Limnol. Oceanogr., 40(7), 1995, 1290–1301

Flow-dependent herbivory and growth in zooxanthellae-free soft corals

Katharina E. Fabricius
Australian Institute of Marine Science, PMB 3, Townsville, Queensland 4810, and Center of Marine Tropical Ecology, Klagenfurter Str./ Geo, 28359 Bremen, Germany

Amatzia Genin
The Hebrew University, H. Steinitz Marine Biological Laboratory, POB 469, Eilat 88103, Israel

Yehuda Benayahu
Department of Zoology, Tel Aviv University, Ramat Aviv 69978, Israel

Abstract

The diet of *Dendronephthya hemprichi* and three other abundant soft corals in the northern Red Sea consists mainly of phytoplankton, a food source so far unknown for cnidarians. We present a carbon budget for this species, synthesizing field data on somatic growth, food intake, and respiration. In situ rates of phytoplankton uptake and addition of polyps were affected in a similar and nonlinear fashion by flow, with optimal values observed at ~15 cm s^{-1}. The size of polyps increased with increasing flow between 1 and 32 cm s^{-1}. Zooplankton capture was selective for weakly swimming bivalve and gastropod larvae and contributed <5% to the corals' carbon demand for growth and respiration and about two to three orders of magnitude less than the carbon gained by phytoplanktivory. The ability of octocorals to feed on phytoplankton is probably related to the narrowly spaced pinnules on their tentacles as well as morphological and behavioral adaptations to living in strong flow. The utilization of phytoplankton, which has nearly an order of magnitude higher biomass than zooplankton, is probably the principal mechanism allowing an azooxanthellate cnidarian to be highly productive in oligotrophic reef waters.

Soft corals (Cnidaria: Octocorallia) are, after the reef-building stony corals, the secondmost common benthos component in many Indo-Pacific coral reefs (Benayahu and Loya 1981; Tursch and Tursch 1982). Nonetheless, little is known about their nutrition. The epidermis of octocorals contains few small stinging cells (nematocysts) and poor ciliary and flagellar structures compared with scleractinians (Mariscal and Bigger 1977). Their tentacles are branched so that rows of narrowly-spaced pinnules are arranged in a comblike structure around each of the eight polyp tentacles. These features appear more suitable for feeding on small particles and uptake of dissolved organic material than for zooplankton capture. Octocorals are thus markedly different from scleractinian corals, which have nonpinnate tentacles with numerous highly differentiated nematocysts. A few studies on tropical (Lewis 1982) and temperate (Sebens and Koehl 1984) octocorals have confirmed their ability to capture zooplankton. Other studies (Patterson 1984; Spongaule and LaBarbera 1991) characterized soft corals as passive suspension feeders without investigating their natural food composition or particle sizes. Overall, the assumption that all cnidarians are carnivores has long been the common convention (Muscatine 1973; Brusca and Brusca 1990).

The asymbiotic soft coral *Dendronephthya hemprichi* is highly abundant in flow-exposed reef habitats of the northern Red Sea but is virtually absent in flow-protected habitats (L. Karp unpubl.). *D. hemprichi* is highly productive, and newly deployed manmade surfaces down to 80-m depth can be covered with colonies up to 30 cm tall after only a few months (H. Fricke unpubl. data). In contrast to the great majority of other reef-inhabiting octocorals, both of the orders Alcyonaceae (soft corals) and Gorgoniaceae (sea fans), *D. hemprichi* does not contain endosymbiotic algae (zooxanthellae). In symbiotic stony and soft corals, carbon translocation from the symbiotic algae and nutrient recycling between algae and host contribute to high levels of biological productivity. The question of how zooxanthellae-free heterotrophic cnidarians can be highly productive in coral reefs has not been addressed.

As passive suspension feeders, octocorals depend on the ambient currents to transport food particles through their filter structures. Rates of particle uptake are com-

Acknowledgments

We thank all staff and members of the H. Steinitz Marine Biology Laboratory, Eilat, Israel, where this study was carried out. Thanks to J. Trager for the loan of parts of the flow-chamber systems, Z. Dubinsky and R. Vago for the loan of the respirometers, and A. Post, B. Lazar, M. Kiflawi, J. Jacobs, and D. Klumpp for many discussions and comments on the ms.

K.F. was supported by the German-Israeli Science foundation, MINERVA, and the research was funded by the Wolfson Foundation administered by the Israel Academy of Science granted to A.G.

Contribution 724 of the Australian Institute of Marine Science.

monly related to water flow in a nonlinear fashion (Shimeta and Jumars 1991), and the flow speed at which particle capture reaches a maximum varies according to size and morphology of the filter feeder (Patterson 1984; McFadden 1986). Various studies have demonstrated the great importance of water flow for filter feeders, influencing distribution ranges (Sebens and Done 1993), colony growth, size, and morphology (Jokiel 1978; Helmuth and Sebens 1993), and rates of gas exchange (Patterson et al. 1991). The lack of photosynthetically fixed carbon should make the azooxanthellate *D. hemprichi* particularly dependent on currents to carry food into the reach of this suspension feeder.

We characterize natural food composition and in situ rates of food uptake and growth of *D. hemprichi,* provide evidence for phytoplankton ingestion, and present a carbon budget for this asymbiotic cnidarian.

Material and methods

The animals—The investigation focused on *D. hemprichi,* although phytoplankton utilization was also studied in three other common asymbiotic octocoral taxa in the northern Red Sea, the nephtheid species *Dendronephthya sinaiensis* and *Scleronephthya corymbosa* and the gorgonian *Acabaria* sp. All taxa have a fan- or tree-shaped morphology and are brightly colored. *D. hemprichi* colonies are up to eightfold ramified. Their polyps are small, with a diameter of 3.2–4 mm (0.8-mm oral disc diameter, 1.2–1.6-mm tentacle length) and 18–20 pinnules on each tentacle with 60–80-μm gaps between the narrow pinnules. The species is characterized by great morphological variability, affecting the coloration of polyps, colony stem and sclerites, and the growth form of the colonies. Feeding experiments were carried out on the most common morph (red polyps, orange sclerites, quite variable colony shape), whereas at least five different morphs were used in the growth experiments.

This taxon commonly propagates asexually by shedding large quantities of colony fragments with 5–8 polyps (Dahan and Benayahu in prep.). For the experiments, we produced colony clones by taking advantage of this natural mode of asexual reproduction and the tendency of fragments to firmly attach to the substrate by growing rhizoidal structures from the base of their stems. Naturally produced fragments and branches cut off large colonies were put in running-water tanks with the floors of the tanks covered by 10 × 10-cm PVC plates. Fragments and branches attached to the plates in ~10 d. These colonies could then be transported and manipulated with minimal disturbance of the sensitive animals.

Colony contraction by soft corals causes large errors in linear measurements, volume, or wet weight determination. Fortunately in *D. hemprichi,* the biomass of the polyps was uniform, therefore the correlation between the number of polyps and the ash-free dry weight (AFDW) of colonies was highly significant (Fig. 1; $R^2 = 0.88$, $N = 107$, $P < 0.001$). The regression coefficient was not significantly different for different morphs growing at the same site under similar conditions. Thus, all experiments were normalized by using the number of polyps as a measure for colony biomass.

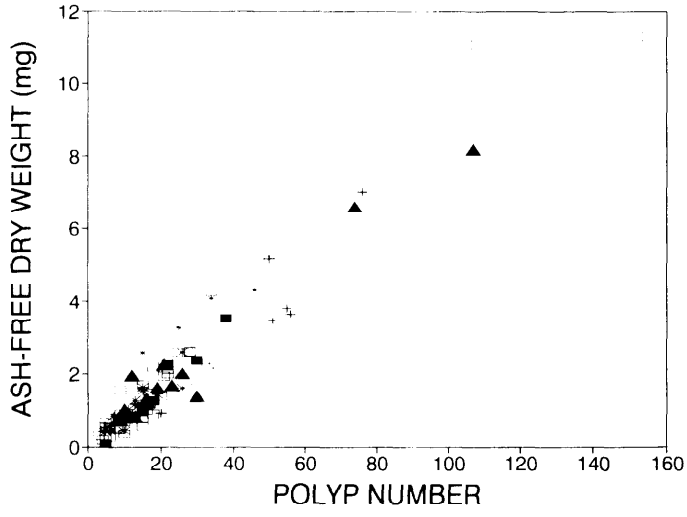

Fig. 1. Correlation between colony biomass (AFDW) and number of polyps per colony in *Dendronephthya hemprichi* ($N = 107$, $R^2 = 0.88$). The symbols represent different morphs distinguished by coloration and growth form (□: red polyps, orange sclerites, bushy or flattened colony shape; ■: pink, sparse polyps, yellow sclerites; ∗: purple polyps, dark purple sclerites, commonly flattened, fan-shaped colonies; +: white polyps and sclerites, flattened colonies; ▲: yellow polyps and sclerites, stout growth). Some of the variability is due to different flow environments from which the colonies were sampled.

Study sites—All experiments were carried out in 1993 at the H. Steinitz Marine Biological Laboratory in Eilat, Israel. Wherever possible, experiments were performed in the field. The reefs off the laboratory experience an average flow of 4.8 cm s^{-1} and usually low wave action (A. Genin unpubl. results). The species under investigation were rare on natural substrates but highly abundant on artificial structures elevated off the bottom, such as ropes of anchoring buoys, fences, and poles of jetties. Most of the study animals were obtained from the poles of the oil pier in Eilat at a water depth of 10–28 m.

Flow manipulation—In situ flow enhancement was achieved with submerged pumps as described by Genin et al. (1994). Four pumps (hereafter named "pump setup") were positioned 40-m offshore at 5-m depth. Experimental flow speeds ranged from 4 to 35 cm s^{-1}, depending on the distance from the pump. This range encompassed a substantial part of the flow variations *D. hemprichi* experiences at its natural habitats in the Red Sea. Extensive colony depredation, particularly by chaetodonids, in preliminary experiments forced us to cage the pump setup. Two cages (120 × 60 × 60 cm) made of plastic-coated chicken mesh (30 × 45-mm mesh size) were used. No predation was observed thereafter. The cages weakened the ambient flow by < 10%. A third cage, used to create low-flow conditions, had its vertical walls coated with woven plastic material and reduced the am-

bient current to 1–2 cm s^{-1}. The flow speed inside and outside the cages and around individual transplanted colonies was measured by the video-dye technique (Colman et al. 1984). All cages were elevated 0.5 m off the bottom to prevent accumulation of sediment and detritus. The ambient flow speed and direction near the pump setup at 0.5 m above bottom was monitored throughout the experimental period with an electromagnetic current meter (InterOcean model S4) that recorded the measurements for 1 min every tenth minute.

Feeding ecology—The presence of phytoplankton in the gastrovascular cavities (coelenterons) was assessed by epifluorescence microscopy. For each taxon examined, polyps of six freshly collected colonies were dissected and immediately checked for fluorescence under blue light. Because phytoplankton fluorescence penetrated the pieces of coral tissue only weakly, the observations allowed only a qualitative assesment.

The weight of chlorophyll *a* and its degradation products (pheopigments) in a known number of polyps (20–30) were fluorometrically quantified with a Turner 10-000r fluorometer (filter set 10-042) after 24 h of dark extraction in cold (4°C) 90% acetone solution of the complete fragments (Parsons et al. 1984). The effectiveness of the 24-h extraction was controlled for by putting 80 fragments through a second and third 24-h extraction period in fresh acetone after the first and second extractions, 4.0% (±1.3 SD) and 0.8% (±0.3) of the chlorophyll *a* remained, indicating that one 24-h extraction removed >95% of all Chl *a*. The concentration of Chl *a* in the ambient water during our experiments was measured with 0.7-μm glass-fiber filters (GF/F). Attempts to use the conventional technique of determining the incorporation of ^{14}C-labeled algae by *D. hemprichi* in a 3-liter aereated flow chamber were not successful due to the experimental requirement of several hours of exposure in a small volume of water and *D. hemprichi's* requirement of continuous and fast water replenishment. Three sets of feeding experiments were based on this method of quantifying plant-derived pigment concentrations in the colonies.

In feeding experiment 1, we measured rates of chlorophyll decomposition in the gastrovascular cavities of starved colonies in the laboratory (October 1993). Five colonies were put in a 30-liter aereated flow chamber with flow velocities of 4–9 cm s^{-1} and a continuous supply of unfiltered seawater pumped from 5-m depth about 40-m offshore. After 3 d, when the colonies were presumably in a steady state of ingestion and digestion, we stopped the supply of untreated seawater and replaced it with 0.7-μm GF/F-filtered seawater. Chlorophyll content in the polyps and in the chamber water was then measured hourly in the first 10 h and every 3 h in the following 35 h. Branches were clipped off the colonies and subsampled (six branchlets of 20–30 polyps from each branch, 163 branchlets in total), and polyp number was microscopically determined and photopigment contents measured as described above. At 6-h intervals, 50% of the water was replaced with freshly filtered seawater.

In feeding experiment 2, rates of phytoplankton intake in the gastrovascular cavities were measured by reversing the decomposition experiment (October 1993). Twenty-three colonies were incubated in repeatedly exchanged filtered seawater in the flow chamber for 3 d. The results of feeding experiment 1 indicated that by that time the phytoplankton contents of the gastrovascular system were very low. The filtered water was then replaced by a continuous supply of new unfiltered seawater. Successive measurements of pigment concentrations were carried out over 48 h following the same sampling protocol as described above. The flow speed in front of each individual colony, analyzed by video-tracking the traveling speed of natural particles in the water, ranged from 4.0 to 9.6 cm s^{-1}. Rates of phytoplankton ingestion were calculated by linear regression analysis on increase in chlorophyll contents over the first 14 h in 30 colonies. The calculation was based on the assumption that the digestion of cell walls was slow and no significant chlorophyll decomposition took place within the first hours. In order to address possible diurnal effect on feeding behavior, we carried out the experiment both after dawn (93 colony samples, 20 water samples) and after dusk (209 colony samples, 32 water samples). Daily rates of chlorophyll intake were compared with chlorophyll concentrations in the water, and clearance rates were determined as the volume of seawater cleared of phytoplankton per unit time. Clearance efficiency was calculated as the phytoplankton intake rate normalized by the phytoplankton flux through an imaginary plane with the size of a polyp's tentacle crown (9.6±1.2 mm^2) (Shimeta and Jumars 1991).

Additional food items such as naked flagellates and herbivorous microzooplankton might have contributed to the Chl *a* contents in the gastrovascular system of *D. hemprichi*. To control for this possibility, we repeated feeding experiment 2 by exposing five starved colonies to laboratory algae cultures (*Nannochloropsis, Isochrysis, Tetraselmis*) diluted in filtered seawater after microscopic examination had confirmed that the cultures were free of contamination with microzooplankton. Chl *a* concentrations in the colonies were assessed after 20 h of exposure (N = 30 colony samples).

The influence of flow speed on rates of in situ phytoplankton ingestion was measured twice (15–17 August and 14–16 September) in feeding experiment 3. Numbered plates carrying a total of 35 colonies (5–8 cm high) were suspended for 3 d on wires in front of the pumps 10–50 cm away from the flow straighteners. Three times per day, water samples were taken from within the cages and the state of expansion and contraction of the colonies recorded. After 3 d, the colonies were brought back to the laboratory for pigment extraction (N = 210 colony samples).

Feeding on zooplankton was examined both in situ and in the laboratory (May and June 1993). In feeding experiment 4, branches of colonies in the field were collected for zooplankton gut content analysis during two nights and two days. In the first night, 10 colonies growing on plates were exposed to the ambient flow of 3.4 cm s^{-1} (range, 1.1–4.7 cm s^{-1}). During the second night, five colonies were kept in front of the flow setup, exposed to current speed of 18 cm s^{-1}, while five other colonies were exposed to ambient flow averaging 3.1 cm s^{-1} (range,

0.2–9.6 cm s^{-1}). Four braches were collected from each colony at 2-h intervals during the nights (at 2200, 2400, 0200, and 0400 hours). At the same time, zooplankton availability in the water was estimated by pumping water for 20 min from the vicinity of the experimental setup to a zooplankton net (100-μm mesh) with a submerged rotary pump at a pumping rate of 13.7 m^3 h^{-1}. At various times during the day, 10 colonies were collected from different flow-exposed locations to check for gut contents during daytime. Colonies and plankton samples were immediately preserved in 5% buffered formaldehyde.

A total of 8,625 polyps of 30 colonies from the field were dissected under the microscope, and zooplankton items found in the gastrovascular cavities were separated, counted, and preserved. The size of all items found in the guts and 200 randomly chosen items from each water zooplankton sample were measured with a video-recording technique. Preserved specimens were recorded by a CCD camera (Sony DXC-10IP) mounted on a dissecting microscope. The length of recorded individuals was measured with an image-processing technique (frame-grabbing card and Globalab software. Selectivity was calculated from the coefficient of prey preference $\alpha_i = r_i p_i^{-1} [\Sigma(r_i p_i)^{-1}]^{-1}$ (Chesson 1978), which compares the probability for prey capture (type i, fraction in gut contents r_i) with the probability of prey encounter (fraction of prey in water sample p_i).

In feeding experiment 5, we examined the zooplankton-capture efficiency of *D. hemprichi* in a laboratory experiment. Expanded colonies were put in a 5-liter flow chamber at 0, 1, and 5 cm s^{-1} flow speed to which natural living zooplankton were added. Live zooplankton were collected by gently filtering pumped seawater in a 100-μm net submerged in a large container. Encounters between the coral and zooplankton were recorded for ~40 min each with a video Camcorder (Sony Hi 8, model V700e) and later analyzed by playing back the tapes using a Sony VCR and the above frame-grabbing technique. Measured parameters included prey type and size, duration of contact between prey and polyp, number of tentacles involved, and feeding success (prey capture or escape).

Determination of growth rates in the field—Relationships between flow and the growth rate of *D. hemprichi* were investigated with the pump setup. Timers on the pumps simulated the intermittent, tidally determined characteristic of the currents in the gulf (Genin et al. 1994). A 5-h period of enhanced flow was followed by 3 h of inactivated pumps, delayed by 45 min a day. Colony clones were established by cutting hundreds of branchlets, 5–20 polyps in size, off five differently colored mother colonies collected at separate locations. The five clones were randomly distributed over 20 PVC plates and positioned on the bottom of an aerated aquarium with running seawater. The polyp number decreased by up to 20% during the rhizoid production. After ~10 d, the rhizoids had stopped growing, and newly gained biomass was apparently invested into addition of polyps and stem growth of the now firmly attached colonies. The position, color, and number of polyps of the 20–30 established colonies

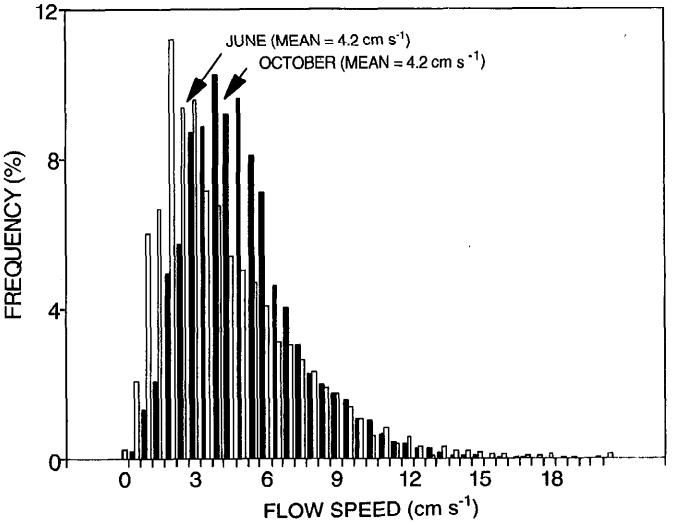

Fig. 2. Flow conditions at the pump setup (40-m offshore, 5-m depth) during the growth experiments. Frequency distribution of flow speeds in the June (4 June–3 July 1993: open bars) and October experiments (11 October–10 November 1993: closed bars).

per plate were recorded, and the plates were photographed and transferred to the pump setup at sea. Every 3–5 d, the colonies were counted and checked for potential signs of predation and the cages and pumps were cleaned. After 30 d, the plates were taken back to the laboratory, and growth increment, defined as change in the number of polyps, was microscopically determined. We determined possible flow effects on the biomass of individual polyps by measuring the AFDW of 30 fragments at the beginning of the experiment and 102 fragments at the end.

The experiment was run twice, 4 June–3 July and 11 October–10 November 1993. The mean ambient flow was similar during both runs (4.2 vs. 4.8 cm s^{-1}), with a maximum of 20 cm s^{-1} and occasional periods of almost zero flow (Fig. 2). Wave-generated flow at the 5-m-deep site was negligible. Currents were mostly longshore (northeast–southwest), with varying flow directions in the first experiment (June) and a predominance of northeastward direction in the second experiment (October–November).

Metabolic demand and carbon budget—The oxygen consumption of 8–12-cm-tall colonies was measured in self-contained underwater respirometers with six 3-liter deployment chambers (technical descriptions of a prototype given by Klumpp et al. 1987). The respirometers were set up outdoors in a 15-m^3 tank with running seawater and kept in semi-darkness (15 μEinst m^{-2} min^{-1}) in order to minimize oxygen production by phytoplankton. The water in the chambers was automatically replaced every 20 min, and oxygen, temperature, and light were recorded by averaging five readings every minute. Measurements of O_2 consumption followed the protocol of Fabricius and Klumpp (1995). Propelled water movement in the chambers was probably faster than it was in the feeding experiments described above, and highly turbulent. Due to the short incubations between chamber

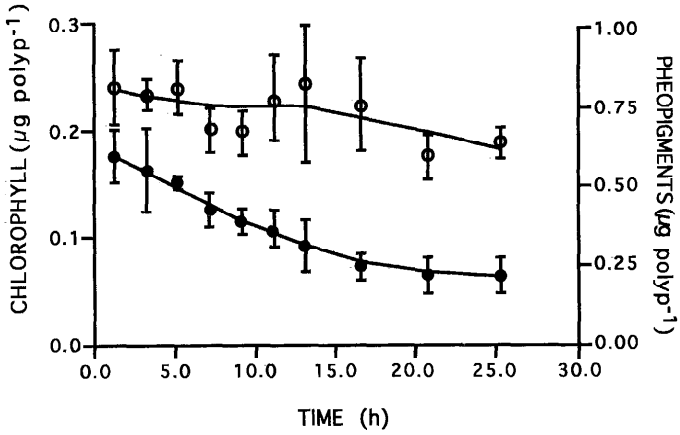

Fig. 3. Changes in Chl *a* (●) and pheophytin (○) contents per polyp of a *Dendronephthya hemprichi* colony after transfer into 0.7-μm-filtered, phytoplankton-free seawater (*see text*). Each point represents the mean of 12 samples from two sampling periods (±1 SD). Curves fitted with LOWESS smoothing.

flushings, O_2 concentrations in the chambers never deviated more than 15% from that of the fresh seawater. Patterson et al. (1991) clearly demonstrated the effect of flow on rates of gas exchange in marine invertebrates. However, because of the complicated flow conditions and the oscillating O_2 concentrations in the deployment chambers, we did not attempt to adjust our measured rates of respiration to the flow speeds used in the carbon budget. Calculation of the metabolic carbon demand RE was based on a respiratory quotient (RQ) of 0.8 (Hatcher 1989), a polyp biomass of 0.08 mg of AFDW, and a biomass exponent (Patterson 1992) of 1.0 which best fit the data.

The respiratory carbon demand was compared with carbon gained by zooplankton and phytoplankton feeding and carbon investment in colony growth. Conversion factors were based on the assumptions that follow. Chl *a*: phytoplankton C = 1: 60 (Taguchi et al. 1988), phytoplankton assimilation efficiency = 70% (as commonly found for marine organisms feeding on microalgae, Wotton 1992), and carbon content of the individually measured zooplankton items (M_z, in μg C) in relation to body length (S, in μm) was estimated as: $\log M_z = 2.23(\log S) - 5.58$ (Rodriguez and Mullin 1984). We assumed a zooplankton digestion time of 6 h to extrapolate mass of gut contents to daily zooplankton ingestion. The soft coral *Sarcophyton trocheliophorum* digested *Artemia* nauplii within 4 h (Lewis 1982). The digestion of copepods and shelled molluscs is probably slightly slower.

Statistical analyses—Statistical analyses were done with SYSTAT 5.03 (Wilkinson 1988) and Statistica (StatSoft Inc.). The locally weighted robust regression (LOWESS, Cleveland 1979) was used for graphic presentations due to the unequal time intervals of our data points. Piecewise linear regression with breakpoint, with weighed least squares and the quasi-Newton algorithm to estimate and minimize the loss function, was used to describe nonlinear relationships (Gill and Murray 1974). Cochran tests were used to test for homogeneity of variances before ANOVA, and data were transformed to reduce heteroscadiscity (Underwood 1981). Tukey's pairwise comparison technique was used in combination with ANOVA for posthoc comparisons of means (Lund and Lund 1983).

Results

Feeding ecology—High concentrations of phytoplankton cells (several hundred per polyp) of 3–20-μm size were found in the gastrovascular cavity of freshly collected *D. hemprichi* from flow-exposed sites. Neither phytoplankton nor other sources of epifluorescence were found in the polyps after colonies were kept in the laboratory for 2–3 d in filtered seawater or in unfiltered water but under conditions of low flow. A thin film of epiphytic algae was commonly found on the lowest part of the colony's stem, and this part was excluded from later chlorophyll extractions. Large numbers of phytoplankton cells also were found in the coelenterons of *D. sinaiensis, S. corymbosa,* and the gorgonian *Acabaria* sp. Unlike *D. hemprichi,* these three taxa showed high levels of autofluorescence in tentacle tissue and spicules. Floristic assessment of the phytoplankton ingested by all four taxa indicated a strong selection of eucaryotes. Very few cyanobacteria (size, <3 μm) were observed, although their numbers and biomass in the ambient water greatly exceed those of eucaryotes (D. Lindell and A. Post unpubl.). Flow-cytometry techniques would allow us to test whether low numbers of cyanobacteria in the coelenterons were the consequence of greater difficulty in observation (their fluorescence is weaker than that of eucaryotic cells) or whether there is a selectivity against very small particle sizes by the colonies.

Chl *a* concentration in the gastrovascular cavity of *D. hemprichi* decreased significantly after the colonies were transferred to phytoplankton-free, filtered water in feeding experiment 1 (Fig. 3). Chl *a* gradually decomposed in the initial 14 h at a mean rate of 0.006 μg polyp^{-1} h^{-1} (N = 102, SE = 0.002, $P < 0.001$) or 3.5% h^{-1}. Changes in pheopigment concentrations varied, resulting in no significant trend over that period ($R^2 = 0.0015$, $P > 0.05$). At the same time, the ratio of Chl *a* to pheopigment in the polyps dropped by 0.012 h^{-1}, reaching levels a fifth to an eighth of those in the ambient seawater after ~ 15 h (0.08–0.13 vs. 0.69). In freshly collected polyps before the beginning of starvation, the value of this ratio was 0.4 times that in ambient seawater. These processes provided evidence for phytoplankton digestion (Welschmeyer and Lorenzen 1985), as discussed below.

When starved corals were reintroduced to natural seawater or filtered seawater with laboratory algae added (feeding exp. 2), phytoplankton accumulated in their gastrovascular system. Accumulation of phytoplankton from natural seawater was gradual, and retention rates depended on the flow speed (Fabricius et al. 1995). Over about the first 10 h, Chl *a* concentrations in colonies seemed to increase linearly, with rates ranging from 0.006 to 0.029 μg Chl *a* polyp^{-1} h^{-1} (Table 1). Equivalent car-

Table 1. Increase of plant pigments in the gastrovascular system of previously starved *Dendronephthya hemprichi*. Linear correlation on pigment concentrations sampled in the initial 10 h and between 10 and 48 h after measurements started. Number of colony samples—*N*.

Flow (cm s^{-1})	*N*	0–10 h		10–48 h	
		μg $polyp^{-1}$ h^{-1} ± SE	R^2	μg $polyp^{-1}$ h^{-1} ± SE	R^2
		Chlorophyll *a*			
4–5.9	60	0.0063±0.0033	0.79	0.00001±0.001	0.000
6–7.9	60	0.0104±0.0029	0.92	0.0025±0.0018	0.27
8–9.5	90	0.0291±0.0079	0.93	0.0012±0.0029	0.02
		Total pigments			
4–5.9	60	0.0174±0.0052	0.69	0.0067±0.0021	0.63
6–7.9	60	0.0254±0.0213	0.32	0.0183±0.0043	0.79
8–9.5	90	0.0483±0.0189	0.52	0.0142±0.0104	0.64

bon intake values are listed in Table 2. The curve of Chl *a* concentration over time had an asymptotic shape, which suggests a balance between Chl *a* ingestion and decomposition after ~10–12 h. The trend of a slight Chl *a* increase after 10 h was not significant and paralleled a steady Chl a rise in the ambient seawater during the observation time (from 1.8 to 2.7 mg Chl *a* m^{-3} over 48 h). In contrast, the concentration of total photopigments in the colonies continued to increase after 10 h (Table 1), presumably due to slow gut clearance rates and accumulation of indigestible pheopigments in the gastrovascular system. In the two experiments (one started at dusk and one in the morning), ingestion rates were not significantly different within the first 12 h (nested ANOVA, $P > 0.05$). Clearance efficiency increased from 1.7% at 4–6 cm s^{-1} to 4.5% at 8–10 cm s^{-1} (Table 2). Maximal efficiency was therefore equivalent to a clearance rate of 2.8 liters seawater $polyp^{-1}$ d^{-1}.

In feeding experiment 3, in situ relationships between phytoplankton ingestion and flow were generally similar to those found in the flow tank. Phytoplankton intake rates were highest at 15–18 cm s^{-1} and declined at flow speeds above and below this (Fig. 4). At the lowest flow speed of 1–3 cm s^{-1}, colonies contained ~10% of the Chl *a* (0.03–0.08 μg $polyp^{-1}$) of those feeding at optimum flow speed (0.5–0.73 μg $polyp^{-1}$). Chl *a* concentrations varied up to 30% between branches within the same colonies, probably due to local differences in flow exposure and state of expansion. The flow accounted for 65.5% of the total variance in chlorophyll contents (piecewise linear regression, $R^2 = 0.65$, $N = 210$, $P \ll 0.001$, computed breakpoint at 16.1 cm s^{-1} flow and 0.287 μg Chl *a* $polyp^{-1}$). The flow-dependent ingestion rates did not differ significantly between the first and second experiment when intake rates were normalized by the mean ambient Chl *a* concentration during each period (0.26 and 0.29 mg Chl *a* m^{-3}, respectively; nested ANOVA, $P > 0.05$).

Feeding on zooplankton—In contrast to the high intake rates of phytoplankton, we found very little zooplankton

Table 2. Food availability (FA, μg C $liter^{-1}$) and daily carbon intake per polyp (μg C $polyp^{-1}$ d^{-1} ± SE) in *Dendronephthya hemprichi*. Phytoplankton carbon availability estimates are based on plankton biomass measurements 40 m off the coast of Eilat at 5-m water depth over 2×48 h during the experiments. Zooplankton carbon availability estimated during the feeding study (for 20 min each in 2-h intervals through two nights at 2200, 2400, 0200, and 0400 hours) by pumping a known volume of water from the vicinity of the experimental setup to a zooplankton net (100-μm mesh). Zooplankton capture rates are based on in situ observations and extrapolated to daily values assuming a digestion time of 6 h; calculations of phytoplankton intake rates are based on flow chamber experiments with natural seawater (N = 8, 7, 8 colonies). Clearance rate (CR, liters $polyp^{-1}$ d^{-1}) and efficiency (CE, %) are calculated by comparing food intake rates with in situ availability (*see text*).

	Concn m^{-3}	FA	Flow (cm s^{-1})	Ingestion $polyp^{-1}$ d^{-1}	C ingestion	CR	CE
Phytoplankton	0.25 mg Chl *a*	15.0	4–6	0.15 μg Chl *a*	9.0±4.8	0.6	1.7
			6–8	0.25 μg Chl *a*	15.0±4.1	1.0	2.1
			8–10	0.70 μg Chl *a*	41.0±11.4	2.8	4.5
Zooplankton	1,100 items	3.5	1–18	0.088 items	0.2	0.08	0.2
Phyto.: zoo.		1:0.23			1:0.02–1:0.005		

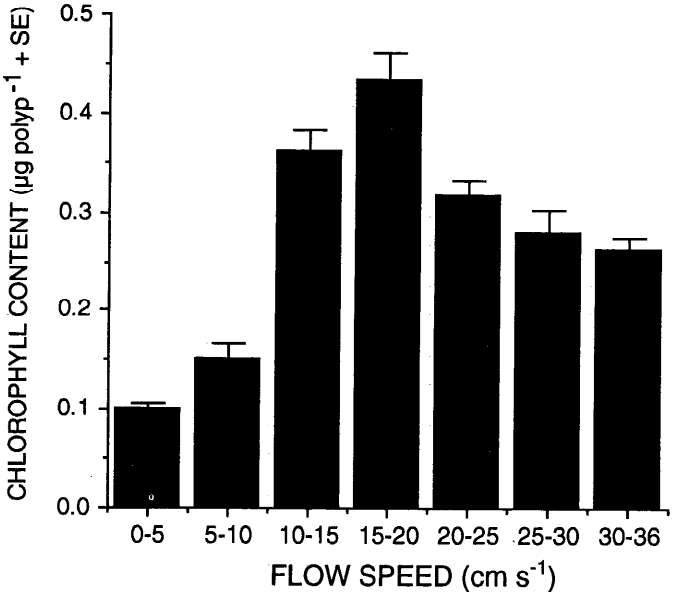

Fig. 4. Chlorophyll *a* concentration in *Dendronephthya hemprichi* exposed for 3 d to different in situ flow speeds (N = 210 samples from 35 colonies). Error bars indicate SE.

prey in the polyps of *D. hemprichi* in the field in feeding experiment 4. On average, there were <0.02 items, or 0.05 µg zooplankton C per polyp, equalling an intake rate of 0.2 µg C polyp^{-1} d^{-1} (Table 3). No differences in flow or times of activity were evident. The prey consisted mostly of small (mostly <700 µm body length) planktonic bivalves, copepods, and gastropods. The Chesson selectivity coefficients indicated a preference for bivalves and gastropods, while copepods were underrepresented in the gut samples. Both clearance rates and clearance efficiencies were an order of magnitude lower than those for phytoplankton (Table 2).

In feeding experiment 5 with expanded colonies in a flow chamber, there were no encounters between zooplankton and polyps at 0–1 cm s^{-1} flow speed, probably because of advection or avoidance behavior of the prey. At 5 cm s^{-1} and around 200 zooplankton items liter^{-1}, encounter rates were probably three to four orders of magnitude higher than in the field, and 400 encounters were recorded. Besides the above-listed taxa, ostracods, amphipods, tintinniids, polychaetes, and fish eggs were found in the coelonterons. These were mostly small and slow-swimming individuals. Items <300 µm were often captured and taken up within 10–20 s. Attempts to capture items ≥750 µm were almost never successful, although in these cases all eight tentacles of *D. hemprichi* were involved, and the zooplankton items escaped after a mean contact time of 50 s. There were no signs of paralysis even in prey held by the tentacles for several minutes or captured two or three times. After 2 h in concentrated zooplankton, polyps contained up to seven prey items (mean, 1.1 polyp^{-1}, N = 80). Thus, food saturation probably does not occur under natural conditions.

Flow-related growth rates and morphology—In the young *D. hemprichi* colonies exposed to different flow velocities in the field, there was a significant effect of flow on the addition of new polyps as well as on polyp size. The greatest increase in polyp numbers, with a daily addition of up to 8%, was found in colonies exposed to 12–17 cm s^{-1} for 15 h d^{-1} (Fig. 5). At 1–3 cm s^{-1}, the average numbers of polyps changed little and the size of many colonies decreased. The increase in polyp numbers over time was linear and size-dependent [linear regression between number of polyps initially (N_0) and after 30 d (N_{30}): at 1–3 cm s^2 flow, N = 76, R^2 = 0.73, $P \ll 0.01$; 4–6 cm s^2, N = 50, R^2 = 0.68, $P \ll 0.01$; 17–20 cm s^2, N = 67, R^2 = 0.64, $P \ll 0.01$]. The mean daily rate of polyp addition was independent of the initial polyp number (1–3 cm s^2, N = 76, R^2 = 0.14; 4–6 cm s^2, N = 50, R^2 = 0.02; 17–20 cm s^2, N = 67, R^2 = 0.16; $P > 0.05$ in each case). Sixty-nine percent of the variation in increase in polyp numbers of the 418 colonies of the second experiment was accounted for by flow exposure. Piecewise linear regressions computed the breakpoint at 13.0 cm s^{-1}. No statistical difference was found between growth rates in the June and October experiments (nested ANOVA, $P > 0.05$), between growth rates of the different color morphs (nested ANOVA, $P > 0.05$) or in mortality be-

Table 3. Zooplankton in the gastrovascular cavity (prey comp., %±SD) of 8,625 polyps from 30 field-collected *Dendronephthya hemprichi* colonies (189 items in total) compared to the zooplankton availability (zoo. comp., %±SD) at the study site during the experiment (mean of three 200-item subsamples each from seven 4.6-m^3 water samples collected over two nights). α—Chesson's (1978) index of prey preference. Carbon approximations (zoo. C, µg C polyp^{-1}) based on Rodriguez and Mullin (1984).

Prey type	Prey comp.	Zoo. comp.	α	Body length (µm ± SD)		Zoo. C
				Gut contents	Water samples	
Bivalvia	47.6±24.2	10.1±4.7	0.68	367±101	345±35	0.0144
Gastropoda	15.3±7.3	9.0±4.0	0.25	537±425	340±51	0.0108
Copepoda	34.4±18.7	68.9±6.9	0.07	573±368	563±72	0.0280
Euphausiaceae	0	2.7±1.0	0	—	815±443	—
Tunicata	0	2.1±1.9	0	—	1,363±621	—
Others	2.6±3.2	7.2±3.6	—	678±130	226±323	(<0.001)
Sum	100 (N=189)	100 (N=1,200)	1.0	mean: 508±217 µm	mean: 532±73 µm	0.0532

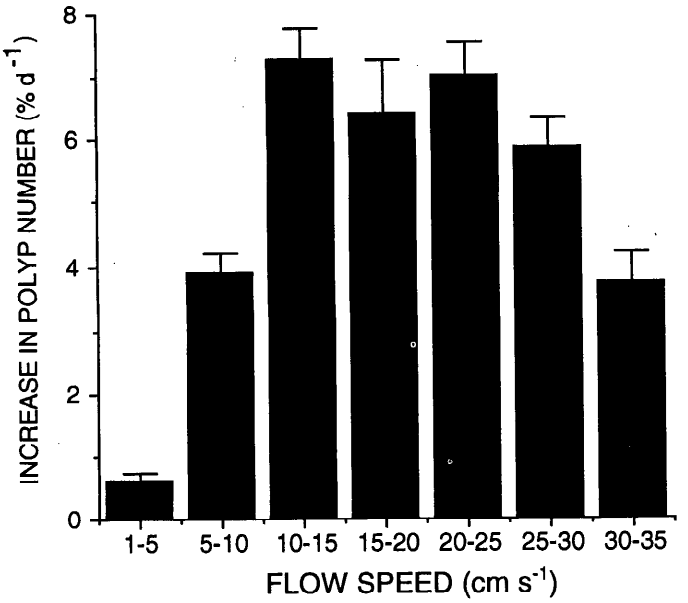

Fig. 5. In situ growth rates of 704 young *Dendronephthya hemprichi* in the field, measured as change in polyp numbers over 30 d. Error bars indicate SE.

tween flow treatments (ANOVA, $P > 0.05$; mean mortality in the June and October experiments: 19.8 ±17.7% SD, $N = 217$, and 23.5 ±11.7%, $N = 704$, respectively).

Colonies exposed to flow of 1–3 cm s^{-1} had significantly smaller polyps than those exposed to higher flow (Fig. 6). Within the range of flow speeds tested, the mean polyp biomass increased steadily with increasing flow speed. The effect of flow on the AFDW of the polyps was highly

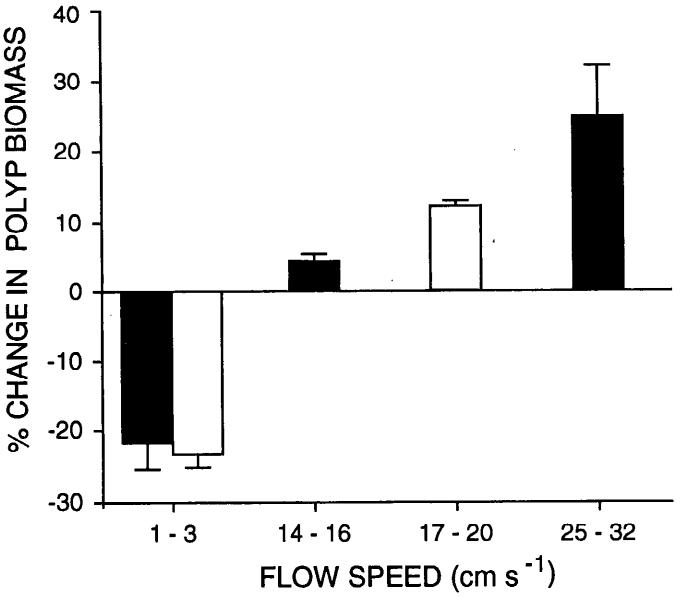

Fig. 6. Flow effect on polyp biomass (AFDW) in *Dendronephthya hemprichi*. Colonies grew under different flow conditions for 30 d. Open bars—June experiment; closed bars—October experiment. Error bars indicate SE.

Table 4. Daily growth rates of small colonies of *Dendronephthya hemprichi* in different flow (cm s^{-1}) environments. Daily percent change (±SE) in colony biomass (Δ M $colony^{-1}$) based on increase in polyp numbers within 30 d (Δ polyp No.) and changes in AFDW of polyps (Δ M $polyp^{-1}$). $N = 30$ for each flow category. Each factor contributes differently to colony growth in different flow environments.

Flow	Δ polyp No.	Δ M $polyp^{-1}$	Δ M $colony^{-1}$
	(% ± SE)		
1–3	+0.62±0.12	−0.72±0.24	−0.104±0.06
12–16	+7.12±0.45	+0.14±0.02	+7.27±0.86
25–32	+5.25±0.39	+0.82±0.38	+6.11±1.98

significant. ANOVA on data of June experiment: flow, df = 2, MS = 1.878; error, df = 92, MS = 0.045; $F = 24.165$, $P < 0.001$. Tukey's posthoc pairwise comparison of groups: $P < 0.005$ in each comparison. The ratio of ash weight (mostly spicules) to AFDW was highly variable and not significantly different between treatments.

The above growth rate data were used to calculate the mean biomass change of whole colonies in relation to the flow environment (Table 4). Colonies under conditions of weak flow (1–3 cm s^{-1}) lost on average 0.2% of their biomass per day in spite of a slight rise in polyp numbers. The increase in colony biomass was not significantly different between colonies exposed to medium (12–16 cm s^{-1}) and high (25–32 cm s^{-1}) flow speeds. However, the daily addition of 7.3% to the colony biomass under conditions of medium flow was mostly due to an increase in polyp numbers (Fig. 5), whereas the size of the polyps increased only little (Fig. 6). In contrast, the growth of colonies from the high-flow treatment, which added an average of 6.1% to their original biomass, was a combined effect of addition in polyp number and increased polyp size.

Metabolic demand of D. hemprichi—The mean daily carbon consumption, measured on six colonies in underwater respirometers and standardized by the AFDW of the colonies, was 6.46±1.32 mg C g^{-1} AFDW d^{-1} (± SD) or 2.72±0.52 μg C $polyp^{-1}$ d^{-1} (Table 5). A linear

Table 5. Oxygen consumption and respiratory carbon demand in young *Dendronephthya hemprichi* colonies in respiration chambers. Biomass (AFDW)—M.

Colony	M (g)	Respiration (μmol O_2 min^{-1})	(mg C g^{-1} M d^{-1})	(μg C $polyp^{-1}$ d^{-1})
1	0.86	0.40	6.18	2.64
2	0.46	0.18	4.49	1.92
3	0.87	0.49	7.62	3.25
4	0.84	0.52	8.19	3.50
5	0.56	0.27	5.82	2.49
6	0.31	0.18	5.87	2.51
Mean ± SD			6.46±1.32	2.72±0.52

correlation between respiration and biomass, and a biomass exponent of 1.0, best fit the data: respiration = 0.0074 AFDW ($R^2 = 0.88$, $N = 6$, $P < 0.02$).

Discussion

Our observations and measurements using a variety of methods provide strong evidence that some asymbiotic soft corals ingest considerable amounts of phytoplankton. In the case of *D. hemprichi,* our experiments indicate that ingested phytoplankton is digested by the coral. This conclusion is based on the observed decrease in Chl *a* : pheophorbide in the coral's digestive system, an established indicator of herbivory (Hawkins et al. 1986; Takamura et al. 1993). The ratio of Chl *a* to pheopigments in the gastrovascular contents of freshly collected polyps was only 0.4 times of that in the ambient seawater, presumably because the polyps contained algal cells in various states of digestion. This ratio gradually decreased to very low levels. The decomposition of Chl *a* to pheopigments requires a low pH level and does not occur spontaneously either in the light or in the dark (Welschmeyer and Lorenzen 1985). This suggests that acid digestive fluids hydrolyze and penetrate the algal cell walls (acidity measured for sea anemones: Van-Praet 1985), which facilitates the release of soluble algal components from the cells. Plant-derived gut pigments have been widely used to determine food composition and trophic levels (Kleppel 1988). The chlorophyll contents in colonies fed with laboratory algae cultures free of microzooplankton provide additional evidence that phytoplanktivory is the dominant mode of nutrition in these cnidarians.

The literature on soft-coral feeding is sparse and contradictory. All previous soft-coral feeding studies, except that of Sebens and Koehl (1984), were carried out under laboratory conditions with artificial food or concentrated natural zooplankton of unknown density and without considering the role of water flow in determining behavior, feeding activity, and food encounter rates (e.g. Roushdy and Hansen 1961; Lewis 1982; Farrant et al. 1987). There is a report of the temperate azooxanthellate soft coral *Alcyonium digitatum* feeding on ^{14}C-labeled algae (Roushdy and Hansen 1961). A significant ^{14}C depletion in the medium was measured over 23 h; however, the study failed to provide an appropriate control for algae settlement. Subsequent gut-content analyses on the same genus indicated zooplanktivory (Sebens and Koehl 1984). Farrant et al. (1987) also measured incorporation of labeled phytoplankton in soft coral tissue, with a negative outcome. However, they ended their experiments after digestion times of 2 h, which is probably insufficient time for the corals to break open and digest the cell walls of algae. Plant-digesting carbohydrase (amylase and laminarinase) were found in three soft coral species (genus *Alcyonium*) but not in stony corals during a broadscale screening of marine benthic invertebrates of the Great Barrier Reef (Elyakova et al. 1981).

No evidence for phytoplankton feeding has been found in the few studies examining this feeding mode in scleractinian (stony) corals (e.g. Porter 1974). The biological significance of tentacle pinnules in the Octocorallia group (alcyonarians, gorgonians, and Pennatulaceae), in contrast to their absence in the Hexacorallia (actinarians, stony corals, and zoanthidae), has not been recognized. Finely spaced and narrow pinnules in octocorals apparently allow the capture of particles as small as a few micrometers. Furthermore, some octocorals were found to possess only small and ineffective stinging cells (cnidae), whereas the nematocysts of zooplankton-feeding scleractinian corals are generally highly elaborate and efficient and probably more numerous (Mariscal and Bigger 1977). Feeding on unicellular phytoplankton requires specific biomechanical adaptations because of the low Reynolds numbers resulting from small cell sizes. The arborescent colonies of *D. hemprichi* seem well adapted to this mode of feeding. They embody dense filters with up to eightfold ramifications, and the diameters of the pinnules as the smallest filter elements are only 45–55 μm (gap width between the pinnules, 60–80 μm). With these filter element structures, direct interception of phytoplankton on the pinnules and polyp surface is a likely event at intermediate to fast flow (Rubenstein and Koehl 1977; LaBarbera 1978). Low flow speeds adversely affect phytoplankton intake, probably due to reduced encounter rate by direct interception.

The documented selectivity in zooplankton capture matches findings for other passive suspension feeders with no means to paralyze prey, e.g. the soft coral *Alcyonium siderium* (Sebens and Koehl 1984) and the Red Sea crinoid *Lamprometra klunzingeri* (Rutman and Fishelson 1969). In the absence of effectively paralyzing cnidae, capture success depends on the escape behavior of the prey. Thus, copepods, with their highly evasive abilities, escape more often than the less motile molluscs. Apparent selectivity also could be due to prolonged digestion times and therefore long gut residence of hard-shelled items such as the molluscs.

The characteristic large, spiky sclerites of *D. hemprichi* commonly have been related to predator deterrence. However, the apparent elimination of all *D. hemprichi* in our preliminary uncaged growth experiment, as well as the specific arrangement of these sclerites, suggests that their prime function may be to hold the polyps and polyp bundles upright in strong flow conditions and to allow severalfold coenenchyme expansion and contraction. The mechanical and hydrostatic support of the polyps by large sclerites may explain why maximum food uptake seems to occur at higher flow and over a wider range of flow speeds in *D. hemprichi* than in several other octocorallia. For example, maximum particle capture occurs at 6–12 cm s^{-1} flow in the Caribbean gorgonians *Plexaurella dichotoma, Briareum asbestinum, Eunicea tournefortis,* and *Pseudopterogorgia americana* (Fabricius and Sebens unpubl. data) and at 6–15 cm s^{-1} in three gorgonians from southern Taiwan (Dai and Lin 1993). To some extent, the reduced feeding efficiency under conditions of high flow may be related to polyp retraction and colony con-

traction in *D. hemprichi.* Contraction occurs predominantly at flows of <3 cm s^{-1} and >25 cm s^{-1} (Fabricius unpubl. data). Contraction reduces colony height to ~30% of expanded height, which effectively reduces the coral's filtration area and thus its rate of food ecounter (Shimeta and Jumars 1991).

The nonlinear effect of flow on colony growth is similar to that on phytoplankton intake. The similarity of these curves is strong evidence that growth rates are to some extent limited by rates of food intake at lower or very high flow. A similar influence of flow on colony growth and maximum colony sizes was found for the temperate *A. siderium* (Sebens 1984). The change of biomass investment with increasing flow, either into polyp numbers or polyp size, may help maximize phytoplankton intake rates. At intermediate flow, intake rates will be directly related to the number of polyps, and polyp addition seems to be most advantageous. In contrast, at high flow, intake rates are affected by polyp bending, and biomass investment into polyp strength and stoutness rather than into additional polyps may enhance rates of food intake.

We established a simple carbon budget for *D. hemprichi,* comparing the in situ data on food intake, respiration, and growth in flows of 4–10 cm s^{-1} (Table 6). Due to the number of assumptions and the unknown influence of flow on zooplankton capture and respiration, this budget must be be considered very approximate. However, it can serve to evaluate and compare the magnitude of carbon gains and losses in *D. hemprichi.* Phytoplankton carbon uptake, corrected for an assimilation efficiency of 70%, exceeded zooplankton uptake by two orders of magnitude, with 6.3–28.7 μg C $polyp^{-1}$ d^{-1}, depending on the flow environment (Table 2). Zooplankton ingestion was only 0.2 μg C $polyp^{-1}$ d^{-1} at an assumed digestion time of 6 h, with a similar contribution of copepods and gastropods (Table 3). Daily carbon investment in growth of 3–6 μg $polyp^{-1}$ added to the respiratory carbon demand of 2.7 μg C $polyp^{-1}$ d^{-1}. This calculation assumes size-independent growth rates, as indicated by our data. Thus, zooplankton contributed 2.4–3.5% to the daily carbon requirements of *D. hemprichi.* Phytoplankton ingestion on its own covered the carbon requirements for growth and respiration in *D. hemprichi* more than adequately.

According to our calculations, the ratio between carbon investment in growth and that used for respiration in *D. hemprichi* is 1.1 : 1 to 2.1 : 1, depending on flow. These values are considerably higher than those reported for stony corals. For example, Edmunds and Spencer-Davies (1989) reported 0.24 : 1 to 0.59 : 1 in *Porites porites.* The high investment of carbon into biomass addition makes *D. hemprichi* one of the most productive marine macrobenthos invertebrates known, and this productivity is almost exclusively fueled by phytoplankton. Depending on flow rates, 20–88% of the ingested carbon was allocated to somatic growth and respiration in *D. hemprichi.* The excess carbon could to some extent be accounted for by mucus secretion and leakage of dissolved organic carbon out of the gastrovascular cavities (Schlichter 1982). The experiments were carried out on young, sexually immature colonies. Mature colonies release gametes or colony fragments almost daily (Benayahu unpubl. data) and may therefore require a considerable amount of additional carbon for reproductive functions.

Table 6. Carbon budget (μg C $poly^{-1}$ d^{-1}) for *Dendronephthya hemprichi* under conditions of different flow speeds (cm s^{-1}). Respiration was measured at ~16 cm s^{-1} and is probably lower at lower flow speeds. The effect of flow on zooplankton could not be determined because too few prey were captured. At higher flow speeds, carbon invested in growth is greater than the respiratory carbon demand. Phytoplankton provides sufficient carbon to fuel growth and respiration, whereas zooplankton intake is insufficient. "Excess" represents carbon which is not invested in somatic growth and respiration (*see text*).

Flow	Phyto- + zooplankton ingestion		Respiration		Growth		Excess
4–6	6.3±0.2	=	2.7	+	3	+	0.8
	100%		41.5%		46.1%		12.3%
6–8	10.5±0.2	=	2.7	+	3.9	+	4.1
	100%		25.2%		36.4%		38.4%
8–10	28.7±0.2	=	2.7	+	5.7	+	20.5
	100%		9.3%		19.7%		70.9%

To date, cnidarians have been considered strictly carnivorous (Brusca and Brusca 1990). Our work clearly shows that this generalization is incorrect. The inability to feed on zooplankton seems widespread among soft corals of the Great Barrier Reef (K. Fabricius unpubl. data on *Sinularia* 2 spp., *Sarcophyton* 3 spp., *Cladiella* sp., *Nephthea* sp., and *Paralemnalia digitiformis*), and 12 of the most common symbiotic soft coral genera on the central Great Barrier Reef were unable to cover their carbon requirements by photosynthesis (Fabricius and Klumpp 1995). Phytoplankton carbon in waters around coral reefs is commonly an order of magnitude more abundant than zooplankton carbon (Roman et al. 1990). Thus, an adaptation to feed on phytoplankton can be advantageous in the reef environment where zooplankton are heavily depleted by both vertebrates and invertebrates (Porter 1974; Hamner et al. 1988; Genin et al. unpubl. data). Indeed, some earlier studies suggested that phytoplankton uptake by the entire coral-reef community can be substantial (e.g. Glynn 1973; Sorokin 1991) without referring to the community members utilizing this resource. An evaluation of the extent of herbivory among cnidarians and other filter-feedere is required to assess the main pathways of phytoplankton import into the coral reef system.

References

BENAYAHU, Y., AND Y. LOYA. 1981. Competition for space among coral-reef sessile organisms at Eilat, Red Sea. Bull. Mar. Sci. **31:** 514–522.

BRUSCA, R. C., AND G. J. BRUSCA. 1990. Invertebrates. Sinauer.

CHESSON, J. 1978. Measuring preference in selective predation. Ecology **59:** 211–215.

CLEVELAND, W. S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Am. Stat. Assoc. **74:** 829–836.

COLMAN, R. S., H. CRENSHAW, D. L. MEYER, AND J. R. STRICKLER. 1984. A non-motorized dye injector for visualization of flow in situ and its use with coral reef crinoids. Mar. Biol. **83:** 125–128.

DAI, C. F., AND M. C. LIN. 1993. The effects of flow on feeding of three gorgonians from southern Taiwan. J. Exp. Mar. Biol. Ecol. **173:** 57–69.

EDMUNDS, P. J., AND P. SPENCER-DAVIES. 1989. An energy budget for *Porites porites* (Scleractinia), growing in a stressed environment. Coral Reefs **8:** 37–43.

ELYAKOVA, L. A., N. M. SHEVCHENKO, AND S. M. AVAEVA. 1981. A comparative study of carbohydrase activities in marine invertebrates. Comp. Biochem. Physiol. **69B:** 905–908.

FABRICIUS, K. E., Y. BENAYAHU, AND A. GENIN. 1995. Herbivory in asymbiotic soft corals. Science **268:** 90–92.

———, AND D. W. KLUMPP. 1995. Wide-spread mixotrophy in reef-inhabiting soft corals: The influence of depth, and colony expansion and contraction on photosynthesis. Mar. Ecol. Prog. Ser. **126:** 145–152.

FARRANT, P. A., M. A. BOROWITZKA, R. HINDE, AND R. J. KING. 1987. Nutrition of the temperate Australian soft coral *Capnella gaboensis:* 2. The role of zooxanthellae and feeding. Mar. Biol. **95:** 575–581.

GENIN, A., L. KARP, AND A. MIROZ. 1994. Effects of flow on competitive superiority in scleractinian corals. Limnol. Oceanogr. **39:** 913–924.

GILL, P. E., AND W. MURRAY. 1974. Numerical methods for constrained optimization. Academic.

GLYNN, P. W. 1973. Ecology of a Carribean coral reef. The *Porites* reef flat biotope: Part 2. Plankton community with evidence for depletion. Mar. Biol. **22:** 1–21.

HAMNER, W. M., M. S. JONES, J. H. CARLETON, I. R. HAURI, AND D. MCB. WILLIAMS. 1988. Zooplankton, planktivorous fish, and water currents on a windward reef face: Great Barrier Reef, Australia. Bull. Mar. Sci. **42:** 459–479.

HATCHER, A. 1989. RQ of benthic marine invertebrates. Mar. Biol. **102:** 445–452.

HAWKINS, A. J. S., B. L. BAYNE, R. F. C. MANTOURA, AND C. A. LLEWELLYN. 1986. Chlorophyll degradation and absorption throughout the digestive system of the blue mussel, *Mytilus edulis.* J. Exp. Mar. Biol. Ecol. **96:** 213–223.

HELMUTH, B., AND K. P. SEBENS. 1993. The influence of colony morphology and orientation to flow on particle capture by the scleractinian coral *Agaricia agaricites* (Linnaeus). J. Exp. Mar. Biol. Ecol. **165:** 251–278.

JOKIEL, P. L. 1978. Effects of water motion on reef corals. J. Exp. Mar. Biol. Ecol. **35:** 87–97.

KLEPPEL, G. S. 1988. Plant and animal pigments as trophodynamic indicators, p. 73–85. *In* D. F. Soule and G. S. Kleppel [eds.], Marine organisms as indicators. Springer.

KLUMPP, D. W., A. D. MCKINNON, AND P. DANIEL. 1987. Damselfish territories: Zones of high productivity on coral reefs. Mar. Ecol. Prog. Ser. **40:** 41–51.

LABARBERA, M. 1978. Particle capture by a Pacific brittle star: Experimental test of the aerosol suspension feeding model. Science **201:** 1147–1149.

LEWIS, J. B. 1982. Feeding behaviour and feeding ecology of the Octocorallia (Coelenterata: Anthozoa). J. Zool. Lond. **196:** 371–384.

LUND, R. E., AND J. R. LUND. 1983. Probabilities and upper quantiles for the studentized range. Appl. Stat. **32:** 204–210.

MCFADDEN, C. S. 1986. Colony fission increases particle capture rares of a soft coral: Advantages of being a small colony. J. Exp. Mar. Biol. Ecol. **103:** 1–20.

MARISCAL, R. N., AND C. H. BIGGER. 1977. Possible ecological significance of octocoral epithelial ultrastructure, p. 127–133. *In* Proc. 3rd Int. Coral Reef Symp.

MUSCATINE, L. 1973. Nutrition of corals, p. 77–116. *In* O. A. Jones and R. Endean [eds.], Biology and geology of coral reefs. V. 2. Academic.

PARSONS T. R., Y. MAITA, AND C. M. LALLI. 1984. A manual of chemical and biological methods for seawater analysis. Pergamon.

PATTERSON, M. R. 1984. Patterns of whole colony prey capture in the octocoral, *Alcyonium siderium.* Biol. Bull. **167:** 613–629.

———. 1992. A mass transfer explanation of metabolic scaling relations in some aquatic invertebrates and algae. Science **255:** 1421–1423.

———, K. P. SEBENS, AND R. R. OLSON. 1991. In situ measurement of flow effects on primary production and dark respiration in reef corals. Limnol. Oceanogr. **36:** 936–948.

PORTER, J. W. 1974. Zooplankton feeding by the Caribbean reef-building coral *Monastrea cavernosa,* p. 111–122. *In* Proc. 2nd Int. Coral Reef Symp.

RODRIGUEZ J., AND M. M. MULLIN. 1984. Relation between biomass and body weight of plankton in a steady state oceanic ecosystem. Limnol. Oceanogr. **32:** 361–370.

ROMAN, M. R., M. J. FURNAS, AND M. M. MULLIN. 1990. Zooplankton abundance and grazing at Davies Reef, Great Barrier Reef, Australia. Mar. Biol. **105:** 73–82.

ROUSHDY, H. M., AND V. K. HANSEN. 1961. Filtration of phytoplankton by the octocoral *Alcyonium digitatum* L. Nature **190:** 649–650.

RUBENSTEIN, D. I., AND M. A. R. KOEHL. 1977. The mechanisms of filter feeding: Some theoretical considerations. Am. Nat. **111:** 981–994.

RUTMAN, J., AND L. FISHELSON. 1969. Food composition and feeding behavior of shallow-water crinoids at Eilat (Red Sea). Mar. Biol. **3:** 46–57.

SCHLICHTER, D. 1982. Epidermal nutrition of the alcyonarian *Heteroxenia fuscescens* (Ehrb.): Absorption of dissolved organic material and lost endogenous photosynthates. Oecologia **53:** 40–49.

SEBENS, K. P. 1984. Water flow and coral colony size: Interhabitat comparisons of the octocoral *Alcyonium siderium.* Proc. Natl. Acad. Sci. **81:** 5473–5477.

———, AND T. J. DONE. 1993. Water flow, growth form and distribution of scleractinian corals: Davies Reef (GBR), Australia, p. 557–568. *In* Proc. 7th Int. Coral Reef Symp. V. 1.

———, AND M. A. R. KOEHL. 1984. Predation on zooplankton by the benthic anthozoans *Alcyonium siderium* (Alcyonacea) and *Metridium senile* (Actinaria) in the New England subtidal. Mar. Biol. **81:** 255–271.

SHIMETA, J., AND P. A. JUMARS. 1991. Physical mechanisms and rates of particle capture by suspension-feeders. Oceanogr. Mar. Biol. Annu. Rev. **29:** 191–257.

SOROKIN, Y. I. 1991. Parameters of productivity and metabolism of coral reef ecosystems off central Vietnam. Estuarine Coastal Shelf Sci. **33:** 259–280.

SPONGAULE, S., AND M. LABARBERA. 1991. Drag-induced deformation: A functional feeding strategy in two species of gorgonians. J. Exp. Mar. Biol. Ecol. **148:** 121–134.

TAGUCHI, S., G. R. DITULLIO, AND E. A. LAW. 1988. Physiological characteristics and production of mixed layer and chlorophyll maximum phytoplankton populations in the

Carribean Sea and western Atlantic Ocean. Deep-Sea Res. **35:** 1363–1377.

TAKAMURA, N., J. L. LI, H. Q. YANG, X. B. ZHU, AND T. MIURA. 1993. A novel approach to evaluate feeding by mixed cyprinid species in a chinese integrated fish culture pond using measurements of chlorophyll derivatives and photosynthesis in gut contents. Can. J. Fish. Aquat. Sci. **50:** 946–952.

TURSCH, B., AND A. TURSCH. 1982. The soft coral community on a sheltered reef quadrate at Laing Island (Papua New Guinea). Mar. Biol. **68:** 321–332.

UNDERWOOD, A. J. 1981. Techniques of analysis of variance in experimental marine biology and ecology. Oceanogr. Mar. Biol. Annu. Rev. **19:** 513–605.

VAN-PRAET, M. 1985. Nutrition of sea anemones. Adv. Mar. Biol. **22:** 65–95.

WELSCHMEYER, N. A., AND C. J. LORENZEN. 1985. Chlorophyll budgets: Zooplankton grazing and phytoplankton growth in a temperate fjord in the central Pacific gyres. Limnol. Oceanogr. **30:** 1–21.

WILKINSON, L. 1988. SYSTAT: The system for statistics. Systat, Inc.

WOTTON, R. S. [ED.]. 1992. The biology of particles in aquatic systems. CRC.

Submitted: 14 November 1994
Accepted: 3 April 1995
Amended: 8 June 1995

UNITED STATES POSTAL SERVICE™

Statement of Ownership, Management, and Circulation
(Required by 39 U.S.C. 3685)

1. Publication Title	2. Publication No.	3. Filing Date
Limnology and Oceanography	0 0 2 4 - 3 5 9 0	23 October 1995
4. Issue Frequency: Eight times per year in Jan., Mar., May, June, July, Sept., Nov., Dec.	5. No. of Issues Published Annually: 8	6. Annual Subscription Price: $175.00

7. Complete Mailing Address of Known Office of Publication *(Street, City, County, State, and ZIP+4) (Not Printer)*
American Society of Limnology and Oceanography, 810 E 10th St., Lawrence, KS 66044-8897 US

8. Complete Mailing Address of Headquarters or General Business Office of Publisher *(Not Printer)*
American Society of Limnology, 810 E 10th St., Lawrence, KS 66044-8897 USA

9. Full Names and Complete Mailing Addresses of Publisher, Editor, and Managing Editor *(Do Not Leave Blank)*
Publisher *(Name and Complete Mailing Address)*
American Society of Limnology and Oceanography, 810 E 10th St., Lawrence, KS 66044-8897 US

Editor *(Name and Complete Mailing Address)*
Raelyn Cole, Limnology and Oceanography, School of Oceanography, Box 357940, University of Washington, Seattle, WA 98195-7940 USA

Managing Editor *(Name and Complete Mailing Address)*
Raelyn J Cole School of Oceanography, Box 357940, University of Washington, Seattle, WA 98195-7940 USA

10. Owner *(If owned by a corporation, its name and address must be stated and also immediately thereafter the names and addresses of stockholders owning or holding 1 percent or more of the total amount of stock. If not owned by a corporation, the names and addresses of the individual owners must be given. If owned by a partnership or other unincorporated firm, its name and address as well as that of each individual must be given. If the publication is published by a nonprofit organization, its name and address must be stated.) (Do Not Leave Blank.)*

Full Name	Complete Mailing Address
American Society of Limnology and Oceanography	810 E 10th St., Lawrence, KS 66044-8897 US

11. Known Bondholders, Mortgagees, and Other Security Holders Owning or Holding 1 Percent or More of Total Amount of Bonds, Mortgages, or Other Securities. If none, check here. ☒ None

Full Name	Complete Mailing Address

12. For completion by nonprofit organizations authorized to mail at special rates. The purpose, function, and nonprofit status of this organization and the exempt status for federal income tax purposes: *(Check one)*
☒ Has Not Changed During Preceding 12 Months
☐ Has Changed During Preceding 12 Months
(If changed, publisher must submit explanation of change with this statement)

PS Form **3526**, October 1994 *(See Instructions on Reverse)*

13. Publication Name	14. Issue Date for Circulation Data Below
Limnology and Oceanography	June '94- May '95

15. Extent and Nature of Circulation	Average No. Copies Each Issue During Preceding 12 Months	Actual No. Copies of Single Issue Published Nearest to Filing Date
a. Total No. Copies *(Net Press Run)*	5375	5400
b. Paid and/or Requested Circulation (1) Sales Through Dealers and Carriers, Street Vendors, and Counter Sales *(Not Mailed)*		
(2) Paid or Requested Mail Subscriptions *(Include Advertisers' Proof Copies/Exchange Copies)*	4893	4709
c. Total Paid and/or Requested Circulation *(Sum of 15b(1) and 15b(2))*	4893	4709
d. Free Distribution by Mail *(Samples, Complimentary, and Other Free)*	5	5
e. Free Distribution Outside the Mail *(Carriers or Other Means)*	0	0
f. Total Free Distribution *(Sum of 15d and 15e)*	5	5
g. Total Distribution *(Sum of 15c and 15f)*	4898	4714
h. Copies Not Distributed (1) Office Use, Leftovers, Spoiled	477	686
(2) Return from News Agents		
i. Total *(Sum of 15g, 15h(1), and 15h(2))*	5375	5400
Percent Paid and/or Requested Circulation *(15c / 15g x 100)*	99%	99%

16. This Statement of Ownership will be printed in the November 1995 issue of this publication ☐ Check box if not required to publish.

17. Signature and Title of Editor, Publisher, Business Manager, or Owner — Date
Raelyn J Cole — 23 October 1995

I certify that all information furnished on this form is true and complete. I understand that anyone who furnishes false or misleading information on this form or who omits material or information requested on the form may be subject to criminal sanctions *(including fines and imprisonment)* and/or civil sanctions *(including multiple damages and civil penalties).*

Instructions to Publishers

1. Complete and file one copy of this form with your postmaster on or before October 1, annually. Keep a copy of the completed form for your records.
2. Include in items 10 and 11, in cases where the stockholder or security holder is a trustee, the name of the person or corporation for whom the trustee is acting. Also include the names and addresses of individuals who are stockholders who own or hold 1 percent or more of the total amount of bonds, mortgages, or other securities of the publishing corporation. In item 11, if none, check box. Use blank sheets if more space is required.
3. Be sure to furnish all information called for in item 15, regarding circulation. Free circulation must be shown in items 15d, e, and f.
4. If the publication had second-class authorization as a general or requestor publication, this Statement of Ownership, Management, and Circulation must be published; it must be printed in any issue in October or the first printed issue after October, if the publication is not published during October.
5. In item 16, indicate date of the issue in which this Statement of Ownership will be printed.
6. Item 17 must be signed.

Failure to file or publish a statement of ownership may lead to suspension of second-class authorization.

PS Form **3526**, October 1994 *(Reverse)*