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Elemental Composition of the Coral *Pocillopora damicornis* Exposed to Elevated Seawater Ammonium[1]

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ABSTRACT: The elemental composition (C, N, and P) of zooxanthellae and host tissue from the coral *Pocillopora damicornis* (Linnaeus) was determined after maintenance in flowing seawater with 20-μM and 50-μM ammonium enrichments for periods of 2 to 8 weeks. Compared with ambient seawater controls, total zooxanthellar nitrogen (μg N cm^{-2} colony surface) increased four-fold during exposure to 20 μM ammonium. This resulted from increases in N content of zooxanthellae and in zooxanthellae population densities. C : N ratios of zooxanthellae decreased from 19.7 ($\pm$4.0) to 10.3 ($\pm$3.0), and N : P ratios increased from 21.4 ($\pm$3.1) to 30.4 ($\pm$2.2) after 8 weeks in 20 μM ammonium. Zooxanthellae from the 8-week 50-μM ammonium corals had values of 8.9 ($\pm$0.6) for C : N and 40.4 ($\pm$2.3) for N : P. Coral animal C, N, and P content were not affected by ammonium-enriched seawater. The C : N ratio of coral animal tissue was 5.2 ($\pm$0.0), and the N : P ratio was 20.1 ($\pm$0.2) after 8 weeks in 20-μM ammonium seawater. There were no changes in host C : N, N : P, or C : P with ammonium enrichment. Thus, most of the N from the elevated seawater ammonium is retained by the zooxanthellae of *P. damicornis*, rather than by the animal tissue. Accordingly, sustained high concentrations of ammonium are likely to result in increased N storage by zooxanthellae and to affect the relative size of zooxanthellar to animal N pools.

ADDITION OF A LIMITING nutrient increases the size of the resident population of zooxanthellae living within animal hosts, including corals and sea anemones (Cook et al. 1988, Høegh-Guldberg and Smith 1989, Muscatine et al. 1989, Stambler et al. 1991, Stimson and Kinzie 1991, Muller-Parker et al. 1994). Increased densities of zooxanthellae within corals subjected to ammonium [$(NH_4)_2SO_4$] enrichment clearly increase the productivity of the symbiotic association (Høegh-Guldberg and Smith 1989, Dubinsky et al. 1990). However, the effects of added nutrients on the balance between algal growth and animal growth, and the nutrient fluxes and pools of reef corals are not yet well understood. These effects are likely to depend on the nutrient status of the coral zooxanthellae before nutrient enrichment.

There is some evidence that C : N ratios are related to the nitrogen status of symbiotic zooxanthellae. The C : N of zooxanthellae increased with starvation of the host anemone *Aiptasia pallida* (Verrill) in low-nutrient seawater (Cook et al. 1988) and decreased in zooxanthellae in the coral *Stylophora pistillata* Esper with ammonium enrichment of the seawater (Muscatine et al. 1989). Schools of fish that defecate on coral heads also increase the N and P content of coral tissue (Meyer and Schultz 1985). If the ratio of C : N : P reflects the availability of ambient nutrients, as originally proposed by Redfield et al. (1963) and confirmed by studies with

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cultured phytoplankton (e.g., Rhee 1974, 1978) and macroalgae from high-nutrient and low-nutrient environments (Atkinson and Smith 1983, Lapointe et al. 1992), comparisons of the elemental ratios of zooxanthellae isolated from nutrient-enriched and unenriched corals are a rapid way to assess the nutrient status of symbiotic zooxanthellae in corals from different environments.

Knowledge of the C, N, and P content of zooxanthellae is important for relating carbon productivity rates to N and P production and turnover. Current interest in the effect of nutrients on corals relates to the effect of nutrient additions on the nutritional and energetic exchanges between the host animal and its zooxanthellae and to the effect of potential increases in coral reef anthropogenic nutrients on coral growth. Also, the effect of long-term additions of inorganic nutrients on the elemental composition and C : N : P of the separate zooxanthellae and coral fractions is unknown. Continuous additions of nutrient-enriched seawater (N provided as 20 and 50 μM ammonium) to the Hawaiian coral *Pocillopora damicornis* (Linnaeus) resulted in increased densities of zooxanthellae (Muller-Parker et al. 1994). These corals provided the opportunity to explore the effect of ammonium enrichment on the C, N, and P content of corals. Furthermore, we were able to evaluate the utility of the C : N : P ratio as a potential indicator of nutrient status of zooxanthellae in corals.

MATERIALS AND METHODS

The experimental design and details of the maintenance of *P. damicornis* under the different ammonium treatments are described by Stambler et al. (1994). Colonies were maintained in seawater enriched with 20 and 50 μM ammonium, or in ambient seawater (≤ 2 μM NH_4^+), for periods ranging from 2 to 8 weeks. Control corals kept in ambient flowing seawater for 8 weeks served as the zero time point. Corals from the different treatments were separated into animal and zooxanthellae (Muller-Parker et al. 1994), and these fractions were used to prepare samples for elemental analysis. The surface area corresponding to the amount of tissue removed from each coral specimen was obtained by a leaf area measuring device (Li-Cor Model 3100), as described by Muller-Parker et al. (1994).

Freshly isolated zooxanthellae were passed sequentially through 73-μm and 20-μm Nitex screening to remove animal debris, and known volumes were collected by filtration onto glass fiber filters (Whatman GF/F) under vacuum (<250 mm Hg). Precombusted (6 to 8 hr at 500°C) 25-mm GF/F filters were used for the samples for C and N analysis, and noncombusted 25-mm GF/F filters were used for the P samples. Cell counts were taken with a hemacytometer before filtration of samples. One million to 3 million zooxanthellae were collected on filters, which were then rinsed with 3–5 ml of filtered seawater followed by about 200 μl of distilled water to remove salts. Preliminary tests showed that this treatment did not affect the amount of C and N per zooxanthella. All sample sets included appropriate filter blanks and controls (equivalent volumes of seawater filtered). The final filter samples were placed in individual aluminum foil packets and frozen before analysis.

Samples for elemental analysis of the animal fraction were prepared by absorbing a measured volume of each sample into pairs of filters (for separate C and N, and P analyses). Samples of frozen coral animal fraction stored in microfuge tubes were thawed and mixed thoroughly on a vortexer before applying them to the filters. Filters were arranged on a ridged clean piece of aluminum foil, and a total of 400 μl (100 μl at a time) of well-mixed animal sample was placed on each filter using a calibrated micropipette. Filters were dried under a heat lamp between each 100-μl addition so that no sample leaked from the filter. Control filter blanks were prepared by spotting filters with equivalent volumes of filtered seawater. Contamination of filters by handling was avoided by wearing gloves throughout the procedure and using forceps to transfer all filters. Dried filters were stored in individual aluminum foil packets.

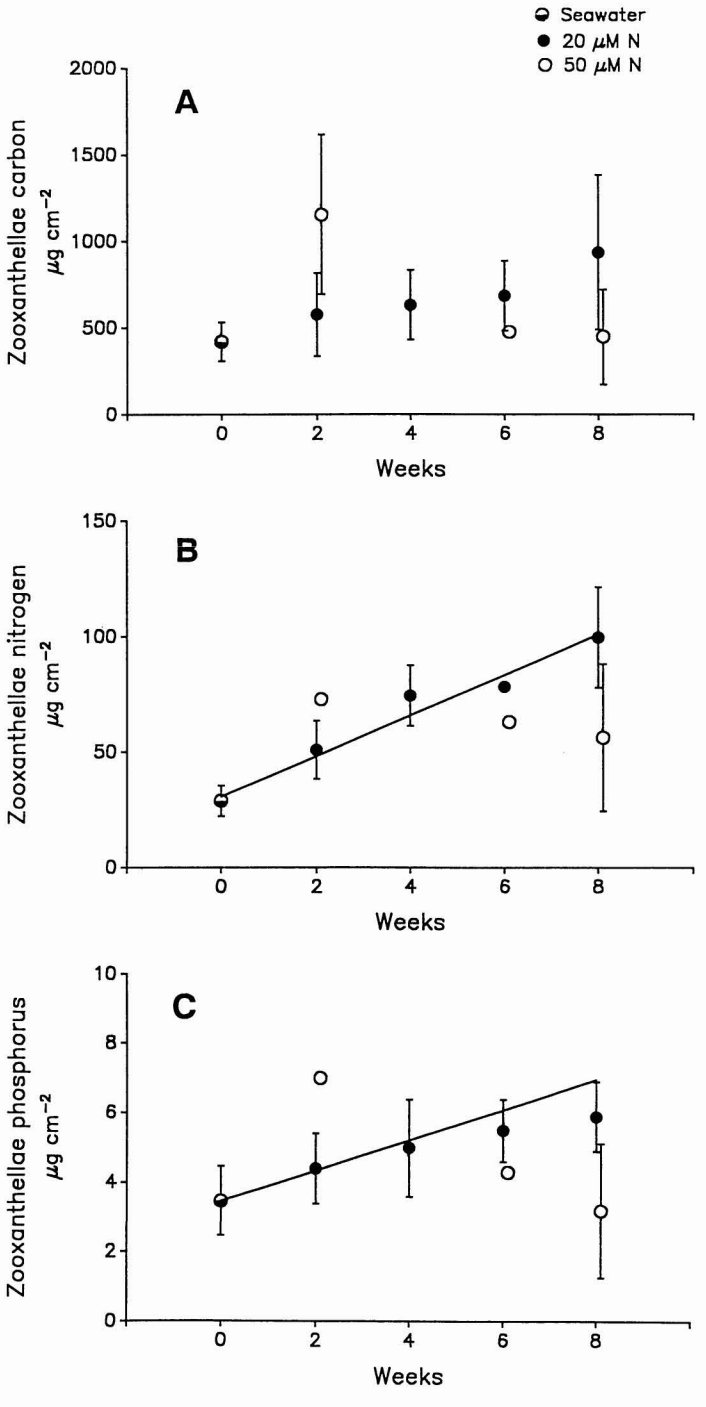

FIGURE 1. Areal C, N, and P content of zooxanthellae in colonies of *Pocillopora damicornis* as a function of time of exposure to 20 μM and 50 μM ammonium additions in seawater. Ambient seawater control colonies maintained under the same light and water flow conditions are used for the zero time point. Data are expressed as the total amount of carbon (*A*), nitrogen (*B*), and phosphorus (*C*) in zooxanthellae per unit colony surface area. $n = 6$ colonies for zero time point, and $n = 2$ for all others except $n = 1$ for the 6-week 50-μM ammonium time point. Error bars are ± 1 SE. The x axis for the 50-μM ammonium data is slightly shifted to the right for clarity. Regression lines are provided for significant effects observed with 20 μM ammonium. *B*: $r = 0.869$, $P < 0.01$; *C*: $r = 0.625$, $P < 0.05$.

Weights of C and N for each filter were determined using an elemental analyzer (Control Equipment Corp. Model 240X). Filters were dried to constant weight before analysis (45°C). Weight of P per filter was measured according to the procedure of Aspila et al. (1976). Each set of analyses included appropriate filter and control seawater blanks that were subtracted from sample results before calculating the C, N, and P content of coral animal and zooxanthellae fractions from volume equivalents.

For statistical purposes, corals maintained in ambient flowing seawater for 8 weeks were presumed to represent corals before the addition of ammonium and were used as the zero time point. The effects of ammonium addition on elemental content and elemental ratios of zooxanthellae and host animal tissue were examined by linear regression over time, using the correlation coefficient (r) to indicate significance of treatments. Elemental ratios were not transformed before analysis.

RESULTS

Figure 1 shows the areal C, N, and P content of zooxanthellae during the 8-week exposure to 20 μM and 50 μM ammonium-enriched seawater. There was a marginally significant ($0.06 > P > 0.05$) trend of increasing C content of zooxanthellae per square centimeter at 20 μM ammonium during this period (Figure 1*A*). Total zooxanthellar N increased four-fold (Figure 1*B*; $P < 0.001$) and total P of zooxanthellae doubled (Figure 1*C*; $P < 0.05$) over the 8-week exposure period to 20 μM ammonium. There were no significant time-related changes in the areal C, N, and P content of zooxanthellae from corals maintained in 50 μM ammonium during the 8-week experiment (Figure 1A–C).

The data in Figure 1 show the changes in total C, N, and P content of zooxanthellae, reflecting both the elemental content of each cell and the areal population density of zooxanthellae in each coral. Figure 2 shows the amount of C, N, and P per zooxanthella isolated from *P. damicornis* after 2 to 8 weeks exposure of the corals to ammonium enrichment. The C and P content of zooxanthellae from corals held in 20 μM ammonium-enriched seawater did not change with time (Figure 2*A*,*C*), but nitrogen per cell increased significantly ($P < 0.05$) over the 8-week period (Figure 2*B*). Different results were obtained for colonies maintained at 50 μM ammonium. There was a significant decline ($P < 0.05$) in C and P content of zooxanthellae during the 8 weeks in 50 μM ammonium (Figure 2*A*,*C*). After 8 weeks, the P content of these cells was half that of zooxanthellae from control corals. The nitrogen content of zooxanthellae from corals exposed to 50 μM ammonium remained constant with time (Figure 2*B*).

The relative changes in C, N, and P of *P. damicornis* zooxanthellae with exposure to added ammonium are shown by the ratios of these elements. The C : N of zooxanthellae from corals kept in 20 μM ammonium-enriched seawater was reduced by half during the first 4 weeks and then remained constant for the next 4 weeks (Figure 3*A*); however, the overall change in C : N with time was not significant ($0.07 > P > 0.06$). The N : P of zooxanthellae in these corals increased by 42% during the 8-week period (Figure 3*B*; $P < 0.05$), with most of the increase resulting from increased N content (cf. Figure 1*B*,*C*). There was no significant change in C : P (Figure 3*C*). N : P also increased in zooxanthellae from corals in the 50-μM ammonium treatment (Figure 3*B*), due in part to the decrease in P content of these algae (Figure 2*C*). Coral zooxanthellae from the 8-week samples had an extremely high N : P of 40. Neither C : N nor C : P of zooxanthellae was affected by exposure of the corals to 50 μM ammonium (Figure 3*A*,*C*).

The C : N and N : P ratios of all zooxanthellae samples from *P. damicornis* were compared with zooxanthellae population densities (zooxanthellae cm^{-2}) to determine if there was a density-dependent effect on elemental ratios. There was no significant correlation of C : N and of N : P with cell density of corals maintained in ambient and in nutrient-stripped seawater.

Figure 4 shows the areal C, N, and P con-

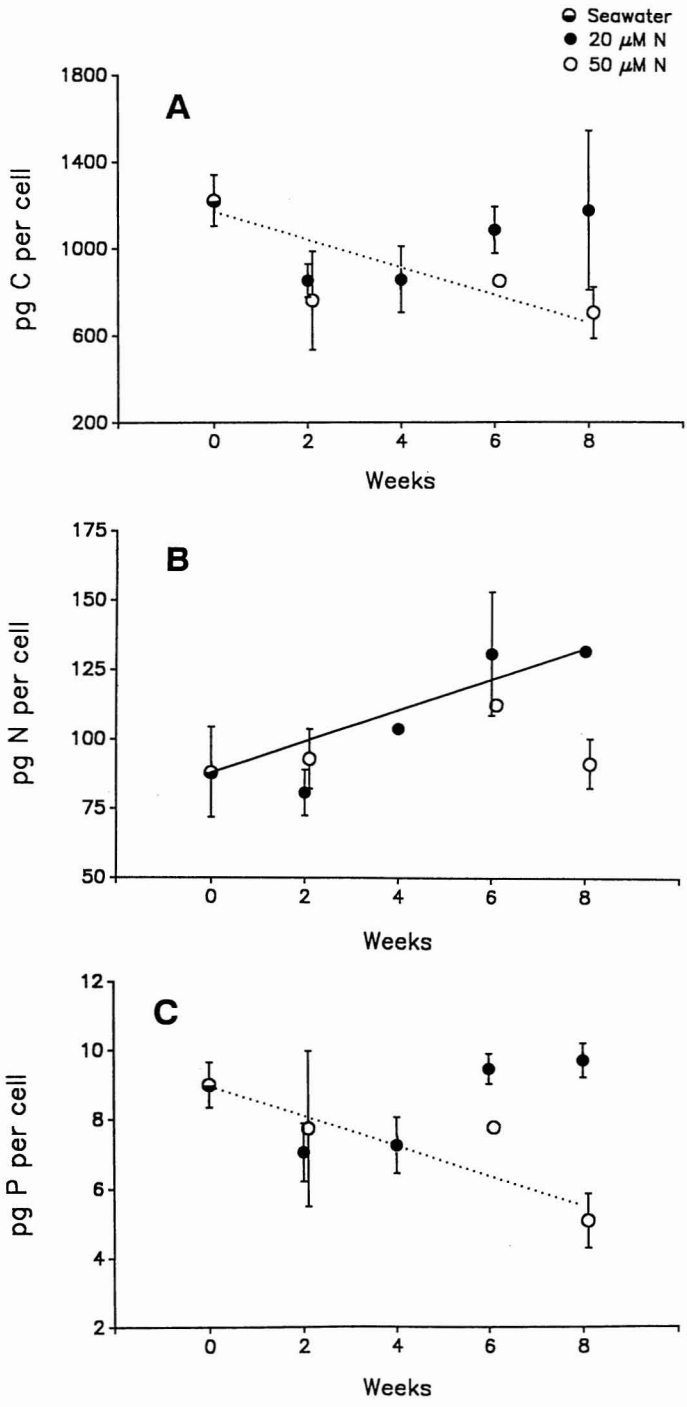

FIGURE 2. C, N, and P content of zooxanthellae in colonies of *Pocillopora damicornis* as a function of time of exposure to 20 μM and 50 μM ammonium additions in seawater. Ambient seawater control colonies maintained under the same light and water flow conditions are used for the zero time point. Data are expressed as the weights of carbon (*A*), nitrogen (*B*), and phosphorus (*C*) per zooxanthella. $n = 8$ colonies for zero time point, and $n = 2$ for all others except $n = 1$ for the 6-week 50-μM ammonium time point. Error bars are ± 1 SE. The x axis for the 50-μM ammonium data is slightly shifted to the right for clarity. Regression lines are provided for significant effects (solid lines: corals in 20-μM ammonium treatment; dotted lines: corals in 50-μM ammonium treatment). *A*: $r = 0.573$, $P < 0.05$; *B*: $r = 0.478$, $P < 0.05$; *C*: $r = 0.612$, $P < 0.05$.

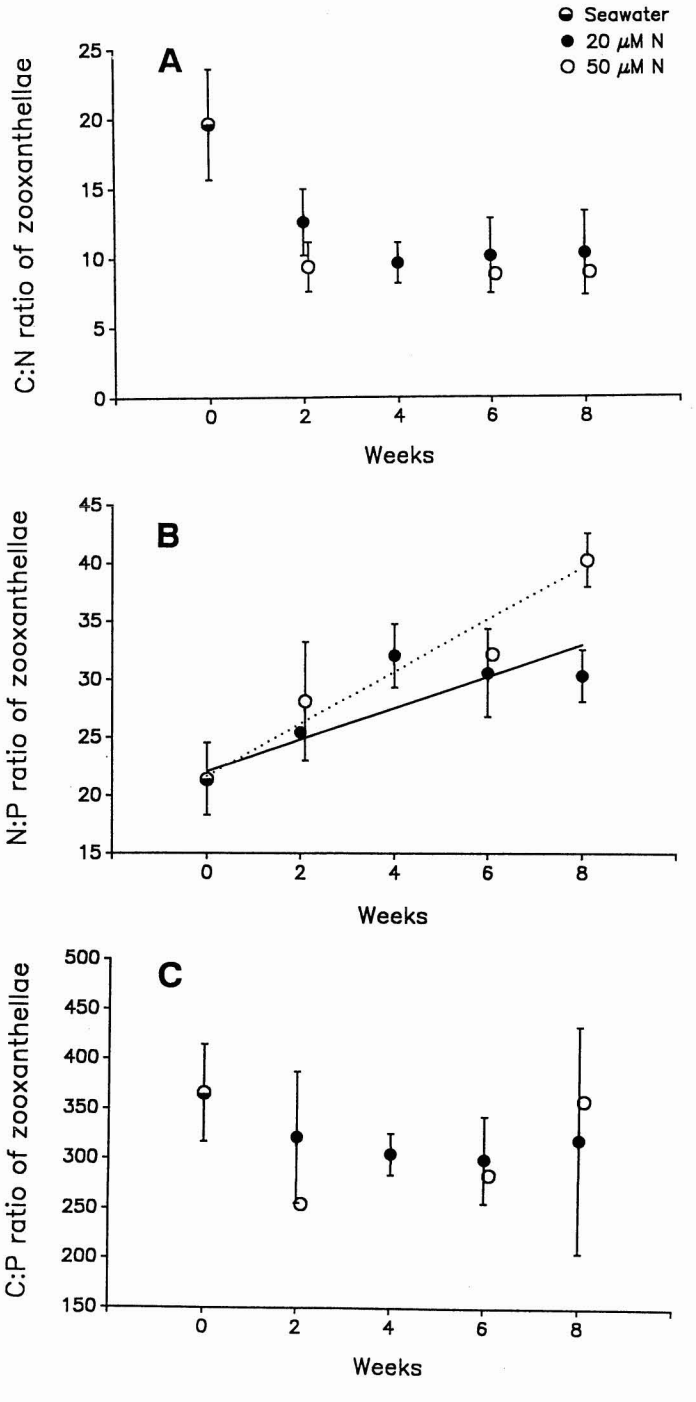

FIGURE 3. C : N, N : P, and C : P ratios (by atoms) of zooxanthellae from individual colonies of *Pocillopora damicornis* as a function of time of exposure to 20 μM and 50 μM ammonium additions in seawater. Ambient seawater control colonies maintained under the same light and water flow conditions are used for the zero time point. C : N (*A*), N : P (*B*), and C : P ratios (*C*) are derived from data in Figure 2 (same conventions). *B*: 20 μM ammonium comparison: $r = 0.532$, $P < 0.05$; 50 μM ammonium comparison: $r = 0.703$, $P < 0.01$.

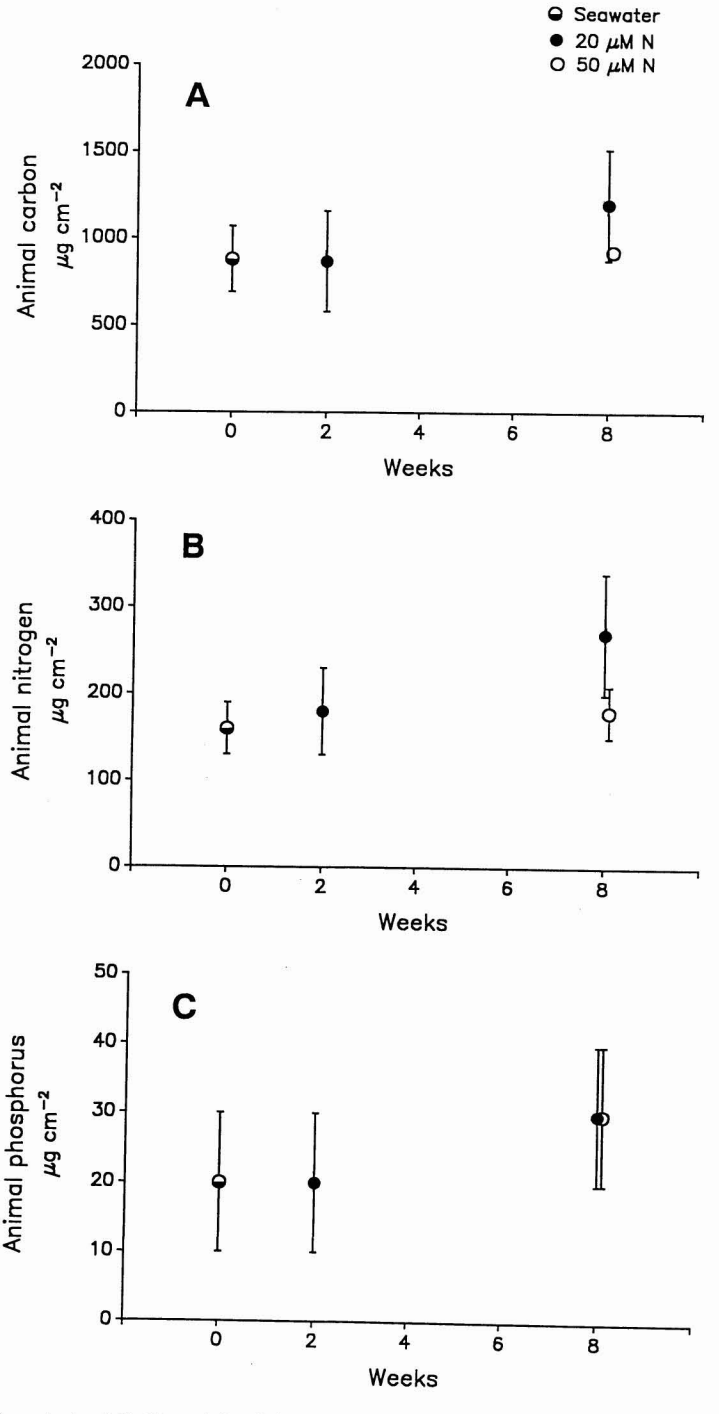

FIGURE 4. Areal content of C, N, and P of the coral animal fraction of *Pocillopora damicornis* colonies as a function of time of exposure to 20 μM and 50 μM ammonium additions in seawater. Ambient seawater control colonies maintained under the same light and water flow conditions are used for the zero time point. $n = 4$ colonies for zero time point, and $n = 2$ for all other time points. Error bars are ± 1 SE. The x axis for the 50-μM ammonium data is slightly shifted to the right for clarity. Data are expressed as the weight of animal carbon per square centimeter (*A*), animal nitrogen per square centimeter (*B*), and animal phosphorus per square centimeter (*C*).

tent of host coral tissue during exposure to ammonium. There were no changes with time in any of these parameters in corals maintained in 20 μM ammonium, in contrast to the increases in N and P of zooxanthellae isolated from these corals. Ammonium-N appears to have been retained by the zooxanthellae, rather than by the animal tissue. The lack of effect on host C, N, and P is reflected in the elemental ratios; there were no changes in host C : N, N : P, or C : P with ammonium addition with time (Table 1). Only two samples of animal tissue were taken from corals exposed to 50 μM ammonium (at 8 weeks), precluding statistical analysis.

Table 1 contains the C : N and N : P ratios of animal tissue and zooxanthellae of *P. damicornis* and shows the amount of C, N, and P in whole coral (sum of animal and algal fractions) and the percentage of each element that is present in the zooxanthellae. A comparison of the zooxanthellae and animal elemental ratios shows that the N : P ratios are similar for both fractions, but C : N ratios are consistently lower in animal tissue and were not changed by ammonium enrichment. Zooxanthellae comprised from 26 to 42% of the total C content of *P. damicornis*, from 13 to 27% of the total N, and from 11 to 28% of total P (Table 1).

DISCUSSION

Effect of Ammonium Enrichment on C, N, and P of Zooxanthellae in Pocillopora damicornis

The addition of 20 μM ammonium to seawater surrounding the colonies of *P. damicornis* resulted in significant increases in the areal N and P content of zooxanthellae (Figure 1). Total areal N content of the zooxanthellae increased four-fold over the 8-week period (Figure 1*B*). This increase was caused by an increase in the density of zooxanthellae (Muller-Parker et al. 1994) and in N per cell (Figure 2*B*). The increase in areal P of zooxanthellae was due solely to an increase in zooxanthellae population density, because P per cell did not change as a function of time of ammonium addition (Figure 2*C*). The C content of zooxanthellae was not affected by the length of exposure to 20 μM ammonium (Figures 1*A*, 2*A*). Because the population density of zooxanthellae increased over this period, the lack of change in C indicates that these cells lost C and gained N during the experiment. In the 50-μM ammonium treatment, the C and P content of zooxanthellae was significantly reduced with time (Figure 2*A*,*C*). This decline in C per cell with ammonium addition is consistent with a decline in starch and lipid observed in morphometric analyses of micrographs of zooxanthellae (Berner and Izhaki 1994). However, areal C and P were not affected (Figure 1*A*,*C*), presumably because of an increase in the numbers of zooxanthellae with time.

The increase in N content of zooxanthellae from *P. damicornis* colonies maintained at 20 μM ammonium could result from an increase in either one or more of the following cellular constituents: amino acid pools, protein, or chlorophyll. Results of biochemical analyses performed on zooxanthellae from the same specimens eliminated free amino acids and protein as N pools. McAuley (1994) found no differences in the size of the amino acid–N pools of zooxanthellae from ammonium-enriched *P. damicornis* and corals maintained in ambient seawater. Although Achituv et al. (1994) observed an initial increase in zooxanthellae protein during the first month of enrichment with 20 μM ammonium, protein content declined during the second month. The significant increases in chlorophyll content of zooxanthellae exposed to 20 μM ammonium (Muller-Parker et al. 1994) may account for the higher N in these cells. There is also the possibility that ammonium is directly stored by zooxanthellae. It is interesting that maintenance of the host in ammonium did affect the amino acid pools of zooxanthellae in a symbiotic anemone; Ferrier (1992) found that zooxanthellae isolated from *Aiptasia pallida* maintained for 4 weeks in 20 μM ammonium exhibited higher concentrations of basic amino acids.

The C and P content of zooxanthellae from corals in the 50-μM ammonium treatment declined during the 8-week period (Fig-

TABLE 1

Elemental ratios and amount of C, N, and P in the coral *Pocillopora damicornis* exposed to 20 μM ammonium and 50 μM ammonium-enriched seawater for 8 weeks

	ANIMAL			ZOOXANTHELLAE						ZOOXANTHELLAE		
P. damicornis	C : N	N : P	C : P	C : N	N : P	C : P	TOTAL C (μg/cm^2)	TOTAL N (μg/cm^2)	TOTAL P (μg/cm^2)	% OF TOTAL C	% OF TOTAL N	% OF TOTAL P
Ambient seawater												
Avg.	6.37	26.57	172	19.66	21.41	365	1,236	182	18	26	13	15
SE	0.40	4.36	35	3.99	3.12	49	310	36	6	4	1	2
n	4	4	4	8	8	8	4	4	4	4	4	4
20 μM ammonium 2 weeks												
Avg.	5.64	17.10	96	12.59	25.45	321	1,443	227	27.3	39	23	16
SE	0.34	0.02	6	2.40	0.38	66	534	63	8	2	1	1
20 μM ammonium 8 weeks												
Avg.	5.21	20.12	105	10.31	30.38	320	2,138	368	36.7	42	27	20
SE	0.03	0.22	2	3.00	2.24	114	765	91	8	6	1	2
50 μM ammonium 8 weeks												
Avg.	6.25	14.92	88	8.92	40.41	359	1,381	235	32.2	29	22	11
SE	0.84	5.80	24	0.65	2.31	6	322	65	4	13	8	7

The 20-μM ammonium treatment corals also were sampled 2 weeks after enrichment. $n = 2$ except where indicated (ambient seawater corals).

ure 2*A*,*C*). Achituv et al. (1994) found that the lipid content of zooxanthellae isolated from 50 μM ammonium-enriched corals was extremely low. Whether the low C, N, P, and lipid content of these zooxanthellae resulted from shrinkage of algal cells in response to the high ammonium or from changes in the biochemical composition of the zooxanthellae cannot be determined without appropriate cell size measurements. It is possible that the high ammonium concentration was toxic to the zooxanthellae and that the anomalous trends observed reflect a response to a stressful nutrient environment.

C : N : P ratios reflect the nutritional history of organisms. The elemental ratios of the zooxanthellae were clearly affected by the ambient ammonium concentration to which the coral was exposed, although only the N : P ratio of zooxanthellae showed a significant increase with time of exposure to both 20 and 50 μM ammonium (Figure 3). However, the C : N of zooxanthellae dropped immediately from 20 to <10 after 2 weeks of ammonium treatment (Figure 3*A*).

Elemental ratios are often associated with changes in the growth rate of the algae. The near-Redfield ratios of oceanic phytoplankton were used to suggest nutrient-saturated growth rates for these algae (Goldman et al. 1979), although others have reasoned that Redfield ratios can occur when growth is limited by other factors (Tett et al. 1985). Because the accumulation of nitrogen in zooxanthellae with 20 μM ammonium enrichment increased after 1 month of exposure to N (Figure 2*B*), it is likely that the increased growth rate of zooxanthellae in response to additions of both 20 and 50 μM ammonium (Høegh-Guldberg 1994) accounted for the steady N content and for the reduction of C and P during this period. After 6 weeks, the C and P levels of zooxanthellae exposed to 20 μM ammonium were similar to the levels in zooxanthellae in control corals kept in unenriched seawater (Figure 2*A*,*C*), indicating that zooxanthellae stored nitrogen primarily during the second month of ammonium enrichment.

Our data show the importance of a baseline (or zero time point) for comparison of elemental ratios of algae subjected to different nutrient regimes. For example, the C : N of N-enriched *P. damicornis* zooxanthellae (Figure 3*A*, Table 1) was higher than C : N ratios of cultured zooxanthellae maintained in nutrient-enriched media (Domotor and D'Elia 1984; unpublished data) and of zooxanthellae isolated from well-fed sea anemones (*Aiptasia pallida* [Cook et al. 1988]). Based on the Redfield ratio for phytoplankton growing in seawater with unlimited nutrient supply of C : N : P ratio of 106 : 16 : 1, we might infer that *P. damicornis* zooxanthellae from N-enriched corals had high C : N ratios. However, the C : N of zooxanthellae from the ambient seawater control corals was twice as high (Figure 3*A*).

It is therefore likely that the elemental composition of zooxanthellae is species-specific and quite variable. Comparison with an extensive data set for Bermuda corals (G.M.P., C.B.C., and Porter, unpublished data) shows that the C : N of *P. damicornis* zooxanthellae from corals maintained in ambient seawater is about twice that of the zooxanthellae in the Atlantic corals *Montastrea annularis* (Ellis & Solander) and *Madracis mirabilis* (Duch. & Mich.) from Bermuda, but the N : P of *P. damicornis* zooxanthellae is lower. The C : N and N : P of N-enriched *P. damicornis* zooxanthellae are similar to those of zooxanthellae from the field populations of the Atlantic corals *M. annularis* and *Madracis mirabilis* (G.M.P., C.B.C., and Porter, unpublished data).

Effect of Ammonium Enrichment on C, N, and P of Animal Tissue of Pocillopora damicornis

It is clear that most of the effects of seawater ammonium enrichment are observed in changes in the areal N content of zooxanthellae (Figure 1) and not in the animal tissue (Figure 4). Unlike zooxanthellae, the N content of the coral animal tissue did not increase significantly with time during exposure to 20 μM and to 50 μM ammonium (Figure 4*B*). The highest N content of animal tissue, obtained in corals maintained in 20-μM ammonium-enriched seawater for 8 weeks

(Figure 4*B*), is consistent with an increase in protein content obtained by Muller-Parker et al. (1994), but was a small and nonsignificant increase compared with that observed in zooxanthellae from the same corals (Figure 1*B*). However, the number of animal tissue samples analyzed was limited and may have contributed to the lack of effect observed with time. If animal assimilation of ammonium occurred, the amount assimilated is relatively small in comparison with assimilation of N by the zooxanthellae. Furthermore, Achituv et al. (1994) concluded that the biochemical composition of the coral animal tissue, including protein, remained constant under all treatments. Høegh-Guldberg and Smith (1989) observed a slight (also nonsignificant) increase in animal tissue protein content with ammonium addition to two species of corals. Muscatine et al. (1989) obtained no differences in protein, lipid, and carbohydrate content of animal tissue from *Stylophora pistillata* exposed to added nutrients. Using $^{15}NH_4^+$, Lipschultz and C.B.C. (unpublished data) found that the zooxanthellae of *P. damicornis* had a higher rate of ammonium assimilation over 24 hr than did the animal tissue. However, they did find appreciable incorporation of ammonium-N into host macromolecules at the end of the study.

This is the first report of the C, N, and P composition of the separated animal and algal fractions of a coral. Other investigators have reported on the elemental ratios of whole coral tissue. The C : N of coral tissue in *Stylophora pistillata* ranged from 6.26 to 4.86 (Muscatine et al. 1989), and the N : P of two Caribbean corals ranged from 21 to 26 (Meyer and Schultz 1985). The N : P ratios of animal tissue and zooxanthellae in *P. damicornis* are similar, but C : N ratios are consistently lower in animal tissue (Table 1). Ammonium enrichment did not alter animal C : N ratios (Table 1). However, C : N and N : P ratios may provide information about the relative importance of inorganic nutrients dissolved in seawater and nutrients obtained via capture and assimilation of zooplankton prey. By varying the relative input of dissolved inorganic nutrients and food, it may be possible to assess the relative contribution of these sources to the elemental composition of an organism. Nutrient fluxes between the seawater environment and the host are affected by the nutritional status of the zooxanthellae (Muller-Parker et al. 1990, Szmant et al. 1990). A comparison of the relative elemental ratios, in conjunction with knowledge of uptake rates of inorganic nutrients and prey capture rates, may indicate which source is more important.

Ecological Implications

Changes in inorganic nitrogen input affect the nitrogen balance of reef corals, because the relative proportion of zooxanthellar to animal nutrient pools changes with enrichment. These changes are also likely to affect net coral production and the stoichiometry of C, N, and P metabolism on reefs (Atkinson 1988). Our results suggest that corals living in high-nutrient environments will have more N stored in the autotrophic zooxanthellae. The mass balance of C, N, and P will change as the proportion of zooxanthellae to animal biomass changes under different conditions, ranging from conditions that result in loss of zooxanthellae (bleaching) to eutrophic conditions that promote high population densities of zooxanthellae.

Because the nutrient status of zooxanthellae in field corals is difficult to determine without experimental manipulations of the ambient nutrient regime, the use of "indices" of algal nutrient status such as the C : N : P ratios, the ammonium enhancement of dark carbon fixation (Cook et al. 1992, 1994), and amino acid ratios (Flynn 1990) to test the nutrient status of zooxanthellae in field populations of symbiotic anemones and corals is a promising approach. More work is needed to determine the pathways of nutrient acquisition and storage products of nitrogen.

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