Organic carbon cycling in a Caribbean coral reef

Hidden biomass, sneezing sponges, and net heterotrophy

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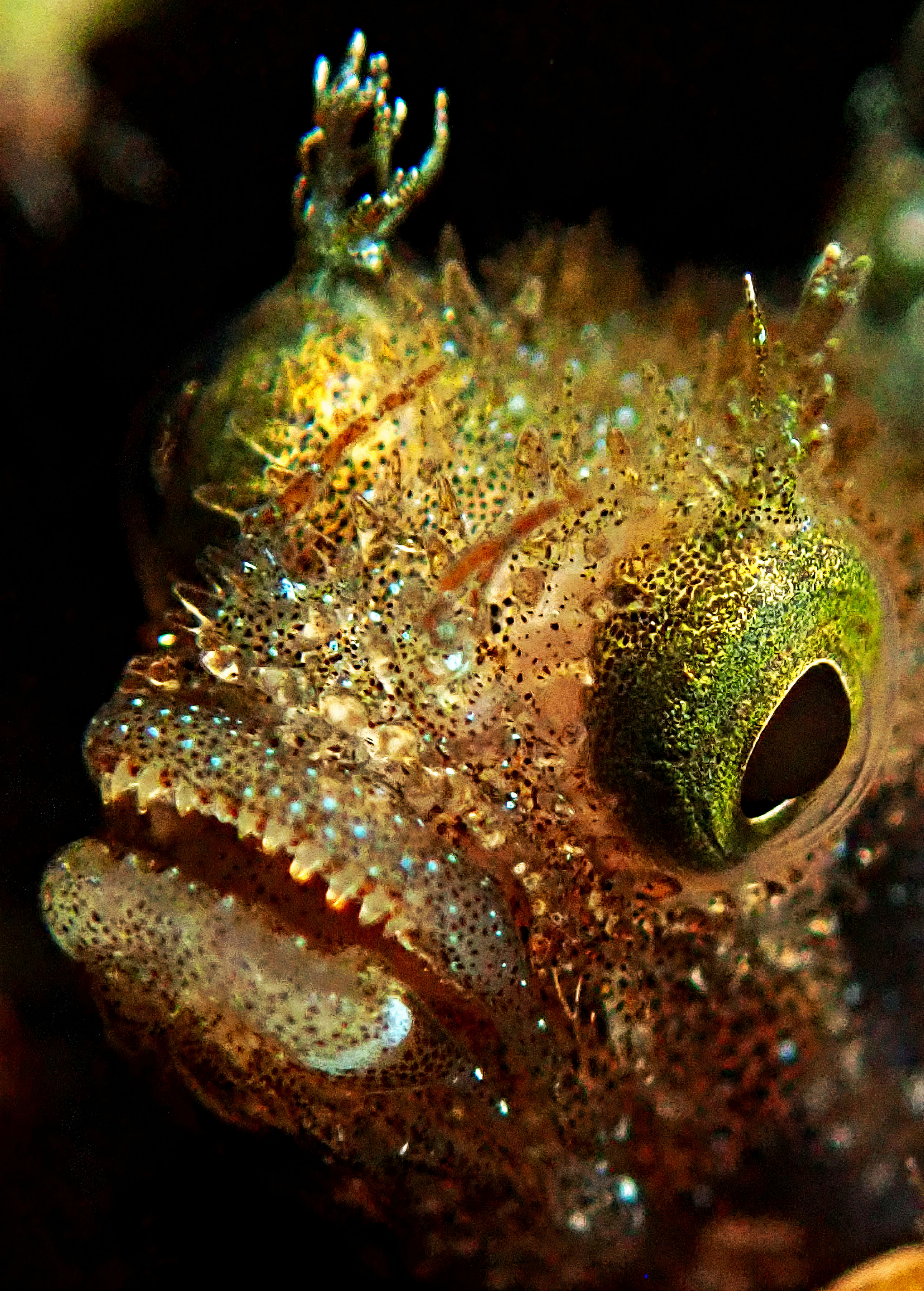

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Appendix

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SUMMARY

In the mid-20st century, coral reefs were shown to harbor exceptionally resilient communities, in which the primary production of reef-building corals and macroalgae is effectively transferred to fishes and invertebrates through grazing and predation. This paradigm shifted in the 1980's after coral populations started to decline noticeably around the world, stimulating research into the functioning of a wide range of taxa inhabiting reefs. Experimental studies showed that microbes and sponges contribute substantially to the cycling of resources by transforming dissolved organic matter (DOM) into particulate matter, thereby making this organic matter available to consumer species that feed on microbial or sponge-derived detritus. However, the extent to which sponges contribute 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 reef community composition, and because the mechanism of detritus production by sponges is still unclear.

This thesis aimed to address these knowledge gaps using biomass surveys of entire reef communities and controlled experiments with living sponges, corals, algae, and several other taxa. The knowledge and data acquired in this thesis were combined with existing data, and are summarized in a food-web model to quantify organic carbon flows on a Caribbean coral reef. This approach provided a suite of empirical data and model predictions that enable us to critically re-assess the balance between biomass production and consumption and test new hypotheses on the cycling and retention of organic matter within modern day coral reefs.

To understand the composition and functioning of coral reef communities, the standing biomasses and resource flows among all major reef organisms need to be quantified. Because the community composition of coral reefs was traditionally assessed as the percentage of the reef substrate (as seen from above) covered by each species, the abundances of cryptic taxa were often not considered in studies of reef communities. In **Chapter 2**, we used photogrammetry to generate 3D models of the reef ecosystem—including cavities, crevices, and overhangs—and to quantify the abundances of all benthic reef organisms inhabiting the leeward reef slope on the Caribbean island of Curaçao in terms of 2D relative cover, 3D surface area, biovolume, and biomass. We describe the scope of these abundance metrics in detail, and found that half of the biomass on the studied reef resided on cryptic surfaces. We also found that encrusting (predominantly cryptic) sponges dominated this reef in terms of biomass, while only representing 2 % of the 2D projected cover. In contrast, macroalgae covered more than 50 % of the projected substrate, but contributed less than 5 % to the total reef community biomass. Our findings highlight that different abundance metrics lead to markedly different perspectives on benthic reef community composition, which needs to be

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considered in assessments of the biogeochemical cycles mediated by these communities.

Recently, the role of sponges in the cycling of organic carbon in coral reef communities has received particular attention. The "sponge loop" describes the transformation of the consumed DOM into detritus by sponges, which thereby becomes available to other animals capable of feeding on sponge-derived detritus. Sponges filter large amounts of water to feed on DOM and plankton, and it is commonly assumed that the detritus released by sponges is expelled with the outflowing water leaving the sponge. In **Chapter 3**, however, we discovered that the Caribbean tube sponge *Aplysina archeri* and an Indo-Pacific sponge of the genus *Chelonaplysilla* expel mucus-embedded sediment particles from their inflow openings. Time-lapse imaging revealed that the mucus-embedded particles were transported against the direction of seawater moving through the sponges' body. The mucus-embedded material aggregated at the sponge surface and was "sneezed" into the environment through periodic body contractions and expansions. Several invertebrates and one species of fish were observed to scavenge on the particulate waste released by *A. archeri*, which contained more organic carbon and nitrogen than particulate matter collected from controls without sponges. These results confirm that sponges with massive growth forms can contribute to the sponge loop by sneezing particulate waste embedded in organic mucus into their environment.

In light of the findings from **Chapters 2** and **3**, the widely reported shifts from coral-dominated to algal-dominated reef communities likely altered food-web interactions and the net balance between biomass production and consumption on present-day coral reefs. To better understand changes in trophic relationships as coral reef communities shift in composition, their food-web structure and community metabolism were explored using a linear-inverse model (LIM) of the organic carbon flows in the community. LIMs estimate unknown or suspected resource flows (e.g., inputs of allochthonous carbon) based on available data for other resource flows within the community (e.g., gross primary productivity (GPP) and respiration of the species) and by assuming that the carbon inputs and outputs for each group or taxon are in "steady state" (i.e., the inputs and outputs balance each other). Although the steady-state assumption is obviously a simplification that does not fully apply to coral reefs, this approach has enabled ecologists to identify missing trophic pathways and compare the relative importance of different carbon flows in natural communities. In **Chapter 4**, we combined the local abundance estimates of the benthic species on the reef reported in **Chapter 2** with published values (e.g., **Chapter 3**) and *in-situ* measurements of the net fluxes of planktonic, detrital, and dissolved organic carbon, and dissolved oxygen (as proxy for primary productivity and respiration) by these species in a new LIM. This approach enabled us to integrate recent insights relevant to the flow of organic carbon within coral reef communities—e.g., the role of cryptic taxa and the sponge loop—and to evaluate the relative importance of these processes to the overall carbon budget of present-day Caribbean reef communities. One of our key findings is that the total respiration rate by the reef community exceeded its primary production. According to the LIM analysis, this net heterotrophy of the coral reef community was supported by the influx of allochthonous plankton and DOM taken up from water masses above the reef. The total standing biomass of the reef represented 8 % of its annual GPP, which gives a mean turnover time of about one month. This high biomass turnover was comparable to that measured on other reefs across different oceans and at different time points spanning several decades. The internal carbon fluxes were dominated by the transformation of dissolved coral and algal photosynthates into detritus through the sponge loop and the well-known microbial loop, which retained comparable amounts of DOM within the reef.

The predictions of the LIM presented in **Chapter 4** were tested *in situ* to validate that our model outcomes represent actual organic carbon fluxes in the field. To this end, portable semi-enclosures (incubation systems that allow some exchange with ambient reef water) were deployed to measure carbon fluxes for m^2-sized segments of benthic reef communities. In **Chapter 5**, we used these portable semi-enclosures to incubate six Caribbean benthic reef communities of different taxonomic composition *in situ*, and to measure their community-wide GPP, respiration, and uptake/release of plankton, detritus, and dissolved organic carbon. By adjusting the abundances assumed by the original LIM, and comparing its community-level predictions with real measurements, for the six reef communities, we showed that community-level GPP, respiration, and net fluxes of plankton and detritus were accurately predicted by the LIM. In contrast, net primary productivity of the entire reef community was best estimated by simply summing fluxes of individual (groups of) taxa. Our measurements corroborate the notion that present-day Caribbean reefs are net sinks of organic carbon. Provided that model outcomes are further validated in the field, LIMs are a useful first approach to quantify food web models of coral reefs, where the uncertainties associated with measured fluxes are generally high.

The research presented in this thesis provides a quantification and analysis of the major biomass stocks and organic carbon flows in a Caribbean coral reef community. In **Chapter 6**, the findings of the preceding chapters are synthesized to illustrate lessons learned and several key assumptions underlying the LIM presented in **Chapters 4** and **5** are analyzed. **Chapter 6** also offers recommendations for continued fundamental research on carbon cycling in coral reef communities, including directions for surveying present-day coral reefs in 3D and open questions pertaining to the mechanisms underpinning detritus

production by sponges. The chapter ends with a perspective on the integration of models and measurements to foster a deeper understanding of how organisms share resources within coral reef communities, at present and in the future.

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SAMENVATTING

In de twintigste eeuw stonden koraalriffen bekend om hun hoge productiviteit en zeer hoge biodiversiteit. Rifbouwende koralen en algen produceren veel energie middels fotosynthese en deze energie wordt vervolgens gebruikt door vissen en ongewervelde dieren via trofische processen zoals begrazing en predatie. Echter, sinds de jaren 80 van de vorige eeuw begonnen koraalgemeenschappen wereldwijd merkbaar af te nemen, waardoor er ook meer wetenschappelijk onderzoek werd gestart naar het fysiologische en ecologische belang van verschillende rifgemeenschappen. Het is bijvoorbeeld pas sinds de afgelopen 10–20 jaar bekend dat microben en sponzen substantieel bijdragen aan de cyclus van organisch materiaal binnen koraalrifgemeenschappen. Sponzen zetten opgelost organisch materiaal (DOM, zoals bijvoorbeeld suikers) om in organische deeltjes (de "poep", of met een netter woord detritus, van de spons). Hierdoor komt dit organisch materiaal beschikbaar voor veel rifbewoners die normaal niet direct van deze voedselbron gebruik kunnen maken. De mate waarin sponzen bijdragen aan het metabolisme van een koraalrif ecosysteem is echter moeilijk te beoordelen, aangezien een groot deel van de sponsgemeenschap niet direct zichtbaar is. Veel sponzen leven onder en in het rif, in zogenaamde cryptische habitatten. Daarnaast is het mechanisme achter detritus productie door sponzen nog niet bekend.

Dit proefschrift heeft tot doel om deze ontbrekende schakels in de organische koolstofcyclus op rifsystemen te ontrafelen door een zo volledig mogelijke inventaris te maken van de totale biomassa van alle rifbewoners, zowel op als onder het rif, en van de opname en afgifte van organische koolstof door deze rifbewoners. Deze metingen zijn vervolgens gebruikt in een voedselweb model om de koolstofcyclus op een hedendaags koraalrif in het Caribisch gebied te kwantificeren. Het model beschrijft de balans tussen de productie en consumptie van biomassa (die historisch in evenwicht was) en berekent hoe groot de uitwisseling is van verschillende bronnen van organisch koolstof (bijvoorbeeld detritus of DOM) tussen verschillende groepen organismen binnen een rifgemeenschap. Het model leverde een reeks aan nieuwe empirische gegevens en voorspellingen op die ons in staat stellen de gevestigde inzichten te beoordelen en nieuwe hypothesen te testen over het importeren, vasthouden en uitwisselen van organisch materiaal in moderne koraalriffen.

Om de samenstelling en werking van hedendaagse koraalrifgemeenschappen beter te begrijpen, moeten de biomassa's en koolstofstromen tussen alle belangrijke riforganismen worden bepaald. De samenstelling van koraalrifgemeenschappen wordt traditioneel gekwantificeerd als het geprojecteerde percentage van de rifbodem (van bovenaf gezien door het maken van een foto) dat door elke soort of groep van organismen wordt bedekt. Hierdoor werden cryptische taxa in voorgaande studies van rifgemeenschappen niet "gezien". In **Hoofdstuk 2** hebben we fotogrammetrie gebruikt om 3D-modellen van het rif ecosysteem te genereren (inclusief holtes, spleten en kleine grotten), om daarmee de hoeveelheden van alle bentische riforganismen te kwantificeren op de Caribische riffen van Curaçao. In deze studie hebben we de 2D relatieve bedekking van de belangrijkste soorten vergeleken met hun bedekking op een 3D-oppervlak, en met hun biovolume en biomassa. We beschrijven hoe deze verschillende bepalingen (2D versus 3D, volume, biomassa) leiden tot een geheel andere kwantificering van de relatieve samenstelling van de rifgemeenschappen. We ontdekten dat de helft van de biomassa op het bestudeerde rif zich op cryptische oppervlakken bevond en dat korstvormende (overwegend cryptische) sponzen een groot deel van de totale biomassa op dit rif vertegenwoordigden, terwijl ze slechts 2% van de 2D geprojecteerde oppervlakte bedekten. Daarentegen bedekten macroalgen meer dan 50% van het geprojecteerde substraat, maar droegen ze minder dan 5% bij aan de totale biomassa van de gehele rifgemeenschap. Deze resultaten laten zien dat verschillende methoden oor het meten van de samenstelling van rifgemeenschappen leiden tot totaal verschillende schattingen van de abundantie van soorten. Hier moet rekening mee worden gehouden als men de biogeochemische cycli op koraalriffen wil bestuderen, zoals de opname en uitwisseling van koolstof tussen organismen op het rif.

De afgelopen jaren is de rol van sponzen op koraalriffen veel groter gebleken dan eerder gedacht. De "sponge loop" of "spons kringloop" beschrijft hoe sponzen, in tegenstelling tot de meeste andere heterotrofe organismen, het abundant aanwezige opgelost organisch materiaal (DOM) uit de verder zeer voedselarme tropische zee kunnen opnemen en dit vervolgens omzetten in organische deeltjes (detritus). Dit spons "afval" is beschikbaar voor andere dieren. Sponzen filteren grote hoeveelheden water om zich te voeden met DOM en plankton, en algemeen wordt aangenomen dat het afval dat door sponzen wordt geproduceerd, wordt uitgestoten met het uitstromende water dat de spons verlaat via hun "osculum" (uitstroomopening). In **Hoofdstuk 3** ontdekten we echter dat de Caribische buisspons *Aplysina archeri* en een Indo-Pacifische spons van het geslacht *Chelonaplysilla* in slijm ingebedde sedimentdeeltjes uitstoten via hun instroomopeningen, de zogenaamde "ostia". Time-lapse video's onthulden dat de in slijm ingebedde deeltjes werden getransporteerd tegen de stroomrichting in van het zeewater dat door het lichaam van de sponzen wordt gepompt. Het slijmerige afval dat uit de ostia kwam, verzamelde zich aan het sponsoppervlak en werd door periodieke samentrekkingen en uitzettingen van het sponslichaam in de omgeving "geniest". We zagen dat verschillende ongewervelde dieren en tenminste één vissoort zich voedden op het in slijm ingebedde materiaal dat werd uitgestoten door *A. archeri*, dat meer organische koolstof en stikstof bevatte dan in het controle experiment met alleen zeewater zonder "sponssnot". Deze resultaten bevestigen

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dat ook de grotere sponzen op het rif kunnen bijdragen aan de spons kringloop door in organisch slijm ingebed fijn afval in hun omgeving te niezen. Bovendien laat dit onderzoek zien dat eerdere studies soms, onbewust, op de verkeerde plek de detritusproductie van sponzen hebben gemeten en daardoor verkeerde conclusies hebben getrokken over bijvoorbeeld het opnemen en doorgeven van voedsel op koraalriffen.

In het licht van de bevindingen uit **Hoofdstukken 2** en **3** heeft de wijdverspreide verschuiving van koralen naar algen waarschijnlijk de voedsel-web interacties en de balans tussen koolstof productie en consumptie op hedendaagse koraalriffen beïnvloedt. Om beter te begrijpen hoe de trofische relaties op een rif veranderen als koraalrifgemeenschappen in samenstelling veranderen, hebben we de structuur van het voedselweb, en met name de koolstofkringloop van het rif, onderzocht met behulp van een lineair-inverse model (LIM). LIMs helpen bij het in kaart brengen van koolstofstromen, zelfs als die stromen niet goed bekend zijn. Daarbij wordt het model gevoed met metingen van de opname en uitstoot van koolstof (bijvoorbeeld door primaire productie en ademhaling van de soorten). Het model onderzoekt alle koolstofstromen tussen koralen, sponzen, algen en andere soortgroepen in de rifgemeenschap, op basis van de aanname dat de koolstof in- en uitvoer voor elke groep of taxon in balans is. Hoewel we weten dat een rif niet perfect in balans is in de tijd (er is vaak sprake van netto groei, of juist afname van soorten) stellen LIMs ecologen in staat de orde van grootte van koolstofstromen tussen verschillende soortgroepen vast te stellen. In **Hoofdstuk 4** hebben we de biomassa bepalingen van de rifgemeenschappen uit **Hoofdstuk 2** gecombineerd met *in-situ* metingen en gepubliceerde waarden (uit bijvoorbeeld **Hoofdstuk 3**) van de netto fluxen van koolstof uit plankton, detritus en opgelost organisch materiaal (DOM) en van zuurstof (als proxy voor primaire productiviteit en ademhaling) om een LIM te maken van de Caribische riffen van Curaçao. We ontdekten dat de bestudeerde riffen zeer productief zijn, maar dat de totale respiratie van het rif hoger was dan de primaire productie. Volgens de LIM-analyse wordt deze netto heterotrofie van de koraalrifgemeenschap ondersteund door de opname van allochtoon plankton en DOM aangevoerd door de oceaanstromingen. De totale biomassa van het rif was 8% van de jaarlijkse bruto primaire productie ("GPP"), wat neerkomt op een gemiddelde turnover van ongeveer een maand. Deze turnover is vergelijkbaar met die van andere riffen in verschillende oceanen en gemeten over meerdere decennia. De interne koolstoffluxen werden gedomineerd door de conversie van opgeloste organische stoffen, geproduceerd door de fotosynthese activiteit van koraal en algen, in detritus door de spons kringloop en door groei van bacteriën via de bekende microbiële kringloop, die beiden vergelijkbare hoeveelheden DOM in het rif vasthielden.

De voorspellingen van het LIM gepresenteerd in **Hoofdstuk 4** zijn gevalideerd op het koraalrif, ofwel “in situ”. Om de natuurlijke koolstofstromen op een rif te bepalen hebben we in **Hoofdstuk 5** incubatietenten (met een oppervlakte van 1 m^2) geplaatst over zes verschillende rifgemeenschappen waarvan de samenstelling en biomassa bekend is. De rifgemeenschappen in deze incubatietenten zijn gedurende 3 tot 4 uur doorgemeten, zowel overdag als ’s nachts. Daarbij hebben we gekeken naar de productiviteit en respiratie van de totale gemeenschap, en naar de opname en uitstoot van opgelost en particulair organische koolstof (bijvoorbeeld bacteriën, fytoplankton, of detritus). De gevonden koolstofstromen zijn daarna vergeleken met de stromen die door het model zijn berekend op basis van de samenstelling en biomassa van de geïncubeerde rifgemeenschappen. Daarnaast zijn de gevonden koolstofstromen vergeleken met de incubaties van individuele soorten uit **Hoofdstuk 4** om te onderzoeken of een LIM nodig is, of dat je individuele metingen van riforganismen ook gewoon bij elkaar kan optellen. Uit ons onderzoek is gebleken dat de LIM in de meeste gevallen een betere schatting maakt van de natuurlijk gemeten waarden, dan wanneer individuele metingen bij elkaar worden opgeteld (dus zonder modelberekening). Het model voorspelt nauwkeurig de bruto productiviteit en respiratie van de rifgemeenschappen, en ook de opname en uitstoot van plankton en detritus. Daarentegen kon de netto primaire productiviteit van de gehele rifgemeenschap het beste worden geschat door simpelweg de koolstofstromen van individuele (groepen) taxa op te tellen. Onze veldmetingen bevestigen het idee dat de huidige Caribische riffen netto heterotroof zijn. De resultaten laten zien dat LIMs een zeer bruikbare manier bieden om het voedselweb van koraalriffen te beschrijven en kwantificeren, hoewel validatie van de modelvoorspellingen in het veld wenselijk blijft.

Het onderzoek in dit proefschrift is een eerste kwantitatieve analyse van de biomassaverdeling en belangrijkste organische koolstofstromen in een Caribische koraalrifgemeenschap. In **Hoofdstuk 6** volgt een synthese van de bevindingen. In dit hoofdstuk worden suggesties gedaan voor toekomstig onderzoek, bijvoorbeeld om uit te zoeken hoe het beste koraalriffen te analyseren in 3D en wat het onderliggende fysiologische mechanisme is achter de “niezende sponzen”. Ook beschrijft dit hoofdstuk een gevoeligheidsanalyse van de aannames van het LIM gepresenteerd in **Hoofdstukken 4** en **5**. Het hoofdstuk eindigt met een perspectief op de integratie van modellen en metingen om een beter begrip te krijgen van het complexe netwerk van interacties tussen de verschillende organismen in koraalrifgemeenschappen, nu en in de toekomst.

ZUSAMMENFASSUNG

Im mittleren zwanzigsten Jahrhundert hat sich gezeigt, dass Korallenriffe außergewöhnlich widerstandsfähige Gemeinschaften beherbergen, die auf der Primärproduktion von riffbildenden Korallen und Makroalgen basieren. Diese Produktion wird über das Abgrasen und Prädation effektiv auf Fische und Wirbellose übertragen. Die Ansicht, dass Korallenriffgemeinschaften allgemein widerstandsfähig sind, änderte sich in den 1980er-Jahren, nachdem die Korallenpopulationen weltweit merklich abzunehmen begannen, was die Erforschung der Physiologie und Ökologie vieler verschiedener Organismen auf Korallenriffen anregte. Heute ist bekannt, dass Mikroben und Schwämme wesentlich zum Ressourcenkreislauf beitragen: Sie wandeln gelöste organische Stoffe in Partikel um und machen diese dadurch für heterotrophe Arten verfügbar, die sich von Plankton oder vom Detritus (d.h. von toten organischen Überresten) der Schwämme ernähren. Das Ausmaß, in dem Schwämme zum gesamten Riffstoffwechsel beitragen, ist jedoch schwer einzuschätzen. Denn sie sind vor allem in kryptischen Lebensräumen (Höhlen, Spalten und Überhänge) reichlich vorhanden, die in Standardprotokollen zur Untersuchung der Zusammensetzung benthischer Riffgemeinschaften nicht berücksichtigt werden. Hinzu kommt, dass der Mechanismus, wie Schwämme Detritus produzieren, noch unklar ist.

Diese Dissertation zielte darauf ab, die oben genannten Wissenslücken zu schließen, indem Biomassenuntersuchungen ganzer Riffgemeinschaften und kontrollierte Experimente mit lebenden Schwämmen, Korallen, Algen und weiteren Riffbewohnern durchgeführt wurden. Das Wissen und die Daten aus dieser Arbeit sind mit vorhandenen Erkenntnissen in einem Nahrungsnetzmodell zusammengefasst, um die Kohlenstoffflüsse eines karibischen Korallenriffes zu quantifizieren. Dieser Ansatz lieferte eine Reihe von empirischen Daten und Modellvorhersagen, die es uns ermöglichten, das Gleichgewicht zwischen Produktion und Verbrauch von Biomasse neu zu bewerten und neue Hypothesen über den Kohlenstoffkreislauf in modernen Korallenriffen zu testen.

Um die Zusammensetzung und Funktionsweise von Korallenriffgemeinschaften zu verstehen, müssen die vorhandenen Biomassen und Ressourcenströme zwischen allen wesentlich vorhandenen Rifforganismen quantifiziert werden. Da die Zusammensetzung der biologischen Gemeinschaften auf Korallenriffen traditionell als Prozentsatz des von jeder Art bedeckten Riffsubstrats (von oben gesehen) charakterisiert worden ist, wurde die Fülle kryptischer Organismen in Studien über Riffgemeinschaften oft nicht berücksichtigt. In **Kapitel 2** beschreiben wir, wie wir mittels Bildmessung und -interpretation 3D-Modelle eines Korallenriffes erstellten–einschließlich Hohlräumen, Spalten und Überhänge. Zudem quantifizierten wir die Häufigkeit aller benthischen Rifforganismen innerhalb des untersuchten Riffhangs auf der südlichen Karibikinsel Curaçao hinsichtlich ihrer traditionell projizierten Flächen sowie ihrer 3D-Oberflächen, Biovolumina und Biomassen. Wir beschreiben den Umfang dieser Metriken im Detail und fanden heraus, dass sich die Hälfte der Biomasse auf dem untersuchten Riff auf kryptischen Oberflächen befindet. Wir ermittelten zudem, dass verkrustende (überwiegend kryptische) Schwämme die Biomasse des Riffs dominieren, während sie aktuell nur 2 % der projizierten 2D-Bedeckung ausmachen. Im Gegensatz dazu bedecken Makroalgen mehr als 50 % des projizierten Substrats, tragen aber weniger als 5 % zur gesamten Biomasse der Riffgemeinschaft bei. Unsere Ergebnisse zeigen, dass verschiedene Abundanzmetriken zu überaus unterschiedlichen Perspektiven auf die Zusammensetzung benthischer Riffgemeinschaften führen, was bei der Bewertung der biogeochemischen Kreisläufe innerhalb dieser Gemeinschaften berücksichtigt werden muss.

In den letzten Jahren hat die Rolle von Schwämmen im organischen Kohlenstoffkreislauf der Korallenriffgemeinschaften besondere Aufmerksamkeit erhalten. Die ‚Schwammschleife' beschreibt die Umwandlung des verzehrten gelösten Kohlenstoffs durch Schwämme in (partikulären) Detritus, der dadurch für andere Tiere verfügbar wird, die sich von diesem ernähren können. Schwämme filtern große Mengen an Wasser zur Aufnahme von Plankton und gelöster Materie, und es wird allgemein angenommen, dass ihre organischen Abfallprodukte mit dem von ihnen abfließenden Wasser ausgestoßen werden. Jedoch entdeckten wir in **Kapitel 3**, wie der karibische Ofenrohr-Schwamm *Aplysina archeri* und ein indopazifischer Schwamm der Gattung *Chelonaplysilla* in Schleim eingedecktes Sediment aus ihren Einströmöffnungen ausstoßen. Durch Zeitrafferaufnahmen konnten wir zeigen, dass die in Schleim eingedeckten Partikel entgegen der Richtung des vom Schwamm generierten Wasserstroms transportiert wurden. Das schleimige Material aggregierte an der Schwammoberfläche und wurde durch periodische Körperkontraktionen und -ausdehnungen in die Umgebung ‚geniest'. Wir dokumentierten zudem, wie mehrere wirbellose Tiere und eine Fischart den von *A. archeri* freigesetzten Abfall fraßen, der mehr organischen Kohlenstoff und Stickstoff enthielt als das organische Material aus den Kontrollmessungen. Diese Ergebnisse bestätigen, dass massiv wachsende Schwämme zur Schwammschleife beitragen können, indem sie partikulären Abfall in organischen Schleim einbinden und in ihre Umgebung niesen.

An vielen heutigen Korallenriffen werden die Riffgemeinschaften zunehmend von Makroalgen anstelle von Korallen dominiert. In Anbetracht der Ergebnisse aus den **Kapiteln 2** und **3** verändert dies dort wahrscheinlich die Interaktionen innerhalb des Nahrungsnetzes und das Gleichgewicht zwischen Biomasse-produktion und -verbrauch. Um die Veränderungen der trophischen Beziehungen in Korallenriffgemeinschaften mit variabler Zusammensetzung besser zu

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verstehen, untersuchten wir das Nahrungsnetz und den Stoffwechsel der Riffgemeinschaft mit linear-inversen Modellen (LIMs) der Kohlenstoffflüsse innerhalb der Gemeinschaft. LIMs schätzen unbekannte oder vermutete Ressourcenflüsse (z. B. Einträge von externem Kohlenstoff aus dem offenen Ozean) auf der Grundlage verfügbarer Daten für andere Ressourcenflüsse innerhalb der Gemeinschaft (z. B. Bruttoprimärproduktivität und Atmung der Organismen). Dies geschieht unter der Annahme, dass sich die Gesamteinträge und -austräge von Kohlenstoff für jede Gruppe oder jedes Taxon in einem ‚stationären Zustand' befinden bzw. sich ausbalancieren. Obwohl ein solches Gleichgewicht für Rifforganismen in der Natur unwahrscheinlich ist, hat die Annäherung Ökologen in die Lage versetzt, bisher unbekannte trophische Verbindungen zu identifizieren und die relative Bedeutung verschiedener Kohlenstoffflüsse in natürlichen Gemeinschaften zu vergleichen. In **Kapitel 4** kombinierten wir die in **Kapitel 2** berichteten lokalen Biomasseschätzungen der benthischen Riffbewohner mit veröffentlichten Werten (z. B. aus **Kapitel 3**) und zusätzlichen *in-situ* Messungen der Nettoflüsse von Plankton, Detritus, gelöstem organischem Kohlenstoff und gelöstem Sauerstoff (als Proxy für Primärproduktivität und Atmung) durch diese Riffbewohner in einem LIM. Dieser Ansatz ermöglichte es uns, aktuelle Erkenntnisse zu integrieren, die für den Fluss organischen Kohlenstoffs in Korallenriffgemeinschaften relevant sind – z. B. die Rolle der kryptischen Taxa und der Schwammschleife. Auch konnten wir so die relative Bedeutung dieser Prozesse für das gesamte Kohlenstoffbudget gegenwärtiger karibischer Riffgemeinschaften evaluieren. Eine wesentliche Erkenntnis aus unseren Messungen ist die Tatsache, dass die Gesamtatmungsrate der untersuchte Riffgemeinschaft ihre Primärproduktion überstieg. Laut der LIM-Analyse wurde diese Netto-Heterotrophie der Korallenriffgemeinschaft durch den Zustrom von externem Plankton und DOM unterstützt, die aus den Wassermassen über dem Riff aufgenommen wurden. Die gesamte stehende Biomasse lag bei 8 % der jährlichen Bruttoprimärproduktion, was einer Umschlagszeit von ungefähr einem Monat entspricht. Eine derart kurze Umschlagszeit war vergleichbar mit der relativen Biomasse auf anderen Riffen in verschiedenen Ozeanen und zu verschiedenen Zeitpunkten innerhalb mehrerer Dekaden. Die internen Kohlenstoffflüsse wurden durch die Umwandlung des von Korallen und Algen abgegebenen gelösten Kohlenstoffs in Detritus im Rahmen der Schwammschleife und der länger bekannten mikrobiellen Schleife dominiert. Beide hielten vergleichbare Mengen an gelöstem Kohlenstoff durch dessen Umwandlung zu Partikeln im Riff zurück.

Die in **Kapitel 4** vorgestellten Vorhersagen des linear-inversen Modelles wurden in der Natur getestet, um zu validieren, dass unsere Modellergebnisse die tatsächlichen organischen Kohlenstoffflüsse auf Korallenriffen darstellen. Zu diesem Zweck wurden tragbare, halbisolierte Gehäuse eingesetzt, die einen geringen Austausch mit dem umgebenden Wasser zulassen, um Kohlenstoffflüsse in quadratmeter-großen Segmenten benthischer Riffgemeinschaften zu messen. In **Kapitel 5** beschreiben wir, wie wir ein solches tragbares Gehäuse verwendet haben, um sechs karibische benthische Riffgemeinschaften unterschiedlicher taxonomischer Zusammensetzungen auf dem Riff zu inkubieren. Dies erlaubte es uns, ihre Gesamtraten der Bruttoprimärproduktivität, der Atmung und der Aufnahme von Plankton sowie Aufnahme und Produktion von Detritus und gelöstem organischem Kohlenstoff zu messen. Im Zuge dessen passten wir die vom ursprünglichen LIM angenommenen Häufigkeiten und den Vergleich von dessen Vorhersagen auf Gemeinschaftsebene mit realen Messungen für die sechs Riffgemeinschaften an. So konnten wir zeigen, dass die Bruttoprimärproduktivität, die Atmung und die Nettoflüsse von Plankton und Detritus auf Gemeinschaftsebene mit dem LIM relativ genau vorhergesagt wurden. Im Gegensatz dazu wurde die Nettoprimärproduktivität der gesamten Riffgemeinschaft am besten durch Summierung der Produktivität einzelner (Gruppen von) Taxa geschätzt. Unsere Messungen bestätigen die Vorstellung, dass heutige karibische Riffe Netto-Senken für organischen Kohlenstoff sind. Vorausgesetzt, dass die Modellergebnisse weiterhin im Feld getestet werden, bilden LIMs einen nützlichen ersten Ansatz zur Beschreibung von Nahrungsnetzen in Korallenriffen, wo die Flüsse im Allgemeinen nicht genau gemessen werden können.

Die in dieser Dissertation vorgestellte Forschung bietet eine Quantifizierung und eine Analyse der Biomasseverteilung und organischen Kohlenstoffflüsse in einer karibischen Korallenriffgemeinschaft. In **Kapitel 6** werden die Ergebnisse der vorangegangenen Kapitel synthetisiert, um die gewonnenen Erkenntnisse zu veranschaulichen. Es beinhaltet eine Analyse der zentralen Annahmen, die dem in **Kapitel 4** und **5** vorgestellten LIM zugrunde liegen. **Kapitel 6** bietet auch Empfehlungen für die weitere Grundlagenforschung zum Kohlenstoffkreislauf in Korallenriffgemeinschaften. Einbezogen werden dabei Anmerkungen zur Vermessung heutiger Korallenriffe in 3D und offene Fragen zu den Mechanismen, die Schwämme zum Niesen nutzen. Das Kapitel endet mit einer Perspektive zur Integration ökologischer Modelle und Messungen, um ein tieferes Verständnis dafür zu fördern, wie die Organismen in Korallenriffen gegenwärtig und in Zukunft Ressourcen teilen.

AUTHOR CONTRIBUTIONS

Chapter 2:

N.A.K. and J.M.dG. designed research; N.A.K., M.J.L.Z., and S.J.M. performed research; N.A.K. and J.C. analyzed data; N.A.K. wrote the paper with substantial contributions from J.M.dG., B.M., M.J.A.V., and J.H. All authors read and approved the manuscript.

Chapter 3:

N.A.K. and J.M.dG. designed research; N.A.K. and Y.E. performed research; N.A.K., D.S., and S.P.L. analyzed data; N.A.K. and J.M.dG wrote the paper with substantial contributions from S.P.L, B.M, M.J.A.V., and J.H. All authors read and approved the manuscript.

Chapter 4:

N.A.K. and J.M.dG. designed research; N.A.K., J.M.dG., and J.H. constructed the model. N.A.K., A.J.R., W.J.B., and A.T.K.R. performed research; N.A.K. and J.M.dG. analyzed data; N.A.K. and J.M.dG wrote the paper with substantial contributions from M.J.A.V. and J.H. All authors read and approved the manuscript.

Chapter 5:

N.A.K. and J.M.dG designed research; N.A.K., Y.E., and A.W. performed research; N.A.K. and L.J.dN. analyzed data; N.A.K. wrote the paper with substantial contributions from J.M.dG., M.J.A.V. and J.H. All authors read and approved the manuscript.

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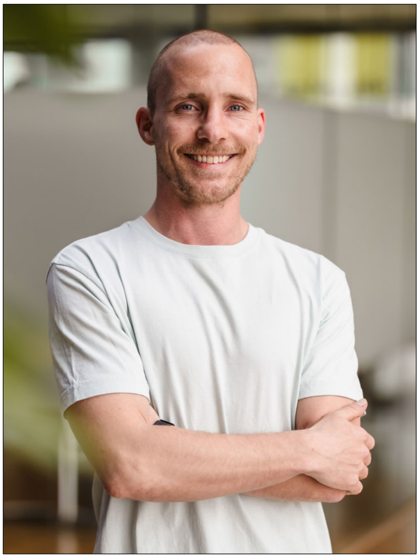
ABOUT THE AUTHOR



Niklas Alexander Kornder was born in Eisenach (Germany) in 1989. Growing up in Cologne in the home of a family with members from both sides of the former Berlin wall, he developed an early appreciation for sciences and a sharp intuition for business. Home-fostered interest in STEM led him to complete a Bachelor of Science in Biosystems Engineering at Bremen University of Applied Sciences (Germany) in 2014. During his bachelor, Niklas assisted animal and plant evolution lectures and took a year abroad as a visiting scholar at Griffith University (Australia), which nurtured a profound passion and concern for the worldwide status of coral reefs.

To expand his knowledge of coral reefs, Niklas moved to the United States to pursue a Master of Science in Environmental Sciences at Nova Southeastern University on a Fulbright Scholarship. While coursing this program, he got certified as an AAUS Scientific diver and contributed to regional restoration efforts for the critically endangered *Acropora* corals. As a graduate researcher at Nova Southeastern University and supervised by Dr. Joana Figueiredo, his research focused on the effects of climate change on coral calcification and coral reef community resilience. Upon completion of the Master's program in 2016, Niklas joined the Raja Ampat Sea Centre in Indonesia, where he contributed to several native islanders-led coral reef conservation projects and obtained his dive master certification. Since 2017, Niklas worked at the University of Amsterdam (The Netherlands) to pursue a Ph.D. in Marine Ecology. Supervised by Dr. Jasper M. de Goeij, he aimed to identify key taxa and processes that drive the productivity and biodiversity of coral reefs. This thesis is the result of his latest efforts.