

Benthic N₂ fixation in coral reefs and the potential effects of human-induced environmental change

Ulisse Cardini^{1*}, Vanessa Bednarz¹, Rachel A. Foster^{2,4} and Christian Wild^{1,3}

¹Coral Reef Ecology Group (CORE), Leibniz Center for Tropical Marine Ecology (ZMT), Fahrenheitstr. 6, 28359 Bremen, Germany

²Max Planck Institute for Marine Microbiology, Celsiusstr. 1, 28359 Bremen, Germany

³University of Bremen, Faculty of Biology and Chemistry (FB 2), Bremen, Germany

⁴current address: Department of Ecology, Environment, and Plant Sciences, Stockholm University, SE-10691 Stockholm, Sweden

*corresponding author:

Ulisse Cardini

Tel: +49(0)421/238 00-138

Fax: +49(0)421/238 00-30

Email: ulisse.cardini@zmt-bremen.de

Supplementary Information

Supplementary Table 1. Values in this Table have been collected from the available literature and used to produce the graph in Fig. 3. Rates of N₂ fixation have been extrapolated from the text when possible, and the original conversion factor used by the authors has been reported. If no conversion was available, but only C₂H₂ reduction rates were reported, the conservative 4:1 conversion ratio has been used. ARA = Acetylene Reduction Assay, ¹⁵N₂ = labeling incubations with isotope ¹⁵N₂. Only studies with rates normalized to surface area are shown.

Substrate	Methods	Ratio (mol C ₂ H ₂ :1 mol N ₂)	N ₂ fixation rates (mg N m ⁻² day ⁻¹)	Location	References
Scleractinian corals	ARA	4.00	3.32 ± 3.70	Eilat, Israel	Shashar <i>et al.</i> (1994b)
	ARA	4.00	0.29 - 1.13	Great Barrier Reef, Australia	Davey <i>et al.</i> (2008)
	ARA	3.45	9.75 ± 8.18	Eilat, Israel	Shashar <i>et al.</i> (1994a)
	ARA	4.00	2.90 ± 2.19	Eilat, Israel	Shashar <i>et al.</i> (1994a)
	ARA	4.00	3.69 ± 1.60	Eilat, Israel	Shashar <i>et al.</i> (1994a)
	ARA	4.00	5.24 ± 0.25	Eilat, Israel	Shashar <i>et al.</i> (1994a)
	ARA	4.00	3.69 ± 4.96	Eilat, Israel	Shashar <i>et al.</i> (1994a)
	ARA	3.45	7.21 ± 2.69	Eilat, Israel	Shashar <i>et al.</i> (1994a)
	ARA	3.45	0.68 ± 0.45	Eilat, Israel	Shashar <i>et al.</i> (1994a)
	ARA	3.00	0.00 - 8.40	Akumal, Mexico	Lesser <i>et al.</i> (2007)

Other cnidarians	ARA	4.00	30.0 ± 11.93	Eilat, Israel	Shashar <i>et al.</i> (1994b)
	ARA	4.00	0.08 ± 0.25	Eilat, Israel	Shashar <i>et al.</i> (1994b)
Sponges	ARA	4.00	0.19 ± 0.34	Eilat, Israel	Shashar <i>et al.</i> (1994b)
Macro/Turf Algae	ARA	3.45	0.44 - 1.07	Great Barrier Reef, Australia	Larkum <i>et al.</i> (1988)
	ARA	3.45	8.18 ± 12.05	St. Croix, US Virgin Island	Williams and Carpenter (1997)
	ARA	4.00	22.69 ± 9.24	Kaneohe Bay, Oahu, Hawaii	Williams and Carpenter (1998)
	ARA	3.45	10.36 ± 0.56	Eilat, Israel	Shashar <i>et al.</i> (1994b)
Limestone/Dead corals	ARA	4.00	0.00 - 42.16	Great Barrier Reef, Australia	Wilkinson <i>et al.</i> (1984)
	ARA	4.00	0.51 ± 0.78	Eilat, Israel	Shashar <i>et al.</i> (1994b)
	ARA	3.45	10.72 ± 11.30	Great Barrier Reef, Australia	Larkum <i>et al.</i> (1988)
	ARA + ¹⁵ N ₂	3.30	2.12	Tuamotu Atoll, French Polynesia	Charpy-Roubaud <i>et al.</i> (2001)
	ARA	3.45	1.05 - 25.98	Great Barrier Reef, Australia	Davey <i>et al.</i> (2008)
	ARA	3.45	3.61 - 15.98	Great Barrier Reef, Australia	Larkum (1988)
	ARA	3.45	62.23 ± 31.94	Eilat, Israel	Shashar <i>et al.</i> (1994b)
	ARA	3.45	4.68 - 30.79	Great Barrier Reef, Australia	Larkum (1988)
Carbonate sands	ARA	3.00	0.06 - 0.26	Great Barrier Reef, Australia	Werner <i>et al.</i> (2008)
	ARA + ¹⁵ N ₂	3.00	1.80	Barbados	Patriquin and Knowles (1975)
	ARA	4.00	1.10 - 8.50	Great Barrier Reef, Australia	Wilkinson <i>et al.</i> (1984)
	ARA	3.00	0.30 - 2.40	Puerto Rico	Corredor and Capone (1985)
	ARA	4.00	0.13 - 4.08	Bermuda	O'Neil and Capone (1989)
	ARA	4.00	0.71 - 5.17	Puerto Rico	O'Neil and Capone (1989)
	ARA	4.00	0.07 - 0.69	San Salvador, Bahamas	O'Neil and Capone (1989)
	ARA	4.00	0.20 - 1.30	Great Barrier Reef, Australia	O'Neil and Capone (1989)
	ARA + ¹⁵ N ₂	3.16	2.00 - 10.00	Moreton Bay, Australia	O'Donohue <i>et al.</i> (1991)
	ARA	3.00	1.68 - 4.37	Great Barrier Reef, Australia	Capone <i>et al.</i> (1992)
	ARA + ¹⁵ N ₂	1.80 - 3.00	0.40 - 3.90	Tuamotu Atoll, French Polynesia	Charpy-Roubaud <i>et al.</i> (2001)
	ARA	3.45	21.87 ± 19.61	Eilat, Israel	Shashar <i>et al.</i> (1994b)
	ARA + ¹⁵ N ₂	3.45	0.34 ± 0.09	Great Barrier Reef, Australia	Larkum <i>et al.</i> (1988)

	ARA + ¹⁵ N ₂	3.45	0.81 ± 0.30	Great Barrier Reef, Australia	Larkum <i>et al.</i> (1988)
	ARA	4.00	8.21 ± 2.70	New Caledonia	Charpy <i>et al.</i> (2007)
Microbial mats	ARA	4.00	16.40 ± 5.40	New Caledonia	Charpy <i>et al.</i> (2007)
	ARA + ¹⁵ N ₂	1.60	8.00	Tuamotu Archipelago, French Polynesia	Charpy-Roubaud and Larkum (2005)
	ARA	4.00	110.00	Enewetak Atoll, Marshall Islands	Mague and Holm-Hansen (1975)
Seagrasses	ARA + ¹⁵ N ₂	3.16	19.00 - 40.00	Moreton Bay, Australia	O'Donohue <i>et al.</i> (1991)
	ARA + ¹⁵ N ₂	4.40	145.00	Great Barrier Reef, Australia	Iizumi and Yamamuro (2000)
	ARA	3.00	16.00 - 47.00	Gulf of Carpentaria, Australia	Moriarty and O'Donohue (1993)
	ARA	3.00	13.00 - 19.00	Gulf of Carpentaria, Australia	Moriarty and O'Donohue (1993)
	ARA	3.00	25.00	Gulf of Carpentaria, Australia	Moriarty and O'Donohue (1993)
	ARA	n.a.	28.00	Jamaica	Blackburn <i>et al.</i> (1994)
	ARA	n.a.	0.03	Florida, USA	McRoy <i>et al.</i> (1973)
	ARA	3.00	5.00 - 24.00	Biscayne Bay, Florida, USA	Capone and Taylor (1980)
	ARA	3.00	5.10 - 9.00	Bimini Harbour, Bahamas	Capone <i>et al.</i> (1979)
	ARA	3.00	27.00 - 140.00	Barbados	Patriquin and Knowles (1972)

References

- Blackburn T, Nedwell D, Wiebe W (1994) Active mineral cycling in a Jamaican seagrass sediment. *Marine Ecology Progress Series*, **110**, 233-239.
- Capone DG, Dunham SE, Horrigan SG, Duguay LE (1992) Microbial nitrogen transformations in unconsolidated coral-reef sediments. *Marine Ecology Progress Series*, **80**, 75-88.
- Capone DG, Penhale PA, Oremland RS, Taylor BF (1979) Relationship Between Productivity and N₂ (C₂H₂) Fixation in a *Thalassia testudinum* Community. *Limnology and Oceanography*, **24**, 117-125.
- Capone DG, Taylor BF (1980) N₂ fixation in the rhizosphere of *Thalassia testudinum*. *Canadian Journal of Microbiology*, **26**, 998-1005.
- Charpy-Roubaud C, Charpy L, Larkum AWD (2001) Atmospheric dinitrogen fixation by benthic communities of Tikehau Lagoon (Tuamotu Archipelago, French Polynesia) and its contribution to benthic primary production. *Marine Biology*, **139**, 991-997.
- Charpy-Roubaud C, Larkum AWD (2005) Dinitrogen fixation by exposed communities on the rim of Tikehau atoll (Tuamotu Archipelago, French Polynesia). *Coral Reefs*, **24**, 622-628.
- Charpy L, Alliod R, Rodier M, Golubic S (2007) Benthic nitrogen fixation in the SW New Caledonia lagoon. *Aquatic Microbial Ecology*, **47**, 73-81.

- Corredor JE, Capone DG (1985) Studies on nitrogen diagenesis in coral reef sands. In: *The Fifth International Coral Reef Congress*. (eds Gabrie C, Toffart JL, Salvat B) pp Page, Tahiti, French Polynesia.
- Davey M, Holmes G, Johnstone R (2008) High rates of nitrogen fixation (acetylene reduction) on coral skeletons following bleaching mortality. *Coral Reefs*, **27**, 227-236.
- Iizumi H, Yamamuro M (2000) Nitrogen fixation activity by periphytic blue-green algae in a seagrass bed on the Great Barrier Reef. *Japan Agricultural Research Quarterly*, **34**, 69-73.
- Larkum AWD (1988) High rates of nitrogen fixation on coral skeletons after predation by the crown of thorns starfish *Acanthaster planci*. *Marine Biology*, **97**, 503-506.
- Larkum AWD, Kennedy IR, Muller WJ (1988) Nitrogen fixation on a coral reef. *Marine Biology*, **98**, 143-155.
- Lesser MP, Falcon LI, Rodriguez-Roman A, Enriquez S, Hoegh-Guldberg O, Iglesias-Prieto R (2007) Nitrogen fixation by symbiotic cyanobacteria provides a source of nitrogen for the scleractinian coral *Montastraea cavernosa*. *Marine Ecology Progress Series*, **346**, 143-152.
- Mague TH, Holm-Hansen O (1975) Nitrogen fixation on a coral reef. *Phycologia*, **14**, 87-92.
- Mcroy CP, Goering JJ, Chaney B (1973) Nitrogen fixation associated with seagrasses. *Limnology and Oceanography*, **18**, 998-1002.
- Moriarty D, O'donohue M (1993) Nitrogen fixation in seagrass communities during summer in the Gulf of Carpentaria, Australia. *Marine and Freshwater Research*, **44**, 117-127.
- O'donohue MJ, Moriarty DJW, Rae ICM (1991) Nitrogen fixation in sediments and the rhizosphere of the seagrass *Zostera capricorni*. *Microbial Ecology*, **22**, 53-64.
- O'neil JM, Capone D (1989) Nitrogenase activity in tropical carbonate marine sediments. *Marine Ecology Progress Series*, **56**, 145-156.
- Patriquin D, Knowles R (1972) Nitrogen fixation in the rhizosphere of marine angiosperms. *Marine Biology*, **16**, 49-58.
- Patriquin DG, Knowles R (1975) Effects of oxygen, mannitol and ammonium concentrations on nitrogenase [C₂H₂] activity in a marine skeletal carbonate sand. *Marine Biology*, **32**, 49-62.
- Shashar N, Cohen Y, Loya Y, Sar N (1994a) Nitrogen-fixation (acetylene reduction) in stony corals - evidence for coral-bacteria interactions. *Marine Ecology Progress Series*, **111**, 259-264.
- Shashar N, Feldstein T, Cohen Y, Loya Y (1994b) Nitrogen-fixation (acetylene reduction) on a coral reef. *Coral Reefs*, **13**, 171-174.
- Werner U, Blazejak A, Bird P *et al.* (2008) Microbial photosynthesis in coral reef sediments (Heron Reef, Australia). *Estuarine Coastal and Shelf Science*, **76**, 876-888.
- Wilkinson CR, Williams DM, Sammarco PW, Hogg RW, Trott LA (1984) Rates of nitrogen-fixation on coral reefs across the continental-shelf of the central Great Barrier Reef. *Marine Biology*, **80**, 255-262.
- Williams SL, Carpenter RC (1997) Grazing effects on nitrogen fixation in coral reef algal turfs. *Marine Biology*, **130**, 223-231.
- Williams SL, Carpenter RC (1998) Effects of unidirectional and oscillatory water flow on nitrogen fixation (acetylene reduction) in coral reef algal turfs, Kaneohe Bay, Hawaii. *Journal of Experimental Marine Biology and Ecology*, **226**, 293-316.