Sources of Organic Carbon to Coral Reef Flats

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ABSTRACT. Simultaneous measurement of the gross and net primary production of the benthic community and the net input of organic carbon delivered by currents to the coral reef flat of the north shore of Moorea, French Polynesia, confirms that carbon fixation by bottom-dwelling autotrophs, including algal symbionts in corals and benthic free-living algae, is the major source of new organic matter to this system. However, particulate organic carbon, including plankton, detritus, and macroalgal fragments originating primarily on the fore reef and reef crest and carried onto the reef flat by currents contributes up to 13% of the net organic carbon input to the zone nearest the reef crest. These results are typical of the many reef flats worldwide that experience unidirectional flow.

Darwin (1842) was the first to note the paradox presented by the high biomass and rich diversity of coral reef communities despite their location in warm, nutrient-poor waters. Coral reefs are now known to be among the most productive ecosystems in the world, with areal rates of carbon fixation rivaling those of agricultural crops (Hatcher, 1988) even though water-column nutrients, especially the nitrogen and phosphorous required for growth of the main primary producers (bottom-dwelling algae and algal symbionts within corals), are in very low concentrations. Explaining this paradox has been a major theme spanning decades of research on these fascinating systems. Proposed solutions to the paradox have included tight recycling of nutrients between symbiotic algae (zooxanthellae) and their coral hosts, nutrients supplied by upwelling, remineralization within the reef framework, nutrient exchange between various reef zones with some acting as sinks and others as sources, the production of low-quality organic matter requiring less nitrogen and phosphorous to create, and, finally, large amounts of nutrients delivered by currents (Hatcher, 1990; Atkinson and Falter, 2003; Atkinson, 2011).

However, currents flowing over coral reef flats deliver not just nutrients but also organic carbon originating from the fore reef and offshore as particles of phytoplankton, zooplankton, microbes, and detritus and as dissolved carbohydrates, lipids, and proteins. While photosynthesis by reef algae and algal symbionts creates new organic carbon from CO_2, flow-delivered organic matter also represents an input of new organic carbon that can be utilized by reef consumers. The magnitude of this horizontal input of particulate and dissolved organic carbon (POC and DOC) to coral reef flats has been measured much less frequently than new carbon added through photosynthesis, and not since the classic study of Odum and Odum (1955) have both sources been estimated simultaneously on the same reef.

Figure 1 illustrates the major sources and sinks of organic carbon in a section of coral reef flat that experiences unidirectional flow. The figure shows POC and DOC flowing into a defined volume from upstream. Myriad processes occur between the benthos and the water column and within the water column itself that serve to remove, transform, or add material to the POC and DOC pools within the volume. Removal processes include consumption of POC by fishes and invertebrates and sedimentation to the seafloor followed by decomposition by microbes and detritovores. Likewise, DOC may be removed by uptake, sorption, and remineralization by heterotrophic bacteria or it may become adsorbed to organic or mineral surfaces. Production processes include POC produced by organisms as tissue growth, propagules, molts, mucus, and fecal pellets, some of which may exit the control

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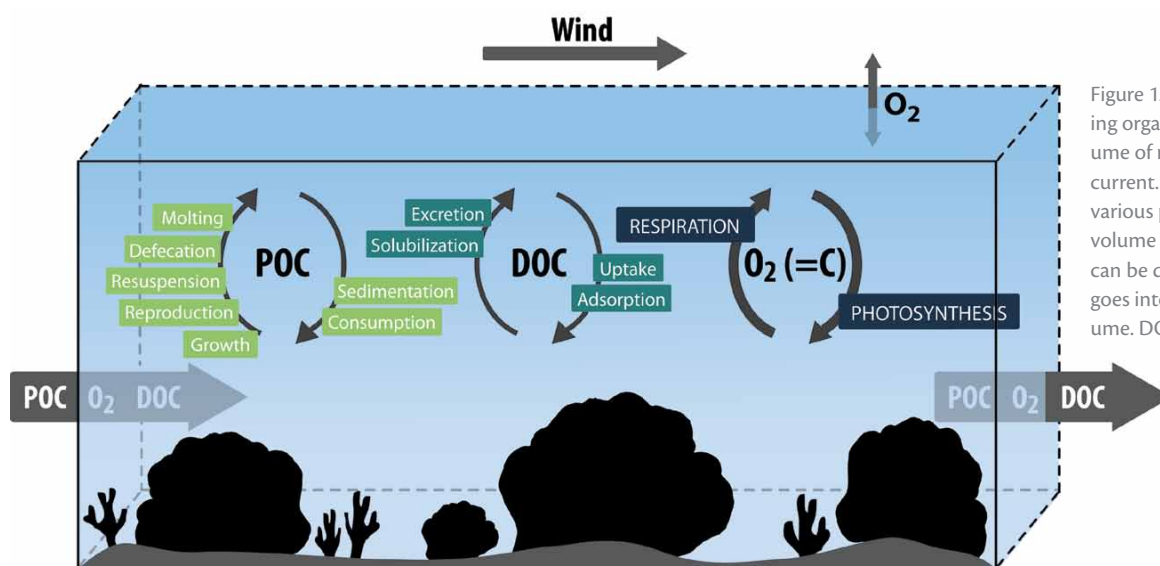
Figure 1. Processes increasing and decreasing organic carbon within a defined volume of reef where there is a unidirectional current. While the rates of most of the various processes occurring within the volume are not known, the net changes can be determined by measuring what goes into and comes out of the volume. DOC = dissolved organic carbon. POC = particulate organic carbon.

volume. Direct exudation, excretion, and egestion by reef organisms and microbes can be a net source of DOC within the control volume. Finally, new carbon is produced within the control volume through the fixation of CO_2 by photosynthesizing algal symbionts in corals, turf algae, macroalgae, benthic (bottom-dwelling) diatoms, and phytoplankton.

During the process of photosynthesis, approximately one molecule of oxygen (O_2) is generated for every atom of carbon fixed. In respiration, approximately one molecule of oxygen is taken up for every atom of carbon released as CO_2. Thus, changes

in oxygen concentration (factoring in wind-dependent O_2 exchange at the sea surface) have been used as a proxy for carbon fixation and respiration in these systems (Sargent and Austin, 1949; Falter et al., 2008). Measuring the change in oxygen concentration from upstream

to downstream, during the day, when both photosynthesis and respiration are occurring, allows net primary production of the whole community to be estimated (net production = daytime carbon fixation – respiration). Measuring the decrease in oxygen from upstream to downstream at night, when only respiration is occurring, and assuming that the daytime community respiration rate is similar to that at night allows estimation of the gross primary production of the whole community (gross production =
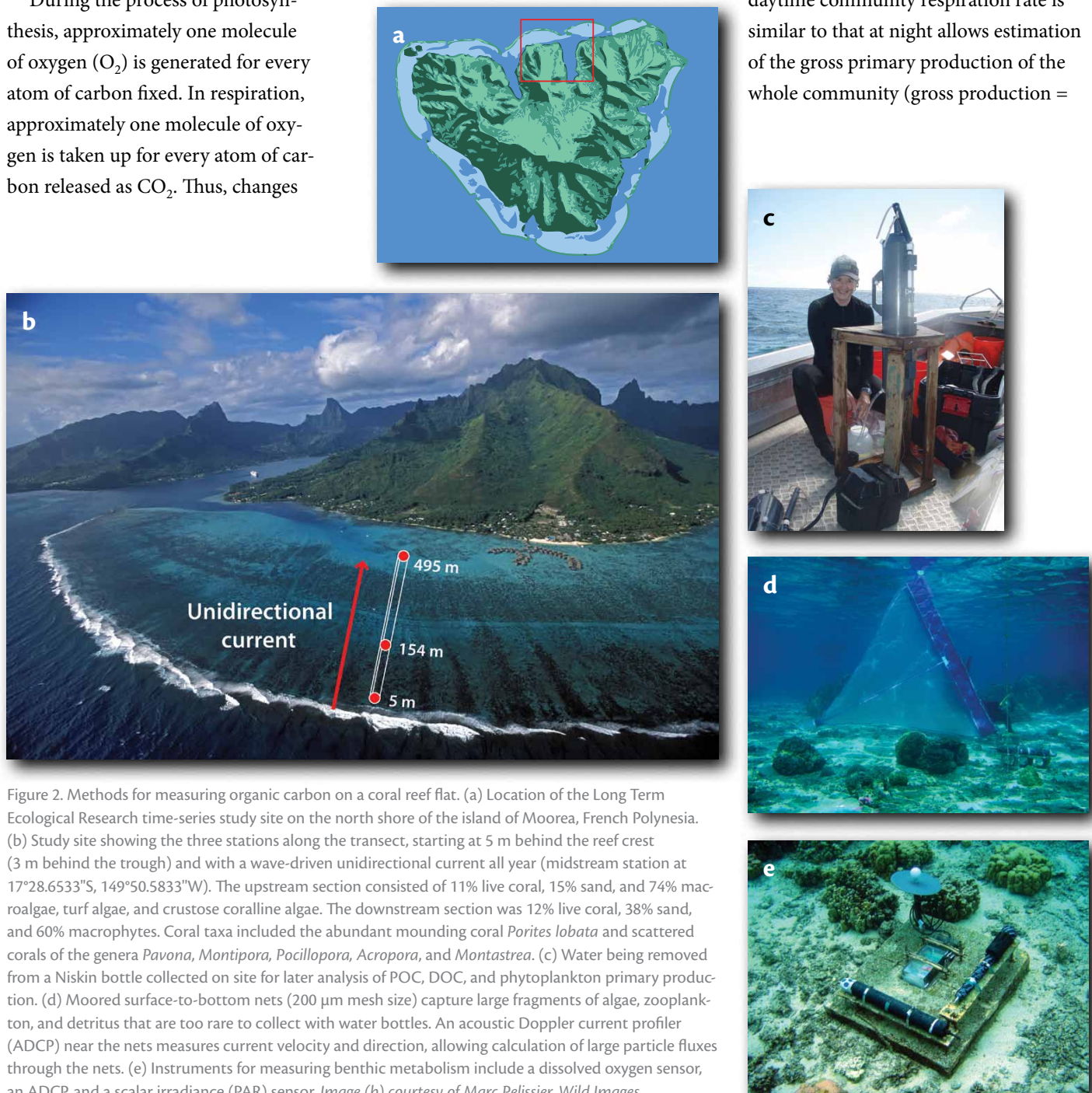
Figure 2. Methods for measuring organic carbon on a coral reef flat. (a) Location of the Long Term Ecological Research time-series study site on the north shore of the island of Moorea, French Polynesia. (b) Study site showing the three stations along the transect, starting at 5 m behind the reef crest (3 m behind the trough) and with a wave-driven unidirectional current all year (midstream station at 17°28.6533"S, 149°50.5833"W). The upstream section consisted of 11% live coral, 15% sand, and 74% macroalgae, turf algae, and crustose coralline algae. The downstream section was 12% live coral, 38% sand, and 60% macrophytes. Coral taxa included the abundant mounding coral *Porites lobata* and scattered corals of the genera *Pavona, Montipora, Pocillopora, Acropora*, and *Montastrea*. (c) Water being removed from a Niskin bottle collected on site for later analysis of POC, DOC, and phytoplankton primary production. (d) Moored surface-to-bottom nets (200 μm mesh size) capture large fragments of algae, zooplankton, and detritus that are too rare to collect with water bottles. An acoustic Doppler current profiler (ADCP) near the nets measures current velocity and direction, allowing calculation of large particle fluxes through the nets. (e) Instruments for measuring benthic metabolism include a dissolved oxygen sensor, an ADCP, and a scalar irradiance (PAR) sensor. *Image (b) courtesy of Marc Pelissier, Wild Images*

net production + respiration). Likewise, measurement of POC and DOC entering and exiting the volume with currents reveals community-wide net changes to these carbon pools. While knowing input and output to the volume tells us little about the processes that alter organic carbon pools within the volume itself, they reveal the relative significance of the various organic carbon sources to the ecology and carbon cycling of the reef.

The site of the Moorea Coral Reef Long Term Ecological Research (MCR LTER) time-series study of benthic community metabolism on the north shore of Moorea is ideal for investigating new organic carbon sources to a coral reef flat. This site (Figure 2a,b) is typical of many island reef flats in that it experiences wave-driven, unidirectional currents as POC and DOC-laden waters flow over the very shallow (20–50 cm) reef crest onto the reef flat and toward shore (Hench et al., 2008). Three stations were sampled on the 490 m long transect parallel to the direction of flow: upstream (1.5 m deep), midstream (3 m deep), and downstream (3 m deep), dividing the transect into two sections (Figure 2b). Dye and drogue studies verify that these stations were in the same flow streamlines. The upstream section is an MCR time-series site where rates of net community primary production and respiration were calculated from the upstream-downstream difference in dissolved oxygen (DO) concentration, current speed, and air-sea DO flux biannually (Smith and Marsh, 1973; Carpenter and MacIntyre, 2010).

Figure 2 illustrates typical modern sampling methods for assessing organic carbon input and output to the reef flat. Seawater samples for determination of carbon fixation by phytoplankton (using standard ^{14}C-bicarbonate methods for 24-hour incubations; USJGOFS, 1996; Alldredge and Carlson, 2011) and concentrations of DOC and POC < 200 μm in size (Shipe et al., 2002; Nelson et al., 2011) were collected by snorkelers at two to three depths at each station with Niskin bottles (Figure 2c). Large particles > 200 μm entering and exiting the transect, including algal fragments, fronds of the macroalgae *Sargassum pacificum* and *Turbinaria ornata*, zooplankton, fecal pellets, and detritus were too rare to be accurately sampled with water bottles and instead were collected by moored surface-to-bottom plankton nets that acted like windsocks underwater (Figure 2d). Total POC and DOC flux at each station can be calculated using current velocities determined with acoustic Doppler current profilers (Figure 2d,e). Finally, scalar irradiance and benthic community carbon fixation and respiration were measured with light and oxygen sensors at each station (Figure 2e).

Table 1 summarizes the organic carbon budget for May 3–9, 2011, when current velocities ranged from 9 to 18 cm s^{-1}. Benthic autotrophy accounted for an average of 87% of gross new organic carbon input to the upstream portion of the control volume with flow-delivered organic carbon accounting for almost 13%. Of this horizontal input of POC, 61% came from large, rare particles collected in the plankton nets, including fragments of benthic algae, crustacean molts, meroplankton, and large fecal pellets that clearly originated from the fore reef and reef crest rather than from oceanic waters. Suspended particles collected with moored nets in other studies have also been dominated by particles largely of reef origin (Odum and Odum 1955; Johannes and Gerber 1974). Because most of these large particles settled out or were consumed in the upstream section, the downstream section experienced little net horizontal input, and 99% of the new organic carbon added to the downstream portion came from benthic autotrophy. Phytoplankton primary production in the water column over both sections was insignificant (< 0.7%), and no consistent depletion or augmentation of DOC from the water column could be resolved. Because the DOC pool in surface seawater is large (> 65 μmol L^{-1}), slight removal of DOC from the water column

Table 1. Mean input (± standard error) of new organic carbon to the two sections of the transect on the north shore of Moorea, French Polynesia, in May 2011.

Sources of New Organic Carbon	Distance Behind Reef Crest			
	5–154 m		154–495 m	
	mmol C m^{-2}d^{-1}	%	mmol C m^{-2}d^{-1}	%
Gross benthic carbon fixation	512 ± 23	86.8	*373	99.3
Gross water column carbon fixation	1.8 ± 0.1	0.3	2.6 ± 0.2	0.7
Net input of POC from horizontal flow	76 ± 13	12.9	0	0
Net input of DOC from horizontal flow	0	0	0	0
Total New Organic Carbon Input	590 ± 36	100	*376	100

*Benthic carbon fixation at the downstream section was estimated assuming production was similar to the upstream section, but proportionately lower due to higher sand cover, and that production by benthic microphytes in the sand was minimal (Suzumura et al., 2002).

could represent a considerable carbon input to the pelagic microbes or benthic community and suggests the need for further investigation.

Table 2 compares the reef flat on the north shore of Moorea with other reef flats around the globe. Over time, the reef flat in Moorea is highly productive, with gross primary production (GPP) over three years averaging about 1,180 to 1,700 mmol C m^{-2} d^{-1}, slightly higher than the 250 to 1,250 mmol C m^{-2} d^{-1} reported for other reef flats. Although this Moorean reef flat is net autotrophic over time (Table 2), skies were periodically overcast during the study period in May. This reduced photosynthesis and resulted in net heterotrophy of the reef, with community respiration exceeding community carbon fixation during that time. The net input of organic carbon from flow-delivered POC and phytoplankton production was only sufficient to counterbalance 25% of the net carbon

loss due to community respiration over this period. Periodic net heterotrophy is common on coral reefs (Table 2), although over time, if the reef is to flourish and grow, autotrophy must exceed heterotrophy as it does in Moorea.

Flow-delivered organic carbon in Moorea was slightly higher than the range of 0–45 mmol m^{-2} d^{-1} reported for other reefs (Table 2), although only Odum and Odum (1955) and the MCR LTER data allow comparison of flow-delivered organic carbon and benthic primary production simultaneously. In general, the high benthic primary production of reef flats and the comparatively low input of organic carbon delivered by currents support the contention that coral reef flats are relatively independent of their surrounding oceanic waters with regard to input of organic carbon. Lack of POC removal in water flowing over coral reefs has been documented previously in the Comoro

Archipelago (Houlbreque et al., 2006). Some reefs, including the north shore of Moorea (Schrimm et al., 2002), can experience net export of organic matter (Hata et al., 1998). Benthic autotrophy clearly dominates new carbon input, although flow-delivered organic carbon may increase in importance at high current velocities and in the zone directly behind the reef crest where a larger, more robust community of microbial and detrital consumers and distinctive energy flow and community dynamics might be expected. However, unique particles originating offshore, such as some phytoplankton and zooplankton, may be disproportionately important to certain fish and benthic consumers on the reef and represent important input from oceanic waters. Finally, the carbon fixation and growth of the various autotrophs in the reef community require nutrient input and ultimately are dependent on nitrogen and phosphorous

Table 2. Primary production and net uptake of flow-delivered particulate organic carbon (POC) previously reported for various hard coral reef flats.

Location	Primary Production (mmol C m^{-2} d^{-1})		Input from Flow Sources (mmol POC m^{-2} d^{-1})	Data Sources
	Gross	Net		
Marshall Islands	512–1,248	0–720	37–45	Sargent and Austin (1949); [†]Odum and Odum (1955); Smith and Marsh (1973); [††]Johannes and Gerber (1974)
Guam	864	320		Marsh (1974)
Hawaii	256–928	−352–384		Kohn and Helfrich (1957); Kinsey (1979); Falter et al. (2008)
Great Barrier Reef	768–832	−192–198		Kinsey (1979); Barnes and Devereaux (1984)
Japan			5–7	Hata et al. (2002)
Comoro Archipelago			0	Houlbreque et al. (2006)
Laccadive Archipelago			27	[††]Tranter and George (1969)
Moorea	640–1,696	0–288		Sournia et al. (1981); Gattuso et al. (1993); Andrefouet and Payri (2000)
MCR LTER	1,184–1,664	96–1,152		MCR LTER multiyear average
MCR LTER	512	−310	0–76	This study

[†]Original data expressed as mass was converted to C assuming 28% organic carbon (the % organic carbon content of net-collected material on the Moorea Coral Reef LTER [MCR] transect)
[††] POC collected only with nets. No water bottle samples collected.

from surrounding waters, the availability of which is mass-transfer limited and dependent on flow rates (Carpenter and Williams, 2007; Atkinson, 2011). While currents may be less important in bringing new organic carbon from surrounding waters to coral reef flats, they remain pivotal in delivering these essential nutrients.

ACKNOWLEDGEMENTS

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