Surviving in a Marine Desert: The Sponge Loop Retains Resources Within Coral Reefs

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effects between duplicates. Although in some cases, this interference can be exploited, for example, by using it to repress gene expression (*5*, *23*), we propose that a more common outcome is the minimization of this interference in gene duplicates that persist over evolutionary time. Whether such minimization is generally accompanied by an increase in regulatory complexity, as seen here, remains to be determined.

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24. Single-letter abbreviations for the amino acid residues are as follows: A, Ala; C, Cys; D, Asp; E, Glu; F, Phe; G, Gly; H, His; I, Ile; K, Lys; L, Leu; M, Met; N, Asn; P, Pro; Q, Gln; R, Arg; S, Ser; T, Thr; V, Val; W, Trp; and Y, Tyr.

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Supplementary Materials

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Surviving in a Marine Desert: The Sponge Loop Retains Resources Within Coral Reefs

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Ever since Darwin's early descriptions of coral reefs, scientists have debated how one of the world's most productive and diverse ecosystems can thrive in the marine equivalent of a desert. It is an enigma how the flux of dissolved organic matter (DOM), the largest resource produced on reefs, is transferred to higher trophic levels. Here we show that sponges make DOM available to fauna by rapidly expelling filter cells as detritus that is subsequently consumed by reef fauna. This "sponge loop" was confirmed in aquarium and in situ food web experiments, using ^{13}C- and ^{15}N-enriched DOM. The DOM-sponge-fauna pathway explains why biological hot spots such as coral reefs persist in oligotrophic seas—the reef's paradox—and has implications for reef ecosystem functioning and conservation strategies.

Coral reefs thrive in oligotrophic tropical seas, but nevertheless belong to the most productive ecosystems on Earth (*1*–*3*). Efficient retention and recycling of carbon and nutrients causes the net production of reefs to be close to zero, despite high gross primary production (*4*). Reef primary producers such as corals and algae release up to 50% of their fixed carbon (*5*, *6*), of which up to 80% immediately dissolves in seawater (*7*). This shunt into the dissolved organic matter (DOM) pool represents a major flow of energy and nutrients on coral reefs (*7*). In the open ocean, microbes enable the transfer of DOM to higher trophic levels through the well-established microbial loop (*8*). Studies on coral reefs have therefore also initially focused on microbes in reef waters and adjacent permeable sediments to understand the fate of DOM in these systems (*7*, *9*–*11*). However, uptake rates by bacterioplankton, in the sense of the microbial loop, are largely insufficient to explain the observed DOM removal on Caribbean and Indo-Pacific reefs (*12*). It therefore remains unclear how the largest source of energy and nutrients on reefs is transferred to higher trophic levels.

Cryptic habitats, for example, the coral reef's crevices and cavities, are identified as major sinks of DOM on Caribbean and Indo-Pacific reefs (*12*). These habitats cover up to two-thirds of the reef's volume, and the biomass of cryptic organisms can exceed that on the open reef (*13*, *14*). DOM removal rates in cryptic habitats on Caribbean reefs (*12*) are comparable to the average gross primary production rates of the entire coral reef ecosystem (*2*). DOM removal rates on Indo-Pacific reefs are lower (*12*) but still account for up to 46% of the average gross reef productivity. Sponges are primarily responsible for total DOM uptake and remove the same amount of DOM from the water column in 30 min as free-living bacteria take up in 30 days (*12*, *15*). Therefore, sponges retain organic matter within the reef community and thereby prevent energy and nutrient losses to the open ocean. Surprisingly however, sponges respire only 42% of the carbon taken up from the surrounding water (*15*, *16*). Assuming that the remaining 58% is used for growth, a biomass increase of 38% of body carbon per day (more than a doubling of biomass every 3 days) would be expected (*16*). In reality, however, the net growth rate of sponges is near zero (*15*, *16*), implying high losses of sponge biomass through a rapid tissue turnover.

A rapid turnover and extensive loss of sponge cells to the surrounding water has been shown for the sponge *Halisarca caerulea (17)*. The sponge's filter cells (choanocytes) divide every 5 to 6 hours, representing the fastest cell cycle found in any multicellular organism to date (*17*). This rapid cell production is counterbalanced by massive shedding of old choanocytes as particulate organic matter (POM or detritus) into the water column (*17*). Massive shedding of POM is also observed in other tropical sponges (*18*, *19*).

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This suggests that sponges use the majority of incorporated carbon to rejuvenate their filter system and maintain a high cell turnover.

We hypothesize here that shed sponge cells (detritus) are subsequently ingested by particle-feeding organisms (detritivores). Sponges thereby make the energy and nutrients stored in the DOM pool available to organisms at higher trophic levels that would otherwise be unable to capitalize on this resource. Because small detritivores (such as crustaceans and polychaetes) are themselves fed upon by larger animals higher in the food web, sponges are at the base of a sponge loop that ultimately recycles energy and nutrients back into the ecosystem in a similar way as the microbial loop does in the open ocean.

To study the proposed DOM-sponge-detritus feedback loop on coral reefs, we tested three key predictions of this hypothesis: (i) sponges take up DOM, (ii) sponges convert DOM into detritus, and (iii) sponge-derived detritus is taken up by detritivores. These three predictions were first tested in flow chambers in a controlled running-seawater aquarium setup (fig. S1) using ^{13}C- and ^{15}N-enriched DOM, extracted from the cosmopolitan marine diatom *Phaeodactylum tricornutum*, as a food web tracer (*20*).

All three key elements were confirmed experimentally (Fig. 1). Four common reef sponge species showed uptake of dissolved organic carbon ($DO^{13}C$) and nitrogen ($DO^{15}N$) (Fig. 1A). All four species subsequently produced ^{13}C- and ^{15}N-enriched detritus (Fig. 1B). The four sponge species converted 11 to 24% of the assimilated $DO^{13}C$ into detritus ($PO^{13}C$) and 18 to 36% of the $DO^{15}N$ into $PO^{15}N$ within 3 hours (Fig. 1, A and B). Control incubations showed that detritus production without sponges was less than 4% of the detritus production in incubations with sponges. Detritivores subsequently fed on the labeled sponge-derived detritus (Fig. 1C). Isotopically enriched detritus, collected from specimens of the four tested sponge species (fig. S2) that were repeatedly fed with ^{13}C- and ^{15}N-enriched DOM (*20*), was added to six cores containing cavity sediments with residing fauna and, in three out of six cores, motile fauna were added (hermit crabs and snails) (fig. S1). Within 6 hours, sponge detritus was incorporated by 17 out of 28 (^{13}C) and 23 out of 28 (^{15}N) specimens of detritivores.

After experimental confirmation of a sponge loop in flow chambers, the question arose whether this newly found pathway could actually be identified in a complex coral reef environment. Therefore, the water exchange of two in situ cryptic reef cavities (75 and 100 liters) with the surrounding reef water was temporarily restricted (*12*, *20*), and ^{13}C- and ^{15}N-enriched DOM was injected into the enclosed cavity at the start of two consecutive incubation periods of 3 hours (fig. S3). Once we restored the water exchange between the water column and the cavities, the presence and fate of labeled DOM were analyzed over the subsequent 45 hours within the main cavity compartments; that is, sponges, sponge-derived detritus, surface sediment, bacterioplankton, nonsponge filter feeders, and motile fauna such as hermit crabs and snails (*20*). The relative abundance of ^{13}C and ^{15}N in these compartments over time provided qualitative

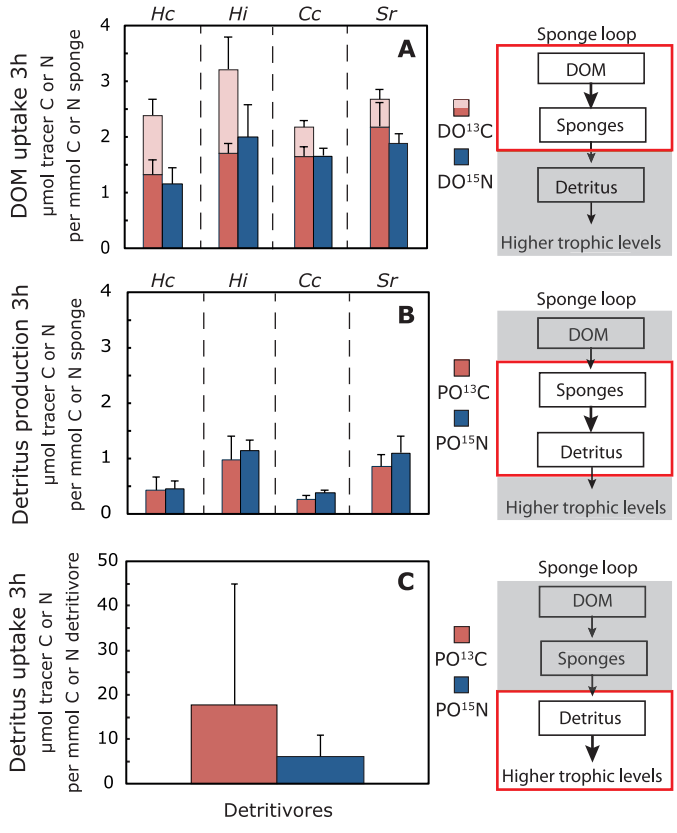

Fig. 1. Fate of DOM tracer ^{13}C (red bars) and ^{15}N (blue bars) through sponge-driven DOM transfer in flow chamber experiments. (**A**) Uptake of tracer DOM ($DO^{13}C$ and $DO^{15}N$; micromoles of tracer per millimole of sponge C or N ± SD; *n* = 4 specimens) by the sponge species *Halisarca caerulea* (*Hc*), *Haliclona implexiformis* (*Hi*), *Chondrilla caribensis* (*Cc*), and *Scopalina ruetzleri* (*Sr*). The uptake of $DO^{13}C$ by sponges is further specified in tissue assimilation (dark red bars) and respiration (light red bars). (**B**) Production of detritus ($PO^{13}C$ and $PO^{15}N$; micromoles of tracer per millimole of sponge C or N ± SD; *n* = 4 specimens) by the sponges HC, HI, CC, and SR. (**C**) Uptake of sponge-derived tracer detritus ($PO^{13}C$ and $PO^{15}N$; micromoles of tracer per millimole of faunal C or N ± SD) by detritivores (*n* = 28 specimens) picked from six cores of reef sediment; three cores were supplemented with hermit crabs and snails.

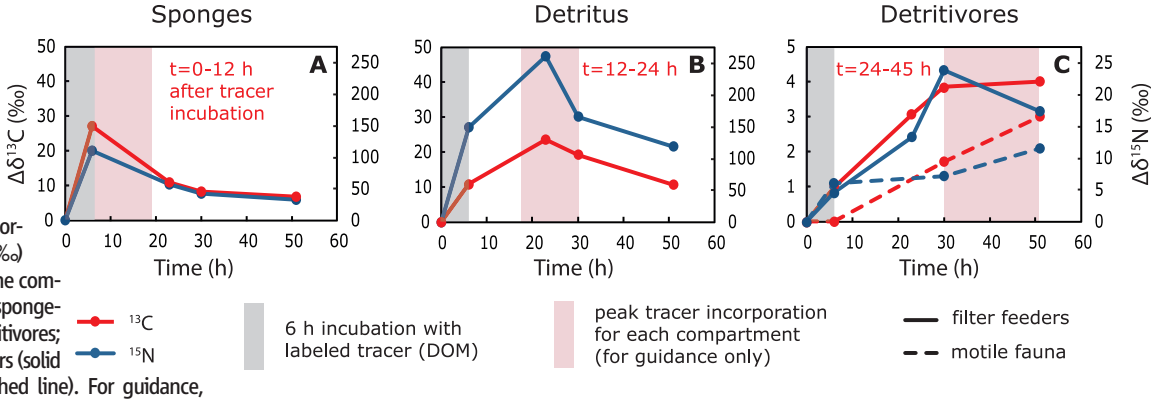

Fig. 2. In situ sponge-driven transfer of tracer DOM (red line, ^{13}C; blue line, ^{15}N) in coral reef cavities after a temporary 6-hour closure (gray shading) and the subsequent 45 hours. The mean above-background isotope tracer incorporation ($\Delta\delta^{13}C‰$ and $\Delta\delta^{15}N‰$) of two cavities is shown for the compartments (**A**) sponges, (**B**) sponge-derived detritus, and (**C**) detritivores; that is, nonsponge filter feeders (solid line) and motile fauna (dashed line). For guidance, the interval of peak tracer incorporation is highlighted for each compartment. *t*, time; h, hours.

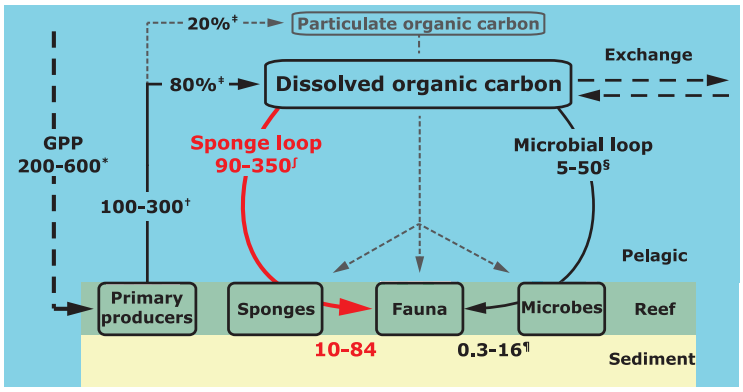

Fig. 3. A simplified scheme of dominant pathways (millimoles of C m^{-2} day^{-1}) of organic carbon transfer on coral reefs in the pelagic (blue), benthic reef (green), and sediment (yellow) ecosystem compartments. The proposed sponge loop (red arrow) is shown in addition to the classical microbial loop. GPP, gross primary production. *(*2*), †(*5*, *6*), ‡(*7*), ʃ(*12*), §(*11*, *12*) ¶(*11*); see (*20*) for details.

evidence in support of our proposed pathway of sponge-driven DOM transfer (Fig. 2). After the introduction of labeled DOM to coral cavities, the uptake of tracer ^{13}C and ^{15}N was first observed in sponges (first prediction: DOM-sponge; mean sponge $\Delta\delta^{13}C$ 27 per mil (‰) and $\Delta\delta^{15}N$ 111‰; Fig. 2A) immediately after the 6-hour incubation period. Between 12 and 24 hours after the incubation, the relative isotope abundance peaked in sponge-derived detritus (second prediction: sponge-detritus; mean detritus $\Delta\delta^{13}C$ 24‰ and $\Delta\delta^{15}N$ 261‰; Fig. 2B). The sponge-derived detritus was finally transferred into motile fauna and nonsponge filter feeders after 45 hours (third prediction: detritus–higher trophic levels; steady increase to a detritivore $\Delta\delta^{13}C$ 3 to 4‰ and $\Delta\delta^{15}N$ 12 to 17‰; Fig. 2C). The ^{13}C:^{15}N ratio of sponge-derived detritus was lower than the ^{13}C:^{15}N of the sponges (Fig. 2, A and B), indicating that the detritus was relatively enriched in N. The DOM-derived $\Delta\delta^{13}C$ or $\Delta\delta^{15}N$ in the surface sediment or the bacterioplankton was generally lower than 2‰, indicating limited uptake by these compartments.

The seemingly paradoxical observation that productive ecosystems such as coral reefs thrive in nutrient-poor waters can only be explained through processes ensuring efficient capture, retention, and recycling of energy and nutrients. Such tight recycling mechanisms involve microbial processing of coral- and algal-derived DOM in the water column and permeable reef sands (*7*, *11*). Here we show that, in addition to the transfer of DOM via bacteria to fauna (*8*), sponges transform the majority of DOM into particulate detritus, a pathway that has hitherto not been recognized (Fig. 3). The underlying mechanisms of DOM uptake and rapid cell turnover in sponges are not yet fully understood. Sponges form close associations with microorganisms, forming so-called holobionts, and both sponge cells and microbes can assimilate DOM (*16*), although their relative contributions remain largely unknown. The sponge loop nevertheless greatly enhances our growing understanding of the efficiency that typifies coral reefs, thus supporting reef life, increasing biodiversity (*21*, *22*,) and maintaining high productivity. Sponges not only recycle the energy retained in DOM but also provide reef fauna with a source of nutrients (such as N), thereby fertilizing the coral reef ecosystem. The efficient and fast uptake, retention, and release (*23*) of nutrients within the originally oligotrophic ecosystem by sponges may also catalyze nutrient-induced shifts in the coral-algal-microbe community after eutrophication, often associated with coral reef degradation (*24*, *25*). Top-down–controlled shifts from coral- to sponge-dominated reefs have been predicted (*26*) and recorded in the Caribbean (*27*, *28*), but still sponges are rarely considered in analyses of alternative stable states on coral reefs. Other oligotrophic ecosystems where sponges are abundant, such as deep-sea cold-water coral reefs and temperate Mediterranean reefs, may also sustain the functioning of a sponge loop. Deep-sea sponges contribute substantially to the respiration of cold-water reef communities (*29*) and produce large amounts of detritus (*30*). Mediterranean reefs are dominated by (cryptic) sponges, of which several abundant species are found to take up DOM (*31*). Although this study shows the presence of the sponge loop mainly qualitatively, DOM turnover by sponges (*15*) approaches the daily gross primary production of the entire reef ecosystem (*2*, *4*), suggesting that this energetic pathway is of great ecological importance (Fig. 3). Recognition of the key role of sponges in coral reefs has, consequently, implications for studies on ecosystem services and conservation strategies in ecosystems where sponges are a ubiquitous component.

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Supplementary Materials

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Materials and Methods
Figs. S1 to S3
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