Ratio of Energy and Nutrient Fluxes Regulates Symbiosis between Zooxanthellae and Corals[1]

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ABSTRACT: Ambient irradiance levels determine the rate of carbon influx into zooxanthellae at any given time, and thereby the energy available for the whole coral symbiotic association. Long-term photoacclimation of zooxanthellae to the time-averaged light regime at which the host coral grows results in optimization of light harvesting and utilization. Under high irradiance light harvesting is reduced, thereby avoiding photodynamic damage, whereas under low light, photon capture and quantum yield are maximized. Most of the photosynthate produced by the algae is respired. However, the capability of the zooxanthellae and the coral to retain carbon beyond that required to meet their respiratory needs depends on the availability of the commonly limiting nutrients, nitrogen and phosphorus. Therefore, the ratio of the flux of these nutrients into the colony to that of the photosynthetically driven carbon flux will regulate the growth of the zooxanthellae and of the animal. Nutrients acquired by predation of the coral on zooplankton are available first to the animal, whereas those absorbed by the zooxanthellae from seawater as inorganic compounds lead first to growth of the algae.

IT HAS BEEN an accepted dogma in coral biology that the extensive spatial and long-term temporal success of coral reefs in the oligotrophic littoral of tropical seas stems from the symbiotic association between endocellular microalgae (the zooxanthellae) and the host hermatype. It is this association that allows corals and coral reef communities to thrive in spite of the low concentrations of nitrogen and phosphorus in the oligotrophic ambient waters (Muscatine and Porter 1977). It is this oligotrophy that also causes the striking paucity of phyto- and zooplankton in these "blue deserts," limiting the availability of particulate food as an alternate nutrient source.

In this mutualistic symbiosis the algae contribute their capability to harness sunlight to the photosynthetic production of high-energy compounds, mainly carbohydrates. These are produced in great excess of that needed to support the basic metabolic needs of the zooxanthellae. However, because these compounds have a very high $C : N$ ratio, they cannot by themselves support multiplication of the algae. The excess photosynthate, which may reach as much as 95% of the total, is "translocated" to the host animal, a process stimulated by "host factors" that dramatically increase the excretion of assimilated carbon compounds by the algae (Muscatine 1967, Sutton and Høegh-Guldberg 1990). The translocated carbon compounds are more than enough to provide for the respiratory needs of the host (Muscatine et al. 1984), although, as is also the case for the zooxanthellae, they cannot support growth of animal tissue. These energy-rich, nitrogen-poor products of photosynthesis were termed "junk food" because of their insufficiency as food for growth (Falkowski et al. 1984).

In return for fixed carbon, the zooxanthellae gain access to the high nitrogen and phosphorus metabolic waste products of their

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host. Thereby the colony retains and recycles these precious substances, which in the absence of the algae would have been excreted into the sea and lost to the system. In addition to photosynthetic capability, the two partners in the coral symbiosis also differ in that the animal is an avid and efficient predator on zooplankton, an important source of nitrogen, while the zooxanthellae are capable of assimilating inorganic nitrogen and phosphorus compounds inaccessible to the animal. However, it is important to bear in mind that under normal reef conditions both of these sources are very limited. Therefore, although the very efficient uptake by the zooxanthellae of nutrients produced by the host animal assures recycling of these resources and prevents their loss from the association (Rahav et al. 1989), this cannot account for growth or "new production."

The effects of the modulation of the flux of carbon into zooxanthellate corals in response to different light intensities, as those encountered at different depths, has been examined in some detail, mostly in a series of studies of the common Red Sea coral *Stylophora pistillata* Esper (Falkowski and Dubinsky 1981, Muscatine et al. 1983, 1984, Dubinsky et al. 1984, Falkowski et al. 1984, Porter et al. 1984). It has been found that the zooxanthellae photoacclimate within a week to a new irradiance level and that the host also responds to this change. Among the reported differences between high (HL)- and low-light (LL) corals were differences in areal chlorophyll *a*. These were a result of up to four-fold increases in the concentration of this pigment in the LL zooxanthellae. This difference was clearly mirrored on the ultrastructural level, as a corresponding difference in thylakoid area (Dubinsky et al. 1984, Berner et al. 1987).

In most cases, photoacclimation was reported to occur primarily on the cellular level of the zooxanthellae, and their densities remained around 10^6 cells cm^{-2} (but see also Dustan 1979 and Titlyanov 1991). However, under extremely low irradiance the algae are confined to the side of the colony facing the light (Figures 1 and 2).

The strategy of photoacclimation in the zooxanthellae of *S. pistillata* is by change in size, not in the number, of photosynthetic units (Falkowski and Dubinsky 1981), although this may not be true for all zooxanthellae (Chang and Trench 1982). It was also found that the HL zooxanthellae had higher dark respiration and light-saturated photosynthetic rates and lower quantum yields than their LL counterparts (Falkowski and Dubinsky 1981, Dubinsky et al. 1984, Porter et al. 1984). The animal responses to the different light regimes included higher respiration and calcification in the HL corals (Dubinsky et al. 1983, Porter et al. 1984). In those studies it was also concluded that in *S. pistillata*, under high light, photosynthesis is sufficient to provide substrata for both animal and algal respiration, which is not the case in LL colonies, which have to supplement algal photosynthesis by animal predation (Falkowski et al. 1984).

In a subsequent series of studies the effect of added nutrients and of feeding on *Artemia salina* (Linnaeus) nauplii on *S. pistillata* was examined (Muscatine et al. 1989, Dubinsky et al. 1990, Falkowski et al. 1993). Although nutrient-enriched colonies changed within 3 weeks to nearly black, whereas the controls remained ivory colored, making them look like LL and HL colonies, this change resulted not from change in the pigment content in the zooxanthellae as was the case in photoacclimation, but from an up to five-fold increase in algal population. Nutrient enrichment brought about additional changes in the interrelation between the zooxanthellae and the coral. Division rate of the zooxanthellae increased (Høegh-Guldberg 1994), but their photosynthetic rates on a per-cell basis decreased, probably resulting from carbon limitation in the dense algal population (Dubinsky et al. 1990). The fraction of photosynthate translocated to the host also decreased.

In studies on the effect of nutrient enrichment done in Hawaii with *Pocillopora damicornis* (Linnaeus), it was also found that nutrient enrichment resulted in increased algal density (Stambler et al. 1991). In those studies nutrient enrichment also led to significantly reduced calcification rates (Stimson
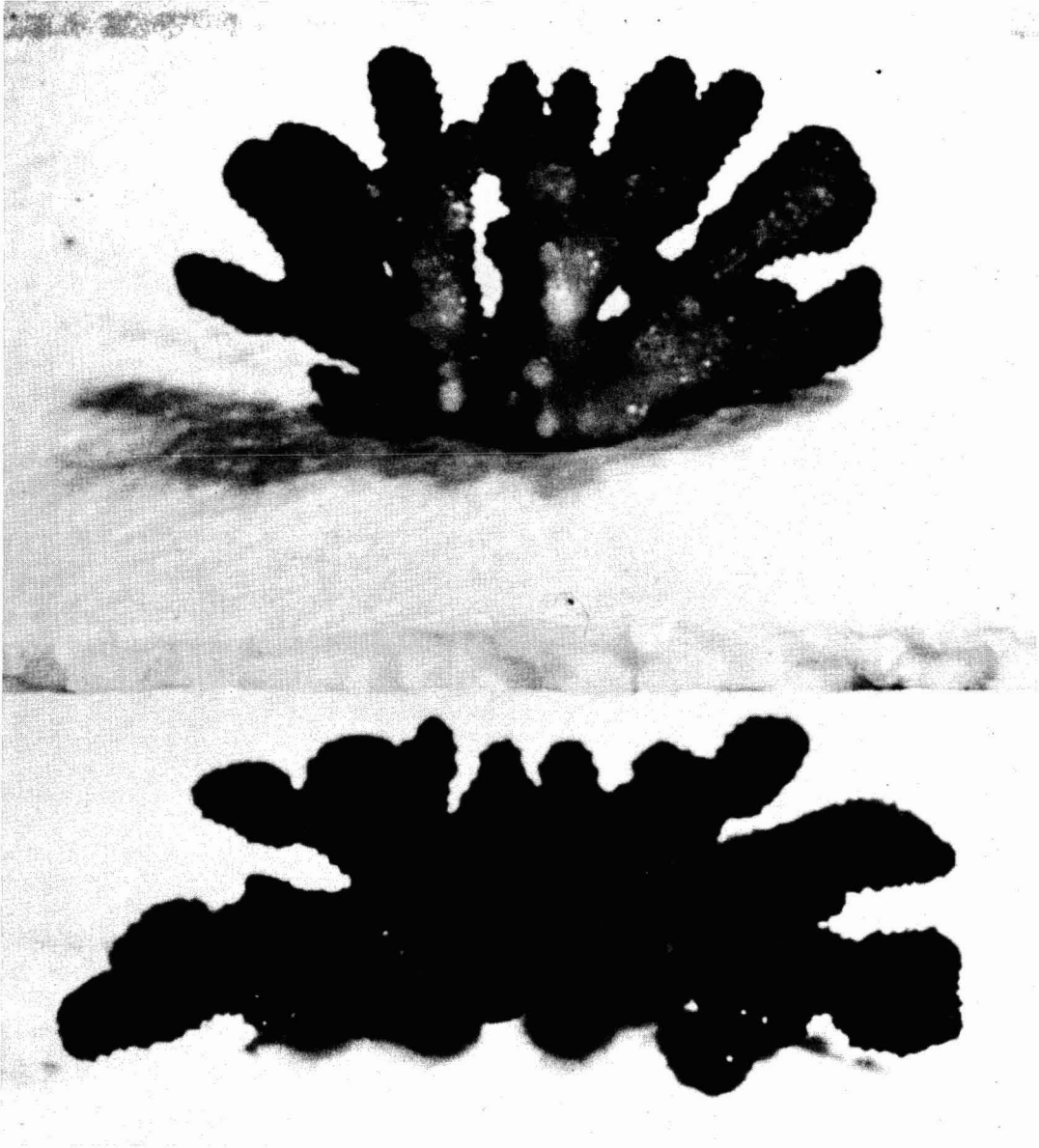
FIGURE 1. *Stylophora pistillata* colony from a deep, shaded crevice. The dark side is the one facing the light; the side facing the rear wall, reflected in the mirror, is nearly white.

1992). Nitrogen enrichment was also reported to weaken the skeletal architecture of corals (Yamashiro 1992) and slow down its growth (Stambler et al. 1991).

In this study we examine the possible interactions between the underwater light and nutrient fields surrounding corals. The effects of light and of nutrients were hitherto studied separately, and we shall attempt to integrate the concepts that emerged from these studies.
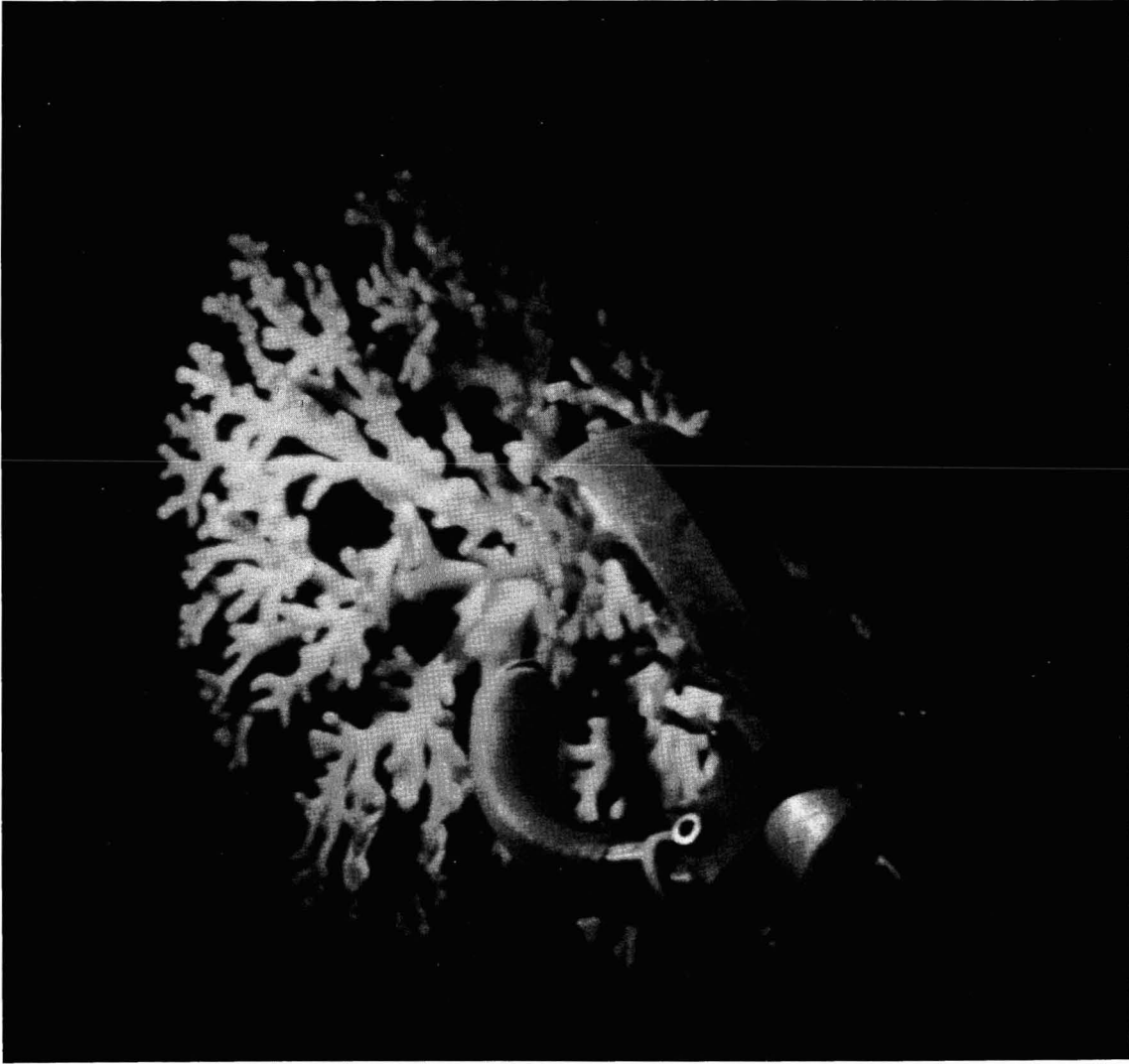
FIGURE 2. *Stylophora pistillata* at 66 m in the Gulf of Elat, northern Red Sea. Zooxanthellae are found only on the up-facing, dark surface; none are on the down-facing side (shown).

Light and Nutrient Flux

When corals exposed to various light intensities are compared, two interesting questions emerge. First, in LL corals, photosynthesis alone cannot account for all of the colony respiration; therefore such colonies have to supplement zooxanthellae autotrophy with heterotrophic animal predation on zooplankton (Falkowski et al. 1984). Indeed, under low light most corals remain with their tentacles extended continuously (Figure 3). Second, why should HL corals, which have more photosynthate produced than that needed to support respiration (Figure 4*a* and *b*), still have to hunt for zooplankton. Although such HL colonies usually extend their tentacles only after sundown, why should they extend them at all? Yonge (1930:54) wrote "Corals as a general rule, expand only
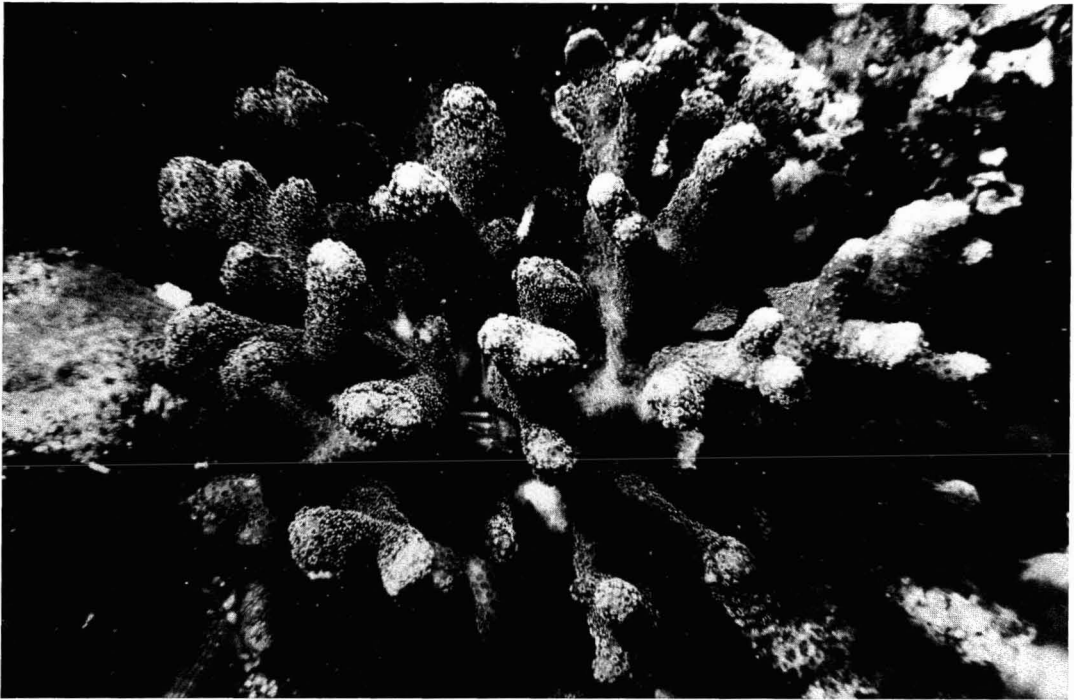
FIGURE 3. *Stylophora pistillata* colony growing under low light. Polyps remain constantly extended.

at night when, as the results of the investigations on plankton will make abundantly clear, their food is most abundant." There is no doubt that these corals are hunting quite efficiently the zooplankton that rises at night from deeper waters.

Because the nutrient concentration to which LL and HL corals are exposed does not differ, we would assume that they do not differ in their nutrient status. However, this seems not to be the case. To grow, both zooxanthellae and coral have to acquire carbon and nitrogen at the same ratios found in their biomass, but assuming that inorganic nitrogen intake by the zooxanthellae is controlled by its concentration in the water, that of carbon is governed by photosynthesis and, thereby, by irradiance. Therefore, although LL colonies acquire carbon and nitrogen at the C : N ratio of 9.97, HL colonies acquire them at a 30.15 ratio (Falkowski et al. 1984, Muscatine et al. 1984). From this follows that while at low light corals may be only slightly

nitrogen-limited and, assuming that respiration preferentially uses high C : N compounds, may in fact not be nitrogen-limited at all, HL corals have to be severely nitrogen-limited, although both grow in the same water. In an analysis of the products of photosynthesis in corals growing at different depths, it was indeed found that in deep-water corals a much higher fraction of photosynthetically assimilated ^{14}C was incorporated into amino acids than in shallow-water (HL) corals (Bil' et al. 1992).

We suggest that, unlike LL colonies, HL corals do not hunt zooplankton for their carbon but rather for their nitrogen (Atkinson 1992). Of course, the nutrient requirement of the zooxanthellae population also depends on algal numbers. Indeed, under reduced densities of zooxanthellae, like those occurring in partially bleached coral colonies, the algae are nutrient sufficient (Cook et al. 1992).
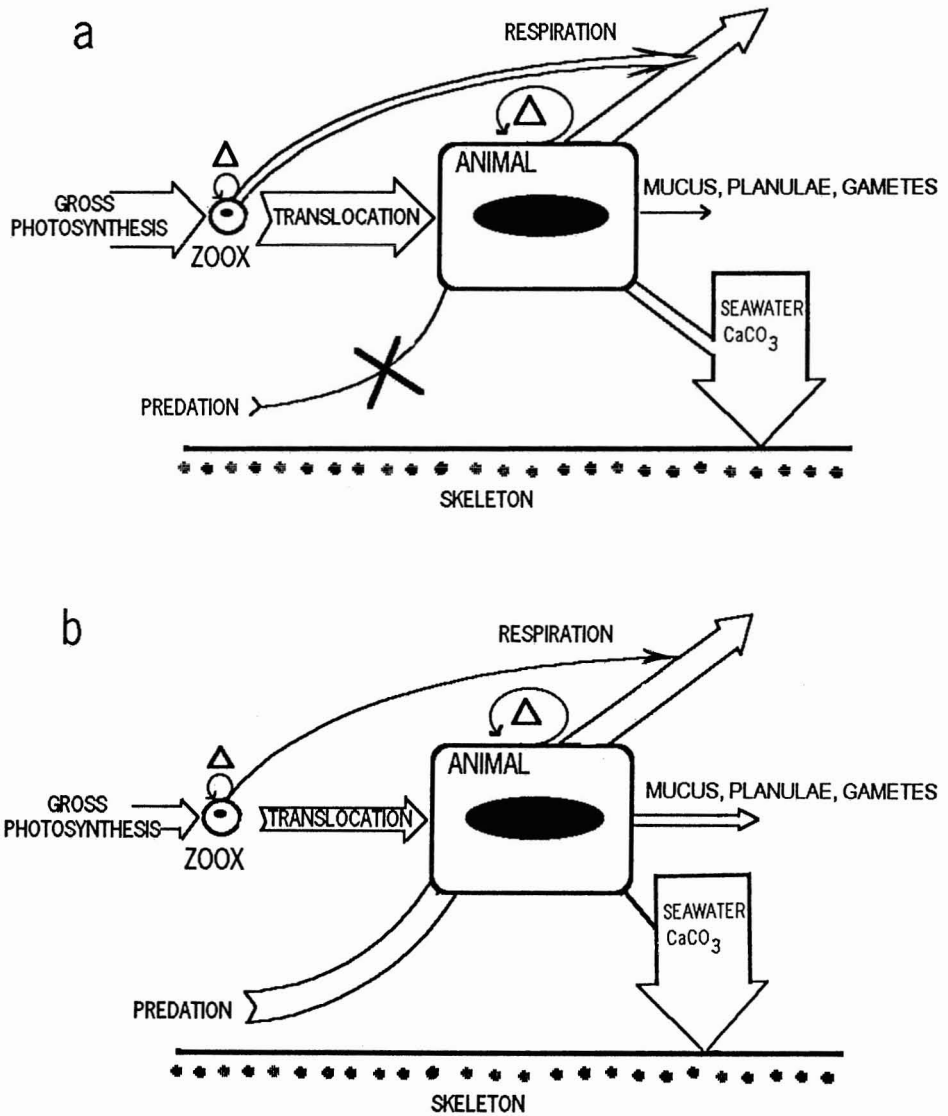
Although it is easy to see why LL corals

FIGURE 4. Carbon budget for 24 hr in HL (*a*) and LL (*b*) colonies of *Stylophora pistillata* (redrawn after Falkowski and Dubinsky 1981).

would extend their tentacles continuously, to capture as much of the scarce zooplankton as possible, we do not have an explanation of the daylight retraction of tentacles by most (not all) shallow-water corals, as may be seen in Figures 5–7 (Abe 1939). In the Red Sea and in the Caribbean (Porter 1974), this is indeed the rule, with very few exceptions,

such as *Goniopora lobata* Edwards & Haime. However, this may not be a universal phenomenon (Lasker 1979) and is not the case in Hawaiian reefs. An analogous situation was described when *S. pistillata* colonies from different depths and irradiance levels were compared for their prey hunting and killing efficiency (E. A. Titlyanov, V. A. Leletkin, and
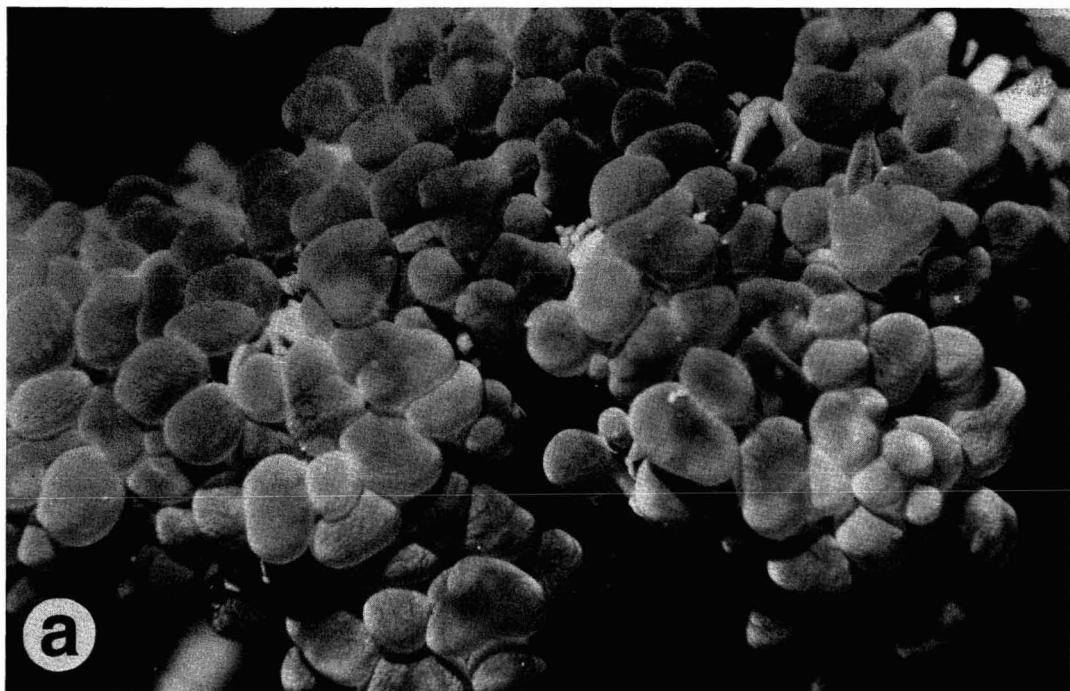
FIGURE 5. The Red Sea coral *Pleurogyra sinuosa* (Dana): (*a*) during daytime, with polyps contracted, vesicles extended; (*b*) at night with polyps fully extended, nematocyte batteries visible, vesicles collapsed.
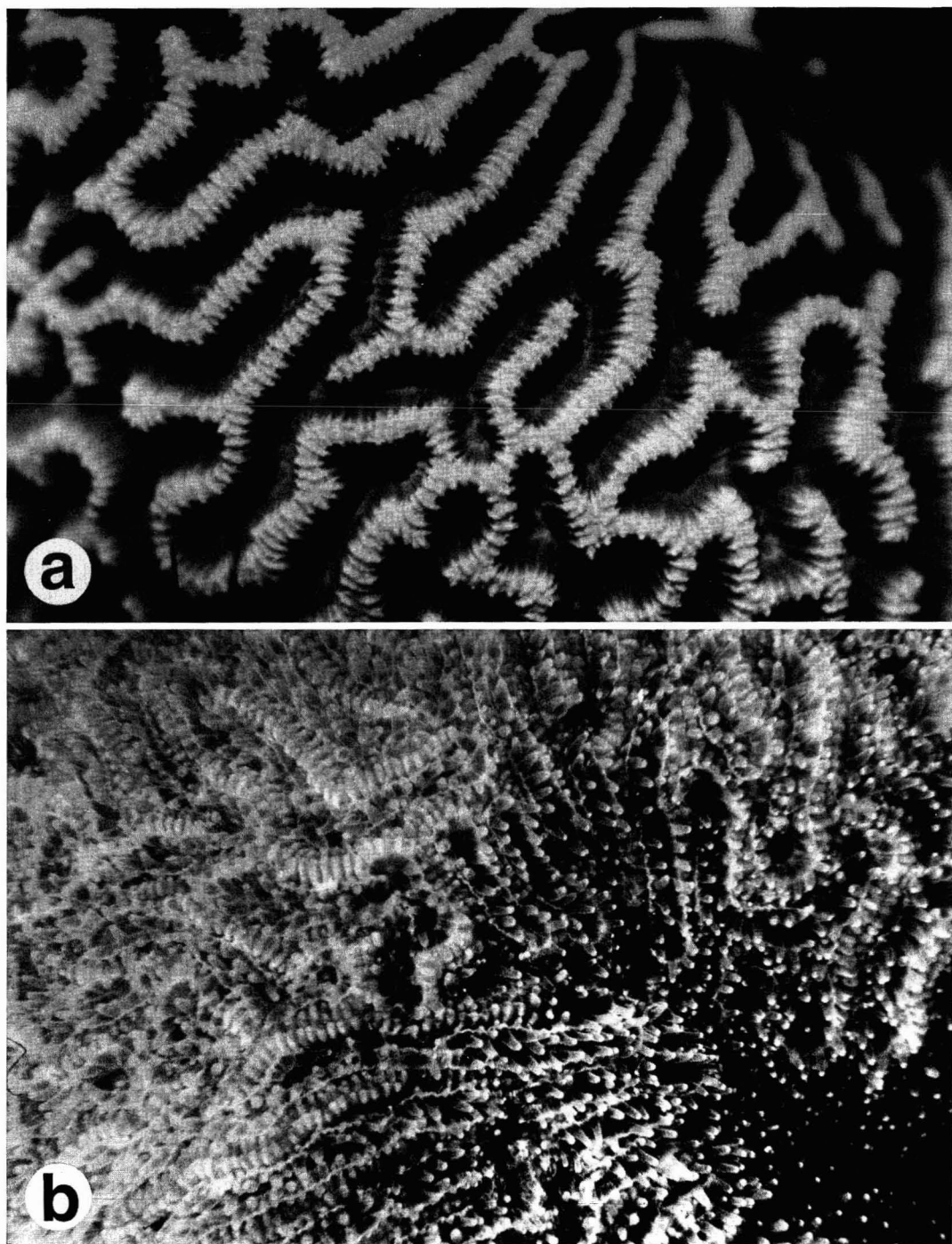
FIGURE 6. The Red Sea coral *Platygyra lamellina* (Ehrenberg): (*a*) during daytime, with polyps contracted; (*b*) at night, with polyps fully extended.
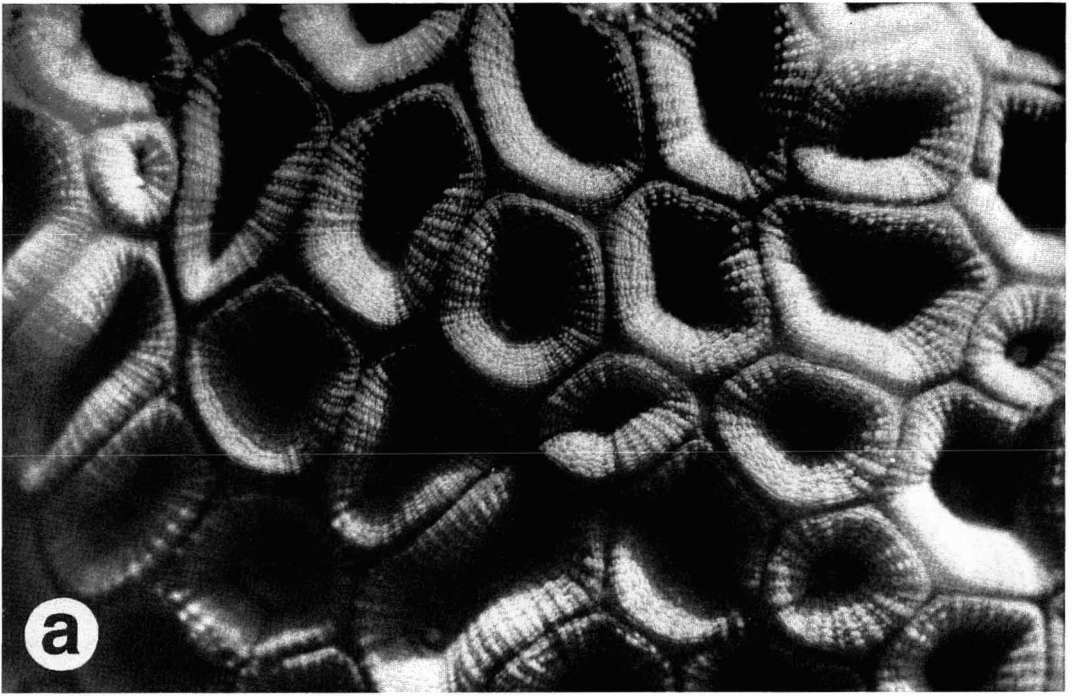
FIGURE 7. The Red Sea coral *Favites flexuosa* (Dana): *a* and *b* as in Figure 6.

Z.D., unpublished data). In all cases HL colonies showed lower prey-hunting efficiency than the deep-water, LL colonies.

The Effects of Nutrient Enrichment and Feeding on Carbon Flux

If we examine the energy and nutrient relationships from the nutrient end, we may find some additional interesting interactions. Because to increase in numbers zooxanthellae have to acquire on the order of one atom of nitrogen for every seven carbon atoms, it follows that any carbon in excess of this ratio will be either respired or translocated to the host. In corals exposed to elevated nutrient levels, the zooxanthellae, instead of acting like a carbon-moving conveyer belt translocating "junk food" to the coral host, retain seven carbon atoms for every nitrogen atom absorbed from the water. This results in two changes in the symbiotic association. Less carbon is translocated to the host, the C : N

ratios in the algae decrease (Muscatine et al. 1989, Muller-Parker et al. 1992), and the algae are able to use photosynthetically produced carbon skeletons for the synthesis of nitrogen-containing molecules required for cell multiplication, such as amino acids and nucleotides. The algal population increases two- to five-fold in numbers, with their respiratory needs being satisfied before those of the coral. As a result of this growth in algal population, the increased algal population becomes carbon-limited, producing less photosynthate per cell (Dubinsky et al. 1990); of the total produced, more is respired, and more is retained, ending up as new zooxanthellae cells.

It also was shown that if the coral is fed zooplankton, not only will the coral tissue be able to grow, as is shown in an increase in animal protein (Muscatine et al. 1989), but as a result of enhanced metabolism (Rahav et al. 1989) and digestion the zooxanthellae will be provided with nitrogen by "reverse trans-
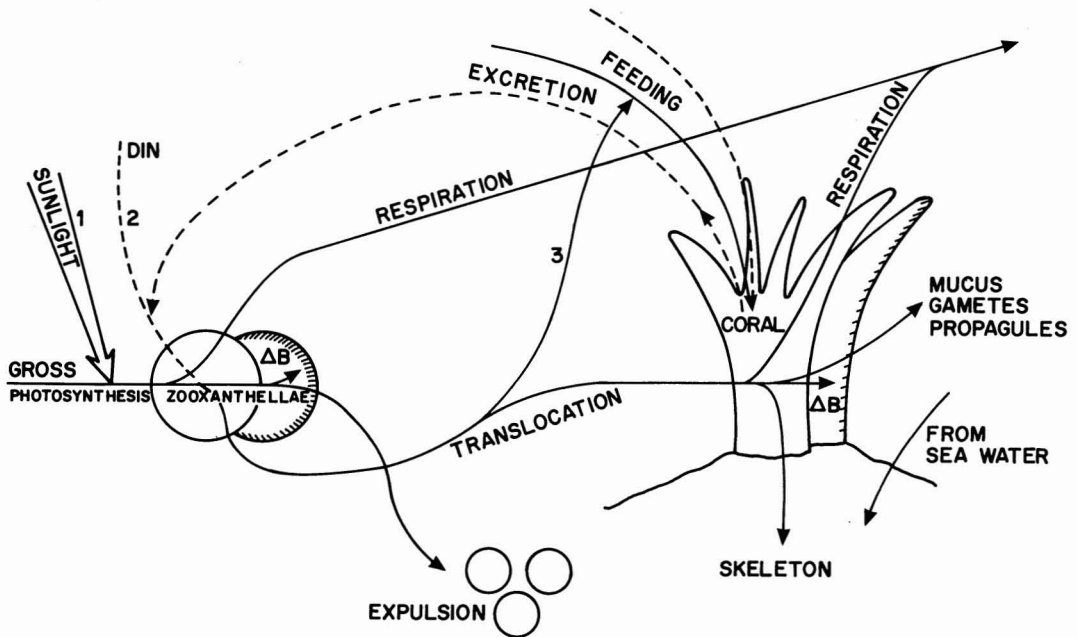

FIGURE 8. Interactions between nitrogen and carbon fluxes in zooxanthellate corals. Light and dissolved inorganic nitrogen control the allocation of carbon to either proliferation of algae or translocation to host. Translocation affects the importance and intensity of feeding. Solid arrows represent carbon fluxes, dashed lines fluxes of nitrogen. 1 and 2 are the main external forcing functions; 3 is an internal feedback loop. Shaded areas represent biomass growth.

location." Feeding on zooplankton, by increasing nitrogen supply, will reduce the uptake of ammonium from the water by the zooxanthellae, as was shown using ^{14}C methylamine, a nonmetabolizable ammonuim analogue (D'Elia and Cook 1988). Al-Moghraby et al. (1992) recently reported that feeding Galaxea fascicularis (Linnaeus) polyps reduced their uptake of free amino acids from the water.

Conclusions

Figure 8 summarizes the main interactions and feedback mechanisms connecting light intensity, nutrient level, and feeding in zooxanthellate corals: (1) Under constant nutrient concentration, light intensity determines the onset of nutrient limitation; as light increases, C : N ratios exceed Redfield ratios. (2) The availability of other nutrients, mainly nitrogen, determines the fate of photoassimilated carbon. Under high C : N ratios, most carbon goes into respiration, calcification, and excreted mucus, whereas low C : N ratios favor increases in zooxanthellae density, reduce translocation, and slow down calcification. (3) Feeding on zooplankton by the coral under low light provides carbon for metabolism. Under high light it supplies both algae and animal with nitrogen.

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