13. Brand, U., Grunewald, M., Hobe, M., and Simon, R. (2002). Regulation of CLV3 expression by two homeobox genes in Arabidopsis. Plant Physiol. *129*, 565–575.

14. Lenhard, M., Jürgens, G., and Laux, T. (2002). The WUSCHEL and SHOOTMERISTEMLESS genes fulfil complementary roles in Arabidopsis shoot meristem regulation. Development *129*, 3195–3206.

15. Zhou, Y., Yan, A., Han, H., Li, T., Geng, Y., Liu, X., and Meyerowitz, E.M. (2018). HAIRY MERISTEM with WUSCHEL confines CLAVATA3 expression to the outer apical meristem layers. Science *361*, 502–506.

16. Stuurman, J., Jaggi, F., and Kuhlemeier, C. (2002). Shoot meristem maintenance is controlled by a GRAS-gene mediated signal from differentiating cells. Genes Dev. *16*, 2213–2218.

17. Engstrom, E.M., Andersen, C.M., Gumulak-Smith, J., Hu, J., Orlova, E., Sozzani, R., and Bowman, J.L. (2011). Arabidopsis homologs of the petunia hairy meristem gene are required for maintenance of shoot and root indeterminacy. Plant Physiol. *155*, 735–750.

18. Schulze, S., Schafer, B.N., Parizotto, E.A., Voinnet, O., and Theres, K. (2010). LOST MERISTEMS genes regulate cell differentiation of central zone descendants in Arabidopsis shoot meristems. Plant J. *64*, 668–678.

19. Zhou, Y., Liu, X., Engstrom, E.M., Nimchuk, Z.L., Pruneda-Paz, J.L., Tarr, P.T., Yan, A., Kay, S.A., and Meyerowitz, E.M. (2015). Control of plant stem cell function by conserved interacting transcriptional regulators. Nature *517*, 377–380.

20. Xin, W., Wang, Z., Liang, Y., Wang, Y., and Hu, Y. (2017). Dynamic expression reveals a two-step patterning of WUS and CLV3 during axillary shoot meristem formation in Arabidopsis. J. Plant Physiol. *214*, 1–6.

Symbiosis: High-Carb Diet of Reef Corals as Seen from Space

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High levels of phytoplankton visible in satellite imagery are correlated with an increased uptake of carbon compounds by corals. This suggests that corals rely less on carbon production by photosynthetic symbionts when other resources are plentiful, and that the changes in the acquisition mode of carbon can be inferred by remote-sensing techniques.

Tropical coral reefs are key habitats affected by climate change and direct human activities. Despite covering a relatively small area of the ocean, they sustain a significant part of all marine biodiversity. Adding to the global value of these ecosystems, the livelihoods of half a billion people, many of them in developing nations, depend on naturally functioning 'healthy' reefs [1]. The high biodiversity and valuable ecosystem services of coral reefs are directly related to their exceptionally high productivity in otherwise nutrient-poor oceans. This apparent contradiction was first observed by Charles Darwin and became subsequently known as the Darwin Paradox. Corals have evolved different strategies to fulfil their nutritional needs in such resource-poor conditions. The coral animals commonly represent a colonial association of numerous hungry mouths surrounded by tentacles equipped with powerful, poisonous stinging cells — ready to paralyse and swallow nearby zooplankton to acquire vital carbon, nitrogen and phosphorus compounds [2]. In addition, they host unicellular photosynthetic symbionts in the cells of their 'stomach lining'. These symbionts transfer substantial amounts of photosynthetically fixed carbon, in the form of sugars and lipids, to the coral host. This carbon supply can cover a large part of the energy demands of the coral host [3], but apparently, two forms of nutrient acquisition are still not enough at times. In addition, corals can directly take up carbon, nitrogen, and phosphorus, in both dissolved organic and inorganic forms, through their dermal cell layer [4,5]. Physiological experiments under controlled laboratory conditions have revealed that corals can modulate their focus on the different pillars of this so-called mixotrophic nutrition; for instance, by increasing the uptake of particulate food when nutrients in dissolved inorganic forms in the water are low [6] or when the carbon-providing symbionts have been lost [7] (Figure 1).

Recent research has shown that some coral-reef ecosystems may not be as poor as previously thought, since new dissolved inorganic nutrients are regularly provided from deeper, nutrient-rich water layers through upwelling, internal waves, and vertical mixing [8,9]. Does this have implications for the way corals meet their nutritional needs? A new study by Fox *et al.* [10] in this issue of *Current Biology* shows that corals can indeed shift their focus towards the uptake of carbon from the environment when reef waters show high levels of primary production. Notably, the authors have inferred this on the global scale by analysing imagery of coral-reef waters taken from space together with the analysis of stable isotopes accumulated by the corals and their symbionts.

There is an increasing awareness that large-scale oceanic processes need to be taken into consideration when we want to

Figure 1. Coral reef on O'ahu, Hawaii.
Stony corals rely on multiple trophic strategies that enable them to build reefs in nutrient-poor waters. However, the clarity of the water around this Hawaiian coral reef is deceptive: The phytoplankton biomass in near-shore reefs around many Pacific Ocean islands is considerably higher than in the surrounding open ocean [8]. Under such conditions, corals can change the focus between the different forms of nutrition and take up more carbon compounds from the environment.

understand the local response of coral reefs to various forms of natural and human-induced stress [11,12]. Fox and colleagues [10] used a clever combination of large-scale proxies, sensitive analytical methods, and mathematical modelling to tackle the challenge of taking the 'bigger oceanic picture' into account. The result is a nice example that demonstrates how higher levels of nutrients in the water may induce changes in trophic strategies of corals.

First, the authors utilised remote-sensing products to classify a number of coral reef regions of high and low productivity around the world. This was done by using chlorophyll in surface waters as a proxy for the amount of phytoplankton and an indicator of elevated nutrient concentrations. Fox and colleagues then analysed a large number of coral samples from these regions and, among other parameters, determined the ratio between heavy and light carbon isotopes from the coral animals and their photosynthetic symbionts. This ratio varies depending on the source of carbon; specifically, the carbon-rich compounds produced by symbiont photosynthesis have a different isotopic signature than those found in the corals' food items. If the carbon-isotope signatures of corals and their symbionts are very similar, it can be concluded that the coral animals received carbon compounds mostly from their photosynthetic partner organism. Differing carbon isotope signatures in the two partners indicate that the host animals relied more on the uptake of carbon compounds from the environment. Fox and colleagues show that in regions where the amount of phytoplankton in the water is low, the carbon isotope signatures of corals and their symbionts are more similar than in regions with high productivity. This indicates that the coral animals have incorporated a different source of carbon in highly productive reefs. These observations point to a switch in the strategies by which corals sustain their metabolism in nutrient-rich environments with potential effects on the functioning of the main reef-building organisms [7,13].

Although the study of stable isotope ratios enables great insights into the nutritional physiology of symbiotic corals, these methods also have some limitations. It is difficult, for instance, to quantify how much the additional uptake of carbon from the environment contributes to the overall nutrition of the corals. In the presented data, the variability of carbon isotope signatures between different regions is substantially larger than the changes in the difference between coral hosts and their symbionts. Hence, other regional factors also affect the isotopic signatures and complicate quantitative analyses. An interesting question emerges: in which form(s) do the corals take up the environmental carbon compounds? Reef-building corals do not appear to fancy a vegetarian diet, and only some species seem to make use of phytoplankton as a food source [14]. Furthermore, the analysis of stable nitrogen isotopes conducted as part of this study does not show the same clear trend as the carbon markers. If the corals were feeding on their favourite dish, zooplankton, it could be expected that the specific carbon and nitrogen signatures of the food items should both leave their trace in the consumer. However, this does not seem to be the case. This could be due to the fact that feeding may not always induce interpretable changes in the nitrogen isotopic signature of corals [15] or that the incorporated carbon compounds are not derived from particulate food. It is well established that corals are able to take up sugars from the water column [16]; perhaps the corals treat themselves to polysaccharides exuded by the plentiful phytoplankton [17] in regions of high productivity. Future research will tell! Last, but not least, the work by Fox and colleagues [10] underlines the potential of remote-sensing techniques to predict physiological responses of corals to their environment. Already now, the probability that corals experience a heat-stress-induced collapse of the symbiotic association (resulting in the infamous and often-fatal coral bleaching) is routinely monitored across the globe with the help of remote-sensing products. Also, the paper adds to the rising awareness that phytoplankton play an important role in locally modulating the bleaching response during episodes of heat stress. This can be, for instance, in a mitigating way by reducing harmful light stress [18] or in aggravating form by competition for dissolved inorganic nitrogen and phosphorus compounds that are vital to maintain temperature-stress tolerance [11,19,20]. Now, multifactorial physiological experiments should clarify how the change in nutritional patterns observed by Fox and colleagues affect the functioning of the symbiotic association under stress.

REFERENCES

1. Ferrario, F., Beck, M.W., Storlazzi, C.D., Micheli, F., Shepard, C.C., and Airoldi, L. (2014). The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. Nat. Commun. *5*, 3794.
2. Ferrier-Pagès, C., Hoogenboom, M., and Houlbrèque, F. The role of plankton in coral trophodynamics. In Coral Reefs: An Ecosystem in Transition, Z. Dubinsky and N. Stambler, eds. (New York: Springer), pp. 215–229.
3. Muscatine, L., McCloskey, L.R., and Marian, R.E. (1981). Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration 1. Limnol. Oceanogr. *26*, 601–611.
4. Houlbrèque, F., and Ferrier-Pagès, C. (2009). Heterotrophy in tropical scleractinian corals. Biol. Rev. *84*, 1–17.
5. Ferrier-Pagès, C., Godinot, C., D'Angelo, C., Wiedenmann, J., and Grover, R. (2016). Phosphorus metabolism of reef organisms with algal symbionts. Ecol. Monogr. *86*, 262–277.
6. Rosset, S., D'Angelo, C., and Wiedenmann, J. (2015). Ultrastructural biomarkers in symbiotic algae reflect the availability of dissolved inorganic nutrients and particulate food to the reef coral holobiont. Front. Mar. Sci. *2*, 103.
7. Hughes, A.D., and Grottoli, A.G. (2013). Heterotrophic compensation: a possible mechanism for resilience of coral reefs to global warming or a sign of prolonged stress? PLoS One *8*, e81172.
8. Gove, J.M., McManus, M.A., Neuheimer, A.B., Polovina, J.J., Drazen, J.C., Smith, C.R., Merrifield, M.A., Friedlander, A.M., Ehses, J.S., Young, C.W., *et al*. (2016). Near-island biological hotspots in barren ocean basins. Nat. Commun. *7*, 10581.
9. Wolanski, E., and Delesalle, B. (1995). Upwelling by internal waves, Tahiti, French Polynesia. Cont. Shelf Res. *15*, 357–368.
10. Fox, M.D., Williams, G.J., Johnson, M.D., Radice, V.Z., Zgliczynski, B.J., Kelly, E.L.A., Rohwer, F.L., Sandin, S.A., and Smith, J.E. (2018). Gradients in primary production predict trophic strategies of mixotrophic corals across spatial scales. Curr. Biol. *28*, 3355–3363.
11. D'Angelo, C., and Wiedenmann, J. (2014). Impacts of nutrient enrichment on coral reefs: new perspectives and implications for coastal management and reef survival. Curr. Opin. Environ. Sustain. *7*, 82–93.
12. Lowe, R.J., and Falter, J.L. (2015). Oceanic forcing of coral reefs. Annu. Rev. Mar. Sci. *7*, 43–66.
13. Riegl, B., Glynn, P.W., Wieters, E., Purkis, S., D'Angelo, C., and Wiedenmann, J. (2015). Water column productivity and temperature predict coral reef regeneration across the Indo-Pacific. Sci. Rep. *5*, 8273.
14. Leal, M.C., Ferrier-Pagès, C., Calado, R., Thompson, M.E., Frischer, M.E., and Nejstgaard, J.C. (2014). Coral feeding on microalgae assessed with molecular trophic markers. Mol. Ecol. *23*, 3870–3876.
15. Hoogenboom, M., Rottier, C., Sikorski, S., and Ferrier-Pagès, C. (2015). Among-species variation in the energy budgets of reef-building corals: scaling from coral polyps to communities. J. Exp. Biol. *218*, 3866–3877.
16. Stephens, G.C. (1960). Uptake of glucose from solution by the solitary coral, Fungia. Science *131*, 1532.
17. Myklestad, S.M. (1995). Release of extracellular products by phytoplankton with special emphasis on polysaccharides. Sci. Total Environ. *165*, 155–164.
18. Maina, J., Venus, V., McClanahan, T.R., and Ateweberhan, M. (2008). Modelling susceptibility of coral reefs to environmental stress using remote sensing data and GIS models. Ecol. Model. *212*, 180–199.
19. Rosset, S., Wiedenmann, J., Reed, A.J., and D'Angelo, C. (2017). Phosphate deficiency promotes coral bleaching and is reflected by the ultrastructure of symbiotic dinoflagellates. Mar. Pollut. Bull. *118*, 180–187.
20. Wiedenmann, J., D'Angelo, C., Smith, E.G., Hunt, A.N., Legiret, F.-E., Postle, A.D., and Achterberg, E.P. (2013). Nutrient enrichment can increase the susceptibility of reef corals to bleaching. Nat. Clim. Change *3*, 160–164.