LINKAGE OF BACTERIOPLANKTON DEPLETION AND NITRATE ACCUMULATION IN CORAL REEF WATERS WITH CRYPTIC SUSPENSION FEEDERS IN CAVITIES

Contributors: Sander R. Scheffers, Rolf P.M. Bak, Fleur C. van Duyl

Reports on reef degradation are accumulating at an alarming rate, but are mostly restricted to describing striking phenomena such as physical damages, coral bleaching and coral diseases. The importance of other kinds of changes is acknowledged, but few studies include changes in coral reef water quality with respect to suspended organic matter and inorganic nutrient concentrations, which may affect the trophodynamics on coral reefs. It is hypothesised that enhanced loads of inorganic nutrients and organic matter in the water, are beneficial to the growth and spatial cover of marine plants and heterotrophic benthic suspension feeders at the expense of corals. Benthic suspension feeders in cavities do not directly compete with corals for space, but supply the reef with extra inorganic nutrients after consuming predominantly allochthonous pico-and nanoplankton from the ocean.

left: A coral cavity on the reef slope of Curaçao (Netherlands Antilles)

right:: 3D-reconstruction of the geometry of the coral cavity shown in the photograph. Inner surface area is 2.47 m^2 and volume is 0.23 m^3.

We studied the diversity, cover and composition of cryptofaunal communities in relation to the physical characteristics of cavities along the coast of Curaçao (Netherlands Antilles) and assessed the role of cavity biota in the benthic-pelagic coupling. Cavities, the virtually inaccessible undersides of overhanging corals and holes in the Holocene and/ or Pleistocene reef framework, form the largest habitat of cryptic organisms on coral reefs. The cryptic reef fauna is highly diverse and includes suspension feeders such as polychaetes, bryozoans, tunicates, bivalves and sponges. We assessed the role of these cryptic communities as consumers of the very small but numerous bacteria flowing over the reef and their role as mineralizers of organic matter. Suspension feeding by cryptic communities may account for the widespread and unexplained observations of strong gradients in pico-and nanoplankton over reefs. The cryptic suspension-feeding fauna therefore potentially forms a quantitatively important sink of microorganisms and a link in reef trophodynamics.

For obtaining basic knowledge on cavity geometry and structure, a new device, the cave-profiler, was developed. With this device cavities were measured at varying depths on the reef slope along the coast of Curaçao. This way the 3D geometry, inner surface substratum area and volume of cavities was explored. Typical volume and surface area for slope cavities was ca 100 litres and 1.5 m^2 respectively. At 15 meters depth, the surface area within the cavities is up to 8 times larger than the surface area of the projected reef. An endoscopic digital video camera was used to penetrate the cavities and study the cryptofauna. Digital images, together with sampling for identification, were used to quantify the cover of cryptic organisms and identify the species. More than 60% of the inner cavity surface is covered with encrusting suspension feeders of which sponges were the most abundant. Forty different sponge species were identified of which 14 commonly occurred in cavities (e.g. *Desmanthus incrustans, Diplastrella megastellata*). Several a-biotic factors (turbidity, water movement, light) contributed to explaining the cryptobenthic zonation. Calcareous algae dominated in cover in the frontal part and encrusting sponges in the rear part of cavities.

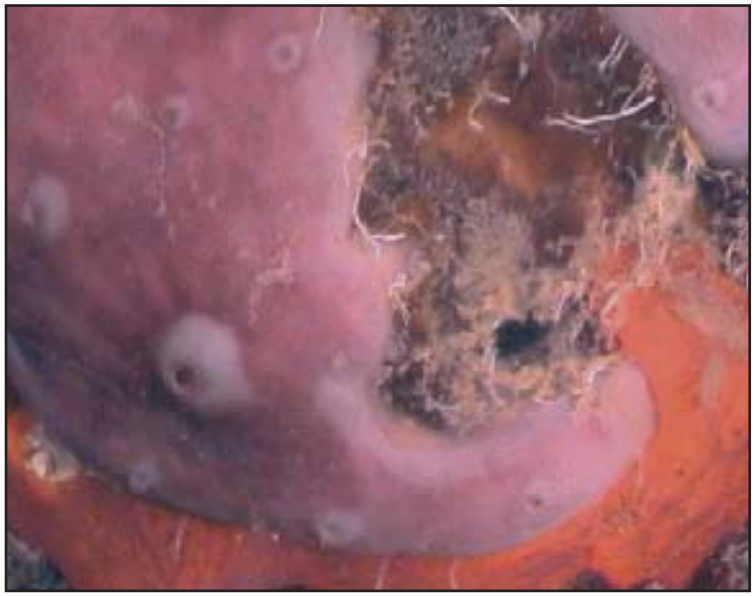
Year round comparisons of bacterial densities in cavity water with ambient reef overlying water for cavities along the coast revealed an average depletion of bacteria of 50% (ranging from 1-60%) in cavity water. Within cavities gradients in bacterial densities from the middle of the cavity to the wall covered with encrusting suspension feeders, a further 30% depletion occurs, establishing the role of encrusting suspension feeders in the bacterioplankton depletion in cavities.

We found that under the replete inorganic nutrient concentrations in open coral cavities dissolved organic carbon (DOC) consumption by bacterioplankton exposed to cavity water is 2 times enhanced compared to such consumption in reef overlying ambient water. With seawater cultures we demonstrated that this was due to the higher inorganic nutrient concentrations in

cavity water and apparently not to higher bioavailable DOC concentrations in cavities, indicating that cavities are definitely not net sources of labile DOC.

With *in situ* experiments in closed-off cavities we showed that biota in cavities are a quantitatively important sink of bacterioplankton (0.62 $mgC.l^{-1}.d^{-1}$; 30.1 $mgC.m^{-2}$ inner cavity surface substratum.d^{-1}), a sink of SiO_4^{2-} and a source of dissolved inorganic nitrogen (0.67 $mmol\ N.m^{-2}$ inner cavity surface substratum.d^{-1}). As expected, higher (up to 60 mg bacterial $C.m^{-2}$. inner cavity surface substratum.d^{-1}), but still comparable rates were found in open cavities in which we accounted for the water exchange. Water exchange rate coefficients in cavities varied between 0.00004 and 0.0088 s^{-1} with a median exchange rate of 0.0038 s^{-1} (residence time of 4.4 min). Net effluxes of DIN and DIP occurred from open cavities (1.44 and 0.31 $mmol.m^{-2}$ cavity surface area.d^{-1} respectively). Significant net effluxes of NH_4 from cavities did not occur. On the contrary, NH_4 often disappeared in open cavities. The net NO_3 efflux exceeded the net DIN efflux suggesting that cavities are hot spots of nitrification. The differences in inorganic nutrient concentrations (NO_3, DIN) between ambient reef overlying water and cavity water declined with increasing water exchange, indicating conservative mixing with constant net inorganic N release rates from cavity surfaces. The relation between bacterioplankton depletion and water exchange in cavities pointed to non-conservative mixing, suggesting that bacterioplankton removal rate by cryptic suspension feeders increased with increasing exchange up to a threshold exchange and subsequently dropped to a significantly lower level. This illustrates that the hydrodynamic conditions in coral cavities affect and set boundaries to matter uptake by cryptic suspension feeders.

Coral cavities are quantitatively important net sinks of bacterioplankton and net sources of dissolved inorganic nitrogen (NO_3) and DIP (open cavities only). Cavities net released NO_3, but did not release net NH_4 or net labile DOC. Based on our results we argue that cryptic biota cannot live merely of the reef production but are dependent on the food advected to them by the ocean water passing the reef. As such cryptic suspension feeders play an important role in reef trophodynamics by incorporating ocean derived organic matter in the reef benthos and supply the reef with extra inorganic nutrients. Our results indicate that coral reefs should be considered as open in stead of closed ecosystems. Allochthonous nutrition of coral reef biota may contribute to explaining the Darwinian paradigm of a biologically diverse and extremely productive ecosystem surrounded by oligotrophic waters.



Encrusting sponges in cavities (scale ca. 4x5 cm)