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Herbivory in Asymbiotic Soft Corals

Katharina E. Fabricius,* Yehuda Benayahu, Amatzia Genin

A zooxanthellae-free soft coral from the Red Sea feeds almost exclusively on phytoplankton, a mode of nutrition so far unknown for corals. Herbivory was also found in three other azooxanthellate soft corals. In tropical oligotrophic waters, phytoplankton biomass density may be an order of magnitude higher than that of zooplankton. Use of this resource allows these azooxanthellate cnidarians to be highly productive in flow-exposed oligotrophic reef waters.

Soft corals are an important group of sessile marine invertebrates in tropical and temperate waters. They are the second most common benthos component in coral reefs of the Indo-Pacific and the Red Sea, in which their abundance can be higher than that of hard corals (*1*). Their feeding organs are characterized by relatively poorly developed stinging cells (nematocysts) (*2*), and their tentacles are branched so that rows of narrowly spaced pinnules are arranged in a comblike structure around each of the eight polyp tentacles. Thus, the surface area used for passive suspension feeding in soft corals is much larger than in stony corals, whose tentacles do not carry pinnules.

We have studied the diet of the common reef-inhabiting soft coral *Dendronephthya hemprichi* from the northern Red Sea and assessed the composition of its food and rates of food intake in field experiments. Most reef-inhabiting corals live in symbiosis with unicellular algae (zooxanthellae), which translocate enough photosynthetically fixed carbon to the host to fully cover the host's carbon demand in its characteristically nutrient-depleted environment (*3*). *Dendronephthya hemprichi* does not contain zooxanthellae but is successful in coexisting with or even outcompeting symbiotic reef corals. The arborescent colonies embody dense filters with up to eightfold ramification, and the pinnules are the smallest filter elements, with diameters of only 45 to 55 μm. Gap width between the pinnules is 60 to 80 μm. These structures seem more suitable for suspension feeding than for predatory capture of prey. We demonstrate here that suspension feeding on phytoplankton is the principal mode of nutrition that fuels this rapidly growing (*4*) soft coral.

Three lines of evidence indicate that *D. hemprichi* feeds on phytoplankton: (i) Epifluorescence microscopy of the gastrovascular cavity of freshly collected *D. hemprichi* showed high concentrations of small (3 to 20 μm) phytoplankton cells (*5*). (ii) Chlorophyll a degraded to phaeopigments in actively feeding colonies, a process indicative of phytoplankton digestion (*6*). (iii) Phytoplankton gradually accumulated in starved corals after their reintroduction to natural seawater.

The observations under the epifluorescence microscope confirmed that *D. hemprichi* was free of autofluorescence and epiphytic algae and did not contain zooxanthellae. A great majority of the ingested algae were eukaryotes, whereas very few blue-green algae were taken in. This contrasts to the great proportion of blue-green algae in cell numbers and biomass in phytoplankton populations of tropical waters (*7*) and may be related to the small size of blue-green algae cells (<3 μm).

The concentrations of phytoplankton pigments (chlorophyll a and its degradation products, phaeopigments) in the corals were quantified in order to estimate rates of phytoplankton intake and decomposition. Concentrations were determined fluorometrically, after a standard acetone-extraction technique (*8*), in colony branches with a known number of polyps (*9*). For the experiments, colonies 4 to 5 cm tall growing on small polyvinyl chloride plates were kept in a flow chamber (18 cm by 15 cm in cross section) in continuously replaced seawater. The plates were suspended on metal-free wire away from the glass walls in such a way that each colony was exposed to unobstructed laminar flow of 4 to 10 cm/s (*10*).

The chlorophyll a gradually decomposed to phaeophytin in the gastrovascular cavities of the colonies. Ten colonies were kept in natural seawater in the flow chamber. After 3 days of feeding on the natural phytoplankton, the ratio of chlorophyll a to total photopigments in the colonies was 0.23 (±0.04 SD), as compared with 0.69 ± 0.02 SD in the seawater. The seawater in the flow chamber was then replaced by filtered water (filter pore width was 0.7 μm), and the changes in concentrations of plant-derived pigments in the colonies were recorded over 48 hours by random sampling of branch tips of the colonies for pigment extraction. Within the first 14 hours, chlorophyll concentrations decreased at a rate of 3.5% per hour in these starving colonies, whereas phaeopigment concentrations did not change. Around 14 hours after the ini-

K. E. Fabricius, Australian Institute of Marine Science, Post Mail Box Number 3, Townsville Q4810, Australia, and Zoological Institute, University of Munich, Karlstrasse 23, 80333 Munich, Germany.
Y. Benayahu, Department of Zoology, Tel Aviv University, Ramat Aviv 69978, Israel.
A. Genin, The Hebrew University, H. Steinitz Marine Biological Laboratory, Post Office Box 469, Eilat 88103, Israel.
*To whom correspondence should be addressed.

Table 2. Mechanical and physiological properties of *Drosophila* flight muscle. Values given are mean ± SEM. The sample size for minimum elastic storage is smaller because not all flight sequences contained portions in which $P_{acc} > P_{aero}$.

Properties	Values
(ζ) Efficiency (%)	11.0 ± 0.06 (N = 26)
(α_{min}) Minimum elastic storage (%)	11.3 ± 1.31 (N = 16)
Muscle power (W kg^{-1} of thorax)	39.9 ± 1.44 (N = 26)
Muscle stress (kN m^{-2})	40.4 ± 4.01 (N = 26)

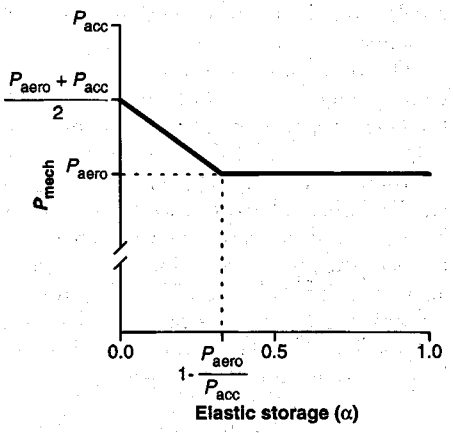

Fig. 3. Predicted mechanical power (P_{mech}) as a function of elastic storage. The graph plots Eq. 4 under the condition that P_{acc} is greater than P_{aero}. The maximal value of mechanical power is 1/2 (P_{acc} + P_{aero}) when α = 0. As elastic storage increases, P_{mech} decreases linearly toward P_{aero}. Mechanical power remains constant with increases in elastic storage above the critical value of $\alpha = 1 - P_{aero}/P_{acc}$.

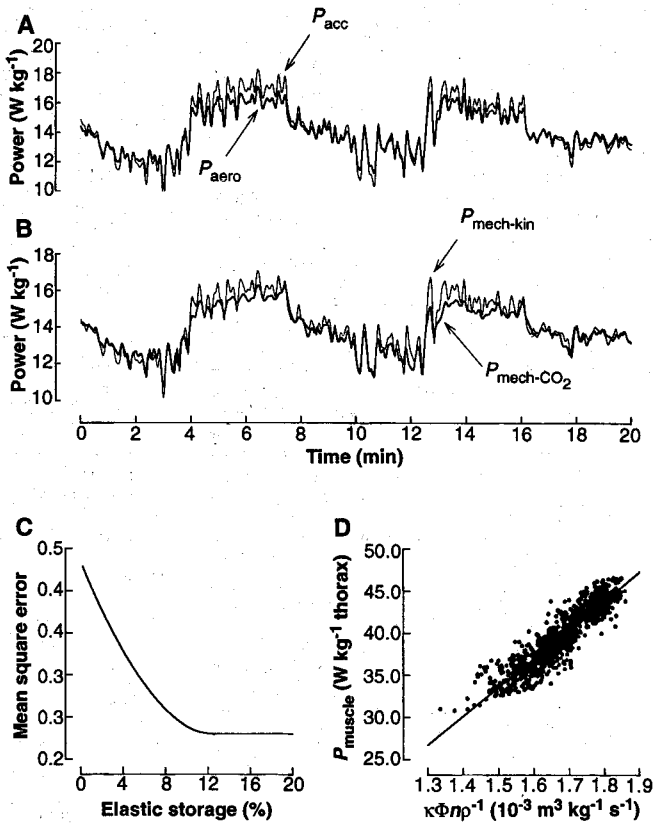

Fig. 4. (**A**) Comparison of predicted aerodynamic and inertial power during flight. The calculations are based on wingbeat frequency and stroke amplitude wave forms sampled at 1 Hz and so represent the power requirements averaged over many wingbeat periods. Although P_{acc} (thin trace) exceeds P_{aero} (thick trace) throughout most of the flight sequence, there are several sequences in which P_{aero} is larger. During these times, muscle efficiency may be estimated according to Eq. 6, yielding an average value of 11%. (**B**) Comparison of mechanical power based on respirometry ($P_{mech\text{-}CO_2}$, thick trace) and kinematics parameters ($P_{mech\text{-}kin}$, thin trace) for the same data set as in (A). The kinematic estimate of P_{mech} is based on an elastic storage of 12%, the minimum value of α that generated the lowest MSE with the respirometry data. (**C**) The MSE between the respirometric and kinematic estimates of P_{mech} as a function of percent of elastic storage [same data set as in (A) and (B)]. (**D**) Muscle power plotted against the product of strain, frequency, and density. Power was determined from the respirometric estimate of mechanical power, with the use of thoracic mass as an estimate of muscle mass [same data set as in (A), (B), and (C)]. Muscle strain was calculated by multiplication of stroke amplitude Φ by a scaling factor κ of 0.0037 rad^{-1}, which would generate a 1% strain at the mean stroke amplitude of 2.7 rad. The slope of this line gives a stress estimate of 34.3 kN m^{-2} (r^2 = 0.845).

proached the critical value of $1 - P_{aero}/P_{CO_2}$. The minimum elastic storage α_{min} is defined as the shoulder value of elastic storage above which the MSE remains constant. Values for minimum elastic storage determined by this method were typically about 11% (Table 2). The actual capacity for elastic storage could be higher, but it would not cause a further reduction in the power requirements for flight and would therefore not be detectable by this method.

In addition to allowing estimation of the degree of elastic storage, knowledge of muscle efficiency permits calculation of the specific power output of the flight muscle. Use of thoracic mass as an estimate of muscle volume yields an estimate of about 40 W kg^{-1} for the mechanical power of *Drosophila* asynchronous musculature (Table 2). The specific power output of muscle is thought to be linearly related to muscle stress (σ), stroke amplitude, and wingbeat frequency as (7):

$$P_{muscle} = \frac{\sigma\kappa\Phi n}{\rho} \quad (7)$$

where ρ is muscle density and κ is a constant relating stroke amplitude to muscle strain. By assuming that average wingbeat amplitude results in 1% muscle strain, we may use Eq. 7 to estimate the stress within the power muscles during flight. Respirometrically estimated muscle power output is plotted as a function of $\kappa\Phi n\rho^{-1}$ in Fig. 4D. The slope of this relation is muscle stress, which was on average 40 kN m^{-2} (Table 2). This value is low for insect muscle (8), but reduced stress is expected of muscles operating at high frequency because a large proportion of the internal space is taken up by mitochondria (7).

The results of this kinematic and respirometric analysis of *Drosophila* have general implications for the energetics of insect flight. First, we calculated a mechanical efficiency of about 10% for asynchronous muscle. Unless this value is radically different in other species, the results suggest that many insects must maintain an energy balance not through the use of extraordinarily efficient muscles but through elastic storage. The benefits of elastic storage are not as large in *D. hydei* as they might be in other species, because the difference between the average inertial and aerodynamic power requirements is quite small. However, in many other species, the requirements for inertial power may be up to six times those of aerodynamic power (9), and elastic storage would offer substantial energetic savings. Further, by consideration of the interaction between inertial and aerodynamic power, it appears that the amount of elastic storage required to minimize energy requirements during flight might be lower than previously expected. In *D. hydei*, we find that elastic storage greater than 10% would not affect the energy balance during flight. Taking the ratio of inertial and aerodynamic power for a variety of larger insects (9) yields minimum elastic storage values ranging from about 35 to 85%. The insect wing hinge is known to contain the protein resilin (10), which is among the most elastic materials known. It is quite reasonable to expect that, as in *Drosophila*, the thoracic structures of many insects are capable of the minimum elastic storage necessary to minimize the energetic costs of flight.

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tiation of the measurements, the ratio of chlorophyll a to total photopigment reached an average value of 0.13 ± 0.04 SD (Fig. 1A). From this time on, both chlorophyll and phaeopigment concentrations dropped at similar rates. The decrease in chlorophyll a in starved corals and its degradation to phaeopigments are clear indicators of digestion of phytoplankton trapped in the gastrovascular cavity (*11*).

To determine rates of phytoplankton intake, successive pigment measurements were carried out on 20 actively feeding colonies kept in the flow chamber with continuously replaced natural seawater. Before the experiments, the colonies were kept in filtered seawater for 3 days, hence their gastrovascular systems were free of phytoplankton at the beginning of the measurements. Rates of chlorophyll a intake depended on the flow environment of the colonies (Fig. 1B). Within the first 10 to 12 hours, intake rates were 0.0063 ± 0.0032 μg of chlorophyll a per polyp per hour (± SD) in colonies exposed to a flow of 4 to 5.9 cm/s (linear regression analysis over the first 10 hours: $N = 60$, $R^2 = 0.79$). At a flow rate of 6 to 7.9 cm/s, intake rates were higher (0.0104 ± 0.0029 μg per polyp per hour) ($N = 60$, $R^2 = 0.92$), and at a flow rate of 8 to 10 cm/s, intake rates were 0.0291 ± 0.0079 μg per polyp per hour ($N = 90$, $R^2 = 0.93$). These rates equal 9.0 ± 4.8, 15 ± 4.1, and 41.0 ± 11.4 μg of carbon per polyp per day, respectively, if a chlorophyll a to phytoplankton carbon mass conversion factor of 1:60 is assumed (*12*). Ambient chlorophyll a concentrations in the seawater averaged 0.25 mg/m^3(15 mg of carbon per cubic meter) during the experiments. The phytoplankton clearance efficiency, calculated by normalization of phytoplankton intake rates by the flux through an imaginary plane with the area of the polyp's cross section (9.6 ± 1.2 mm^2), increased from 1.7% (at a flow rate of 4 to 5.9 cm/s) to 4.5% (at a rate of 8 to 10 cm/s).

In contrast to the high rates of intake of phytoplankton, we found very little zooplankton prey in the polyps of *D. hemprichi* (*13*), with an average of less than 0.02 items per polyp (mostly planktonic mollusks and copepods). Mean prey size was 508 μm, and the rate of zooplankton carbon intake was 0.21 μg of carbon per polyp per day. Phytoplankton filtration supplied two orders of magnitude more carbon to the diet of *D. hemprichi* than did zooplankton capture. The concentration of zooplankton carbon in the seawater during the experiment averaged 3.5 mg of carbon per cubic meter (*14*).

A microscopic examination of three other reef-inhabiting asymbiotic octocorals (*D. sinaiensis*, *Scleronephthya corymbosa*, and *Acabaria* sp.) showed that the gastrovascular cavities of these species also contained large quantities of phytoplankton cells. Mechanisms of phytoplankton intake by octocorals and biochemical adaptations to this diet are still unknown (*15*). To date, cnidarians have been considered carnivorous (*16*). Our work clearly shows that this generalization is incorrect.

A major question addressed by tropical reef studies is how do the corals maintain their high levels of biological productivity in a nutrient-impoverished environment (*17*). One explanation is the symbiotic association with zooxanthellae. Efficient retention of food particles carried over the reef is a second mode of energy supply. Zooplankton, and detritus with bacteria attached, have been discussed as main nutrient sources for the predominately filter-feeding coral reef inhabitants (*18*), whereas phytoplankton has until now been neglected in most trophic studies of coral reefs and reef invertebrates, despite its great biomass. It is now imperative to evaluate the extent of herbivory among cnidarians and other filter-feeding reef benthos in order to assess the contribution of phytoplankton to the high gross productivity of reefs.

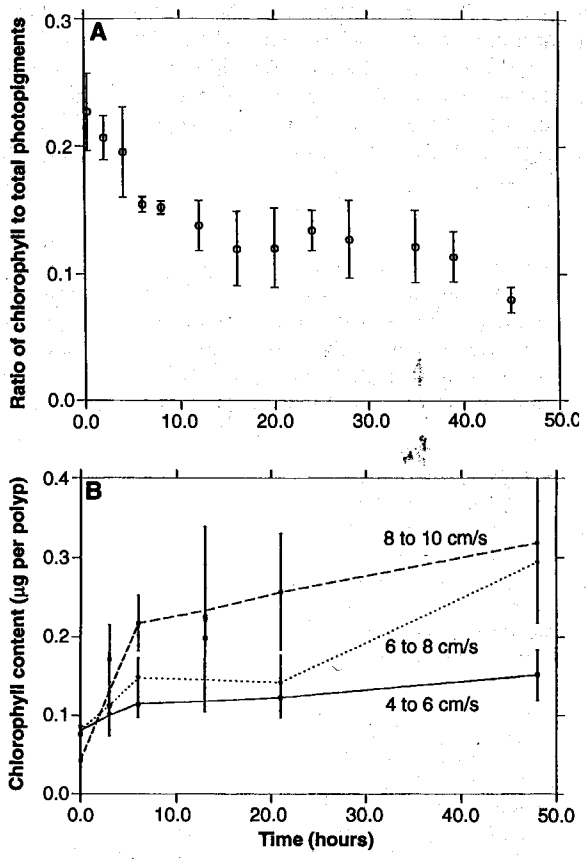

Fig. 1. (**A**) Decrease in the ratio of chlorophyll a to total plant-derived photopigments in polyps of *D. hemprichi* over time. The curve shape is the result of a steady decrease in chlorophyll a concentrations within the polyps, due to decomposition to phaeopigments. Photopigment concentrations remained initially constant but began to drop after about 12 to 15 hours. The decreasing ratio of chlorophyll a to total photopigments is evidence for the digestion of the ingested phytoplankton by this soft coral. Each data point averages six measurements from a colony kept in the flow chamber in filtered water (filter pore width, 0.7 μm). Error bars indicate 1 SD. (**B**) Increasing chlorophyll a concentrations in actively feeding colonies of *D. hemprichi* after a period of starvation. Colonies were in natural seawater at a flow rate of 4 to 10 cm/s. Each data point averages 36 samples from six colonies (24 samples from four colonies after 14 hours). Data points are connected with Lowess Smoothing, a nonparametric regression function. Error bars represent 1 SD. The asymptotic shape of the chlorophyll curves suggests a steady state after about 12 hours, in which the chlorophyll a ingestion rates equalled the chlorophyll a decomposition to phaeopigments.

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The observations under the epifluorescence microscope confirmed that *D. hemprichi* was free of autofluorescence and epiphytic algae and did not contain zooxanthellae. A great majority of the ingested algae were eukaryotes, whereas very few blue-green algae were taken in. This contrasts to the great proportion of blue-green algae in cell numbers and biomass in phytoplankton populations of tropical waters (*7*) and may be related to the small size of blue-green algae cells (<3 μm).

The concentrations of phytoplankton pigments (chlorophyll a and its degradation products, phaeopigments) in the corals were quantified in order to estimate rates of phytoplankton intake and decomposition. Concentrations were determined fluorometrically, after a standard acetone-extraction technique (*8*), in colony branches with a known number of polyps (*9*). For the experiments, colonies 4 to 5 cm tall growing on small polyvinyl chloride plates were kept in a flow chamber (18 cm by 15 cm in cross section) in continuously replaced seawater. The plates were suspended on metal-free wire away from the glass walls in such a way that each colony was exposed to unobstructed laminar flow of 4 to 10 cm/s (*10*).

The chlorophyll a gradually decomposed to phaeophytin in the gastrovascular cavities of the colonies. Ten colonies were kept in natural seawater in the flow chamber. After 3 days of feeding on the natural phytoplankton, the ratio of chlorophyll a to total photopigments in the colonies was 0.23 (±0.04 SD), as compared with 0.69 ± 0.02 SD in the seawater. The seawater in the flow chamber was then replaced by filtered water (filter pore width was 0.7 μm), and the changes in concentrations of plant-derived pigments in the colonies were recorded over 48 hours by random sampling of branch tips of the colonies for pigment extraction. Within the first 14 hours, chlorophyll concentrations decreased at a rate of 3.5% per hour in these starving colonies, whereas phaeopigment concentrations did not change. Around 14 hours after the ini-

K. E. Fabricius, Australian Institute of Marine Science, Post Mail Box Number 3, Townsville Q4810, Australia, and Zoological Institute, University of Munich, Karlstrasse 23, 80333 Munich, Germany.
Y. Benayahu, Department of Zoology, Tel Aviv University, Ramat Aviv 69978, Israel.
A. Genin, The Hebrew University, H. Steinitz Marine Biological Laboratory, Post Office Box 469, Eilat 88103, Israel.
*To whom correspondence should be addressed.