

Feeding on Ultraplankton and Dissolved Organic Carbon in
Coral Reefs: from the Individual Grazer to the Community

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ABSTRACT

Benthic grazing on phytoplankton is a principal trophic pathway in shallow, temperate coastal habitats. Traditionally, studies of benthic-pelagic coupling in coral reefs, where the planktonic community is dominated by minute prokaryotic cells, have focused on zooplankton, rather than the smaller phytoplankton and bacteria, as the principal source of prey. My goal was to study the trophic role of ultra-phytoplankton (<0.01 mm), bacteria, and dissolved organic matter in the coral reef ecosystem on scales ranging from the individual grazer to the whole community.

Mapping the spatial distribution of phytoplankton near coral reefs (*Limnol. Oceanogr.*, **43**, 551) revealed the occurrence of a 1-3 m layer depleted of phytoplankton. The depleted layer was found over several coral reefs but not over sandy sites with similar bathymetry. The extent of the depletion was dependent upon the hydrodynamic conditions. Using state-of-the-art underwater technology, we were able to apply the "Control Volume" approach to measure *in situ* phytoplankton grazing on a scale of a whole coral-reef community (*Oceanography*, **15**, 90). The results indicate that the import of carbon and nutrients via phytoplankton grazing is a major, previously underestimated, trophic pathway in coral reefs.

By developing new methods for *in situ* measurements of feeding-rates (*Limnol. Oceanogr. Methods*, **3**, 46) I was able to measure the diet composition, prey preference patterns, and grazing rates of 15 benthic suspension feeder taxa at the reef. Soft corals (*Limnol. Oceanogr.*, **43**, 354), sponges (*Limnol. Oceanogr.*, **48**, 141), boring bivalves, and ascidians (*Mar. Ecol. Progr. Ser.*, submitted) were found to be efficient phytoplankton grazers. Only sponges were efficient bacteriovores. The yet un-described cryptic fauna inhabiting the outer surfaces of the so-called "bare rocks" was found to be an important sink for phytoplankton (*Coral Reefs*, in press). The preference for ultraplanktonic prey was similar for different grazers, exhibiting a general selectivity for coccoid photosynthetic prokaryotes over both larger or similar-size eukaryotic algae and smaller or similar-size non-photosynthetic bacteria. As this pattern does not maximize carbon or energy gain, it is suggested that at the reef, where carbon is not a rare commodity, suspension feeders have evolved to optimize the gain of other nutrients or to avoid harmful prey taxa.

My new *in situ* technique allowed, for the first time, direct quantification of dissolved organic matter removal by several active suspension feeders. The symbiont-bearing reef sponge *Theonella swinhoei* removed up to 26% ($12 \pm 8\%$, mean \pm 1SD) of the total organic carbon (dissolved and particulate) from the water it filtered during a single passage through its filtration system (*Limnol. Oceanogr.*, **48**, 141). The amount of carbon gained by the sponge from the dissolved pool was an order of magnitude greater than that gained from the total living cells it removed. Evidence for removal of dissolved organic matter (DOM) was also recorded for a coral boring bivalve, a solitary ascidian, and two other sponges. My findings suggest that DOM may be a major component in the nutrition of metazoan and that the role of metazoans in DOM cycling may have been grossly underestimated.

This study revealed the previously overlooked fundamental role of minute phytoplankton and dissolved organic matter in the nutrition of benthic suspension feeders and benthic-pelagic coupling in the complex coral reef community.

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1. Synopsis

This work was initiated about 8 years ago with the discovery that soft, asymbiotic corals are apparently herbivores, ingesting and digesting minute, unicellular algae (phytoplankton) from the flowing water (Fabricius, Benayahu, and Genin, *Science*, **268**, 90, 1995). This finding was rather surprising as corals were widely believed to be carnivores and phytoplankton grazing was not considered significant in coral reef ecosystems. That discovery had triggered interest in the ecological significance of phytoplankton as a nutritious source for soft corals and more generally to the reef ecosystem. During the spring of 1994, when I was doing my bachelor studies in biology, I approached Dr. Genin, seeking a subject for my BSc project. Within two days I found myself in Eilat, diving deep (literally) into the beauty of the reef and the complexities involved with underwater research. Soon after, I discovered that at the reef, no trivial answers were available to even the simplest question, such as "what does that animal eat?" During my BSc project, we discovered that the soft, asymbiotic coral *Dendronephthya* is able to remove significant amounts of phytoplankton from the water passing through its branching colonies. The combination of this field data with laboratory measurements of the rate of chlorophyll destruction within polyp's lumen had allowed us to reevaluate *Dendronephthya's* feeding rates (Appendix I, Fabricius, Yahel, and Genin, *Limnology and Oceanography*, **43**, 354, 1998) which were previously grossly underestimated.

Water samples collected in transects from the reef to the open sea indicated remarkable phytoplankton depletion close to the reef bottom but not over a nearby sandy bottom site. However, a significant unexplained variability existed between different sampling sessions. To improve the accuracy of our phytoplankton measurements, and in order to gain more knowledge of the planktonic community composition, we established a fruitful collaboration with Dr. D. Marie and Prof. D. Vaultot from the CNRS institute in Roscoff, France, one of the worlds leading groups in marine flow cytometry. After two more years, and much field work in Eilat and along the western coast of the Sinai peninsula, we realize that it is mostly hydrodynamics (and not, for example, shifts in grazers behavior or phytoplankton community) that controls the thickness of the depleted layer over the reef (3, Yahel, Post, Fabricius, Marie, Vaultot, and Genin, *Limnology and Oceanography*, **43**, 551, 1998). By tracking water parcels flowing through the artificial "perforated reef", which grows over old barbwire underneath the jetty of Eilat Oil Terminal, we were able to estimate phytoplankton fluxes into that system as the product of water velocity and phytoplankton depletion. Our estimates indicated that phytoplankton feeding can account for the entire respiratory carbon demand of *Dendronephthya* and that phytoplanktonic carbon fluxes into the "perforated reef" were comparable to the highest records of zooplankton fluxes into coral reefs.

Evaluating the role of phytoplankton as a nutritional source for the typical fringing reefs of the Gulf of Aqaba, where soft, asymbiotic corals are sparse, was a much more complex task. While phytoplankton depletion at the reef bottom was evident, the shear and turbulence created by the rough micro-topography hindered simple rate measurements. To resolve this difficulty we have decided to follow two complimentary approaches. One approach was holistic, i.e., we wanted to establish a community scale methodology that will allow reliable quantification of benthic-pelagic mass flux exchanges in the multifaceted environment of exposed reef slopes. Soon, our preliminary flow measurements revealed, that on a meso-scale, the flow field over the reef is even more complex, containing features such as vertical and cross-shore shears. We then realized we needed the help of hydrodynamics engineers to properly design the community scale methodology. This led to the establishment of a successful collaboration with Prof. J R. Kossef,

and Prof. S. G. Monismith from the Dept. of Civil and Environmental Engineering, Stanford University. A joint grant from the BSF allowed us to develop and deploy the "Control Volume" experiments (Appendix II, Genin, Yahel, Reidenbach, Monismith, and Koseff. *Oceanography* **15**, 90, 2002). Using a suit of underwater pump arrays, acoustic current meters, and current profilers, we were able to achieve simultaneous, high resolution, measurements of both the flow and phytoplankton concentration fields over some deep open sections of the reef slope community. The entire setup was replicated twice in the summer 1999 and once again in the winter of 2001. Our preliminary results from the 1999 experiments indicate that the overall grazing rate at the reef was substantial, exceeding previous estimates by an order of magnitude. Import of carbon and nutrients via this grazing is thus a major, previously underestimated, trophic pathway in coral reefs. Independent estimates based on Lagrangian studies, as well as mesocosms experiments yielded similar clearance estimates (Yahel, unpublished data). Buoyancy driven cross-shore flows seems to be an important factors, replenishing the reef with fresh oceanic waters. Data analysis is still in progress as over 2,000 flow cytometry samples and 3,000 chlorophyll samples were collected in these experiments along with a high-resolution data set of physical data. At least three more publications are currently under preparation by the participants of this study.

As a complimentary method, we used a "scaling up" approach, in order to extrapolate phytoplankton-grazing rates of individual grazers to the reef scale. Surprisingly, a comprehensive literature search has found no explicit report of a phytoplanktivorous reef dweller, let alone reports on phytoplankton grazing rates. Moreover, the application of standard method used to measure phytoplankton-grazing rates in temperate and boreal habitats (namely, putting the animals in a laboratory vessel and measuring plankton depletion in the vessel) was clearly inappropriate in the reef environments where many suspension feeders are cryptic and all have tight symbiotic relationships. What we needed was a nondestructive method that would allow us to survey, *in situ*, the feeding rates of different suspension feeders. The reference unit of these feeding rates should have been also readily quantified at the reef (obviously, traditional biomass reference unit are inappropriate for [e.g.] endolithic taxa). To that end I developed and evaluated a technique termed "InEx". InEx is based on the simultaneous, pair-wise collection and comparison of the water **In**haled and **Ex**haled by the animal. Calculations of feeding (or excretion) rates are obtained by multiplying the concentration difference by pumping rate. The latter is concurrently measured by recording the movement of a dye front in a transparent tube positioned within the ex-current jet (Appendix III, Yahel, Marie, and Genin, *Limnol. Oceanogr. Methods*, submitted).

Using InEx we collected over 500 separate measurements of filtration efficiency, pumping rates, diet composition, and selectivity patterns in four sponge species, three tunicate species and five bivalve species, some in the Gulf of Aqaba, and others, in the Indian Ocean. All species studied were found to be phytoplanktivores with varying degree of efficiency and with a distinct preferences pattern for each grazer taxa. In addition to phytoplankton, and non-photosynthetic bacteria removals, measured with a flow cytometer, we have also analyzed inorganic nutrients, respiratory gasses, and total and dissolved organic carbon in many of the InEx pairs. An important, unexpected finding was the discovery of a previously undocumented pathway of carbon flux in benthic habitats. DOC (dissolved organic carbon) appeared to be a major component in the diet of several active suspension feeders at the reef belonging to three remote phyla (Sponges, Tunicates, Mollusks). While we first documented this phenomena back in 1997 (using an un-calibrated Dohrmann TOC analyzer), it required the dedicated help of the world leading authority in DOC analysis, Prof. J.H. Sharp of the Graduates College for Marine Sciences in Delaware, and almost three years of painstaking work (with many excluded samples) to refine the methodology and get a reliable, no equivocal, quantitative measurements of this DOC removal (Chapter 4, Yahel, Sharp, Marie, Häse, and Genin, *Limnol. Oceanogr.* **48**, 150, 2003). Another

interesting and novel phenomenon revealed with InEx is the discovery that reef suspension feeders (bivalves and tunicates) are highly selective in the planktonic bacteria they feed on. These suspension feeders readily retain photosynthetic bacteria as well as non-photosynthetic bacteria with high nucleic acid content but apparently reject other type of bacteria. This selectivity is apparently size independent and thus should be based on a, yet unknown, cell recognition mechanisms. Sponges in contrast are less selective but more efficient filter feeders. An in-depth analysis of these phenomena for three representative species is presented in Chapter 5 (Yahel, Marie, Eckstein, and Genin, *Mar. Ecol. Progr. Ser.*, Submitted).

Finally, phytoplankton-grazing estimates based on the individual based rate measurements (InEx) and the actual abundance of active suspension feeders within the control volume area yielded pumping rates estimates of <15% of the estimated total community grazing rate (Yahel et al. in prep.). It was thus evident that the active suspension-feeders guild cannot be the sole, and probably not even the major, sink for phytoplankton at the reef. Hydraulic phytoplankton filtration through sand (Huettel and Rusch 2000) or reef framework (Haberstroh and Sansone 1999), as well as the activity of coelobite fauna, were all ruled out for Eilat reef slopes. However, laboratory experiments clearly demonstrate that the, yet un-described, cryptic fauna of reef rock surfaces is a major sink for phytoplankton at coral reefs (Chapter 6, Yahel G., Zalogin T., Yahel R. and Genin A., *Coral Reefs*, Submitted).

The studies presented here span over a six-year period. During that time, a few other groups have published follow-up papers (e.g., Fabricius and Dommissé 2000; Richter et al. 2001) or independent studies (e.g., Ribes et al. 1999; Roditi et al. 2000; van Duyl and Gast 2001) related to aspects of phytoplankton grazing and DOC dynamics. In order to avoid confusion and to maintain a clear flow of the scientific background and summary, the Introduction will review the scientific background relevant to the time of the onset of the study and research-plan formulation (1997). References for newer publications (after 1997) will be generally reserved for the relevant chapters and to the concluding section, unless they pertain to recent reviews that summarized older studies.