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In situ depletion of phytoplankton by an azooxanthellate soft coral

Abstract—The in situ removal of phytoplankton by the soft coral *Dendronephthya hemprichi* was investigated by taking small-scale measurements of chlorophyll concentrations around colonies on a reef of the northern Red Sea. The chlorophyll concentration downstream of a 0.75-m-deep colony thicket was depleted by 6.4% (±1.4% SE) compared with the water upstream. Neighboring organisms are thus exposed to water that is significantly depleted of phytoplankton. A 0.75 × 0.1 × 0.1-m passage of actively feeding colonies removed 34 mg of carbon per day from the water, equivalent to ~1.3 times their respiratory carbon demand. Rates of algae intake were also estimated by determining the decrease in gut fluorescence in starved colonies. The in situ depletion technique showed a three- to sixfold greater sensitivity compared with the gut fluorescence technique, and should be preferred as a technique for estimating feeding rates.

Invertebrates known to be efficient filter feeders (e.g. mussels, ascidians, and sponges) can significantly deplete the overlying water column of phytoplankton (Fréchette and Bourget 1985; Petersen and Riisgård 1992; Pile et al. 1996). In a previous study (Fabricius et al. 1995), we characterized several azooxanthellate soft corals as herbivorous filter feeders, and demonstrated that their rates of phytoplankton filtration and their growth rates were related to the ambient flow environment. The study was partially based on the gut fluorescence technique, a commonly used and established method for estimating feeding rates. Estimates based on the gut fluorescence technique are however significantly affected by uncertainties associated with measurements of digestion times (Peterson et al. 1990). We have now developed a method to directly evaluate rates of phytoplankton intake by the soft coral *Dendronephthya hemprichi* that is based on small-scale in situ measurements of chlorophyll concentrations upstream and downstream of colonies. We quantified the contribution of phytoplankton to the carbon demand of *D. hemprichi* in its natural reef environment and compared the resulting carbon budget with that based on gut fluorescence measurements. The technique also allowed us to investigate whether the suspension feeding of this soft coral would affect algae concentrations in its wake and thus modify the food availability of neighboring filter feeders in the reef.

To determine in situ rates of phytoplankton depletion, we compared concentrations of chlorophyll *a* in the water upstream and downstream of a 0.75-m-deep thicket of large (~40 cm tall) *D. hemprichi* colonies. The colonies were transplanted into a stable flow environment generated by submersible pumps and screens erected on the coral reef off the coast of Eilat, Israel (*see* Fabricius et al. [1995] for a description of the pump setup and procedures for chlorophyll measurements). Clouds of fluorescent dye were used to characterize the flow, and indicated that the water passed through the thicket within 20 s (equivalent to an average flow speed of 3.8 cm s^{-1}). The branches farthest upstream experienced ~20 cm s^{-1} flow, whereas colonies within the thicket were exposed to slower turbulent flow conditions. Sixty-eight pairs of water samples were taken upstream and downstream of the thicket at varying times over 3 consecutive days. Four to six water sample pairs per dive were collected with 4-cm-diam (330-ml-vol) pipes. The pipes were closed after 20 s flushing, and upstream and downstream samples were taken ~20 s apart.

Phytoplankton flux and removal, as well as colony biomass and respiration, were calculated for an arbitrary passage with a cross section of 0.1 × 0.1 m and a length of 0.75 m. The flux through the 100-cm^2 cross section was 0.38 liter s^{-1}. Phytoplankton depletion was expressed as the proportion of upstream chlorophyll concentration removed from the water after passing through the passage. The phytoplankton community consisted mostly of synechococcoide cyanobacteria and pico-eukaryotic cells (Lindell and Post 1995; A. Post unpubl. data). The C-to-Chl *a* conversion factor ranges from 24 to >175 in picoplankton communities of tropical shallow water (Campbell et al. 1994; Cloern et al. 1995). We conservatively based our conversion of chlorophyll to carbon weight on a Chl *a*:C multiplication factor of 30. The ash-free dry weight (AFDW) of *D. hemprichi* colonies was estimated by determining the size and volume of four large expanded (10.4–17.9-liter) colonies in situ and measuring their dry weight (6 d at 60°C) and ash weight (2 h at 200°C, then 4 h at 450°C). Their mean biomass was 0.56 (±0.14 SE) g AFDW $liter^{-1}$ per colony. The number of polyps in the passage was estimated as the total AFDW of the colonies in the passage divided by the mean AFDW of a polyp of 90 μg (Fabricius et al. 1995). Calculations of the respiratory carbon consumption, R (mg C d^{-1}), were based on previous measurements (table 5 in Fabricius et al.

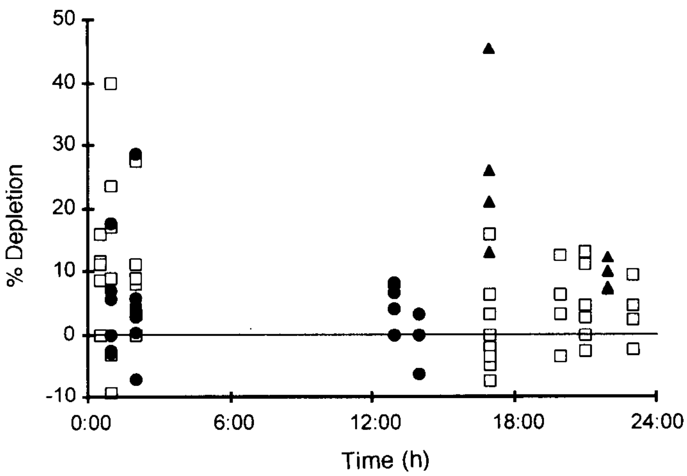

Fig. 1. Percent depletion of chlorophyll downstream of a 0.75-m-wide thicket of the soft coral *Dendronephthya hemprichi*. Average depletion was 6.4 ± 1.4% (SE), $n = 68$. Symbols represent the 3 d of sampling.

1995): $R = 6.46$ (±0.54 SE) × weight. Water clearance rates (ml polyp^{-1} d^{-1}) were obtained by dividing the daily chlorophyll removal per polyp by the ambient chlorophyll concentration.

A second experiment on the rate of chlorophyll ingestion and digestion was undertaken using the gut fluorescence method, modified from our previous study (Fabricius et al. 1995), to compare estimates of phytoplankton ingestion rates with those derived from the in situ depletion experiment. Forty freshly collected small colonies were transferred into a container continuously flushed with 0.2-μm-filtered seawater to prevent further feeding on algae. Chl *a* concentrations in the starved polyps and in the water were measured after 0, 0.5, 1, 2, 3, 6, 8, and 31 h. At each of these times, two fragments with 20–40 polyps were cut from each of four previously unsampled colonies. After determining the number of polyps in each fragment, their chlorophyll was extracted in 90% buffered acetone at 4°C in the dark for 24 h. Hourly ingestion rates were calculated using $I_p = dG$, where I_p is the phytoplankton ingestion rate of a polyp (ng Chl polyp^{-1} h^{-1}), d is the decomposition rate (h^{-1}), and G is the pigment content of the polyp (ng Chl polyp^{-1}) (Peterson et al. 1990). The rate of chlorophyll decomposition was determined by linear regression of log-transformed chlorophyll values over the first 8 h.

The results of the in situ depletion experiment showed that the *D. hemprichi* thicket removed a significant proportion of algae from the water passing through the branches. The Chl *a* concentration downstream of the colonies was 0.035 μg Chl liter^{-1} (±0.008 SE) lower than upstream, equivalent to a depletion of 6.4% (±1.5%) (Fig. 1; paired *t*-test, $t_{(67)} = 4.45$, $P < 0.001$). Assuming that rates of depletion at day and night were similar, the actively feeding colonies in the 0.1 × 0.1 × 0.75-m passage removed 1.126 mg Chl *a*, or 33.8 mg C d^{-1}. The biomass of the colonies in the passage was 4.16 (±1.02) g AFDW, with a rate of respiratory carbon consumption of 26.9 (±9.9) mg C d^{-1}. Therefore, the amount of phytoplankton carbon filtered from the water averaged 8.2 (±1.9) mg C g^{-1} colony AFDW d^{-1}, which is equivalent to 1.3 (±0.38) times the daily respiratory carbon demand of the coral. The seawater upstream of colonies contained on average 0.45 (±0.01) μg Chl *a* liter^{-1}. Fifty-four milliliters of seawater (0.024 μg Chl *a*) was cleared of phytoplankton by a single polyp of *D. hemprichi* per day, providing it with 0.73 μg of phytoplankton carbon.

The gut fluorescence experiment indicated that individual well-fed polyps contained an average of 1.57 (±0.24) ng Chl *a* before starvation in filtered seawater began. During starvation, the chlorophyll concentrations in the polyps decreased at a rate of 11.5% (±1.95%) h^{-1} over the first 8 h. After 31 h, the residual chlorophyll was 18% of the initial value. In unfiltered seawater, in which the colonies were held prior to starvation, the ratio of pheopigments to total plant pigments (pheopigments and chlorophyll) was 25%. In the polyps, this ratio was initially 41%, and increased monotonically to 80% over 31 h. The growing proportion of pheopigments indicated that most of the algae were digested rather than excreted. The rate of phytoplankton carbon intake per polyp was then determined based on the chlorophyll content of well-fed polyps and the rate of chlorophyll decomposition in starving colonies. The estimated rate of intake based on this gut fluorescence measurement was 123 (±22) ng C polyp^{-1} d^{-1}, equivalent to 11–29% of the respiratory carbon demand of the colonies. This estimate was thus three- to sixfold lower than the estimate based on the in situ depletion technique.

Measurements of the in situ phytoplankton depletion indicate that rates of phytoplankton intake in *D. hemprichi* are high and adequate to meet most, if not all, of the respiratory carbon demand of soft corals. In our previous study (Fabricius et al. 1995), we erroneously reported gastrovascular contents in micrograms (instead of nanograms) of Chl *a*, which affected our calculations of rates of phytoplankton intake and the carbon budget. The new measurements validate our original finding that herbivory is the major feeding pathway in this soft coral. The in situ measurements of chlorophyll depletion resulted in estimates of phytoplankton consumption that were considerably higher than those based on the gut fluorescence technique. We stress, however, that carbon budgets, such as the two presented here, can only approximate the magnitude of carbon gain owing to the number of assumptions involved. First, we conservatively assumed a C:Chl weight ratio of 30, an unusually low ratio for tropical shallow-water phytoplankton communities. The carbon intake rate derived from the in situ depletion technique may account for 250% of the respiratory carbon consumption (22–57% derived from the gut fluorescence estimate) if a C:Chl ratio of 60 should be found to better approximate the yearly average. Second, rates of phytoplankton intake depend on flow speed, and chlorophyll concentrations in polyps were eight times higher at a flow speed of 15–20 cm s^{-1} than at 3.8 cm s^{-1} (Fabricius et al. 1995), indicating that the relatively slow flow velocity used in this experiment influenced the rates of chlorophyll depletion measured.

As was the case with *D. hemprichi*, estimates of feeding rates of marine zooplankton were commonly higher when determined by food depletion measurements than estimates derived from the gut fluorescence technique (Conover et al. 1986). Gut contents of 1.6 ng Chl *a* and clearance rates of 54 ml seawater per *D. hemprichi* polyp per day are within the range of values found in herbivorous copepods of comparable body weight (e.g. 0.9–7.7 ng pigments in individual *Calanus pacificus* of ~70 μg C biomass [Landry et al. 1994*a, b*]). A better understanding of the mechanisms involved in phytoplankton intake and digestion by soft corals is required to account for the difference of in situ and gut-based estimates. The gut fluorescence method appears suitable for determining relative rates of food intake (e.g. in various conditions of flow). It also served to confirm that most of the algae were taken in by *D. hemprichi* rather than by the small number of microinvertebrates living among the branches, and that most of the ingested algae were digested rather than excreted. However, direct in situ depletion measurements appear preferable when absolute rates of feeding in marine suspension feeders are evaluated.

Previous studies, most of which were undertaken in temperate waters, have demonstrated the ability of a range of other macrobenthic suspension feeders and planktonic filter feeders to effectively remove plankton from the water (e.g. Anthony 1997). Similarly, the tropical reef-inhabiting *D. hemprichi* significantly reduces phytoplankton concentrations in downstream water, thus creating a particle-depauperate environment for neighboring organisms. Potential implications such as patchiness in microhabitat quality, changes in competitive strength for downstream neighbors, and effects on the benthic community structure in coral reefs deserve further study.

Katharina Fabricius

Australian Institute of Marine Science
CRC Reef Research Centre
PMB 3, Townsville
Queensland 4810, Australia

Gitai Yahel
Amatzia Genin

The Hebrew University
H. Steinitz Marine Biological Laboratory
P.O. Box 469
Eilat 88103, Israel

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