Energy Relationships between *Anemonia sulcata* and its Endosymbiotic Zooxanthellae [*]

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Abstract

The sea anemone *Anemonia sulcata* which is widely distributed in shallow waters along the Mediterranean coast of Israel contains endosymbiotic zooxanthellae in its tissues. Only 50% of the photosynthetically assimilated carbon is utilized by the algae, while the rest is translocated to the animal tissue. The percentage of translocated carbon to the anemone tissue is independent of light intensity and, therefore, does not depend on the total amount of fixed carbon. Under starvation, the percent of translocation increases up to 70%. This translocation of the photosynthetic products from the algae to the animal tissue may provide up to 116% of the animals' respiratory needs under natural conditions. The energy contribution of zooxanthellae to the anemone allows its survival and maintenance under starvation, but for growth, the anemone also needs essential nutrients such as nitrogen and phosphate which have to be obtained through predation.

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1.   Introduction

Various aspects of the association between the sea anemone *Anemonia sulcata* and the zooxanthella *Symbiodinium* sp. found in its tissues have been described (Smith, 1939; Taylor, 1969a,b; Möller, 1978; Schlichter, 1978; Dorselt, 1984; Janssen and Möller, 1981; Tytler, 1981; Tytler and Spencer Davies, 1984; 1986.). In these studies it was found that in nature *A. sulcata* feeds on animal prey (Möller, 1978), and it has been demonstrated that it is capable of utilizing dissolved organic matter (Schlichter, 1978). Nevertheless, it was also shown that the products of algal photosynthesis are essential for the long-term survival of their animal host. The importance of these compounds increases in particular under starvation in captivity. In the dark, starved anemones lost weight at a higher rate than in the light (Smith, 1939; Taylor, 1969a; Janssen and Möller, 1981; Tytler and Spencer Davies, 1986).

The contribution of zooxanthellae to animal respiration (CZAR), (Muscatine, et al., 1981) was studied in a number of organisms. In the case of the clam *Tridacna gigas* the zooxanthellae may supply as much as 100% of the daily respiratory carbon requirement (Fisher et al., 1985). In *Pocillopora damicornis* and *Fungia scutaria* CZAR is in the order of 63–69% (Muscatine et al., 1981).

CZAR also depends on the nutritional state of the host; in the anemone *Anthopleura elegantissima* when starved it was 34–56% and only 8–9% in fed animals (Fitt et al., 1982).

Schick and Dykens (1984) and Zamer and Schick (1987) estimated for the same sea anemone, from the low-intertidal that CZAR was 34–42%, decreasing to 17% in high-intertidal anemones.

The energy input from photosynthesis in the coral *Pocillopora eydouxi* is about twice the amount the animal needs for respiration (Spencer Davies, 1984). In the coral *Porites porites* the animal used only 33% of the energy translocated from the zooxanthellae (Edmunds and Spencer Davies, 1986). In *Stylophora pistillata* products of algal photosynthesis could provide between 143 and 58% of the total carbon and energy requirement of the high and low irradiance adapted colonies respectively (Falkowski et al., 1984; Dubinsky et al., 1984; Muscatine et al., 1984; Porter et al., 1984). The aim of the present study was to describe the carbon budget of the temperate sea anemone *Anemonia sulcata*, and to evaluate the contribution of the photosynthesis of zooxanthellae to this budget.

2.   Materials and Methods

Anemones were collected in shallow water (1–3 m) in a small sheltered harbour at Mikhmoret on the Mediterranean coast of Israel. In this location *A. sulcata* forms dense, continuous "lawns" (Fig. 1).

Most of the study conducted was on these freshly collected anemones, which were considered fed animals (Möller, 1978).

In other cases the anemones were starved in the laboratory for 2–3 weeks. The growth irradiance in the laboratory was 100–300 $\mu E\ m^{-2}\ sec^{-1}$.

Algal densities in animal tissue were determined from homogenate samples. Animals were blotted dry, weighed and homogenized in 100–200 ml of filtered sea water for 2 min in a Molinex blender. Zooxanthellae were counted with a Neubauer hemacytometer in 8 replicates. Algal division rates were estimated from the mitotic index (M.I.) data obtained over 24 hr, at 2 hr interval sampling. In each sampling time, 2 anemones were homogenized as described above and the percentage of dividing cells among 500 cells was determined.

Duration of mitosis, the growth rate μ, and the doubling time T were calculated as described below.
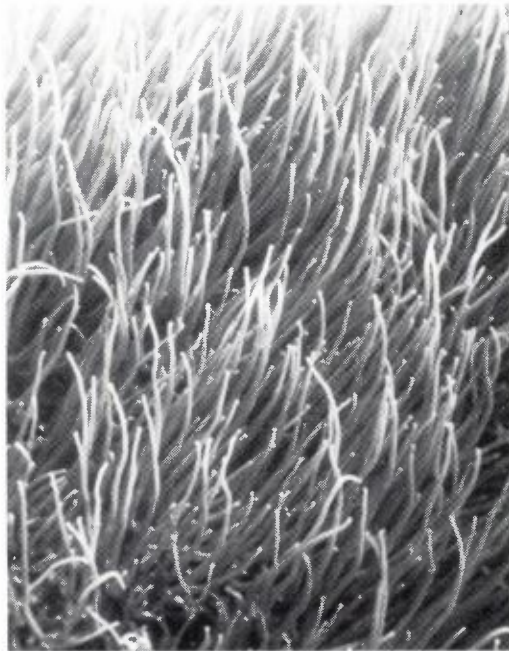

Figure 1. Dense stand of *A. sulcata* at 1 m, Mikhmoret, Israel.

The average daily growth rate of the zooxanthellae, μ, was calculated from eqn. 1 (Wilkerson et al., 1983)

$$\mu = \frac{1}{t} \ln(1 + f_{\max})$$

where t is the total duration of sampling, the duration of sampling was 24 hr, $t = 1$, $f_{\max}$ is maximal mitotic index (M.I.). From this value t_d the duration of division (cytokinesis) was estimated using eqn. 2 (Wilkerson et al., 1983).

$$\mu = \frac{1}{n t_d} \sum_{i=1}^{n} \ln(1 + f_i)$$

where n is the number of samples, f_i is mitotic index of sample i.

The doubling time of the population is T (eqn. 3).

$$T = \frac{\ln 2}{\mu}$$

Dark respiration and photosynthesis-irradiance relationships for whole anemones were determined from changes in O_2 concentration. Anemones were placed in filtered sea water in a $(22 \pm 0.1^\circ$ C) water jacketed glass container with thermostat. Illumination was provided by a slide projector equipped with a quartz-halogen lamp. Desired irradiance levels (0–600 μE m^{-2}s^{-1}) were obtained by attenuating the collimated light beam with various combinations of metal screens. Irradiance incident upon the experimental chamber was measured with a LiCor 185 B light-meter and a quantum sensor, 190SB. Oxygen concentrations were measured with a Yellow Springs Instruments 5331 polarographic electrode connected via a multi-gain amplifier to a recorder, set at 10 mV full scale. The recorder output was calibrated daily against 24 hr air-equilibrated water (100% O_2) and freshly prepared Na_2SO_3 saturated solution (0% O_2), as described in Dubinsky et al. (1987).

Conversion to caloric values was done assuming a 112,000 cal. per mole O_2 equivalence, assuming all carbon to be carbohydrate.

Translocation, as percentage of total carbon assimilation, was estimated from ^{14}C uptake. In ^{14}C incorporation experiments 100 μCurie NaH^{14}CO$_3$ (Amersham) were added to an anemone in 150 ml sea water. Incubations lasted 1–5 hr under irradiance levels of 0–300 μE m^{-2}s^{-1}. At the end of the incubation the water was sampled for excreted dissolved organic carbon (DOC), and the animal was homogenized in unlabelled sea water. Samples of 0.5 ml from the supernatant, following centrifugation for 2 min 1200 pm on a Sorvall RC2-B centrifuge were taken in triplicate. The pellet containing the zooxanthellae was suspended in filtered sea water and 0.5 ml samples were taken, also in triplicate. The samples from all three fractions: sea water, supernatant and pellet were left overnight acidified to pH 2, and subsequently counted in a Lumax: toluene (30:70) scintillation cocktail on a Lumitron MR-300 liquid scintillation counter.

Translocation was calculated assuming ^{14}C in the supernatant to represent photosynthate translocated to the host, while ^{14}C in the homogenate plus ^{14}C in the pellet were considered as total assimilated label. The ratio of the two was converted to percent translocation (Tc), (Muscatine et al., 1983, 1984). From this percentage and total assimilated carbon the contribution of zooxanthellae to animal respiration (CZAR) was calculated following the procedure outlined by Muscatine et al. (1981).

Construction of the model was based on combining the advantages of three different methodologies thereby avoiding their shortcomings.

Photosynthesis and dark respiration data were obtained by the O$_2$ method, which is more reliable than ^{14}C based approaches (e.g. Porter et al., 1984). The partitioning of assimilated carbon between algae and animal was calculated from the percentage of ^{14}C translocated to animal and photosynthesis as measured by O$_2$ electrode. Then again, the partitioning of photosynthetic products retained by the algae, between their growth and their respiration was calculated from the carbon necessary for the algal population increment. This increment was derived from the mitotic index data.

3. Results

Zooxanthellae are distributed throughout the endoderm of *A. sulcata* (Fig. 2,a and b) and their numbers were linearly proportional to the weight of the host (Fig. 3). Therefore, algal density in the tissue was nearly constant, per unit fresh weight, and ranged $4 - 5.6 \times 10^7$ cells g^{-1}.

The diurnal course of the mitotic index (M.I.) is shown in Fig. 4. It is evident that division rate is mostly synchronized, increasing from 0.8% during
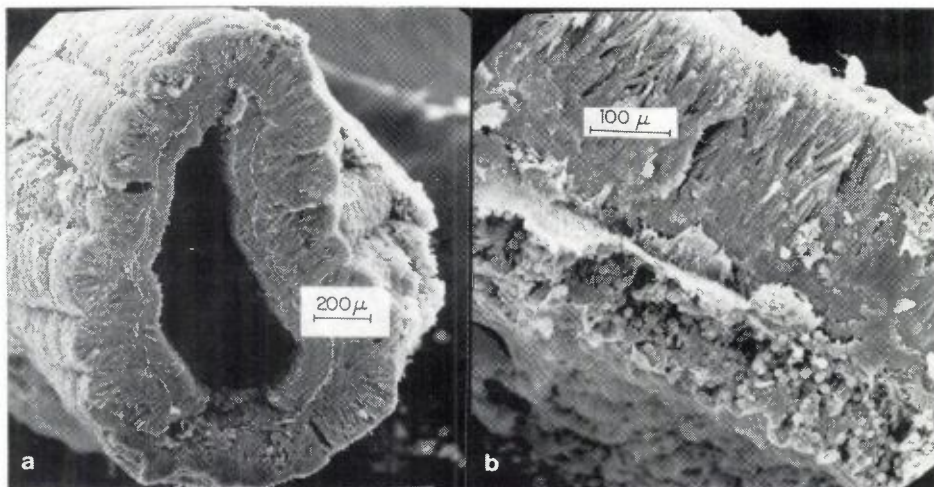
Figure 2(a,b). Transverse scanning electron micrographs through tentacle of
A. sulcata showing zooxanthellae in endoderm surrounding tentacle lumen.
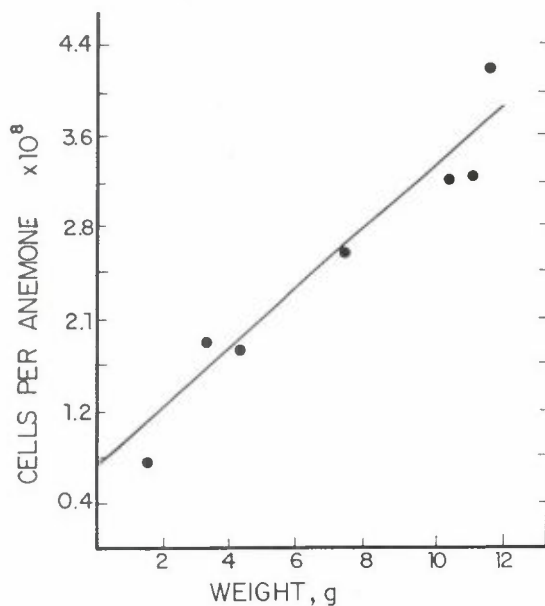

Figure 3. The relation between algal numbers and animal wet weight.

daytime to a peak of 3% around midnight. From these data, duration of cell division (mitosis) was calculated and found to be 15.5 hr and the doubling time (T), 23,45 d. This growth rate and the average algal concentration in the anemone's tissue $(4.5 \times 10^7$ cells $g^{-1})$ result in a daily increment of 1.91×10^6 cells g^{-1}. Assuming 85 pg C cell^{-1} (Muscatine et al., 1984) this addition corresponds to 1.5 cal g^{-1} d^{-1}, as photosynthate ending up as growth in algal biomass.
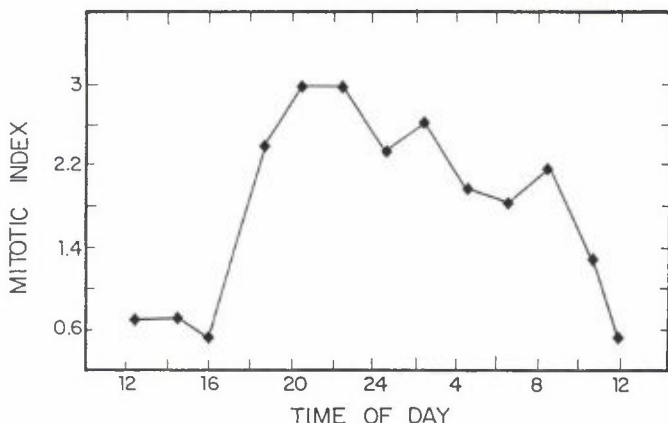

Figure 4. Diel course of changes in mitotic index of *A. sulcata* zooxanthellae.

Dark respiration and photosynthesis of whole anemones

A. sulcata showed a near linear increase in gross photosynthesis between 0 and 200 μE m^{-2}s^{-1}. Above this level maximal, light-saturated photosynthetic rates, P_{max}, of 0.22 μmoles O_2 g^{-1} min^{-1} were attained. At depths of 1–3 m, where *A. sulcata* abounds, 59–90% of subsurface irradiance reaches the anemones, providing on the average around 10 hr a day of saturating irradiance levels — above 200 μE m^{-2}s^{-1}. Under such conditions gross photosynthesis results in 132 μmole O_2 g^{-1} d^{-1} $(= 9.3$ μgO_2 h^{-1} per 10^6 cells) or 14.8 cal g^{-1} d^{-1}. Dark respiration was 115.2 μmole O_2 g^{-1} d^{-1}, utilizing 12.9 cal g^{-1} d^{-1}, thus leaving 14.8–12.9 = 1.9 cal g^{-1} d^{-1} as net productivity, of the whole association. In Table 1 are summarized data showing the partitioning of photosynthetically assimilated ^{14}C among the following fractions: retained in the zooxanthellae, translocated to the animal host, and DOC (dissolved organic carbon), excreted into the water. Anemones, growing in nature at 200 and 1000 μE m^{-2}s^{-1} showed a similar partitioning pattern of ^{14}C among the three examined fractions of nearly 50% translocation and low excretion of DOC.

Table 1. Partitioning of incorporated ^{14}C in freshly collected anemones

Irradiance* during incorporation	Growth* irradiance	Algae	Anemone	DOC
300	1000	49.8%	44.9%	5.9%
	200	46.4%	47.9%	3.7%

* $\mu E\ m^{-2}s^{-1}$

The energy budget of A. sulcata

We present an energy-flow model (Fig. 5) based on results obtained with freshly collected anemones, assumed fed, containing 4.5×10^7 cells g^{-1}, and living at a depth where light-saturated photosynthetic rates are sustained for 10 hr per day. It is evident that under such conditions CZAR exceeds 100% and the algae may amply provide the full carbon needs of the animal for respiration.
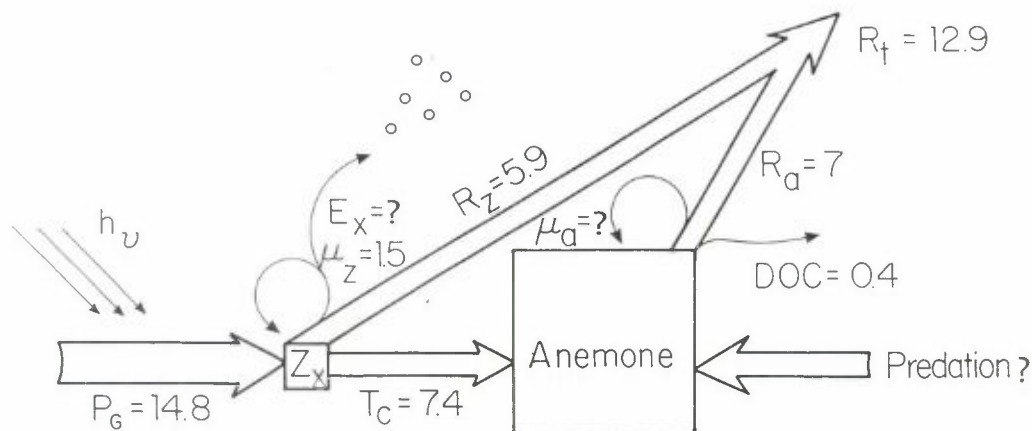

Figure 5. Energy flow in the symbiotic association between zooxanthellae and *A. sulcata* in cal. g^{-1} wet weight d^{-1}.

Effects of starvation on assimilation and translocation

Although the total assimilation rate depends on irradiance level, the distribution among fractions retained, translocated and excreted did not (Table 2).

Table 2. Partitioning of incorporated ^{14}C in anemones starved for 16 days

Irradiance* during incorporation	Algae	Anemone	DOC
50	29.5%	67.5%	3%
100	24%	74.6%	1.5%
300	28%	70.3%	1.7%

* $\mu E\ m^{-2}s^{-1}$

Table 3. Pigmentation and photosynthesis of zooxanthellae

			^{14}C incorporation**	
	Growth*	Pg Chl a	Irradiance during incorporation*	
	irradiance	cell	100	300
Anemones Starved for 16 days	30	2.596	2030	4440
Anemones starved for 7 days	30	3.024	5500	8690
Freshly collected	1000	1.24	14950	10350
anemones	200	1.69	9150	11560

* $\mu E\ m^{-2}s^{-1}$

**dpm μg^{-1} Chl a h^{-1}

At all three irradiance levels, 24–29.5% remained in the algae, 67.5–74.6% were translocated and only 1.5-3% were excreted.

Starving for 16 days in the light, did, however, increase percent translocation (Tables 1 and 2). In the starved anemones nearly 70% of assimilated ^{14}C was translocated to the host, whereas in the freshly collected ones, translocation was below 50%. Table 3 shows the decrease in ^{14}C assimilation by anemones starved for 7 and 16 days, against freshly collected controls. The decrease following 16 days starvation when incubated under 100 $\mu E\ m^{-2}s^{-1}$ was much more pronounced ($\times 4.5$) than under 300 $\mu E\ m^{-2}s^{-1}$ ($\times 2.6$).

4. Discussion

Growth rates (μ) of zooxanthellae symbiotic with *A. sulcata* were derived from data on mitotic index. M.I. of zooxanthellae from *A. sulcata* in nature ranged between 0.4 and 3%, which is below the 10.8% reported for *Mastigias* sp. (Wilkerson et al., 1983) but above values (MI$<$ 1%) found in both *Aiptasia pulchella* and *S. pistillata* (Wilkerson et al., 1983). The values found in the present study are very similar to those reported for the temperate anemone *Anthopleura elegantissima* in California and Washington (Wilkerson et al., 1983).

From the M.I. values and the 1.5 hr duration of mitosis (t_d) doubling time for the algae in *A. sulcata* was calculated to be 23.45 d. This doubling rate is far higher than the growth rate of the animal (Janssen and Möller, 1981). Since algal densities in anemones of all sizes (Fig. 2) were nearly the same, a result similar to that reported by Taylor (1969a), we must assume that part of the algal increment is lost either by digestion or by expulsion. Taylor (1969a) reports the presence of damaged algal cells within the anemone, although in a proportion too low to account for the considerable "overproduction" of algae according to our results. Therefore, it seems plausible to us that most of the "excess" algae are expelled into the water while some replace dead or damaged ones. This hypothesis remains to be tested in further work.

Attempts to construct energy budgets for algal-invertebrate mutualistic associations to compare to our own are few (Falkowski et al., 1984). All of them face difficulties when attempting to partition respiratory costs between algae and animals. This problem has been addressed in a number of ways. Fitt et al. (1982) determined dark respiration of freshly isolated zooxanthellae and assumed this value to be the same as that of the algae within the host. It has, however, been suggested that algal respiration within the host differs from that of isolated zooxanthellae (Muller-Parker, 1984; Smith and Muscatine, 1986).

Awareness of these potential problems resulted in alternative approaches. Muller-Parker (1984) estimated animal respiration alone by measuring that of aposymbiotic animals. Such individuals (or colonies in the case of corals) lack major respiratory substrates obtained by translocation from the algae (Muscatine et al. 1981), and, therefore, their respiratory rates may differ from those of their symbiotic counterparts.

The most commonly applied approach assumes that respiratory rates of zooxanthellae and animal partners are proportional to their respective shares of the associations protein (Muscatine et al., 1983, 1984; Falkowski et al.,

1984). The assumption that the algal and animal fractions have the same respiration rates per unit protein has not yet been confirmed. Further experimental confirmation requires measurement of respirationrates of isolated zooxanthellae and, therefore, would reside on the assumption that the isolated algae maintain the same respiratory rates as those within the host tissue.

We attempted to avoid some of these problems by partitioning the gross photosynthesis, measured by O_2 methodology on intact anemones, between algae and animal according to translocation ratios of assimilated C. From the share of assimilated carbon calculated to be retained by the algae, that allocated for algal growth was subtracted. The remainder was assumed to be used up in respiration. Our data place translocation rates from zooxanthellae in fed *A. sulcata* close to the range of values (40–50%) found in green *Hydra* and *Anthopleura elegantissima* (Trench, 1971; Muscatine, 1974). Values close to 100% were reported for other associations; Steen and Muscatine (1984) found 95% in *Zoanthus sociatus* and Muscatine et al. (1983, 1984) and Falkowski et al. (1984) found 96–99% in *Stylophora pistillata*. While the amount of translocated photosynthate was shown in the present study (Table 3) to depend on irradiance level, the percentage translocated did not.

It is noteworthy that starvation increased translocation from 50% in freshly collected animals to 70% in those starved for 16 days. It may be that the starved host releases less nutrients such as nitrogen and phosphorus normally derived in part from digestion of prey, thereby limiting algal growth rate by increasing C:N and C:P ratios. Under such conditions photosynthesis may proceed resulting in enhanced excretion of compounds devoid of P and N (Dubinsky et al., 1984; Falkowski et al., 1984; Muscatine et al., 1983, 1984).

As far as the ability of the zooxanthellae to provide the metabolic requirements of the host, expressed as CZAR (Muscatine et al., 1981), this has been found to range from 34–56% in *Anthopleura elegantissima* (Fitt et al., 1982) to 143% in *Stylophora pistillata* growing at high irradiance levels, and 53%, in the same coral growing in deep shade (Muscatine et al. 1984; Falkowski et al., 1984). In the case of *A. sulcata* the CZAR was found to reach 110% or sufficient to fully cover the energetic needs of the host. This is similar to the 100% reported for *Tridacna gigas* (Fisher et al., 1985) and is above the 34–42% found in *A. elegantissima* (Fitt et al., 1982), 63–69% in *Pocillopora pistillata* and *Fungia scutaria* (Muscatine et al., 1981) but well below high light adapted *S. pistillata*.

It is important to remember, however, that photosynthesis alone cannot supply the nutrients required by both algal and animal partners of the association, especially nitrogen and phosphorus.

These nutrients are derived in part from dissolved inorganic sources in seawater which are taken up by the zooxanthellae and incorporated by them into various compounds which may subsequently become available to the host (D'Elia, 1977; Crossland and Barnes, 1983; Wafar and Devassy, 1985). Probably, of greater importance is the contribution of nutrients originating in prey captured by the animal and upon digestion becoming available to the algae (Johannes et al., 1970; Falkowski et al., 1984).

The dependence of both, algae and animal on prey capture was clearly confirmed in our study as anemones lost weight with starvation, although kept in the light. Furthermore, algal photosynthetic performance also declined upon prolonged starvation, leading eventually to decreases in algal densities and death of both partners.

Our study further underscores the different contributions of algal photosynthesis and animal predatory skills for the growth and survival of *A. sulcata*. Algal photosynthesis provides all the necessary energy for its metabolic needs and allows survival during prolonged intervals between prey capture events. Feeding by the animal is, therefore, insignificant as a carbon and energy source, but indispensable as the main route for nutrients other than carbon, especially in oligotropic waters such as the Eastern-Mediterranean.

Acknowledgements

REFERENCES

Crossland, C.J. and Barnes, D.J. 1983. Dissolved nutrients and organic particulates in water flowing over coral reefs at Lizard Island. *Aust. J. Mar. Freshwater Res.* **34**: 835–844.

D'Elia, C.F. 1977. The uptake and release of dissolved phosphorus by reef corals. *Limnol. Oceanogr.* **22**: 301–315.

Dorselt, D.A. 1984. Oxygen production in the intertidal anemone *Anemonia sulcata. Comp. Biochem. Physiol.* **78**: 225–228.

Dubinsky, Z., Falkowski, P.G., Post, A.F., and Van Nes, U.M. 1987. A system for measuring phytoplankton photosynthesis in a defined light field with an oxygen electrode. *J. Plankton Research* **9**: 607–612.

Dubinsky, Z., Falkowski, P.G., Porter, Z.W., and Muscatine, L. 1984. Absorption and utilization of radiant energy by light and shade adapted colonies of the hermatypic coral *Stylophora pistillata. Proc. R. Soc. Lond. B.* **222**: 203–214.

Edmunds, P.J., and Spencer Davies, P. 1986. An energy budget for *Porites porites* (Scleractinia). *Mar. Biol.* **92**: 339–347.

Falkowski, P.G., Dubinsky, Z., Muscatine, L., and Porter, J.W. 1984. Light and the bioenergetics of a symbiotic coral. *BioScience* **34**: 705–709.

Fisher, C.R., Fitt, W.K., and Trench, R.K. 1985. Photosynthesis and respiration in *Tridacna gigas* as a function of irradiance and size. *Biol. Bull.* **169**: 230–245.

Fitt, W.K., Pardy, K.L., and Littler, M.M. 1982. Photosynthesis respiration and contribution to community productivity of the symbiotic sea anemone *Anthopleura elegantissima.* (Brandt, 1835). *J. Exp. Mar. Biol. Ecol.* **61**: 213–232.

Janssen, J.H. and Möller, H. 1981. Effect of various feeding conditions on *Anemonia sulcata. Zool. Anz. Jena.* **206**: 161–179.

Johannes, R.E., Kunzel, N.T., and Coles, S.L. 1970. The role of zooplankton in the nutrition of some scleractinian corals. *Limnol. Oceanogr.* **15**: 579–586.

Möller, R.H. 1978. Investigations on the feeding ecology of *Anemonia sulcata. Zool. Anz. Jena* **200**: 369–373.

Muller-Parker, G. 1984. Photosynthesis irradiance responses and photosynthetic periodicity in the sea anemone *Aiptasia puchella* and its zooxanthellae. *Mar. Biol.* **82**: 225–232.

Muscatine, L. 1974. Endosymbiosis of cnidarians and algae. In: *Coelenterate Biology.* L. Muscatine and H.M. Lenhoff, eds. Academic Press, New York, pp. 359–395.

Muscatine, L., Falkowski, P.G., and Dubinsky, Z. 1983. Carbon budgets in symbiotic associations. In: *Endocytobiology.* Vol. II. H.Z.A. Schenk and W. Schemmder, eds. Walter de Gruyter and Co., Berlin, pp. 649–658.

Muscatine, L., Falkowski, P.G., Porter, J.W., and Dubinsky, Z. 1984. Fate of photosynthetic fixed carbon in light and shade adapted colonies of the symbiotic coral *Stylophora pistillata. Proc. R. Soc. Lond. B* **222**: 181–202.

Muscatine, L., McCloskey, L.R., and Marian, R.E. 1981. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnol. Oceanogr.* **26**: 601–611.

Porter, J.W., Muscatine, L., Dubinsky, Z., and Falkowski, P.G. 1984. Primary production and photoadaptation in light and shade-adapted colonies of the symbiotic coral *Stylophora pistillata. Proc. R. Soc. Lond. B.* **222**: 161–180.

Schlichter, D. 1978. On the ability of *Anemonia sulcata* (Coelenterata: Anthozoa) to absorb charged and neutral amino acids simultaneously. *Mar. Biol.* **45**: 97–104.

Schick, J.M. and Dykens, J.A. 1984. Photobiology of the symbiotic sea anemone *Anthopleura elegantissima*: photosynthesis, respiration and behavior under intertidal conditions. *Biol. Bull.* **167**: 608–619.

Smith, H.G. 1939. The significance of the relationship between actinians and zooxanthellae. *J. Exptl. Biol.* **16**: 334–345.

Smith, G.J. and Muscatine, L. 1986. Carbon budget and regulation of the population density of symbiotic algae. *Endocyt.C. Res.* **3**: 213–238.

Spencer Davies, P. 1984. The role of zooxanthellae in the nutritional requirement of *Pocillopora eydouxi. Coral Reefs* **2**: 181–186.

Steen, R.G. and Muscatine, L. 1984. Daily budgets of photosynthetically fixed carbon in symbiotic zoanthids. *Biol. Bul.* **167**: 477–487.

Taylor, D.L. 1969a. On the regulation and maintenance of algal number in zooxanthellae coelenterate symbiosis with a note on the nutritional relationship in *Anemonia sulcata. J. Mar. Biol. Assoc. U.K.* **49**: 1057–1065.

Taylor, D.L. 1969b. The nutritional relationship of *Anemonia sulcata* (Pennant) and its dinoflagellate symbiont. *J. Cell Sci.* **4**: 751–762.

Trench, R.K. 1971. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. I. The assimilation of photosynthetic products of zooxanthellae by two marine coelenterates. *Proc. R. Soc. Lond. B* **177**: 225–235.

Tytler, E.M. 1981. The contribution of zooxanthellae to the energy requirements of the sea anemone *Anemonia sulcata*. Ph.D. thesis, University of Glasgow. 105 pp.

Tytler, E.M. and Spencer Davies, P. 1984. Photosynthetic production and respiratory energy expenditure in the anemone *Anemonia sulcata* (Pennat). *J. Exp. Mar. Biol. Biol. Ecol.* **81**: 73–86.

Tytler, E.M. and Spencer Davies, P. 1986. The budget of photosynthetically derived energy in the *Anemonia sulcata* (Pennat) symbiosis. *J. Exp. Mar. Biol. Ecol.* **99**: 257–269.

Wafar, M.V.M. and Devassy, V.P. 1985. Nitrogen uptake by phytoplankton and zooxanthellae in a coral atoll. *Proc. of the Fifth International Coral Reef Congress* **6**: 24–37.

Wilkerson, F.P., Muller-Parker, G., and Muscatine, L. 1983. Temporal patterns of cell division in natural populations of endosymbiotic algae. *Limnol. Oceanogr.* **28**: 1009–1014.

Zamer, W.Z. and Shick, J.M. 1987. Physiological energetics of the intertidal sea anemone *Anthopleura elegantissima*. *Mar. Biol.* **93**: 481–491.