

**A COMPARISON OF THE GROWTH RATES OF ZOOXANTHELLAE  
AND ANIMAL TISSUE IN THE RED SEA  
CORAL *STYLOPHORA PISTILLATA***

**COMPARAISON DES TAUX DE CROISSANCE DES ZOOXANTHELLES  
ET DES TISSUS ANIMAUX CHEZ LE SCLERACTINIAIRE  
DE MER ROUGE *STYLOPHORA PISTILLATA***

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**ABSTRACT**

Of the net carbon fixed daily by zooxanthellae in the Red Sea coral *Stylophora pistillata*, more than 95% is translocated to the host animal tissue. Of that amount, a fraction is respired by the animal, satisfying 100% of its maintenance respiration needs. The remainder is potentially available for assimilation. The percent contribution of this fraction to animal growth is not easily computed because of the difficulty of measuring coral animal tissue growth rates. From a large data set on mean geometric radius of *S. pistillata* vs. time, we established corresponding surface areas v. time, and knowing the standing stock of animal tissue per unit surface area, were able to calculate the specific growth rate of animal tissue. From these data, the contribution of translocated carbon to animal growth was calculated. Values will be presented and their implications with respect to zooxanthellae expulsion, digestion, and other losses from corals will be discussed.

**. RESUME**

Du carbone net, fixé quotidiennement par les zoanthaires du corail de Mer Rouge *Stylophora pistillata*, plus de 95% provient des tissus de l'animal hôte. De cette quantité, une fraction est reprise par l'animal, satisfaisant 100% de ses besoins respiratoires de maintenance. Le reste est potentiellement disponible pour l'assimilation. Le pourcentage de la contribution de cette fraction à la croissance de l'animal n'est pas facilement évalué à cause des difficultés de mesure des taux de croissance des tissus de l'animal. A partir de nombreuses données sur les moyennes géométriques des rayons de *S. pistillata* au cours du temps, il a été établi des surfaces correspondantes au cours du temps et connaissant la biomasse des tissus animaux par unité de surface, il a été possible de calculer le taux de croissance des tissus animaux. A partir de ces données, la contribution du carbone apporté à la croissance de l'animal a été calculée. Les valeurs sont présentées et leurs implications par rapport à l'expulsion des zooxanthelles, la digestion et autres pertes chez les coraux sont discutées.

## INTRODUCTION

The association of corals and zooxanthellae is impressively constant. The algae not only inhabit all reef-building species but also occur in fairly predictable population densities. These range from 0.6 to  $8.5 \times 10^6$  cells  $\text{cm}^{-2}$ , depending on species and habitat depth (see for example Drew, 1972; Dustan, 1979; Lasker, 1981; Porter et al. 1984; Davies, 1984; McCloskey and Muscatine, 1984; Meyer and Schultz, 1985).

Of considerable interest is the means by which the zooxanthellae population density is maintained in a given coral species. Obviously, the coral animal neither outgrows the symbiotic algae nor is overgrown by them. It therefore can be hypothesized that if a constant zooxanthellae population density is to be maintained, then on the average, the in situ specific growth rate of the zooxanthellae ( $u_z$ ) must be equal to or greater than the specific growth rate of the coral animal tissue ( $u_a$ ), i.e.,

$$u_z \geq u_a.$$

The purpose of this paper is to describe a test of this hypothesis in which independent measurements of  $u_z$  and  $u_a$  for a given coral species are compared. Whereas an estimate of  $u_z$  is easily obtained (see Methods), the estimation of  $u_a$  is more difficult. The reasons for this are outlined by Lewis (1981).  $u_a$  is, in effect, a measure of coral secondary production, estimated in only a few studies (see Lewis, 1981; Davies, 1984; Meyer and Schultz, 1985). Davies (1984) estimated the tissue growth rate of the Pacific coral Pocillopora eydouxi from direct measurement of skeletal growth rate, knowledge of the ratio of skeletal weight to tissue weight, and the assumption that an increment of skeletal growth is accompanied by an increment of animal tissue growth. Similarly, assuming that a unit increase in skeletal surface area is accompanied by a unit increase in tissue biomass, we have attempted to estimate  $u_a$  for the Red Sea coral Stylophora pistillata.

In addition to testing the foregoing hypothesis, the estimation of  $u_a$  is useful in another context. Of the net C fixed daily by the zooxanthellae in S. pistillata, about 99% is translocated to the host animal. In shallow water specimens, translocated C can supply 100% or more of the daily carbon requirement for animal respiration (Muscatine et al. 1984). Any surplus translocated carbon may be used for animal growth. Thus, with knowledge of  $u_a$ , we can evaluate the potential contribution of zooxanthellae translocated carbon to animal growth.

## METHODS

All observations were made in the field, periodically from 1973 to 1982, on Stylophora pistillata (Esper), a dominant coral in the Gulf of Eilat (cf. Loya, 1976).

Specific growth rate of zooxanthellae in S. pistillata was calculated by a method described by Wilkerson et al. (1983; see also Muscatine et al. 1984), such that, for asynchronous populations,

$$u_z = 1/t_d \ln(1 + f) \quad (1)$$

where  $t_d$  is the duration of cytokinesis and  $f$  is the average daily mitotic index, both

estimated as described by Wilkerson et al. (1983).

Specific growth rate of animal tissue was calculated as follows. Loya (1976) and Loya (unpublished) established the relationship between colony size and age for S. pistillata. Colony size was characterized by mean geometric radius ( $\bar{r}$ ), a function of colony length ( $l$ ), width ( $w$ ), and height ( $h$ ), where

$$\bar{r} = 1/2 (lwh)^{1/3} \quad (2)$$

From measurements of 184 colonies every 2-3 months over a 2.5 year period the relationship between age and size was established, where

$$\text{age (years)} = (\bar{r})(0.827 + 0.049) \quad (3)$$

The relationship between  $\bar{r}$  and surface area for S. pistillata was established empirically by McCloskey and Muscatine (1984) for nine shallow water colonies spanning a modest size range as

$$sa = 1.789 \bar{r}^{2.729} \quad (4)$$

Surface area was measured by a dye elution technique (McCloskey and Muscatine, unpublished) indexed to S. pistillata skeleton standards whose surface area was determined with the aluminum foil technique (Marsh, 1970).

On the assumption that an increase in surface area with age is accompanied by a corresponding increase in tissue biomass, it was then possible to calculate the surface area specific growth rate as follows. Knowing the age at  $\bar{r}$  (from Eqn. 3), one may calculate  $\bar{r}$  at age plus one day by the expression

$$\bar{r} + 1 \text{ day} = \bar{r}(\text{age} + 1 \text{ day})\text{age}^{-1} \quad (5)$$

The surface areas at  $\bar{r}$  and  $\bar{r} + 1 \text{ day}$  are then calculated by Eqn. (4), and the daily surface area-specific growth rates ( $u_a$ ) obtained by

$$u_a = [(sa_{+1 \text{ day}} - sa) sa^{-1}] \text{day}^{-1} \quad (6)$$

where  $sa$  and  $sa_{+1 \text{ day}}$  are surface areas at  $\bar{r}$  and  $\bar{r} + 1 \text{ day}$  respectively. The surface area specific weight of carbon added daily as animal tissue growth ( $C_{\text{req}}$ ) is simply

$$C_{\text{req}} = u_a \cdot C \quad (7)$$

where  $C$  is a constant for carbon per unit surface area.

Translocated carbon available for growth of animal tissue (i.e. any carbon remaining after supplying the daily requirement for animal respiration), was calculated from data for S. pistillata given by McCloskey and Muscatine (1984, Tables 1 - 5) from the expression.

$$C_{\text{avail}} = (P_{z\text{net}} \cdot T) - R_a \quad (8)$$

where  $P_{z\text{net}}$  = net carbon produced,  $T$  = fraction of  $P_{z\text{net}}$  translocated, and  $R_a$  = carbon respired by the animal tissue.

The average carbon content of coral tissue was taken as  $522.1 \pm 7.63 \text{ mg C} \cdot \text{g dry wt}^{-1}$  (Lewis, 1981). From data on surface area and tissue dry weight of corals from Barbados (Lewis, 1981) and Guam (Davies, 1984), the calculated average C content per unit surface area of about 10 species of imperforate corals was  $2.70 \pm 1.45 \text{ mg C cm}^{-2}$ .

## RESULTS

The specific growth rate ( $u_z$ ) for shallow water (light adapted) zooxanthellae in S. pistillata is  $0.013 \text{ d}^{-1}$  (Muscatine et al. 1984).

The specific growth rates for animal tissue, as well as the parameters used to calculate them are shown in Table 1. Values of  $u_a$  range from  $0.0014$  to  $0.0047 \text{ d}^{-1}$ , with smaller colonies having higher specific growth rates of animal tissue than larger colonies. It is evident that  $u_z$  is consistently greater than  $u_a$ , ranging from about 3-fold in the smaller, faster growing colonies, to about 9-fold in the larger, slower growing colonies.

Table 1. Growth parameters for light-adapted Stylophora pistillata.

$\bar{r}$ (cm)	age (yrs)	$s_a$ ( $\text{cm}^2$ )	$s_{a+1}$ day ( $\text{cm}^2$ )	$u_a$ ( $\text{d}^{-1}$ )	$C_{\text{required}}$ ( $\mu\text{g cm}^{-2}\text{d}^{-1}$ )	$C_{\text{available}}$ ( $\mu\text{g cm}^{-2}\text{d}^{-1}$ )
1.93	1.596	10.75853	10.80900	.004691	12.726	167.91
4.13	3.415	85.77924	85.96715	.002191	5.927	66.79
4.26	3.523	93.34968	93.54792	.002124	5.746	76.23
4.47	3.696	106.44922	106.66465	.002024	5.475	83.26
4.49	3.713	107.75401	107.97111	.002015	5.451	120.35
4.60	3.804	115.11155	115.33792	.001967	5.320	81.45
4.94	4.085	139.84034	140.09641	.001831	4.953	77.30
5.20	4.300	160.85105	161.13086	.001740	4.705	65.01
6.51	5.383	296.96800	297.38059	.001389	3.756	107.15

Table 1 also shows that the C required for growth ranged from 12.7 to  $3.8 \mu\text{g C cm}^{-2} \text{ d}^{-1}$ , small corals tending to have higher growth rates than large corals. In contrast, C available (from translocation) for growth of animal tissue ranged from 65 to  $167 \mu\text{g C cm}^{-2} \text{ d}^{-1}$  (McCloskey and Muscatine, 1984). Thus, the C available is consistently in excess of the C required for growth, irrespective of coral colony size. As a first approximation, it appears that all of the C required for S. pistillata animal growth (as well as respiration) can potentially be supplied by translocation.

### Discussion

The results of independent measurements of  $u_z$  and  $u_a$  reveal that  $u_z$  for zooxanthellae from S. pistillata is consistently greater than  $u_a$  for the host animal tissue. The differences range from 3-fold in small, faster growing colonies to 9-fold in larger, slower growing colonies. Since the zooxanthellae apparently are growing faster than the host, there must be mechanisms for maintaining a constant population density. Such mechanisms may include expulsion and/or digestion of "excess" zooxanthellae. In a preliminary study, Hoegh-Guldberg et al. (ms. submitted) found that relatively few zooxanthellae are expelled from S. pistillata under field conditions. This observation focuses attention on digestion as a regulatory mechanism for controlling population density in S. pistillata. Digestion of symbiotic algae has been investigated in a range of algae-invertebrate associations (see for example O'Brien, 1980; Hohman et al. 1982; Fitt and Trench, 1983; Colley and Trench, 1985), but remains unstudied in corals.

A growth rate of  $0.013 \text{ d}^{-1}$  is the lowest yet measured for zooxanthellae from corals, and may account, in part, for the very low observed rate of expulsion of zooxanthellae from S.

pistillata. In contrast,  $u_z$  for corals from Jamaica range from  $0.04 \text{ d}^{-1}$  (Montastrea annularis) to  $0.23 \text{ d}^{-1}$  (Dendrogyra cylindrus) (Wilkerson et al., unpublished). In corals with such rapidly growing populations of zooxanthellae, the regulation of population density may be more dependent on expulsion.

The magnitude of the difference between  $u_z$  and  $u_a$  depends on several assumptions. First,  $u_z$  was derived from zooxanthellae from a single large colony (s.a. =  $320 \text{ cm}^2$ ; Porter et al. 1984). We do not know if  $u_z$  is constant or variable with colony size (age). Smith (1984) has shown that zooxanthellae division frequency in the sea anemones Aiptasia pallida

and A. tagetes is independent of polyp size. However, in Aulactinia stelloides, an anemone with zooxanthellae confined largely to the oral disk and tentacles, division frequencies in juveniles are almost double those in adults (Smith, 1984 and ms. submitted). Therefore, if  $u_z$  in S. pistillata varies with colony age, its value is likely to be greater in smaller colonies. A higher zooxanthellae growth rate in small corals would reduce the amount of C available for translocation. Application of our value of  $u_z$  as a constant would tend to err on the conservative side so that differences may be larger than those we observed.

In the calculation of  $u_z$  we assumed  $t_d = 11$  hours (Wilkerson et al. 1983). Since the relationship between  $u_z$  and mitotic index is logarithmic, then at a mitotic index of 1%, values of  $t_d$  greater than 6 hours will not significantly affect the computation of  $u_z$ . If  $t_d$  for zooxanthellae in S. pistillata is less than 6h, the magnitude of  $u_z$  will increase and the difference between  $u_z$  and  $u_a$  would again be larger than those reported here.

The surface area specific growth rates of S. pistillata animal tissue ranged from  $0.0047$  to  $.0014 \text{ d}^{-1}$ , with a mean of about  $0.0022 \text{ d}^{-1}$ . These are in general agreement with the value of  $0.0017 \text{ d}^{-1}$  calculated for Pocillopora eydouxi from Guam from data of Davies (1984), and a mean of  $0.0041 \text{ d}^{-1}$  for 6 species of corals from Barbados (Lewis, 1981). This general set of values represents surface area doubling times of about 6 - 7 months in average size colonies of S. pistillata.

The C required daily for growth of animal tissue is relatively substantial in small colonies but much less in larger colonies. In contrast the C available from translocation is well in excess of these requirements. Any remaining C is presumably available for release as DOC. Although McCloskey and Muscatine (1984) did not assess DOC release by S. pistillata, it

was detected and quantified in a companion study (Muscatine et al. 1984). In that case light and shade-adapted *S. pistillata* released 6% and 50%, respectively, of the net carbon fixed daily by zooxanthellae as DOC. Unfortunately, in that study, surface area was measured by the aluminum foil technique, so the data cannot confidently be compared with those of McCloskey and Muscatine (1984). Nevertheless, if values of carbon required for growth ( $C_{req}$ ) are subtracted from  $P_{znet}$  (from McCloskey and Muscatine, 1984, Table 2) 26 - 52% of the net carbon fixed is available for release as DOC. The occurrence of DOC release of this magnitude by corals has been observed and discussed by Crossland et al. (1980a; 1980b), Davies (1984) and Muscatine et al. (1984).

Of considerable interest is the way in which the various parameters in Table 1 change in relation to the size of the colony. Loya (1976) recognized the difference in growth rates of small vs. large colonies of *S. pistillata*. The data presented here reflect these differences at the level of animal tissue growth rate. Thus as indicated by Smith (1985), it seems that ontogenetic variation poses yet another facet to consider in studies of coral physiology.

Although our data set consists of a small number of observations on colonies representing a modest size range, the fortuitous inclusion of one small and one large colony has prompted us to explore the relationship between surface area and specific growth rate. Such a relationship is depicted in Fig. 1, and reveals that the parameters are related by a power function where  $\log u_a = \log 0.01125 + (-0.367) \log sa$  ( $r^2=1.00$ ).

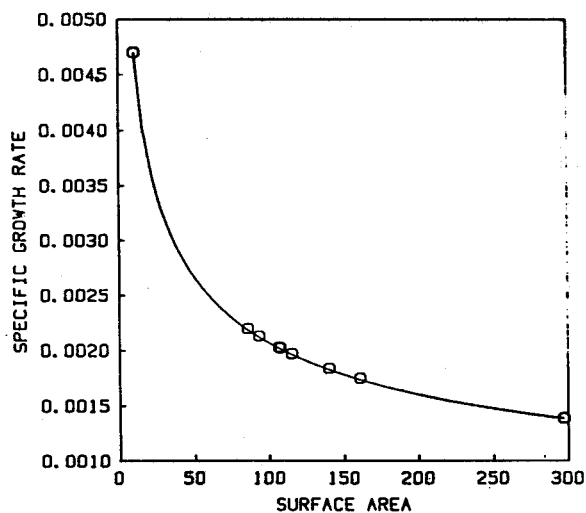


Fig. 1 Specific growth rate ( $u_a$ ) of *S. pistillata* animal tissue as a function of surface area.

In summary, independent measurements of zooxanthellae and animal tissue specific growth rates reveal that the zooxanthellae grow faster than the host. This, of necessity raises questions about how the faster-growing population of algae are regulated. In addition, the data show that carbon translocated from zooxanthellae can satisfy the daily requirement of the coral not only for respiration but also for assimilation and growth. Finally, data are presented which could be interpreted as indicative of substantial export of DOC from a coral.

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