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HOST FEEDING REGIME AND ZOOXANTHELLAL PHOTOSYNTHESIS IN THE ANEMONE, *AIPTASIA PALLIDA* (VERRILL)

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ABSTRACT

Oxygen production was measured in the anemone *Aiptasia pallida* (Verrill) maintained at varying feeding regimes in the laboratory. Host feeding regime had no significant effect on: (1) zooxanthellal gross photosynthesis (GPP_{max}) expressed as $\mu g\ O_2 \cdot \mu g\ chl\ a^{-1} \cdot h^{-1}$ or $\mu g\ O_2 \cdot 10^6$ zooxanthellae$^{-1} \cdot h^{-1}$; (2) the light intensity at which $\frac{1}{2}\ GPP_{max}$ occurs (K_m); or (3) the chlorophyll *a* content of the zooxanthellae. Starvation significantly reduced GPP_{max} expressed as $\mu g\ O_2 \cdot mg$ host protein$^{-1} \cdot h^{-1}$ and zooxanthellal density within the host. Zooxanthellal translocation efficiency was measured by short term incubations of anemones in $NaH^{14}CO_3$. Host feeding regime had no effect on the percentage of ^{14}C translocated to the host.

These results suggest that, under these conditions, starvation did not alter the photosynthetic capability of the zooxanthellae but decreased total photosynthate translocated to the host by decreasing zooxanthellal density within the host.

INTRODUCTION

Much research on zooxanthellae-cnidarian symbioses has focused on metabolite exchange between the symbionts. Most of this work has considered the release of photosynthate by the zooxanthellae (Muscatine, 1967; Von Holt and Von Holt, 1968a; Muscatine and Cernichiari, 1969; Lewis and Smith, 1971; Trench, 1971a; Muscatine *et al.*, 1972; Patton and Burris, 1983) and its subsequent utilization by the host (Muscatine and Hand, 1958; Goreau and Goreau, 1960; Von Holt and Von Holt, 1968b; Muscatine and Cernichiari, 1969; Trench, 1971b, Fitt and Pardy, 1981). In addition to photosynthate translocation there is evidence for movement of organic and inorganic metabolites from host to the zooxanthellae (Cook, 1971; Trench, 1979; Carroll and Blanquet, 1982).

The significance of host metabolite transfer for the zooxanthellae has been examined indirectly by altering host feeding regime and measuring symbiont photosynthesis. In the temperate coral *Astrangia danae* (Milne Edwards & Haime) zooplankton feeding increases zooxanthellal photosynthetic rate (Jacques and Pilson, 1980; Szmant-Froelich, 1981) as well as host protein, lipid, and carbohydrate content (Szmant-Froelich and Pilson, 1980). This indicates that some aspect of host nutritional state affects zooxanthellal photosynthesis (Szmant-Froelich, 1981). Jacques and Pilson (1980) suggest that ammonia production by well fed hosts may be the stimulatory factor. However, the only direct evidence that zooxanthellal photosynthesis is affected by nitrogen is that of Taylor (1978) who has shown that ammonia and urea additions increased photosynthetic rate and excretion by zooxanthellae in *Acropora cervicornis* (Lamarck) *in vitro* and *in vivo*.

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Host-zooxanthellae transfer plays a major role in the nitrogen balance of the symbiosis and the presence of zooxanthellae enhances inorganic nitrogen uptake. For instance, symbiotic individuals of many species take up ammonia while aposymbionts and nonsymbionts excrete ammonia (Cates and McLaughlin, 1976; D'Elia and Webb, 1977; Muscatine and D'Elia, 1978; Muscatine *et al.*, 1979; Muscatine and Marian, 1982). Nutrient uptake rates for isolated zooxanthellae are similar to those for intact coral-zooxanthellae symbioses, further suggesting that it is the zooxanthellae that enhance nutrient uptake (D'Elia *et al.*, 1983). Symbiotic colonies of *A. danae* fed in bright light excrete more nitrogen than starved colonies but less than aposymbiotic colonies (Szmant-Froelich and Pilson, 1977). These results suggest that zooplankton feeding increases host nitrogen production and that zooxanthellae enhance nitrogen retention within the host.

The hypothesis that host metabolism may affect CO_2 availability for the zooxanthellae and the possibility that CO_2 produced by host respiration may stimulate the photosynthetic oxygen evolution of endosymbiotic algae has been investigated in several symbioses. In freshwater systems when the CO_2 concentration is low (<1.0 m*M* HCO_3^-), algal photosynthesis is higher within host cells than when isolated from the host (Reiser, 1980; Phipps and Pardy, 1982), suggesting that host produced CO_2 stimulates photosynthesis (Phipps and Pardy, 1982). However, when the inorganic carbon concentration is elevated (≥1.0 m*M* HCO_3^-), algal photosynthesis is not enhanced within host cells but inhibited (Cantor and Rahat, 1982). In marine systems where the CO_2 concentration is naturally high (>2.3 m*M* HCO_3^-), zooxanthellal photosynthesis is unaffected by inorganic carbon concentration (Burris *et al.*, 1983). These results suggest that host produced CO_2 does not affect zooxanthellal photosynthesis since CO_2 is abundant in most marine systems (Burris *et al.*, 1983).

In this study we examine the relationship between host zooplankton feeding and zooxanthellal photosynthetic oxygen production in the anemone *Aiptasia pallida.* Results suggest that, under laboratory conditions, zooplankton feeding increased the maximum per individual anemone photosynthetic rate by increasing zooxanthellal density within the host.

Materials and Methods

Specimen maintenance

Specimens of *Aiptasia pallida* originally derived from a single individual obtained from Carolina Biological Supply were maintained in artificial sea water (Instant Ocean) at 26 ± 1°C on a 14 h light/10 h dark photoperiod with a light intensity of 65 $\mu E \cdot m^{-2} \cdot s^{-1}$. Aposymbionts were produced by culturing anemones in a theoretical concentration of 10^{-5} *M* 3-(3,4 dichlorophenyl)-1,1 dimethyl urea (DCMU) for 4–5 weeks. Since DCMU is partially insoluble in sea water (Vandermeulen *et al.*, 1972) the actual concentration used was probably less than 10^{-5} *M*. Cultures were either starved, fed to repletion 1× per week, or 3× per week with freshly hatched (24–48 h) *Artemia salina* nauplii for 10 weeks prior to experiments. These treatments provided a large range of individual sizes for experiments. The size range (measured by oral disc diameter and host protein content) of anemones chosen for photosynthetic measurements overlapped considerably between treatments. This was done so that differences in photosynthetic rate between treatments would not be due to individual size differences resulting from the various treatments. With the exception of starved individuals, anemones were used in experiments 24 h prior to their next scheduled feeding.

Photosynthetic measurements

Oxygen flux of individual anemones was measured with a closed respirometry unit. The unit consisted of six 20-ml vials (20 mm dia.) vertically secured in a plexiglass chamber (19.0 cm × 10.5 cm × 7.0 cm) through which constant temperature water (26 ± 1°C) was pumped by a circulating water bath. Each vial contained a magnetic stirbar and was sealed with an oxygen probe (Yellow Springs Instruments, model# 5331) inside a plexiglass cylinder. Vial volume when sealed was 5.4 ml. During acclimation and between measurements vials were continuously flushed with sea water at a flow rate of 2 ml · min^{-1} using a multi-channel peristaltic pump. During measurements flow through the vials was discontinued. A dataplex (Cole-Palmer Dataplex 10, model# 8388) connected to the oxygen probes sequentially scanned each vial and generated a continuous chart recording of O_2 concentration for each vial.

Photosynthetic measurements of individuals from each feeding regime were conducted over several days. Individual anemones from each feeding regime were placed in vials and permitted to attach to the sidewalls and expand (30–45 min). Vials were then placed in the chamber such that the anemone oral disc was perpendicular to the path of light from the light source and preincubated in the dark for 15–20 min prior to a 10–20 min respiration measurement. Net photosynthetic measurements followed respiration measurements. A bank of four incandescent flood lights (Ken-Rad Reflector, 75 Watt, 120 V) was set at varying distances from the chamber to obtain light intensities ranging from 50–400 $\mu E \cdot m^{-2} \cdot s^{-1}$. The intensity of photosynthetically active radiation (400–700 nm) was measured behind the chamber with a Li-Cor Quantum Flux Meter (sensor# LI-190S). Net photosynthetic measurements were determined sequentially at increasing light intensities, with a 15–20 min acclimatization at each light level. An individual anemone spent <4 h in a vial and at no time did the oxygen concentration change >20% from initial values, with most experiments varying <10%. A control vial without an anemone was simultaneously monitored in all experiments to correct for the biological oxygen demand of sea water.

Assuming total respiration rate of host and symbiont in the light was equal to total respiration rate that was measured in the dark we estimated zooxanthellal gross photosynthesis (GPP) of individual anemones at each light intensity by summing the respiration and net photosynthesis measurements. Individual anemone GPP was then expressed as $\mu g\ O_2 \cdot \mu g$ chl $a^{-1} \cdot h^{-1}$, $\mu g\ O_2 \cdot 10^6$ zooxanthellae$^{-1} \cdot h^{-1}$ and $\mu g\ O_2 \cdot mg$ host protein$^{-1} \cdot h^{-1}$ and GPP_{max} and K_m values determined using the Lineweaver-Burk estimate of the right rectangular hyperbola function (McCloskey *et al.*, 1978; Muscatine, 1980).

Chalker (1980, 1981) has advocated use of the hyperbolic tangent function for simulating light saturation curves for photosynthetic oxygen production. Chalker (1981) argues that this function yields a higher r^2 and narrower confidence intervals for the various photosynthetic parameters. Use of the hyperbolic tangent function in this study would not alter the significant differences found in GPP_{max} between treatments since these differences were discerned using values of GPP_{max} estimated from the less powerful right rectangular hyperbola function. Using values of GPP_{max} with narrower confidence intervals generated from the hyperbolic tangent function would only increase the level of significance for GPP_{max} between treatments.

Tissue processing

At the completion of each experiment, anemones were homogenized in 3 ml distilled water with a teflon pestle for 30 s. The resulting suspension was centrifuged

at 3400 rev/min for 3 min and the animal supernatant withdrawn by pipetting. The zooxanthellal pellet was then washed with 2 ml distilled water, centrifuged, and the wash added to the animal supernatant. Supernatant volume was increased to 10 ml with distilled water and replicate aliquots of this anemone fraction were withdrawn and assayed for protein content (Lowry *et al.*, 1951). The zooxanthellal pellet was resuspended in 4 ml by vortexing for 10 s and 1 ml withdrawn and frozen for future zooxanthellae counts. Lysed cells were not observed in these samples and zooxanthellal pellets isolated from other anemones and suspended in distilled water showed no lysis for >1.5 h (at 300×). Six replicate counts of each zooxanthellal sample were made using a hemacytometer. The remaining suspension was centrifuged and the zooxanthellal pellet extracted with 100% acetone for 24 h at −10°C. Solvent extinction was measured with a spectrophotometer (Gilford Instruments, model# 260 or Beckman Instruments, model# DB 1401) and chlorophyll content of the zooxanthellal pellet estimated using the equations of Jeffrey and Humphrey (1975). Tissue processing never took >30 min for any experiment.

Translocation experiments

Groups of three anemones (two symbiotic and one aposymbiotic) were incubated in separate vials with 20 ml Millepore filtered (.45 μm) sea water and allowed to attach and expand. $NaH^{14}CO_3$ was then added (final concentration = 0.25 μCi/ml) and the anemones incubated for 30 min at 26 ± 1°C and 65 $\mu E \cdot m^{-2} \cdot s^{-1}$. Following the incubation, anemones were rinsed three times with Millepore filtered sea water, homogenized, and separated as described previously. Aliquots of the animal and algal fractions were acidified and activity determined with a liquid scintillation counter (Beckman Instruments, model# LS 8000).

Counts per minute of all animal and algal samples were corrected for background, quenching, and counting efficiency and converted to disintegrations per minute. Aposymbiotic anemones in each vial served as controls for animal uptake in all experiments. Replicate aliquots of the animal fractions of all anemones were assayed for protein content and the activity of the animal fractions of symbiotic individuals were corrected for aposymbiont activity on a per unit protein basis.

Mutual contamination of zooxanthellae and host tissue

Contamination of isolated zooxanthellae by host tissue during separation was estimated by incubating aposymbiotic *A. pallida* in Millepore filtered sea water enriched with ^{14}C-glycerol (final concentration = 0.05 μCi/ml) at 26 ± 1°C for 4 h. Individuals were rinsed three times, homogenized for 30 s, and added to non-labelled zooxanthellae. The mixture was vortexed for 10 s, separated, and activity of the zooxanthellal and anemone fractions determined. Four analyses showed contamination of zooxanthellae by ^{14}C of 14.15 ± 1.27% ($\bar{x}$ ± S.E.).

Contamination of host tissue by zooxanthellae during separation was estimated by incubating isolated zooxanthellae in Millepore filtered sea water enriched with $NaH^{14}CO_3$ (final concentration = 0.45 μCi/ml) at 26 ± 1°C and 65 $\mu E \cdot m^{-2} \cdot s^{-1}$ for 5 h. Labelled zooxanthellae were isolated by centrifugation, suspended in unlabelled sea water for 18 h, and then centrifuged. The zooxanthellal pellet was rinsed twice with unlabelled sea water and combined with boiled host homogenate. Boiled homogenate was used since it does not stimulate zooxanthellal liberation of ^{14}C (Muscatine, 1967; Trench, 1971c; Muscatine *et al.*, 1972). The mixture was vortexed for 10 s, separated, and the activity of zooxanthellal and anemone fractions determined. Four analyses showed contamination of host tissue by ^{14}C of 3.69 ± 0.47% ($\bar{x}$ ± S.E.).

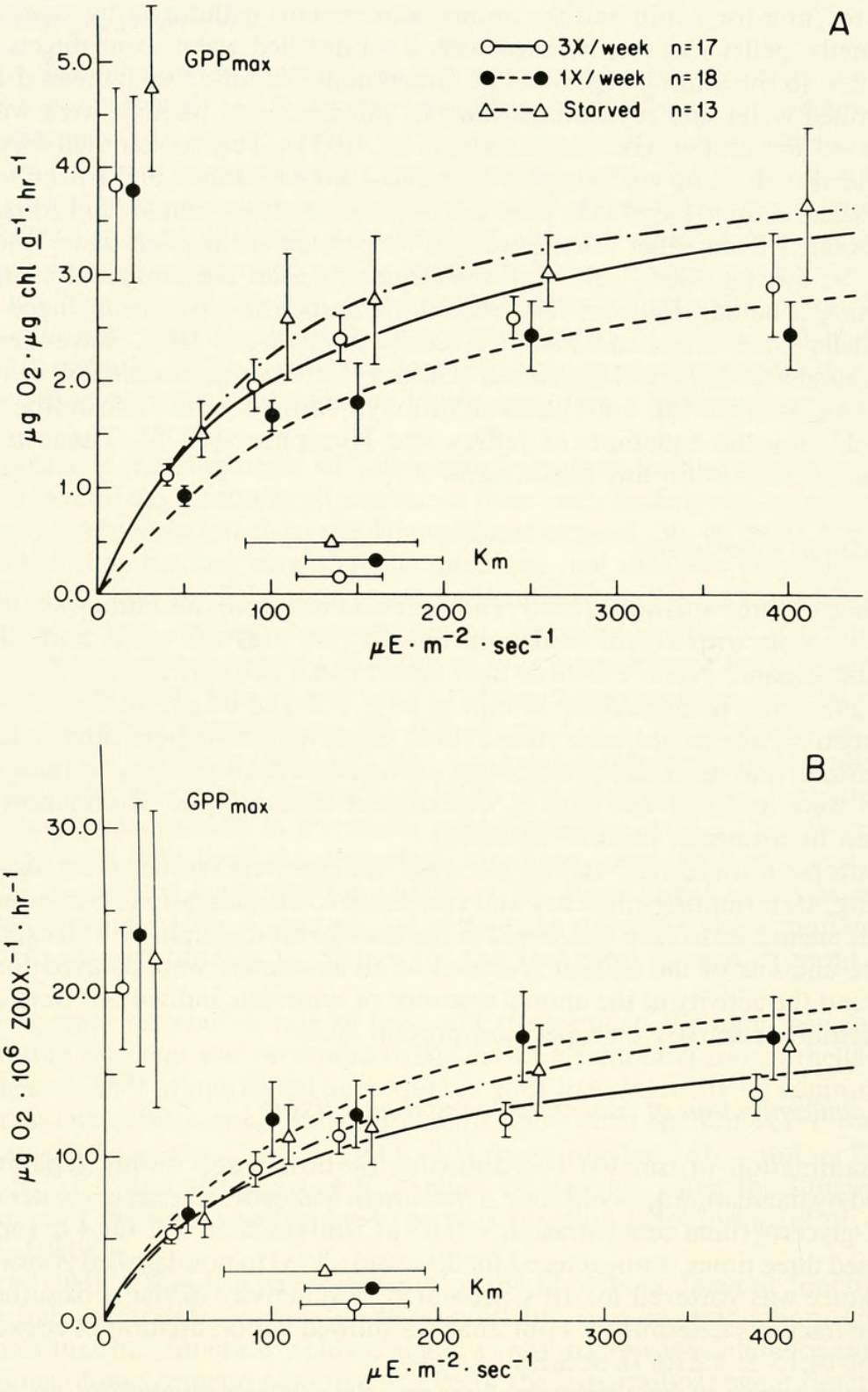

FIGURE 1. Ideal curves of the photosynthesis-irradiance relationship for zooxanthellae from *A. pallida* maintained at varying feeding regimes. GPP_{max} and K_m were calculated from the Michaelis-Menton equation. Bars for GPP_{max} and K_m denote 95% confidence limits; bars for GPP at each light intensity denote standard errors. Points at each light intensity denote the $\bar{x}$ of n measurements and are offset for clarity. A. GPP expressed as $\mu g\ O_2 \cdot \mu g\ chl\ a^{-1} \cdot h^{-1}$. B. GPP expressed as $\mu g\ O_2 \cdot 10^6\ zoox.^{-1} \cdot h^{-1}$. C. GPP expressed as $\mu g\ O_2 \cdot mg\ host\ protein^{-1} \cdot h^{-1}$.

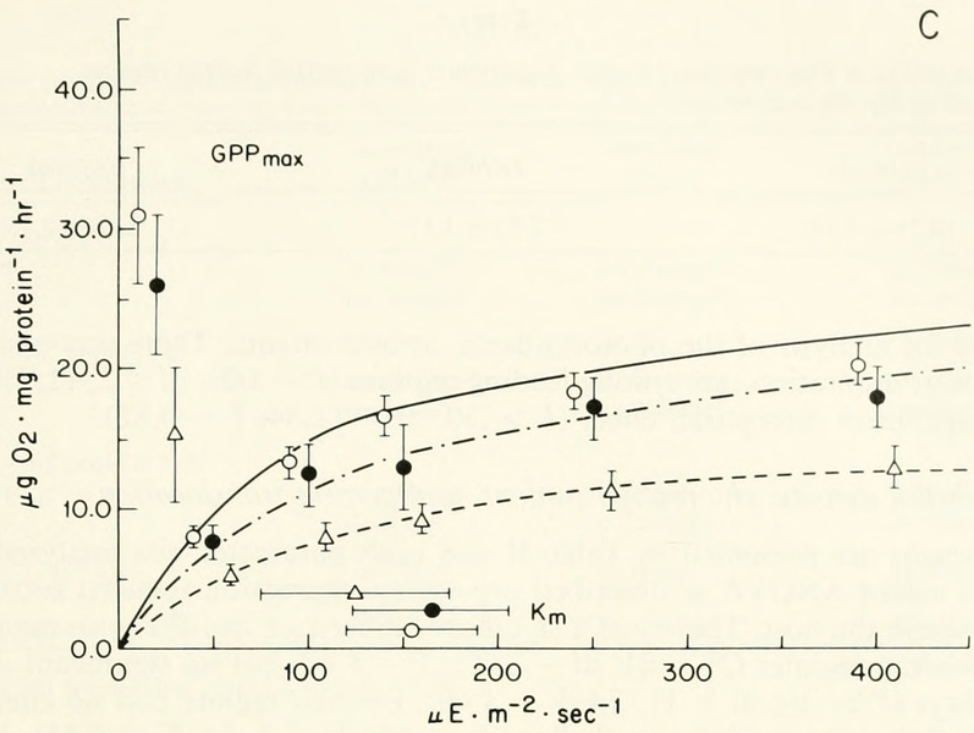

FIGURE 1. (*Continued*)

Activity of zooxanthellal and anemone fractions in the translocation experiments was corrected for mutual contamination as estimated in these experiments.

RESULTS

Zooxanthellal photosynthesis

Results of the photosynthetic measurements are presented in Figure 1a–c. All GPP_{max} and K_m values were analyzed using a two-level nested analysis of variance (ANOVA) for unequal sample sizes (Sokal and Rohlf, 1969) that tested for effects among days within a feeding regime and among feeding regimes. There was no significant difference in GPP_{max} expressed as $\mu g\ O_2 \cdot \mu g\ chl\ a^{-1} \cdot h^{-1}$ ($GPP_{max}/\mu g$ chl *a*, Fig. 1a) among days ($P > .10$; df = 11, 34; F = 1.72) or feeding regimes ($P > .50$; df = 2, 11; F = 0.69). Similarly, K_m for $GPP_{max}/\mu g$ chl *a* showed no significant day ($P > .25$; df = 11, 34; F = 1.22) or feeding regime effects ($P > .75$; df = 2, 11; F = 0.29). Zooxanthellal GPP_{max} expressed as $\mu g\ O_2 \cdot 10^6$ zooxanthellae$^{-1} \cdot h^{-1}$ ($GPP_{max}/10^6$ zoox., Fig. 1b) showed a significant day effect ($P < .001$; df = 11, 34; F = 3.95), suggesting some degree of daily variation in zooxanthellal photosynthetic rate. There was no feeding regime effect for $GPP_{max}/10^6$ zoox. ($P > .50$; df = 2, 11; F = 0.48). K_m for $GPP_{max}/10^6$ zoox. showed no significant feeding regime ($P > .50$; df = 2, 11; F = 0.33) or day effects ($P > .05$; df = 11, 34; F = 1.89). GPP_{max} expressed as $\mu g\ O_2 \cdot mg$ host protein$^{-1} \cdot h^{-1}$ (GPP_{max}/mg protein, Fig. 1c) showed significant day ($P < .05$; df = 11, 34; F = 2.96) and feeding regime effects ($P < .05$; df = 2, 11; F = 4.13). K_m for GPP_{max}/mg protein showed no significant day ($P > .25$; df = 11, 34; F = 1.19) or feeding regime effects ($P > .50$; df = 2, 11; F = 0.35).

Respiration

Total individual respiration was expressed as $\mu g\ O_2 \cdot mg$ host protein$^{-1} \cdot h^{-1}$. Results are presented in Table I and were analyzed using a two-level nested ANOVA as

TABLE I

Respiration rate ($\bar{x} \pm$ 95% confidence limits) of anemones from varying feeding regimes expressed as $\mu g\ O_2 \cdot mg\ host\ protein^{-1} \cdot h^{-1}$

3×/week	1×/week	0×/week
10.26 ± 1.16	7.73 ± 1.17	3.28 ± 2.13

described for analysis of the photosynthetic measurements. There was a significant difference in respiration rate among feeding regimes ($P < .001$; df = 2, 11; F = 28.04) but no significant interaction effect ($P > .50$; df = 11,34; F = 0.82).

Zooxanthellal density, chlorophyll content, and percent translocation

All results are presented in Table II and each parameter was analyzed using a two-level nested ANOVA as described previously. Starvation reduced zooxanthellal density within the host. There was a significant difference in 10^6 zoox. · mg protein^{-1} among feeding regimes ($P < .01$; df = 2, 11; F = 8.42) but no significant difference among days ($P > .10$; df = 11, 34; F = 1.69). Feeding regime had no effect on the chlorophyll *a* content of zooxanthellae ($P > .50$; df = 2, 34; F = 0.55). However, there was a significant day effect for μg chl $a \cdot 10^6$ zoox.$^{-1}$ ($P < .001$; df = 11, 34; F = 5.05), suggesting some variation in zooxanthellal chlorophyll *a* content. Percent translocation from zooxanthellae to host was also unaffected by feeding regime. Analysis of the arcsine transformed data showed no significant day ($P > .75$; df = 9, 12; F = 0.99) or feeding regime effects ($P > .10$; df = 2, 9; F = 4.09).

DISCUSSION

Altering host feeding regime provides a tool for studying possible host effects on the zooxanthellae. Host zooplankton feeding may affect zooxanthellal photosynthetic oxygen production in two fundamental ways, via changes in the number of zooxanthellae within the host or via changes in individual zooxanthellal photosynthesis. Changes in individual zooxanthellal photosynthesis can be further compartmentalized to changes in the size or number of photosynthetic units (PSU's) within the algae. The possibilities and their predicted consequences are presented in Table III and discussed below.

Although changes in PSU size and number were not directly measured these changes should produce definable effects. Thus we can infer certain changes if the observed results are consistent with theoretical predictions. However, the predictions of this response (Table III) were not observed in the data. Feeding regime had no effect on GPP_{max}/chl *a* (Fig. 1a), K_m for $GPP_{max}/10^6$ zoox. (Fig. 1b), K_m for GPP_{max}/

TABLE II

Zooxanthellal chlorophyll a content, zooxanthellal density, and percent translocation to the host by zooxanthellae from Aiptasia pallida *maintained at varying feeding regimes ($\bar{x} \pm$ S.E.)*

	3×/week	1×/week	Starved
μg chl $a \cdot 10^6$ zoox.$^{-1}$	5.31 ± 0.73	5.99 ± 0.62	5.02 ± 0.76
10^6 zoox. · mg protein^{-1}	1.56 ± 0.10	1.24 ± 0.09	0.75 ± 0.09
% Translocation	42.73 ± 2.01	39.93 ± 1.37	45.67 ± 1.22

TABLE III

Possible effects of host zooplankton feeding on zooxanthellal photosynthetic oxygen production

Units of measure	Increasing PSU size	Increasing PSU #	Increasing zooxanthellae #
$\mu g\ O_2 \cdot \mu g\ chl\ a^{-1} \cdot h^{-1}$			
GPP_{max}	decrease*	no change*	no change
K_m	no change*	no change*	no change
$\mu g\ O_2 \cdot 10^6\ zoox.^{-1} \cdot h^{-1}$			
GPP_{max}	no change*	increase*	no change
K_m	decrease*	no change*	no change
$\mu g\ O_2 \cdot mg\ protein^{-1} \cdot h^{-1}$			
GPP_{max}	no change	increase	increase
K_m	decrease	no change	no change
$\mu g\ chl\ a \cdot 10^6\ zoox.^{-1}$	increase*	increase*	no change
$10^6\ zoox. \cdot mg\ protein^{-1}$	no change	no change	increase

* Adapted from Prezelin and Sweeney (1979).

mg protein (Fig. 1c), or μg chl $a \cdot 10^6$ zoox.$^{-1}$ (Table II). These results indicate that host zooplankton feeding did not affect zooxanthellal photosynthesis via changes in PSU size.

A second possibility for changes in individual zooxanthellal photosynthesis is an increase in PSU number. Although GPP_{max}/mg protein increased as predicted (Fig. 1c), there was no increase in $GPP_{max}/10^6$ zoox. (Fig. 1c) or μg chl $a \cdot 10^6$ zoox.$^{-1}$ (Table II). Thus the increased GPP_{max}/mg protein in fed individuals was apparently not due to increasing PSU number within the zooxanthellae.

The final possibility is that zooxanthellal density changed within the host. Although this capability is not evident as a depth related photoadaptive response (Drew, 1972; Lasker, 1977; Dustan, 1982), zooxanthellal density is not static and can be altered by environmental factors (Yonge and Nicholls, 1931a, b; Yonge *et al.*, 1932; Goreau, 1964; Jaap, 1979; Kevin and Hudson, 1979; Fankboner and Reid, 1981). Effects of host starvation on zooxanthellal density appear related to the length of starvation and are somewhat species specific. For instance, prolonged starvation reduces zooxanthellal density in some species (Yonge and Nicholls, 1931b; Smith, 1939; Taylor, 1969; Reimer, 1971) but not in others (Kevin and Hudson, 1979). Two weeks starvation reduces zooxanthellal density in *Astrangia danae* (Szmant-Froelich, 1981) but not in the anemone *Anthopleura elegantissima* Brandt (Fitt *et al.*, 1982). In addition, Franzisket (1970) showed that colonies of four coral species deprived of zooplankton in the light retained zooxanthellae and continued to grow at the same rate as when zooplankton were available. In the experiments reported here, 10 weeks starvation significantly reduced GPP_{max}/mg protein (Fig. 1c), apparently by decreasing zooxanthellal density (Table II). Host alteration of either zooxanthellal growth rate or retention of zooxanthellae associated with starvation may have altered zooxanthellal density.

The effect of host feeding regime on translocation efficiency may also affect the nutrient balance of zooxanthellae and their hosts. For instance, Szmant-Froelich (1981) found that starved *A. danae* colonies fixed less ^{14}C in photosynthesis but "compensated" by translocating more to the host. In this study, percent translocation at 26 ± 1°C was 40–45% regardless of host feeding regime (Table II). This appears

much less than the 63% translocation at 27°C recently reported for *A. pallida* (Clark and Jensen, 1982).

In this study, host feeding regime altered zooxanthellal density (Table II) but had no apparent effect on the zooxanthellal photosynthetic apparatus (Fig. 1a, b; Table II), and no effect on percent translocation by the zooxanthellae (Table II). This suggests that the significantly greater GPP_{max}/mg protein observed in fed individuals (Fig. 1c) was due to higher zooxanthellal densities (Table II) and resulted in fed individual receiving more photosynthate from their zooxanthellae population than starved individuals.

The significance of this increase in available photosynthate for fed individuals compared to starved individuals cannot be readily assessed since any increase in available photosynthate for the host due to increased feeding frequency may be offset by a concomitant increase in host respiration rate. In these experiments total respiration (of animal and algae) of individuals fed 3× per week was approximately 3× that of starved individuals after 10 weeks (Table I). A similar effect of feeding frequency on anemone respiration rate has been reported for other species (Svoboda and Porrman, 1980; Fitt and Pardy, 1981; Fitt *et al.*, 1982). Although feeding regime effects on total respiration rate are not easily partitioned between host and symbionts (*c.f.*, Muscatine and Porter, 1977; Muscatine, 1980; Muscatine *et al.*, 1981), it appears that anemone respiration rate is the major component since symbionts and aposymbionts have similar respiration rates (Pardy and White, 1977; Fitt and Pardy, 1981). In contrast with total respiration, GPP_{max}/mg protein of individuals fed 3× per week was approximately 1.5× that of starved individuals (Fig. 1c). These results suggest that the increased respiration rate associated with feeding was greater than the increased GPP_{max}/mg protein. Regardless of host utilization, however, it appears that fed anemones received more photosynthate from their zooxanthellae than did starved individuals.

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