

Effect of active water movement on energy and nutrient acquisition in coral reef-associated benthic organisms

Christian Wild^{a,b,1} and Malik S. Naumann^a

^aCoral Reef Ecology Group (CORE), Leibniz Center for Tropical Marine Ecology, 28359 Bremen, Germany; and ^bFaculty of Biology and Chemistry, University of Bremen, 28359 Bremen, Germany

Most visitors of Indo-Pacific coral reefs observe underwater an unexpected phenomenon on the seafloor. Some colonies of the soft coral family Xeniidae open and close their polyps, some pulsing in synchronized, and others in unsynchronized, motion. This pulsation behavior represents a striking and fascinating feature because, sessile benthic (coral reef-associated) organisms do not usually show any active body movements. Surprisingly, to date, no study has resolved the

potential reasons and triggering factors for such an unusual and apparently energy-costly behavior. Intensive literature research results in only two related studies from the 1950s. These early investigations indicate that water temperature and some inorganic ions may affect pulsation rates of xeniid soft corals (1, 2), unfortunately without providing further insights into the potential reasons and/or associated benefits of their pulsation. Now, however, in PNAS, Kremien et al. (3) have

succeeded in bringing some light into the darkness. Our colleagues from Israel are able to show, using an interconnected series of in situ observations and laboratory experiments at the Northern Red Sea, that the pulsation movement of the coral reef-associated soft coral species *Heteroxenia fuscescens* leads to increased water flow and turbulence, thereby generating at least two great benefits: (i) enhancement of photosynthesis via fast removal of excess oxygen; and (ii) prevention of refiltration of surrounding water by neighboring polyps.

Previous research revealed that *H. fuscescens* can be considered as an autotrophic plant animal (4), because it can cover its full carbon requirement via intense photosynthesis of its endosymbiotic algae, the zooxanthellae, that occur in extraordinarily high numbers in soft coral tissues. The results presented by Kremien et al. (3) now help to explain why zooxanthellae photosynthesis can be so effective in pulsating xeniid soft corals. In addition, preventing water refiltration by neighboring polyps may not only improve organic carbon supply by stimulating the uptake of particulate organic matter (e.g., detritus, small phyto- and zooplankton) and dissolved organic matter (DOM) (e.g., small carbohydrates, amino and fatty acids) but also enhance organic nitrogen and phosphorus supplies essential for soft coral growth.

Kremien et al. (3) could finally measure and calculate that the energetic cost for pulsation of xeniid polyps is maximal 56% of the total benefit, thereby clearly demonstrating that this is an economically sound investment.

However, active body movements by benthic (often coral reef-associated) organisms generating water flow may have a variety of benefits, going beyond the interesting findings of Kremien et al. (3). In Fig. 1, we

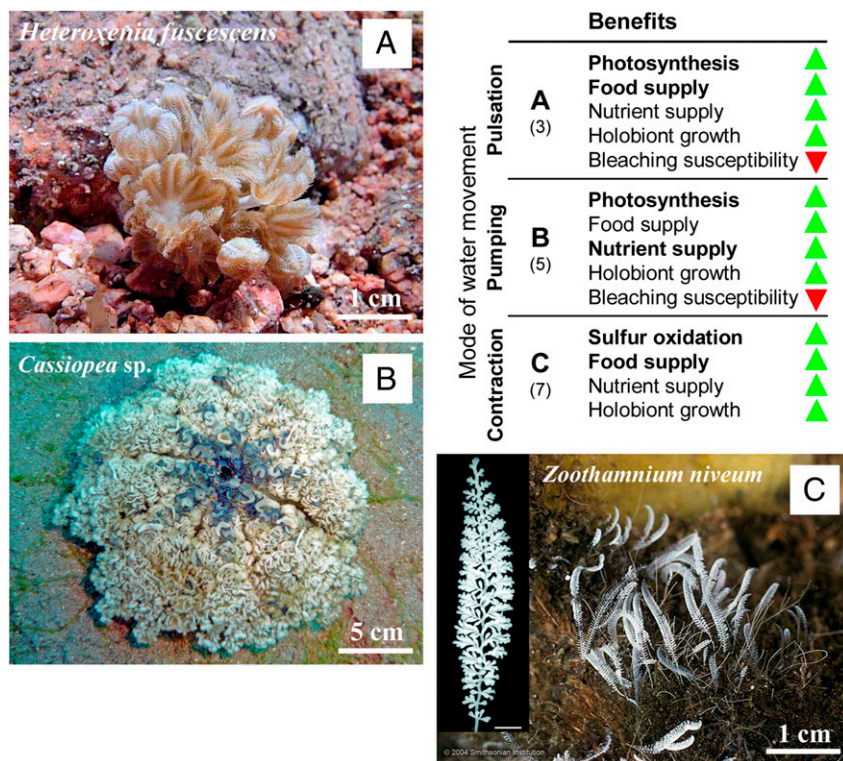


Fig. 1. Benefits of active water movement for (coral reef-associated) benthic organisms. (A) Juvenile soft coral colony of *H. fuscescens* showing unsynchronized pulsating polyps. (B) Medusa of the upside-down jellyfish *Cassiopea* sp. pumping over sandy reef sediments. (C) Colonies of the sessile ciliate *Z. niveum* growing on decaying mangrove wood (courtesy of the Smithsonian Institution); C, Left shows close-up of a single-branched colony harboring ectosymbiotic sulfur-oxidizing microbes. (Scale bar: 0.5 mm.) (Reproduced and modified from ref. 21.) The table at right presents a comparison of proven (in bold) and potential benefits for the three reef-associated organisms (A, B, and C in the table) resulting from respective modes of active water movement. Triangles indicate stimulation (green) or inhibition (red) of processes. Numbers in parenthesis refer to the respective literature source (i.e., refs 3, 5, and 7).

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¹To whom correspondence should be addressed. E-mail: christian.wild@zmt-bremen.de.

summarize proven and potential benefits of active water movement for three different benthic animals associated with coral reef habitats: the key study organism of Kremien et al. (3), *H. fuscescens*, and, as reference organisms, the pumping upside-down jellyfish *Cassiopea* sp. and the contracting sessile ciliate colony *Zoothamnium niveum*. Common for all of these animals is a close association with symbiotic microbes [i.e., either zooxanthellae (*H. fuscescens* and *Cassiopea* sp.) or sulfur-oxidizing ectosymbiotic bacteria (*Z. niveum*)]. Hence, not only the animal host but also the microbes and resulting metabolic communication between both partners may be influenced by the effects of pulsation, pumping, or contraction. We, therefore, refer to all organisms as so-called holobionts in the following.

It becomes clear that benefits of active body movements of benthic marine organisms do not only include enhancement of photosynthesis and prevention of refiltration of surrounding water but also comprise facilitated supply with inorganic compounds, such as fertilizing nutrients (5), and electron donors, such as sulfide (6, 7), via the flow-induced advective transport of pore water from underlying permeable sediments such as reef sands generated by the movements of the respective holobiont. These transport mechanisms exceed diffusive exchange, which takes place without water movement, by orders of magnitude (8) and, thus, can likely promote holobiont growth. For all organisms hosting endosymbiotic zooxanthellae, particularly corals, movement of the holobiont may further reduce their susceptibility to a widespread physiological stress response called bleaching [i.e., loss of zooxanthellae and/or their photosynthetic pigments, primarily caused by elevated temperature in synergy with solar irradiance (9); Fig. 1]. Therefore, holobiont-generated water flows may facilitate the removal of reactive oxygen radicals produced by intense photosynthesis and other toxic metabolites, resulting in potential mitigation of bleaching (10).

From an ecological point of view, pulsating soft corals may, therefore, show higher resilience to temperature-induced bleaching, a climate change-driven global phenomenon increasing in frequency and intensity (9, 11). In addition, soft corals represent superior competitors against hard corals because of powerful chemical defense mechanisms,

including inhibition of larval recruitment via allelopathy (12, 13) and an apparent immunity to impacts of ocean acidification (14). These characteristics may contribute to explain alarming observations in many of today's coral reefs, where soft corals are replacing hard corals (that never pulsate) at a rapid pace within a process called phase shift (9). Thus, pulsating soft corals likely have competitive advantage over hard corals and may become one of the major reef ecosystem engineers in the future.

Such changes in the benthic community composition of coral reefs imply extensive consequences for reef ecosystem functioning and productivity, because hard or soft corals acting as ecosystem engineers control biogeochemical fluxes of inorganic and organic matters very differently (15, 16). Overall, coral reef productivity may not necessarily decrease as a result of a phase shift to dominance of pulsating Xeniids, because the study by Kremien et al. (3) finds a much higher photosynthesis to respiration ratio for the pulsating *H. fuscescens* compared with non-pulsating hard and soft corals. However, this may prove misleading, because, in particular, the generation of stable inorganic carbonate substrates and 3D framework systems important for high reef-associated biodiversity, further enhancing productivity, is not provided by soft corals, which, in con-

trast to hard corals, do not produce rigid aragonite endoskeletons.

The findings by Kremien et al. (3) suggest the availability of substantial excess photosynthetic carbon in pulsating *H. fuscescens*. In hard corals, this organic carbon source is constantly released as mucus or dissolved organic carbon into reef-surrounding waters, where it acts as an energy carrier and particle trap, thereby controlling coral reef biogeochemical element cycling (15, 16). On the contrary, xeniid soft corals do obviously not release substantial amounts of organic matter into their environment (17) and, thus likewise, do not provide this important ecosystem engineering function. As a consequence, available excess photosynthetic carbon may rather be channeled into growth and reproduction of Xeniids, which are fast-growing and often considered invasive, rapidly colonizing stressed or damaged reef areas (18). This behavior may additionally be supported by their pronounced physiological capacity to feed on ambient DOM (17, 19), a trophic strategy likely enhanced by polyp pulsation. Conclusively, benthic community phase shifts to dominance by pulsating xeniid soft corals, as observed currently in many coral reefs (20), may result in the loss of essential ecosystem engineer organisms (i.e., hard corals) and a decline in fundamental aspects of coral reef functioning.

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