapsed” in the field, showing that these sponges “sneeze” and that their mucus-embedded waste is actively consumed by other reef organisms.

In **Chapter 4**, we explore the implications of including cryptic communities and DOM cycling (e.g., sponge loop) in the food web structure of Curaçaoan reef

communities to obtain a better quantitative understanding of the C flows and the balance between the major producers and consumers on present-day reefs. To this end, a comprehensive LIM of the reef's food web was constructed using RStudio (package "LIM", developed by Soetaert and van Oevelen 2009). C flows in the model were constrained using the local abundance estimates reported in **Chapter 2** in combination with published values and *in-situ* measurements of the net fluxes of planktonic, detrital, and dissolved organic C, and dissolved oxygen (as carbon proxy for primary productivity and respiration) by individual reef organisms.

In **Chapter 5**, we test the predictions of the LIM presented in **Chapter 4** by comparing the modeled rates of community-wide fluxes (primary productivity, respiration, and uptake/release of plankton, detritus, and dissolved organic C) against *in-situ* measured rates of these fluxes in six benthic reef communities of varying composition. Reef communities were incubated using tetrahedron-shaped flexible enclosures (0.43 m² planar area, 120 L volume), in which we measured seawater exchange and ambient C concentrations. In addition, we also calculated community-wide fluxes by summing the measured species-specific C fluxes over the taxa on the reef. The deviations between (i) the community-wide fluxes predicted by the LIM model, (ii) those calculated by summing the individual contributions of the different taxa and (iii) the measured community-wide fluxes on the reef were quantified to assess to what degree LIMs can accurately predict C fluxes in coral reef communities.

Finally, in **Chapter 6**, the main findings from all preceding chapters are discussed with respect to existing paradigms in marine food web studies and coral reef ecology. This chapter also includes a sensitivity analysis of important assumptions underlying our LIM. New hypotheses are highlighted and possible directions for ongoing research are discussed.