



UvA-DARE (Digital Academic Repository)

Organic carbon cycling in a Caribbean coral reef

Hidden biomass, sneezing sponges, and net heterotrophy

Kornder, N.A.

Publication date

2023

[Link to publication](#)

Citation for published version (APA):

Kornder, N. A. (2023). *Organic carbon cycling in a Caribbean coral reef: Hidden biomass, sneezing sponges, and net heterotrophy*. [Thesis, fully internal, Universiteit van Amsterdam].

General rights

It is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), other than for strictly personal, individual use, unless the work is under an open content license (like Creative Commons).

Disclaimer/Complaints regulations

If you believe that digital publication of certain material infringes any of your rights or (privacy) interests, please let the Library know, stating your reasons. In case of a legitimate complaint, the Library will make the material inaccessible and/or remove it from the website. Please Ask the Library: <https://uba.uva.nl/en/contact>, or a letter to: Library of the University of Amsterdam, Secretariat, P.O. Box 19185, 1000 GD Amsterdam, The Netherlands. You will be contacted as soon as possible.



Chapter

6

Synthesis

SYNTHESIS

“I have a friend who’s an artist and has sometimes taken a view which I don’t agree with very well. He’ll hold up a flower and say, ‘Look how beautiful it is’, and I’ll agree, and he says ‘I as an artist can see how beautiful this is, but you as a scientist take this all apart and it becomes a dull thing’. And I think that he’s kind of nutty. First of all, the beauty that he sees is available to other people and to me too, I believe, although I may not be quite as refined aesthetically as he is, but I can appreciate the beauty of a flower. At the same time, I see much more about the flower than he sees. I could imagine the cells in there. The complicated actions, which also have a beauty. I mean, it’s not just beauty at this dimension of one centimeter, there’s also beauty at smaller dimensions. The inner structure, also the processes, the fact that the colors and the flower are evolved in order to attract insects to pollinate it is interesting. It means that insects can see the color. It adds a question: Does this aesthetic sense also exist in the lower forms that...why is it aesthetic...all kinds of interesting questions, which the science and knowledge only adds to the excitement and mystery, and the awe of a flower. It only adds. I don’t understand how it subtracts.”

—Richard P. Feynman

The aesthetic beauty of coral reefs has awed people around the world since Darwin described their formation in the 19th century (Darwin 1842). As with the flower in Feynman’s argument, there is much more to coral reefs than their appearance. While aesthetical features of reefs, such as clear waters, colorful hard corals building grand three-dimensional structures, and abundant schools of fish have been on the decline in recent decades (Jackson 1997; Pandolfi et al. 2003), many basic functional attributes of coral reefs, such as their high primary productivity (Davis et al. 2021) and efficient recycling of organic resources (Cinner et al. 2016; Fraser et al. 2020) still persist in many areas around the world.

In this thesis, we address a variety of paradigms relating to the standing biomass stocks, metabolic rates, and organic carbon fluxes in coral reef communities on the shallow reef slope of the island of Curaçao in the Southern Caribbean. We found that a quarter of the benthic community biomass still consists of corals. Sponges, though, comprise half of the community biomass, but largely reside in cryptic spaces that are not considered in standard reef surveys. We confirmed that these reefs are highly productive ecosystems built primarily on the gross primary production of corals and macroalgae. Some of this production is transferred to heterotrophic organisms that directly feed on living biomass (i.e., grazing, predation), however, more production is actively released as organic matter. Like insects feeding on plant nectar, heterotrophic microbes and sponges evolved to live on the rich organic material shed by the primary producers around

them. According to our assessment, microbes and sponges equally contribute to making this resource available to invertebrates and fish that include plankton or sponge-derived detritus in their diets. Notably, we discovered a novel mechanism behind detritus production by sponges that is surprisingly similar to the processes occurring in the respiratory systems of more structured animals, resembling a human sneeze in slow motion. Despite the high primary productivity by producers and efficient retention of locally produced resources by microbes and sneezing sponges, the reef community as a whole was found to be net heterotrophic, thus requiring some form of external organic matter input (e.g., carbon from the open ocean). Many complex cycling pathways in coral reefs have only recently been described and rarely been quantified in unison. Hence, in the spirit of Feynman, our success in understanding and guiding the development of coral reefs through the Anthropocene will depend on how devoted we are to focus not only on the aesthetic features of coral reefs, but also on the internal processes, i.e., “the complicated actions, which also have a beauty.”

Surveying coral reef communities in three dimensions

The common practice of surveying the community composition of coral reefs by photographing them from above does not produce comparative biomass estimates for corals, macroalgae, sponges, and especially cryptic organisms. To obtain a better understanding of how different monitoring approaches affect abundance estimates of all aforementioned groups, in Chapter 2 we quantified the composition of shallow reef communities along the leeward reef of Curaçao using various abundance metrics, including biovolume, biomass, total surface area, and the traditional projected bottom cover. This allowed us to evaluate the impact of surveying coral reefs in different ways. Most importantly, we found that traditional surveys of the percent cover severely underestimated the biomass contribution of some benthic taxa (e.g., encrusting sponges) while they overestimated that of others (e.g., macroalgae). These findings will most likely also be true for other reefs and other benthic marine ecosystems. Surveys of the total three-dimensional (3D) structure within a 1 x 1 m reef area and estimates of the actual biomass (e.g., ash-free dry weight or organic carbon content) of all organisms living on such areas are critical to produce realistic estimates of carbon and nutrient storage and flows within reef communities. Across all ocean basins, the undersides of exposed reef surfaces are generally colonized by crustose coralline algae (CCA), bryozoans, tunicates, polychaetes, and sponges (Winston and Jackson 1984; Wunsch et al. 2000; Richter et al. 2001; Scheffers et al. 2004; Scheffers 2005; van Duyl et al. 2006; de Goeij and van Duyl 2007). We provide cover-to-biomass conversions for many of these reef organisms (Chapter 2) and refer to the extensive list curated by Thomas Brey and colleagues (Brey et al. 2010) for additional conversions. These

cover-to-biomass conversions may help to facilitate estimations of a reef's "true" community composition (i.e., in terms of biomass) and biogeochemical cycling (de Jonge et al. 2019) from simple abundance metrics, such as surface area or geometric volumes.

Although abundance estimates based on projected cover (e.g., Johnson et al. 1995; Arias-Gonzalez et al. 1997; Liu et al. 2009) can generate quick insights into the health of a reef (e.g., coral versus macroalgal cover), such measurements should not be used as proxies for the true abundances of reef organisms. Coral reef ecology would hence benefit from standardized methodologies for 3D assessments of benthic communities. These will improve our ability to characterize carbon and nutrient cycles on coral reefs by including cryptic taxa and adequately considering organisms with upward growth forms (e.g., sponges, gorgonians) and allow for the integration and comparison of various data forms (e.g., surface areas, algal canopy heights, elemental composition of tissues). In addition, the acquired data should involve planar projections of the benthos to ensure comparability with existing census data. Communities that could also be relevant to a coral reef's carbon cycle but were not well characterized in our assessment include macrofauna and microbial communities in sediments (Hewson and Fuhrman 2006; Garren and Azam 2012), endolithic communities (Fine and Loya 2002; Mueller et al. 2014a; Pernice et al. 2020), and cryptobenthic fishes (Brandl et al. 2018; Brandl et al. 2019). Assessing the biomass of these "hidden" taxa would require the destruction of the reef framework and methods that prevent escape of motile organisms.

We quantified the biomass of non-motile reef organisms in as much detail as possible in Chapter 2, to highlight its deviations from other abundance metrics. This approach admittedly made the methodology complex and potentially difficult to replicate. Simpler methodologies to incorporate the 3D topography of reefs and reef organisms are already being developed (Smith et al. 2022). Photographing cryptic communities on reef undersides (e.g., cavities, overhangs) or filming the presence of cryptobenthic fishes could be achieved by developing underwater endoscopes. Similarly, placing artificial cryptic structures into reef frameworks to assess the communities growing on them over extended periods, such as the recently developed Autonomous Reef Monitoring Structures (ARMS), can help determine the abundance and richness of taxa in cryptic habitats (Pearman et al. 2016; Vicente et al. 2021), although it remains unclear to what degree the communities growing on ARMS represent natural cryptic reef communities.

To establish comparable *in-situ* units of cryptic coral reef communities, we build 27 artificial cave structures made of rebar frames and a reef-sand concrete coating—each providing the same shaded surface area under comparable light and flow regimes—, and placed them onto the Curaçaoan reef slope in front of the Carmabi Foundation at 8–12 m depth (Figure 1A). Upon initial colonization by

macroalgae, successional development continued in these artificial “caves”, resulting in an increased dominance of sponges and coralline algae (Figure 1B–D). Once the composition of taxa equals that of the surrounding cryptic communities, the cave units can be used to address several important questions in coral reef ecology. For instance, ARMS could be placed inside the caves to test whether the communities developing on them resemble those in the immediate vicinity. Camouflaged cameras could be positioned to count cryptobenthic fishes and estimate the abundance of motile invertebrates. The caves could also be incubated or periodically sampled under natural versus manipulated conditions (e.g., by adding nutrients or removing specific taxa) to estimate present and expected future compositional changes of cryptic reef communities, as well as the carbon and nutrient flows between coral reef cavities and the outer reef water. Similar studies in natural reef cavities found that cryptic communities release inorganic nutrients, which help sustain the productivity of nearby reef organisms (Rasheed et al. 2002; Scheffers et al. 2004; Slattery et al. 2013). They also found that coral cavities are net sinks of particulate (Richter and Wunsch 1999) and, predominantly, dissolved organic carbon (de Goeij and van Duyl 2007).

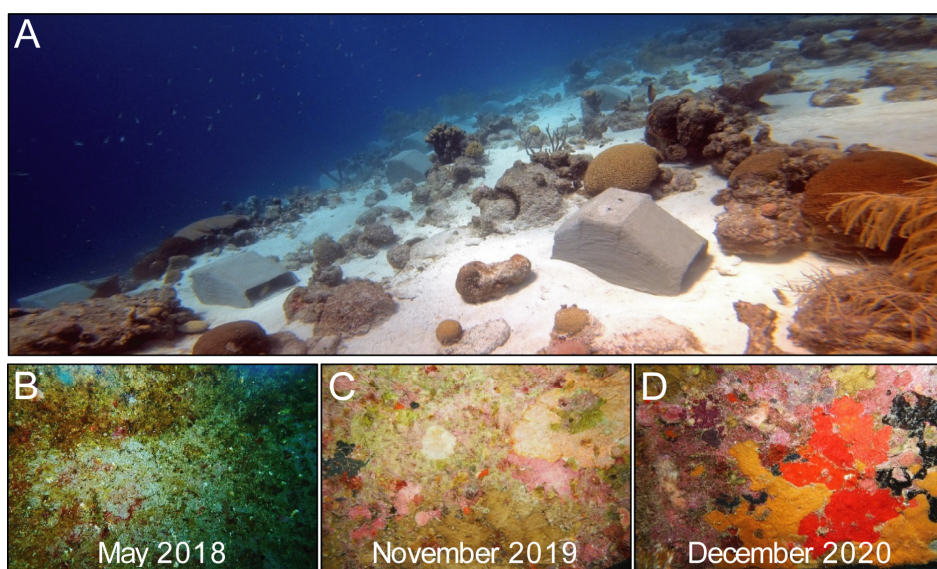


Figure 1. Artificial cave structures deployed on the reef slope on Curaçao (site labeled “Buoy 1” in de Goeij and van Duyl 2007) in December 2017. A total of 27 caves were deployed (A) at similar orientation and 2–3 m distance from each other. The structures are 65 cm long, 40 cm wide, and 15–40 cm high, each harboring 0.7 m² of cryptic surface area inside the caves. These surfaces were photographed yearly to monitor succession (e.g., panels B–D) of the developing cryptic reef communities.

Detritus production by sneezing sponges

The uptake of dissolved organic matter (DOM) by sponges (de Goeij et al. 2008a,b; Rix et al. 2016) and its conversion into detritus (de Goeij et al. 2009) have only recently been described. The production of detritus by sponges supplements the diet of consumer species like motile invertebrates (de Goeij et al. 2013) and fishes (Silveira et al. 2015; Rix et al. 2018). Hence, sponges are important within reef communities by making photosynthates released by benthic primary producers (i.e., DOM) available to organisms at higher trophic levels that cannot feed on DOM, but do feed on particulate detritus. This pathway has been termed the “sponge loop” (de Goeij 2009; de Goeij et al. 2013). However, only encrusting sponges, which are common in cryptic reef habitats, appear to expel significant proportions of their biomass as detritus (12–39 % turnover of organic carbon daily) (Alexander et al. 2014; Rix et al. 2016; de Goeij et al. 2017).

Massive sponges with upward growth forms that grow on light-exposed parts of the reef show low detritus production rates or net uptake of detritus (McMurray et al. 2016; Hoer et al. 2018; Wooster et al. 2019; Maier et al. 2020; Bart et al. 2021b). These observations might be inaccurate, however, due to possible artefacts associated with the methodologies used to measure metabolic fluxes in sponges. The non-invasive “InEx” (later “VacuSIP”) technique (Yahel et al. 2005; Mueller et al. 2014b; Morganti et al. 2016) quantifies the amount of water flowing through a sponge and compares the concentration of (in)organic compounds in seawater entering (In) and exiting (Ex) the sponge. This InEx approach is based on the common assumption that sponges release (in)organic compounds with the processed water through their outflow openings (oscula). However, we discovered in Chapter 3 that massive sponges can expel mucus-embedded particulate waste from their inflow openings (ostia) and sneeze this material into the environment. Specifically, we describe how the massive tube sponge *Aplysina archeri* and another species of the genus *Chelonaplysilla* expel mucus-embedded particles against the direction of seawater flow, transport this material across the sponges’ surface, and finally shed it by sneezing. The expelled material consists largely of inorganic particles (81 %), enriched with organic carbon and nitrogen. The discovery resulted from careful field observations of the build-up and disappearance of mucus on sponges’ surfaces, a thorough screening of anecdotal observations in the old and new literature (e.g., Storr 1976; Strehlow et al. 2017), and a simple experiment to quantify waste production by sponges without the limitations associated with InEx. Sneezes by *A. archeri* were associated with relatively slow (20–50 min) body contractions and occurred every 3–8 h. Time-lapse videography further showed that the mucus-embedded particles expelled from the ostia of massive sponges were eaten by other reef organisms, confirming that both

encrusting and massive sponges can contribute to the sponge loop by producing particulate matter rich in organic carbon and nitrogen.

How can *A. archeri* move mucus against the flow of seawater through its body? In other animals, directed mucus flow is achieved via the whip-like motion of cilia (Brown and Bythell 2005; Mackie et al. 2006; Stannard and O'Callaghan 2006; van der Schans 2007; Conley et al. 2018). Is it possible that sponges use cilia in a similar fashion (Figure 2)? So far, cilia have only been found on the excurrent canal walls of sponges (except in homoscleromorph sponges), but these were not motile (Leys and Hill 2012). By analyzing the individual time-lapse images, we found that the speed of the mucus was one to two orders of magnitude slower than other forms of cilia-driven mucus movement (Sleigh 1989; Hamann and Blanke 2022). Therefore, the movement of mucus in *A. archeri* may represent a novel mechanism of mucus transport in metazoans in need of future exploration. Another unresolved aspect concerns the amount of carbon that is cycled through the sponge loop, regardless of how the material is shed. According to my analysis, the quantities of DOM that are taken up by sponges are comparable to other important carbon flows, mediated by e.g. the microbial loop (Azam et al. 1983), grazing, and predation (Chapter 4).

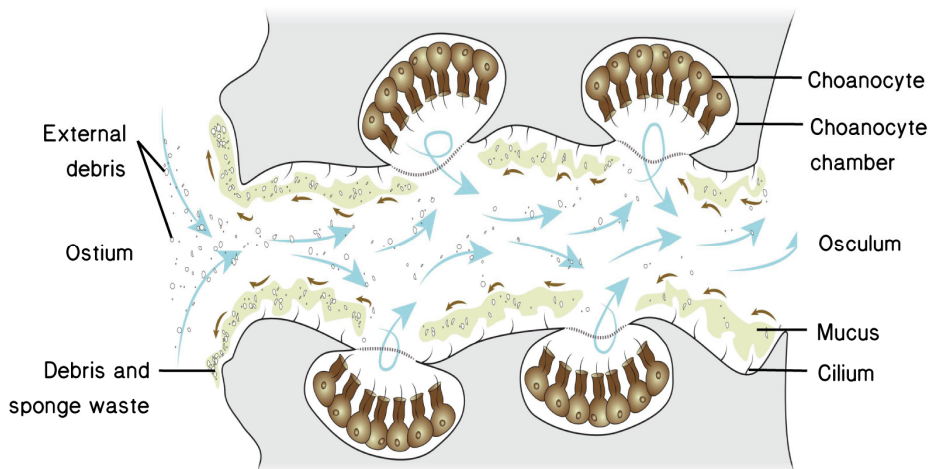


Figure 2. Hypothesized mechanism for mucus-trapped waste transport in *Aplysina archeri*. Sponges draw in water (large blue arrows) via the sinusoidal motion of flagellae at the end of their feeding cells (choanocytes), which are broadly embedded in choanocyte chambers (Bergquist 1978). Water flows from the ostia to the osculum, while mucus is secreted across the sponge pinacoderm and used to transport particulate waste against the water flow (small brown arrows) towards the ostia through the whip-like beating motions of cilia.

A model is only as good as its assumptions

We produced a linear-inverse model (LIM) that estimates the organic carbon flows among resident coral reef taxa on the surveyed reef on Curaçao (Chapter 4) and verified several community-level fluxes predicted by this model in the field (Chapter 5). However, a model is only as good as its assumptions. Figure 3 shows what happens to the LIM results when three major assumptions are removed from the model.

The first major assumption is that each functional group and the entire coral reef community is at steady state. In Chapter 5, we compared the outcomes of our original model with *in-situ* measurements of the metabolism of whole reef communities and found that the steady-state assumption of the LIM improves the model's estimates of the gross—but not net—community-level primary productivity. However, present-day coral reefs and other ecosystems are not in steady state. The bias introduced by forcing this equilibrium assumption upon all functional groups is illustrated by comparing the results of the original LIM (Figure 3A) to those obtained via the “summed fluxes” approach (Figure 3B), where the rate measurements of individual functional groups obtained from incubation experiments are multiplied with their group-specific abundances to calculate total C fluxes (see “C fluxes predicted by summing individual taxa” in Chapter 5). Our estimates of community-level GPP dropped by 39 % from $1890 \pm 408 \text{ mmol C m}^{-2} \text{ d}^{-1}$ (mean \pm SD throughout text) to $1133 \pm 67 \text{ mmol C m}^{-2} \text{ d}^{-1}$ when the steady-state assumption of the LIM was replaced by the summed fluxes approach (i.e., carbon balances were allowed to deviate from zero). Since community respiration using the summed fluxes approach was on average only 21 % lower (from 2227 ± 414 to $1759 \pm 548 \text{ mmol C m}^{-2} \text{ d}^{-1}$), excess respiration was higher (from 337 ± 86 to $626 \pm 552 \text{ mmol C m}^{-2} \text{ d}^{-1}$) and the system was therefore estimated to be more heterotrophic. This result corroborates our earlier notion that the steady-state assumption of LIMs may artificially balance estimates of community GPP and respiration.

The second major assumption is that of elevated daytime respiration with respect to nighttime respiration in phototrophic taxa. When the daily metabolic rates were estimated, using LIM, under the assumption that respiration rates of phototrophic organisms during the day equal their respiration rates at night, we estimated an even larger drop in the modeled reef's community GPP by 55 % (along with a 45 % drop in the respiratory demands) (compare Figure 3A and 3C). This is likely an incorrect assumption in view of the highly elevated (up to 25-fold) daytime respiration rates measured in some corals (Kühl et al. 1995; Schrammeyer et al. 2014). Other benthic primary producers have been found to respire 1.5–3.5 times more carbon during the day than at night, including coralline algae (Furbank and Rebeille 1986; Martin et al. 2013), macroalgae (Langdon et al. 2003), and

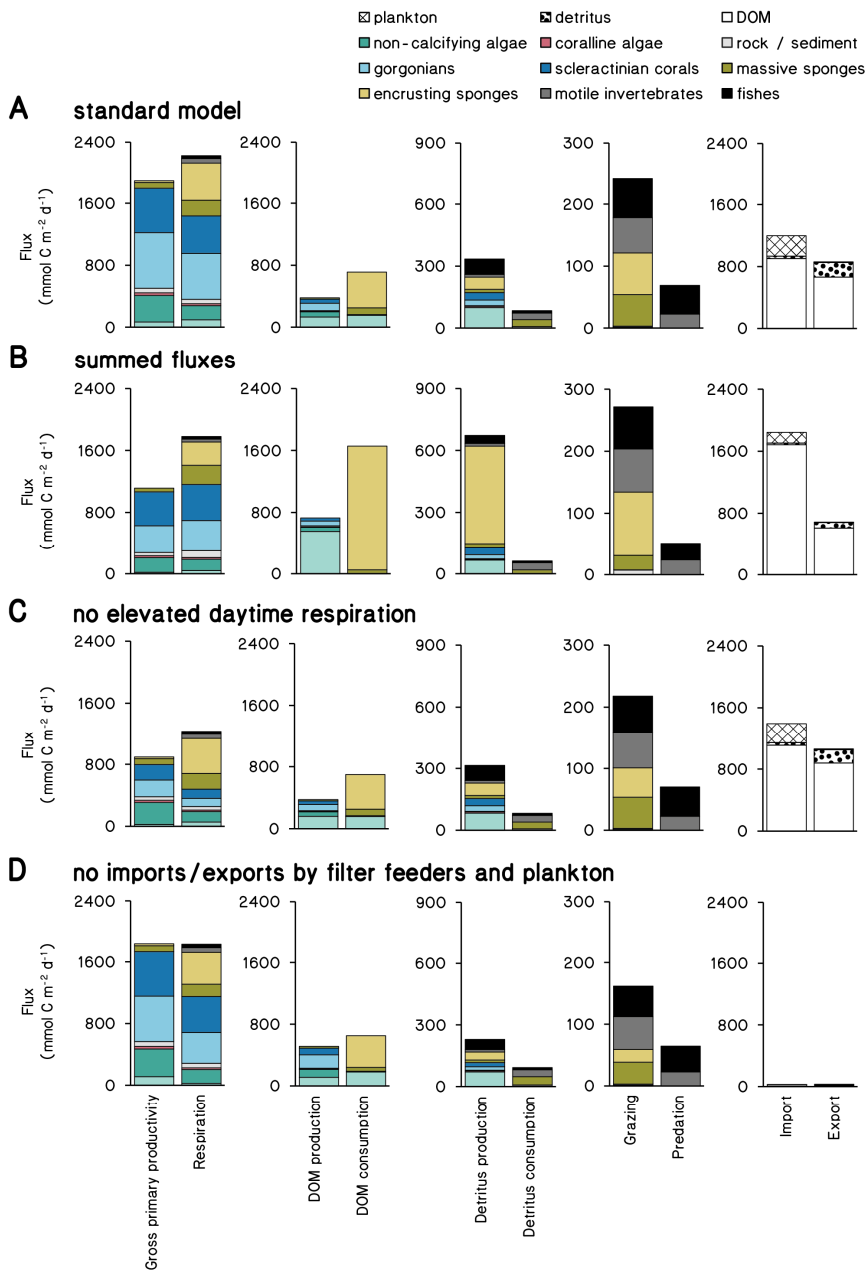


Figure 3. Results of the sensitivity analysis to separately test the impact of three assumptions on the estimated mean organic carbon (C) flows (in $\text{mmol C m}^{-2} \text{d}^{-1}$) within the leeward coral reef of Curaçao at 9–14 m water depth. The processes are partitioned by the contributions of each model compartment (see legend). **A:** Predicted C flows of the linear-inverse model presented in Chapter 4. **B:** The same

predictions as in (A) obtained by summing the average C fluxes of each functional group (i.e., without assuming steady states of coral reef taxa). This “summed-fluxes approach” was presented in Chapter 5. **C:** Output of rerunning the LIM assuming that respiration rates throughout the day remain similar to values measured at night. **D:** Output of rerunning the LIM assuming that system-wide imports and exports of plankton, detritus, and dissolved organic matter (DOM) are limited to mass transfer through the diffusive boundary layer, with no additional exchange between the open ocean and the reef via benthic filter feeders and plankton.

phytoplankton (Pringault et al. 2007). The strong influence of elevated daytime respiration on our model’s estimates of community GPP and R suggests a need to further investigate the diurnal fluctuations of the metabolic rates of benthic primary producers on coral reefs.

The third major assumption concerns our estimates of the carbon imports and exports between local reef communities and the external environment based on our current understanding of benthic-pelagic coupling in coral reefs. While benthic suspension feeders rely on the seawater current to transport carbon to them, but are limited by the formation of boundary layers (Shashar et al. 1996), filter feeders actively pump seawater to access pelagic food sources. In addition, net carbon production or consumption by planktonic organisms over the reef may also export or import carbon into and from the reef. Our original model considered these possible flows at its boundaries, leading to significant imports of DOM and oceanic plankton that balanced the reef community’s excess respiration. However, when carbon imports and exports were “turned off”, the model’s estimated rates of community GPP and respiration were very similar (1833 ± 340 and 1829 ± 340 mmol C m⁻² d⁻¹, respectively) and community net primary productivity approached zero (3 ± 17 mmol C m⁻² d⁻¹) (Figure 3D). It is difficult to quantify the role of oceanic subsidies of organic carbon on reefs. An important step would be to partition the diets of sponges—and possibly other filter feeders (e.g., tunicates, bivalves)—into the consumption of carbon that is locally produced versus the consumption of external carbon imported by the ocean currents. The model could be further improved by deriving imports and exports of carbon from local estimates of shear flow velocities, turbulence, and boundary layer formation using hydrodynamic models (e.g., Rogers et al. 2018). Such models can be coupled with measurements of food concentration gradients in the seawater above the benthic reef community. Our analyses suggest that C imported from the open ocean is essential to sustain the observed present-day heterotrophy of Curaçao’s leeward shallow reef community.

While the estimated gross community metabolism of the studied reef community was sensitive to the assumptions outlined above (Figure 3A-D, left panels), the estimated flows of organic carbon between different functional groups

were relatively robust (Figure 3A–D, central panel columns). Exceptions are the carbon flows associated with the sponge loop, which were sensitive to the assumption of steady state (Figure 3B). DOM consumption and detritus production by encrusting sponges calculated by the summed-fluxes approach were much higher than those same flows predicted by the LIM (compare Figure 3A and 3B). According to the summed fluxes, total DOM consumption by sponges exceeded all other carbon flows. Further, a gap was evident in the budget of detritus, where detritus production by encrusting sponges alone was 8-fold higher than all local consumption and exports of detritus combined (Figure 3B). The large sizes of these organic carbon flows when using the summed fluxes approach suggest that the magnitude of the sponge loop could be suppressed by the LIM. For instance, the mass balancing enforces that detritus produced by sponges needs to be either consumed by other reef fauna or exported from the reef. Since we assumed a relatively low abundance of detritivores on Caribbean reefs (Opitz 1993; Cáceres et al. 2016; Estep et al. 2017), detritus consumption by the reef community was limited, which in turn limited its estimated production in order to meet the assumption of steady states. Export of detritus was not well defined in our model, which focused on the Curaçaoan reef slope between 9–14 m depth. The local shallower waters contain large areas of bare sediment, which are sinks of detritus (Hansen et al. 1992; Wild et al. 2004a). Likewise, deeper reef communities were shown to depend on detritus from shallow reefs to sustain their standing biomass (Slattery et al. 2011; Macartney et al. 2022). In our LIM, detritus imports and exports were estimated based on measurements of the horizontal gradients of suspended detritus between the open ocean and reef water. The model therefore does not account for differences in detritus concentrations at different water depths. Some of the detritus production estimated by the summed fluxes approach, but not by the LIM may represent detritus that is exported to shallower sediment patches or deeper mesophotic reefs beyond the depth range of the studied reef communities. Consequently, taking into account the vertical transport of organic carbon across different areas of the reef ecosystem can help to improve estimates of the internal carbon cycles at each area using LIM. Extending the spatial representation of the model would also require a further understanding of the hydrodynamic transport of DOM, plankton, and detritus across the reef, and their fluxes into the benthos. This information could for instance be obtained by 3D hydrodynamic models in combination with tracing of the incorporation of stable isotopes into benthic reef organisms at various depths, from shallow lagoons to deeper reefs.

Towards comprehensive models in coral reef ecology

Our LIM represents an additional step towards a more comprehensive assessment of the status and dynamic changes of coral reef communities and their functions. We advanced earlier models in two ways. First, we included cryptic reef communities, which in our study area comprised half of the community's total biomass. Second, we represented the abundance of organisms by using their biomass and biovolume instead of projected relative cover. In particular, the use of biomass as abundance metric provides a more accurate representation of erect organisms in the community (i.e., gorgonians and massive sponges), and can be more easily related to biogeochemical fluxes (e.g., C fluxes) on reefs than the classic percent cover.

Based on earlier models, Caribbean coral reefs have historically often been described as self-sufficient systems where respiratory demands roughly equal local productivity (Glynn 1973; Wanders 1976; Adey and Steneck 1985; Hatcher 1988,1990). In contrast, our new results indicate that present-day reefs are net heterotrophic and partly depend on the import of organic carbon transported by the ocean currents. Excess community respiration in our model foremost results from the metabolic activity of encrusting sponges, which predominantly reside on cryptic and hardly accessible reef surfaces. Cryptic communities are well known to be net heterotrophic (Richter and Wunsch 1999; Hudspith et al. 2022) and possibly elevate community-wide respiratory demands on structurally complex reefs where they are relatively more abundant than in flatter, less complex habitats where primary producers dominate the community. This potential dichotomy could be investigated in further detail by comparing community-wide respiratory demands across a sufficient number of coral reefs of different structural complexity and cryptic community abundance. At a larger scale, studies will be needed to obtain a better understanding of the sources and biochemical composition of the organic carbon imported by coral reefs, and whether this external subsidy of organic carbon is mainly produced in open ocean waters, in the local coastal zone, or originates from terrestrial ecosystems.

Another major finding of our model concerns the reef community's turnover time. According to our model, the biomass of the local reef equates to 8 % of its annual gross primary productivity. Computing this relationship for other surveyed reefs across the Caribbean Sea and in the Indo-Pacific throughout the last 70 years yields an average ratio of 8 ± 2 % (range: 6–12 %, $n = 12$ reef communities from 9 studies including Chapter 4). Therefore, one may conclude that the turnover time on coral reefs has remained relatively consistent, despite pronounced changes in the community structures of reefs worldwide (Hughes et al. 2017a,b). Given that the primary productivity and respiration of Caribbean coral reef communities were balanced in the past, our model results suggest that the studied reef community

has become net consumptive, with little change to the turnover time due to allochthonous subsidies that compensate the community's additional respiratory demand. Long-term time series of food webs across coral reefs in various geographical regions would be needed to test this hypothesis and could shed more light on the mechanisms that stabilize turnover times in coral reef communities.

Our model can be expanded to predict the contribution of reef organisms to other biogeochemical cycles in aquatic ecosystems. A relevant next step is to introduce resources beyond organic carbon, such as nitrogen, phosphorous, and silica. Conveniently, the model can incorporate stoichiometric relationships obtained by isotope tracer measurements. Stable isotopes have been widely used to determine nutrient flows between coral reef taxa (e.g., Naumann et al. 2010b; McMahon et al. 2016). A more complex challenge is to incorporate inorganic carbon into our model framework. Coral reefs grow via the accretion of calcium carbonate, predominantly due to the calcification of reef-building corals (Goreau 1963; Allemand et al. 2011). However, calcification on coral reefs is increasingly hampered by ocean acidification, i.e., the gradual decline in ocean pH and carbonate availability as a consequence of rising atmospheric CO₂ levels (Silverman et al. 2009; Eyre et al. 2018; Cornwall et al. 2021). Hence, long-term changes of the flows of organic carbon on reefs will have to consider the deposition and destruction of inorganic carbon as well (Gattuso et al. 1999; Perry and Alvarez-Filip 2019). Studies on the carbonate chemistry of reef organisms (e.g., Allison et al. 2014; de Bakker et al. 2018; Tansik et al. 2021) and entire reef ecosystems (e.g., Eyre et al. 2014; DeCarlo et al. 2017; McMahon et al. 2019) provide a suite of data on species- and community-level rates of calcification and carbon dissolution, as well as potential relationships (e.g., between photosynthesis and calcification) that can be included in our model to estimate both the organic and inorganic carbon fluxes in coral reef communities.

The ability of LIMs to predict carbon flows in food webs can be used in forward models that address other ecological concepts, such as trophic cascades (Shurin et al. 2002; Knight et al. 2005), alternative stable states (Beisner et al. 2003), and community-level responses to environmental disturbances (Alva-Basurto and Arias-González 2014; Cornwall et al. 2021). A simple and straightforward integration is to use the (time-dependent) abundances of organisms predicted by the forward models as inputs into our food web framework. The resulting food webs provide information on the allocation of resources across the different benthic organisms and the availability of essential food sources, such as detritus and dissolved organic matter, and how these are affected by, e.g., changes in trophic structure or shifts to alternative stable states. Changes to the cycling of resources can then be introduced back into the forward models, and so forth, to better resolve how the functioning of coral reef communities relates to their food web structure

over time. Models of carbon and nutrient flows in coral reefs are relatively unexplored. As I have demonstrated in this thesis, integrating measurements of carbon and nutrient flows in LIMs can yield novel insights that improve our understanding of coral reef communities and how they will develop throughout this century.

SUPPLEMENTARY INFORMATION

Supplementary data & code

This chapter contains supplementary data and code, available at figshare.com (DOI: 10.21942/uva.22592944). Additional requests regarding these resources should be directed to and will be fulfilled by the lead contact, Niklas A. Kornder (niklaskornder@gmail.com).

Code S1. This R script defines ranges and relationships for the carbon flows of the linear-inverse model presented in Chapter 4, but under the alternative assumption that respiration rates of phototrophic organisms during the day equal their respiration rates at night. The text can be saved in R's current directory as "file_name.input" to rerun the model using Code S1 of Chapter 4. The text behind exclamation marks is purely descriptive. The structural elements of the script are explained in Soetaert & van Oevelen (2009).

Code S2. Similar to Code S1, however, the alternative assumption here is that imports and exports of carbon to and from the modeled system are limited.

Data S1. Output of the linear-inverse model presented in Chapter 4, but under the alternative assumption that respiration rates of phototrophic organisms during the day equal their respiration rates at night. Each column represents a single flow of C between two compartments of the model and lists all 10000 model solutions for that flow. See Box 1 in Chapter 4 for a description of the abbreviations of the functional groups.

Data S2. Similar to Data S1, however, the alternative assumption here is that imports and exports of carbon to and from the modeled system are limited.