

**PHOTOSYNTHESIS, RESPIRATION, AND CONTRIBUTION
TO COMMUNITY PRODUCTIVITY OF THE SYMBIOTIC
SEA ANEMONE *ANTHOPLEURA ELEGANTISSIMA* (Brandt, 1835)**

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Abstract: The photosynthetic and respiratory physiology of the sea anemone *Anthopleura elegantissima* (Brandt, 1835), living in association with the endosymbiotic dinoflagellate *Symbiodinium* (= *Gymnodinium*) *microadriaticum* Freudenthal, was investigated in anemones that were fed and starved for 2 wk under laboratory conditions or newly collected from the intertidal zone. The photosynthetic performances of this association were similar to those of marine phytoplankton and intertidal seaweeds. Light saturation for *Anthopleura elegantissima* occurred between 125–350 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and inhibition was not observed at intensities up to 1550 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Weight-specific gross photosynthetic rates decreased with increasing anemone size and were similar for fed, starved, and newly collected anemones. Gross photosynthetic rates were positively correlated with chlorophyll *a* content and number of zooxanthellae. Weight-specific respiration rates also decreased with increasing anemone size. Fed anemones respired at rates about twice those of starved anemones and *A. elegantissima* measured within 10 h of collection had respiration rates similar to starved anemones. Gross photosynthesis to respiration (P : R) ratios were a function of the nutritional state of the anemones, typically ranging from 2.0 to 3.0 for starved anemones, but seldom over 1.0 for fed anemones. Estimates of the relative contribution of carbon from the zooxanthellae to the host (animal) respiratory carbon depended on host nutritional state, averaging $\approx 13\%$ for fed anemones and 45% for starved or newly collected anemones. Photosynthetic rates were similar to temperate intertidal seaweeds having low surface to volume ratios. Calculations of the contributions of anemones to intertidal gross primary production (48–151 $\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) fall within the range of temperate intertidal seaweed populations.

INTRODUCTION

Most studies addressing productivity of algal symbioses have dealt with invertebrate-zooxanthellae associations found on coral reefs (see McCloskey *et al.*, 1978; Muscatine, 1980 for reviews). While the ecological and geological importance of these associations to hosts such as reef-building corals is unquestionable, there are other animals that contain endosymbiotic zooxanthellae living in temperate waters which may also be important in the productivity as well as the structure of benthic communities (e.g., see

Taylor, 1968; Kevin & Hudson, 1979; Szmant-Froelich & Pilson, 1980; Taylor & Littler, in press). One such host is the anemone *Anthopleura elegantissima*, found intertidally on the west coast of North America from British Columbia to northern Mexico (Hand, 1955). *A. elegantissima* is one of the most abundant invertebrates in the southern California rocky intertidal (Littler, 1980a), being second highest in percent cover (3%) to the barnacle *Chthamalus fissus* Darwin (4%) and second highest in biomass (24 g dry wt · m⁻²) to the mussel *Mytilus californianus* Conrad (49 g dry wt · m⁻²). *Anthopleura elegantissima* occurs in clonal aggregations as well as having a solitary form (Francis, 1979), and is typically found in association with the dinoflagellate *Symbiodinium* (= *Gymnodinium*) *microadriaticum* Freudenthal. These endosymbiotic algae translocate photosynthetic products to the host (Trench, 1971a,b,c) which contribute to structural components and metabolism (Muscatine & Cernichiari, 1969; Smith *et al.*, 1969; Trench, 1971a; Fitt & Pardy, 1981). Some northern populations of *Anthopleura elegantissima* may contain an unidentified green alga in addition to or instead of zooxanthellae (Muscatine, 1971; O'Brien, 1978, 1980).

In the present study we document the photosynthetic performance of *A. elegantissima* (Brandt, 1835) that contained only zooxanthellae, by measuring respiratory and photosynthetic rates of different sized animals. In addition, we address the role of nutritional state of the host in the respiratory physiology and productivity of *A. elegantissima*. Finally, we compare the contribution of *A. elegantissima* to total intertidal productivity with that of common intertidal seaweeds, and interpret its role in view of factors influencing patterns of distribution, abundance, and productivity.

MATERIALS AND METHODS

EXPERIMENTAL ORGANISMS

Specimens of *A. elegantissima* were collected intertidally from Campus Point, University of California, Santa Barbara. All individuals used in each experiment were from the same clone and contained endosymbiotic zooxanthellae. For 2 wk preceding experiments individual anemones were maintained in the laboratory in Petri dishes in running sea water on a 14:10 h light:dark photoperiod at light intensities of 10–17 $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. All maintenance and experiments were performed at $20 \pm 1^\circ\text{C}$, the ambient ocean temperature at the time of collection. Half of the anemones were fed daily to repletion with frozen shrimp while half were starved. In some experiments *A. elegantissima* were collected at dusk and maintained in the dark in running sea water for 7 h prior to the experiments. Experiments on these freshly collected animals were completed within 24 h of collection.

GAS EXCHANGE MEASUREMENTS

The photosynthesis–light intensity (PI) response was determined by two methods. For fed and starved anemones maintained in the laboratory, oxygen and carbon-dioxide

flux were measured simultaneously in the filtered sea water surrounding an individual anemone enclosed in a 0.6-l Plexiglas chamber containing a magnetic stirring bar. Oxygen flux was recorded continuously on a chart recorder from an IBC (Model No. 160) differential oxygen analyzer. Carbon-dioxide exchange was determined by measuring pH with an Orian (model 801A) Ionanalyzer using standard curves described by Beyers (1970). In practice, individual anemones were preincubated in the chamber for 15 min in the dark before respiration measurements were made. Photosynthetic determinations followed the respiration measurements. Light from an incandescent floodlight was filtered through neutral density filters to obtain intensities ranging from 0 to $1160 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. The light intensity was measured at the top of the anemone with a Lambda Quantum Meter. Photosynthetic rates were determined in steps at increasing light levels, each measurement taking 5 to 15 min. An individual anemone generally spent < 2 h in the chamber and at no time did oxygen or carbon dioxide concentrations change $> 25\%$ from initial values, most experiments varying $< 10\%$. A control chamber without an anemone was monitored simultaneously to correct for the biological oxygen demand in the sea water. This procedure was followed on four fed and four starved anemones. Fed animals were analyzed 12–24 h after feeding. The photosynthetic quotient (PQ), defined as the ratio of oxygen produced to carbon dioxide consumed during photosynthesis was calculated for each anemone at each light intensity tested.

In the second method, four *A. elegantissima* were collected intertidally and analyzed within 24 h by the Winkler titration method (Strickland & Parsons, 1972). Individual anemones in 125-ml stoppered flasks were exposed to natural illumination at different times of day for periods ranging from 0.5 to 2 h. Flasks were shaken immediately before sampling. Changes in oxygen concentration were determined by subtracting oxygen levels in control flasks containing only sea water from the experimental flasks.

Weight-specific gas exchange was measured on nine fed and eight starved anemones plus 12 newly collected anemones in total darkness and in natural sunlight (saturating intensities ranging from $700\text{--}1500 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ by the Winkler titration method). Individual anemones were incubated at $20 \pm 1^\circ\text{C}$ in 250-ml flasks for 0.5 to 2 h between 0900 and 1500. Oxygen concentrations changed $< 25\%$, with most experiments varying $< 10\%$. The P : R ratio, defined as the ratio of gross photosynthesis to respiration, was calculated for each anemone.

The I_k value (Yentsch & Lee, 1966) was used to compare photosynthesis light response curves. This value corresponds to the light intensity occurring at the intersect of the light-dependent portion of the curve with the level of maximum photosynthesis.

All respiratory and photosynthetic rates were standardized to submerged weight and to surface area. Submerged weight (also known as reduced weight) was determined by weighing each anemone while it was submerged in sea water (see Muscatine, 1961; Sebens, 1980). Since the zooxanthellae are concentrated in the tentacles and oral disk region, a two-dimensional surface area was calculated from the radius of each anemone (distance from center of oral disc to tip of expanded tentacles).

CHLOROPHYLL DETERMINATION

Twenty-three *A. elegantissima*, were collected for chlorophyll analysis. After 2 wk of daily feeding or starvation, submerged weights were measured and chlorophyll *a* content determined. Each anemone was cut into small pieces with a razor blade and macerated in a tissue grinder with 90% acetone containing a few mg of MgCO₃. Pigments were extracted in closed containers in the dark at 4 °C under nitrogen gas for 12 to 24 h. Samples were subsequently re-homogenized with a tissue grinder, centrifuged at 1500 × *g*, and absorbance of the supernatant measured at 630 and 663 nm using a Varian Techtron 634 spectrophotometer. Chlorophyll *a* concentrations were calculated by the method of Jeffrey & Humphrey (1975). The remaining pellet was extracted an additional 48 h with fresh 90% acetone and never yielded > 5% of the total chlorophyll *a* found in the first extraction; the whiteness of the pellet indicated that most of the chlorophyll was extracted.

Numbers of zooxanthellae per animal were measured from samples of homogenates of four anemones. Replicate counts of symbionts were made using a hemocytometer. Amount of chlorophyll *a* was determined as described above. Two fed anemones (0.01 and 0.13 g submerged weight) and two starved anemones (0.01 and 0.10 g submerged weight) were analyzed.

CONTRIBUTION OF TRANSLOCATED ZOOXANTHELLAE CARBON TO ANIMAL RESPIRATORY CARBON

Percent contribution of translocated zooxanthellae carbon to the host (animal) respiratory demand (CZAR) was calculated by the method of Muscatine & Porter (1977) and Muscatine *et al.* (1981). Briefly,

$$\frac{\left(\begin{array}{cc} \text{total carbon} & \text{carbon respired} \\ \text{assimilated by} & \text{by zooxanthellae} \\ \text{zooxanthellae/day} & \text{during daytime} \end{array} \right) (\% \text{ translocation})}{(\text{carbon required by animal/day})} \times 100.$$

For our calculations, the following assumptions were made and values used (see discussions of Muscatine & Porter, 1977; McCloskey *et al.*, 1978; Muscatine, 1980; and Muscatine *et al.*, 1981; for analysis of these and other assumptions used in CZAR calculations).

(1) Since it is not possible to measure respiration of zooxanthellae in the light while they are in the host, the amount of respiration is estimated as a proportion of the total symbiotic anemone's dark respiration based on biomass ratios. For *A. elegantissima*, zooxanthellae : animal protein biomass ratios range from 0.03 to 0.19 (McKinney, 1978). However, other biomass ratios for *A. elegantissima* go as low as 0.0033 (Muscatine, 1974). A biomass ratio of 0.09 was used in the calculations, based on the mean value obtained by McKinney (1978).

(2) A minimum estimate of 10 h of saturation photosynthesis per day was chosen. The actual daily period of maximum photosynthesis for field animals would depend on weather conditions and the season.

(3) Oxygen exchange rates were converted to equivalent carbon units assuming $PQ = 1$ and $RQ = 1$ (see Fitt & Pardy, 1981; Muscatine *et al.*, 1981; this study).

(4) Respiration in the dark = respiration in the light.

(5) Estimates for in vitro translocation of fixed ^{14}CO by zooxanthellae isolated from *A. elegantissima* range from 40–50% (Trench, 1971b). A conservative value of 40% was arbitrarily selected.

PRODUCTIVITY

Percent cover data from 10 different locations in southern California averaged from four seasonal assessments in 1975–1976 for *A. elegantissima*, intertidal seaweeds, and sand cover were tabulated from Littler (1977). Data from two of these sites, Coal Oil Point near Santa Barbara, and Dutch Harbor on San Nicolas Island, were selected for detailed analyses of productivity of *A. elegantissima* and the intertidal seaweeds present because this anemone was abundantly represented at these two locations. Percent cover data were converted to dry weight with site-specific regression data (Littler, 1977, 1979). Where no regression data were available for a species at a particular study site, data from another site or from a morphologically similar seaweed was used. Gross productivity of each species was calculated by multiplying the dry weight of their standing stocks by individual photosynthetic rates per unit dry weight from Littler & Murray (1974a) and P. Taylor (pers. comm.). Where no photosynthetic data were available for a given species, the mean photosynthetic rate ($2.2 \text{ mg C} \cdot \text{g dry wt}^{-1} \cdot \text{h}^{-1}$) was used. Gross production rates for each species were subsequently converted to percentages of the total amount of carbon fixed for the entire community of primary producers.

RESULTS

PHOTOSYNTHESIS—LIGHT INTENSITY RESPONSES

Representative PI curves for oxygen exchange are given in Fig. 1 for two *A. elegantissima* of similar size, one fed and one starved. Other fed and starved animals had similar PI responses. Anemones measured within 24 h of collection had PI curves similar to those of starved anemones maintained in the laboratory. Maximum photosynthesis occurred above $125\text{--}350 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. I_k values were 120 ± 40 (mean \pm SD) $\mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ($n = 8$). There were no measurable differences in the I_k values between fed, starved, and newly collected anemones. Photoinhibition was not evident up to intensities of maximum natural illumination ($2000 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ in air = $1550 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ at the surface of the anemone in a flask in 10 cm of sea water).

Carbon dioxide values were either identical or slightly less than the oxygen values at each light intensity. The PQ varied between 0.95 and 1.30 in the range of light intensities examined ($20\text{--}1160 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$). There was more variability in the PQ, especially towards higher values, below saturation; whereas above saturation the PQ stabilized between 0.95 and 1.15.

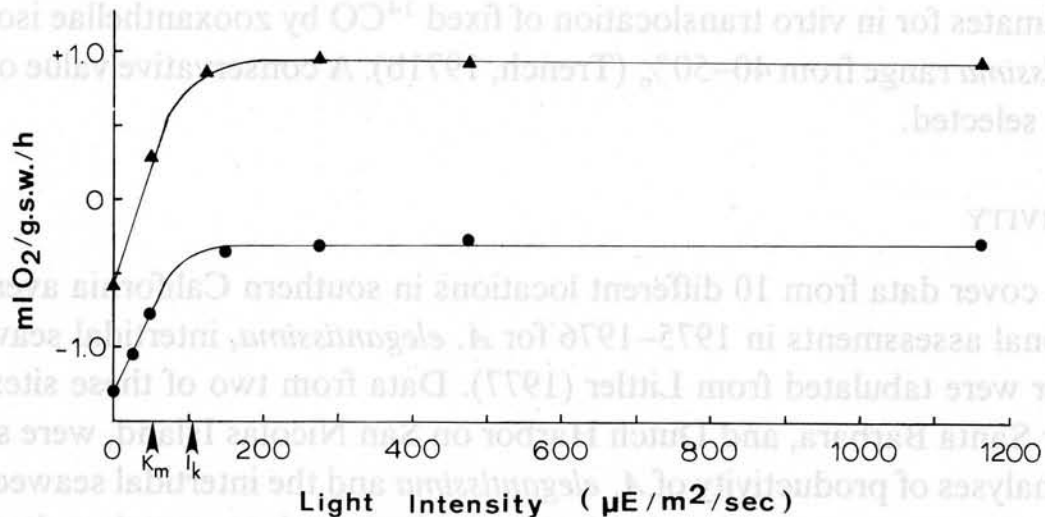


Fig. 1. Photosynthetic response of two similarly sized ($0.08\text{--}0.09$ g submerged wt) *Anthopleura elegantissima* to different light intensities after 2 wk of daily feeding (●) or starvation (▲).

TABLE I

P : R ratios (gross photosynthesis : respiration) of *Anthopleura elegantissima* and percent contribution of zooxanthellae translocated carbon to daily host respiration carbon requirements (CZAR): P : R and CZAR were determined for fed and starved anemones after maintenance in the laboratory for 2 wk and for "field" anemones < 12 h after their collection.

	P : R	CZAR (%)
Fed	0.93 ± 0.23 (8)	12.9 ± 3.2 (8)
Starved	2.55 ± 0.57 (9)	42.8 ± 9.4 (9)
Newly collected	2.78 ± 0.61 (12) n.s.	46.6 ± 10.1 (12) n.s.

* $P < 0.001$; t -test. n.s., $P > 0.05$.

Fig. 1 also illustrates a major difference in the photosynthetic response of fed and starved symbiotic anemones. Fed anemones seldom showed positive net photosynthesis due to high respiration. In comparison, starved and newly collected anemones always produced more oxygen at P_{max} than they consumed in the light (Table I). Starved and newly-collected anemones exhibited significantly greater ($P < 0.05$, t -test) P : R ratios than those of their fed counterparts.

PHOTOSYNTHESIS

Weight-specific maximum gross photosynthetic rates were allometric; smaller anemones produced more oxygen per unit weight than larger anemones (Fig. 2b). There was

TABLE II

Regression analysis of rates of oxygen consumption ($\text{ml O}_2 \cdot \text{g submerged} \cdot \text{wt}^{-1} \cdot \text{h}^{-1}$) and chlorophyll *a* ($\text{mg Chl } a \cdot \text{g submerged wt}^{-1}$) by *Anthopleura elegantissima* of different submerged weights (g) for log transformed data ($\log y = b(\log x) + \log a$): conditions as in Table I.

Condition	<i>n</i>	Slope (<i>b</i>)	SE	Intercept ($\log a$)	<i>R</i> ²		
					Correlation coefficient	Comparison of slopes	Comparison of intercepts
Respiration							
Field	12	-0.460	0.092	-0.627	0.85**	n.s.	n.s. *** ***
Starved	9	-0.428	0.197	-0.606	0.64*		
Fed	8	-0.446	0.113	-0.263	0.85**		
Photosynthesis (gross)							
Starved	9	-0.324	0.125	-0.079	0.70*	n.s.	n.s.
Fed	8	-0.305	0.184	-0.159	0.56 ^a		
Starved and fed	17	-0.407	0.095	-0.226	0.74**	n.s.	n.s.
Field	12	-0.456	0.124	-0.190	0.76**		
Chlorophyll <i>a</i> (fed and starved)	23	-0.545	0.083	-2.82	0.82**	n.s.	n.s.

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. ^a $0.05 < P < 0.1$, n.s., $P > 0.05$.

no significant difference ($P > 0.05$, Table II) in maximum levels of photosynthesis of fed, starved, and newly-collected anemones (Table II). In addition, P_{\max} varied $< 20\%$ between 0830 and 1630 in natural illumination. Weight-specific chlorophyll *a* content decreased with increasing anemone size with similar slopes for anemones in fed and starved conditions (Fig. 2a). The slopes of weight-specific photosynthesis and chlorophyll *a* regression lines were not significantly different ($P > 0.05$, Table II).

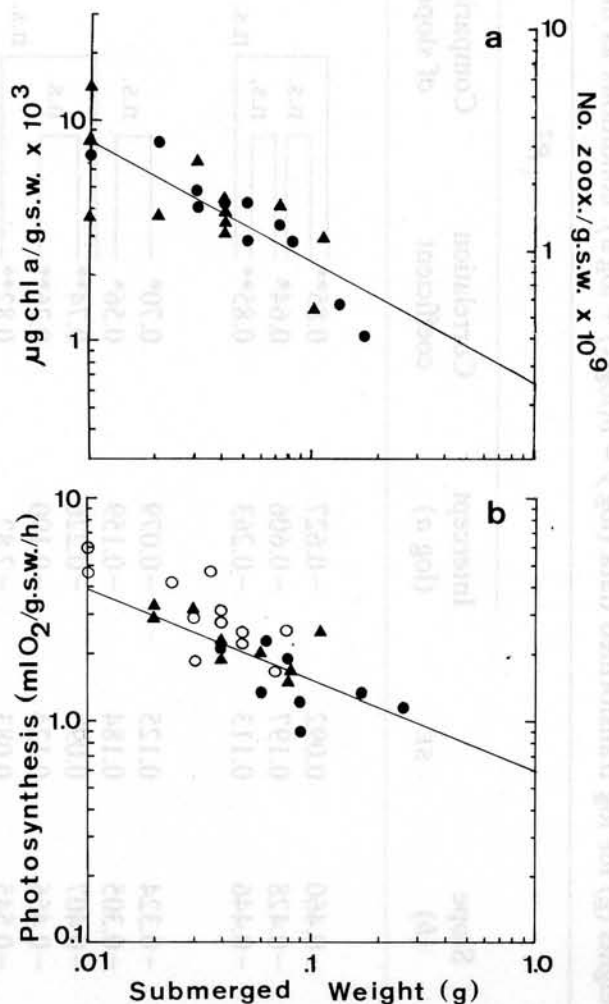


Fig. 2. a, relationship of chlorophyll *a* content and number of zooxanthellae in *Anthopleura elegantissima* to weight; b, relationship of maximum gross photosynthesis of *A. elegantissima* to weight; ●, fed; ▲, starved; ○, newly collected; see text.

TABLE III

Number of zooxanthellae and chlorophyll *a* content per zooxanthella for two large and two small *Anthopleura elegantissima*: *n*, number of fields counted.

Submerged wt (g)	Condition	No. of zooxanthellae \pm SD $\times 10^6$	g Chl <i>a</i> $\times 10^{-12}$ /zooxanthella
0.01	Starved	1.16 \pm 0.24 (8)	2.9
0.01	Fed	1.11 \pm 0.34 (14)	2.7
0.10	Starved	7.03 \pm 1.19 (10)	2.2
0.13	Fed	7.32 \pm 2.05 (12)	2.7
			Mean = 2.6 \pm 0.3 (<i>n</i> = 4)

An analysis of four anemones showed that animals of similar size contained approximately the same number of zooxanthellae regardless of nutritional state. In addition, small anemones had more zooxanthellae per unit weight than larger anemones (Table III). The amount of chlorophyll *a* per zooxanthella did not appear to vary with size or nutritional state ($= 2.6 \pm 0.3 \text{ g Chl } a \times 10^{-12}/\text{zoox.}, n = 4$) and was similar to values obtained by McKinney (1978) for the same anemone ($= 2.2 \pm 1.1 \text{ g Chl } a \times 10^{-12}/\text{zoox.}, n = 22$) (Table III). Consequently, the chlorophyll *a* content (Fig. 2a) was used to estimate the number of zooxanthellae in each anemone.

RESPIRATION

Respiration rates of *A. elegantissima*, measured as oxygen consumed per unit weight per hour, decreased with increasing weight (Fig. 3). In addition, oxygen consumption

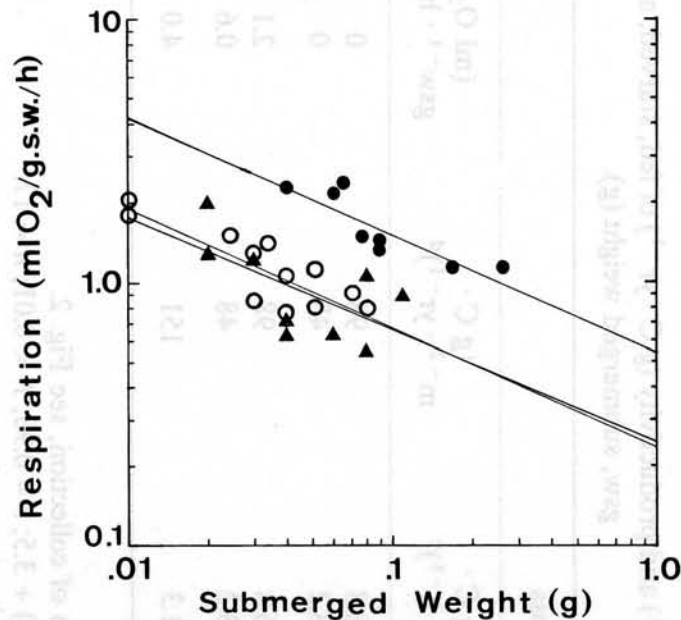


Fig. 3. Relationship of respiration of *A. elegantissima* to weight: symbols as in Fig. 2.

of fed anemones was approximately twice that of starved and newly collected anemones (Fig. 3, Table II). Respiration rates of *A. elegantissima* in this study ranged from 20–164% of the gross photosynthetic rates, depending on nutritional state and anemone size, and did not differ when measured in the daytime or nighttime.

CZAR

The calculated daily contribution of photosynthetically fixed carbon translocated to the host (Table I) accounted for a significantly lower ($P < 0.05$, *t*-test) percentage of the host's respiratory requirements in fed anemones ($\approx 13\%$) than in starved and newly-collected anemones ($\approx 45\%$).

TABLE IV

Gross and net photosynthesis ($\text{ml O}_2 \cdot \text{h}^{-1}$ or $\text{mg C} \cdot \text{h}^{-1}$) and productivity ($\text{g C} \cdot \text{yr}^{-1}$) of fed, starved, and newly collected "field" *Anthopleura elegantissima*: gsw, submerged weight (g).

Nutritional condition	Size (gsw)	Gross			Net		
		($\text{ml O}_2 \cdot \text{gsw}^{-1} \cdot \text{h}^{-1}$) ^a	($\text{mg C} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) ^c	($\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) ^d	($\text{ml O}_2 \cdot \text{gsw}^{-1} \cdot \text{h}^{-1}$) ^a	($\text{mg C} \cdot \text{m}^{-2} \cdot \text{h}^{-1}$) ^c	($\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$) ^d
Fed	0.01	3.9	26.8	98	0	0	0
Fed	0.20	1.1	13.2	48	0	0	0
Starved	0.01	3.9	26.8	98	2.1	14.4	53
Starved	0.20	1.1	13.2	48	0.6	7.2	26
Field ^b	0.01	6.0	41.3	151	4.0	27.5	100

^a From Table II.

^b Maximum value from anemones measured within 12 h of collection, see Fig. 2.

^c ($\text{Surface area in cm}^2$) = $430 \times (\text{submerged weight in g}) + 3.5$; $r = 0.96$; $P < 0.01$; $n = 17$.

^d Calculated on the basis of 10 h of maximum photosynthesis per day.

PRODUCTIVITY

Gross and net photosynthetic rates were determined for the size range of anemones used in our experiments from Figs. 2 and 3 and converted to grams of carbon standardized to submerged weight and area (Table IV). Weight-specific photosynthesis of large anemones was less than a third of that of the smallest. Gross and net production of *A. elegantissima* over the period of 1 yr was calculated on the basis of 10 h of maximum photosynthesis per day (Table IV) and ranged from 48–151 g C · m⁻² · yr⁻¹ depending on the size on the anemones. As mentioned earlier, the net primary productivity of fed anemones was essentially zero due to increased respiration. Net production for starved anemones was about half the gross production.

TABLE V

Percent cover and contribution to total gross photosynthesis of intertidal algae and invertebrates from Coal Oil Point, Santa Barbara and Dutch Harbor, San Nicolas Island: total carbon fixed for a "typical" m² area of intertidal was 1.88 g C · h⁻¹ for Coal Oil Point and 1.36 g C · h⁻¹ for San Nicolas Island; —, alga was not present.

Species	Coal Oil Point		San Nicholas Is.	
	% Cover	% Ps	% Cover	% Ps
<i>Phyllospadix</i> sp.	23.0	24.4 ^b	9.6	46.6 ^b
Rhodophycean turf	15.6	3.9 ^c	—	—
<i>Egria menziesii</i>	11.1	46.4 ^b	—	—
<i>Gigartina canaliculata</i>	8.1	5.5 ^c	19.8	19.0 ^c
<i>Ulva lobata</i>	3.6	2.1 ^d	2.5	3.6 ^d
<i>Cryptopleura violacea</i>	2.1	0.5 ^d	—	—
Blue green	1.8	1.1 ^d	5.2	4.4 ^d
<i>Plocamium cartilagineum</i>	1.4	0.2 ^d	—	—
<i>Corallina vancouveriensis</i>	1.1	0.4 ^c	5.0	2.9 ^c
<i>Chaetomorpha linum</i>	—	—	8.5	4.2 ^c
Ralfsiaceae	—	—	2.2	0.1 ^c
<i>Cladophora columbiana</i>	—	—	1.7	0.3 ^c
<i>Smithora naiadum</i>	—	—	1.6	1.1 ^e
<i>Porphyra lanceolata</i>	—	—	1.5	0.9 ^d
<i>Lithophyllum proboscideum</i>	—	—	1.4	0.7 ^d
Other macrophytes ^a	9.8	7.7 ^e	10.1	11.0 ^e
<i>Anthopleura elegantissima</i>	15.4	7.5/1.4 ^f	5.5	5.4/1.0 ^f
Other invertebrates	4.6	0	21.0	0
Total	97.6		95.6	

^a Less than 1% cover for individual species.

^b Photosynthesis data from Littler & Murray (1974).

^c Photosynthesis data from P. Taylor (pers. comm.), collected at Dutch Harbor, San Nicolas Island, Sept. 1979.

^d Photosynthesis data from Littler (unpubl.).

^e Mean photosynthetic values (see p. 215) used in calculations.

^f Range of values from maximum photosynthetic rates of smallest (0.01 g submerged wt) animals to lowest photosynthetic rate by largest (0.2 g submerged wt) animal.

The overall contribution of *A. elegantissima* to gross intertidal primary production at Coal Oil Point and Dutch Harbor was calculated from percent cover, regression of cover on weight, and photosynthesis per weight data and compared to similar calculations for the major intertidal seaweeds at the same locations. The relative contributions of *A. elegantissima* and seaweeds to the overall intertidal primary productivity is given in Table V. At Coal Oil Point the contribution of *A. elegantissima* was between 1.4 and 7.5% of the total (depending on size of anemones used in the calculations), while at San Nicholas Island it is between 1.0 and 5.4%. Since nearly all of the anemones at these sites are small clonal animals (see below), the actual value is probably closer to the upper estimate.

DISTRIBUTION

Analysis of cover data for 10 intertidal habitats in southern California revealed a positive correlation (except for the site at Santa Cruz Island) with the amount of sand cover and abundance of *A. elegantissima* (Table VI). Highest densities and cover of *A. elegantissima* were documented at Coal Oil Point and San Nicolas Island where rocky outcroppings were completely surrounded by sand and exposed to the direct force of the surf and swell. Because of sand inundation both study sites were missing most of the upper barnacle and mussel zones (Littler, 1977) typically present in exposed rocky areas of high *A. elegantissima* densities in the Pacific Northwest (Sebens, 1977). As with the other locations studied, the highest sand cover occurred during the winter

TABLE VI

Relationship of abundance and percent cover of *Anthopleura elegantissima* to percent cover of sand at 10 intertidal locations in Southern California: numbers are means of four (seasonal) surveys made in 1975–1976, unless otherwise noted; –, no data available; peak, tide height (m) where maximum % coverage of anemones or sand occurs; peak % cover, range of % cover in the peak areas; compiled from Littler (1977).

Location	Anemones				Sand	
	% Cover	$n \cdot m^{-2}$	Peak	Peak % Cover	Peak	Peak % Cover ^a
Fisherman Cove, Santa Catalina Is.	0.1	9	0.6–1.5	1	none	0
Cave Canyon, Santa Barbara Is.	0.4	11	0.3–1.2	1	none	0
Wilson Cove, San Clemente Is.	0.1	–	–	1	none	0
Ocean Beach, San Diego	0.1	–	0.6–1.8	1	none	0
Corona del Mar	1.0	10	0.6–0.9	3	0.3–0.9	3
White's Point, Los Angeles	1.4	32	0–0.9	2–3	0–1.2	12
Cuyler Harbor, San Miguel Is.	1.8	56	0.3–1.5	2–5	0.3–1.5	9
Willows Anchorage, Santa Cruz Is.	2.6	46	0.3–1.2	5–17	none	0
Dutch Harbor, San Nicholas Is.	5.5	136	0.3–0.9	10–20	0.3–0.9	44
Coal Oil Point, Santa Barbara	15.4	412	0.3–0.9	20–44	–0.6–0.6	51

^a Data from winter and spring surveys.

and spring months (Littler, 1977), although the Coal Oil Point study site had zones of persistent sand cover throughout the year. *A. elegantissima* covered over 20 and 40%, respectively, at San Nicolas Island and Coal Oil Point at some intertidal zones (Table VI). Most of the cover of *A. elegantissima* in these areas was made up of small (0.01 to 0.02 g submerged weight) clonal anemones (Taylor & Littler, in press; unpubl. obs.).

The presence of *A. elegantissima* in sand inundated areas may be due to the ability of this anemone to withstand both scouring and burial better than other macrophytes and macroinvertebrates. Observations at low tides indicate that anemones may remain buried for three months or more, corroborating estimates of three months burial (Sebens, 1977; Taylor & Littler, in press) and five months burial (G. Hodson, pers. comm.).

DISCUSSION

The effect of host nutritional state on the respiratory physiology of algal/invertebrate symbioses has only recently been addressed. Our results indicate that recently fed anemones consumed about twice as much oxygen as similarly-sized starved anemones and confirm the preliminary results of Fitt & Pardy (1981) using *A. elegantissima* and Svoboda & Porrmann (1980) using *Aiptasia diaphana*, as well as experiments on *Hydra viridis* containing zoochlorellae (Pardy & White, 1977). The result of this increase in respiration reduced the apparent net photosynthetic output of the organism (note that gross photosynthesis did not change), and thus lowered the P : R ratio.

This phenomenon has important implications in studies that use respiratory and photosynthetic rates to calculate CZAR (e.g. Muscatine & Porter, 1977; Muscatine, 1980; Muscatine *et al.*, 1981). These measurements are used to estimate potential energetic significance of endosymbiotic algae to their hosts, often in situ, where the nutritional state is not usually known. While the actual amount of carbon translocated to the host may be the same for fed and starved anemones, the apparent contribution is lower for fed animals than for starved animals. Changes in respiration rates due to host nutritional state may be responsible for some of the variation in CZAR estimates from in situ studies.

Results of studies on other zooxanthellae-coelenterate associations suggest that translocated carbon may account for higher respiration in symbiotic host species when compared to aposymbiotic host species (Svoboda, 1978), and in symbiotic hosts kept in high versus low light intensities (Svoboda & Porrmann, 1980). Fed and starved aposymbiotic *Anthopleura elegantissima* have respiration rates indistinguishable from symbiotic anemones of similar size (Fitt & Pardy, 1981, unpubl. data), implying that fed and starved respiration rate differences in this association are due primarily, if not solely, to the metabolic demands associated with external food sources rather than with translocated photosynthetic products.

A. elegantissima analyzed within 10 h of field collection had respiration rates,

P : R ratios, and CZAR estimates essentially identical to starved anemones maintained in the laboratory, suggesting that these anemones were not metabolizing an external food source at the time of collection.

The factors responsible for the allometric relationship between respiration and weight in *A. elegantissima* appear to be different than those determining the similar relationship between gross photosynthesis and weight. Respiration per unit body weight declines with increasing body weight as a power function of the body weight, expressed by the equation:

$$\log_{10} V_{O_2} = \log_{10} a + b \log_{10} W,$$

where V_{O_2} = rate of oxygen uptake ($\text{ml O}_2 \cdot \text{weight}^{-1} \cdot \text{h}^{-1}$), W = body weight, a = y intercept, and b = the slope. The slope b usually falls between (-1 and 0) for most organisms, as a result of allometric increases in metabolic function with growth (Kleiber, 1932; Zeuthen, 1953; Gould, 1966; Schmidt-Nielsen, 1974). For sea anemones, slopes range from -0.14 to -1.95 (Newell & Northcroft, 1967; Sassaman & Mangum, 1970; Sebens, 1981; Shick *et al.*, 1979; Walsh & Somero, 1981). Our slopes for *A. elegantissima* in sea water are roughly two to three times those obtained by Shick *et al.* (1979) for this species. However, slopes of weight regressions of weight specific respiration for a single marine species have been shown to vary with temperature (Widdows, 1978; Walsh & Somero, 1981), exposure to air (Shick *et al.*, 1979), and feeding (Widdows, 1978).

Photosynthesis of the anemones also declined as a power function with increasing weight. In this case, photosynthetic rates are correlated with the number of zooxanthellae, the source of the observed photosynthesis. Zooxanthellae in *A. elegantissima* are found predominantly in the endoderm of tentacles and the oral disc. The data in Fig. 2 suggest that the number of zooxanthellae in this layer may increase with increasing anemone size in a manner similar to a surface-to-volume relationship and therefore account for the observed weight-specific relationships of photosynthetic rates and number of zooxanthellae. Svoboda & Porrmann (1980) also found a decrease in chlorophyll a with increasing size of the anemone *Aiptasia diaphana*. However, they noted that the number of zooxanthellae per mg of animal protein was similar in animals of all sizes, implying that either zooxanthellae from larger anemones contained less chlorophyll a per zooxanthella than those from smaller animals or a higher proportion of non-protein biomass in large anemones. Our anemones were all from the same clone and light regime and we found no difference in chlorophyll a per zooxanthella.

McKinney (1978) noted an apparent increase in CZAR with increasing size of *A. elegantissima*. This observation may be explained if photosynthesis per unit weight increases as a greater power of weight than does respiration. Our regression lines do not have significantly different slopes (Table II); however, CZAR in starved animals increased from 34 to 56% while fed animals increased from 8 to 19% over the size range of 0.01 to 1.0 g submerged weight.

The photosynthetic response of *A. elegantissima* is typical of most marine algae and

phytoplankton, as well as other zooxanthellae-coelenterate symbioses (c.f. Beyers, 1966; Crossland & Barnes, 1977; Wethey & Porter, 1977; Chalker & Taylor, 1978; Kevin & Hudson, 1979; Chalker, 1981; Trench *et al.*, 1981). At low light intensities oxygen and carbon dioxide exchange rates increase linearly with increasing light intensity. Saturation occurs at external light intensities that are less than half of noontime intensities. Photoinhibition was not apparent in *A. elegantissima* at natural light intensities reaching the surface of the anemone up to $1550 \mu\text{E} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. We know of no reports of photoinhibition occurring in any intact zooxanthellae symbioses at natural light intensities (Muscatine, 1980).

Photosynthetic rates of temperate intertidal seaweeds with low surface-to-volume ratios, such as crustose, saccate, and thick sheet-like forms (Kanwisher, 1966; Littler, 1980b) are comparable to rates measured for *A. elegantissima*. The PQ values are within the range of values calculated for phytoplankton (Fogg, 1965; Lewis, 1974; Burris, 1981). A PQ of ≈ 1.2 is thought to indicate the synthesis of proteins in phytoplankton, whereas a PQ of ≈ 1 suggests carbohydrate production (Myers, 1949; Fogg, 1959). The significance of PQ in animal-algal symbioses is not clear, due primarily to the fact that PQ of the animal-algal association probably differs from PQ of the zooxanthellae.

Productivity of this anemone is best expressed in "gross" terms, since this value represents the total amount of carbon fixed photosynthetically, while net productivity will vary with the respiration rate. For instance, respiration rates of *A. elegantissima* ranged from 20–164% of gross production rates, depending on nutritional state and size of the anemone, whereas intertidal seaweeds typically have respiration rates ranging from 1 to 26% of their gross photosynthetic rates (Kanwisher, 1966; Littler & Murray, 1974a; King & Shramm, 1976; Ramus *et al.*, 1977). Gross production of *A. elegantissima* ranges from 48–151 $\text{g C} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$, depending on the size of the animals. This estimate is within the range given for some intertidal algal populations in southern California (Littler & Murray, 1974b), but an order of magnitude lower than production rates given for tropical reef corals (e.g., see Taylor, 1973; Smith, 1974; Muscatine, 1980) and about one-fifth of values determined for the temperate symbiotic corals *Plesiastrea urvillei* (Kevin & Hudson, 1979) and *Astrangia danae* (Jacques *et al.*, 1977). These differences may relate to a larger ratio of host respiratory biomass to number of zooxanthellae in anemones compared to corals (Muscatine, 1974).

The existence of a temperate habitat where one of the major primary producers is an animal containing an endosymbiotic plant has interesting implications. In this respect *A. elegantissima* is similar to reef corals, where tight recycling of nutrients between zooxanthellae and host resembles a miniature self-contained "food chain" (Lewis, 1973; Muscatine, 1973). However, there are two noticeable differences between reef corals and *A. elegantissima*. Whereas algae form the base of many temperate intertidal food chains (Paine, 1966; Paine & Vadas, 1969; Dayton, 1975; Hodgson, 1980; Kitting, 1980) there are few predators known to eat *A. elegantissima*. Sebens (1977) documented predation of *A. elegantissima* by the nudibranch *Aeolidia papillosa* and the leather star *Dermasterias imbricata*; however, these predators appear to be rare

in *Anthopleura elegantissima* habitats in southern California (Littler, 1979). Other predators on *A. elegantissima* include *Epitonium tinctum* Carpenter and *Opalia funiculata* Carpenter, small gastropods classified as "macroparasites" (Taylor & Littler, in press). Their effect on the abundance and distribution of *Anthopleura elegantissima* is thought to be minimal (Breyer, 1981). In contrast, a number of animals are important consumers of reef corals, including starfish (Endean, 1973; Glynn, 1974), urchins (Bak & Van Eys, 1975; Glynn *et al.*, 1979), gastropods (Glynn *et al.*, 1972; Hadfield, 1976), crustaceans (Robertson, 1970; Glynn *et al.*, 1972) and fish (Randall, 1974; Neudecker, 1979). Secondly, calculations of CZAR for *A. elegantissima* tend to be less than half of those made on reef corals (see Muscatine & Porter, 1977; McCloskey *et al.*, 1978; Muscatine *et al.*, 1981), indicating a greater dependence of *A. elegantissima* on external food sources. Corroborating evidence lies in the fact that starved *A. elegantissima* lose weight even in the light (Muscatine, 1961; Sebens, 1980). This is in contrast to some reef corals which have been shown to survive and grow without external sources of food in sea water for extended periods of time (Kawaguti, 1965; Franzisket, 1969, 1970; Johannes, 1974; Wellington, pers. comm.).

Seasonality, temperature, water quality, and numerous other variables that are known to affect photosynthesis were not considered in our calculations of productivity. However, the purpose of this exercise was not to provide absolute numbers for production of *A. elegantissima* and intertidal seaweeds, but to suggest that symbiotic *A. elegantissima* fix carbon at rates similar to photosynthetic algae that live in the same habitat, and that in some locations *A. elegantissima* function not only as consumers (Sebens, 1981) but also as major primary producers. As evidence, our calculations suggest that *A. elegantissima* ranks among the top five primary producers at Coal Oil Point and San Nicolas Island, where there is extensive coverage of the small clonal form. There are intertidal zones at these two locations in which *A. elegantissima* is not only the dominant macroinvertebrate in terms of number and percent cover (Littler, 1977; Taylor & Littler, in press) but also, by our calculations, the dominant primary producer.

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REFERENCES

- BAK, R. P. M. & G. VAN EYS, 1975. Predation of the sea urchin *Diadema antillarum* Philippi on living coral. *Oecologia (Berlin)*, Vol. 20, pp. 111–115.
- BEYERS, R. J., 1966. Metabolic similarities between symbiotic coelenterates and aquatic ecosystems. *Arch. Hydrobiol.*, Vol. 62, pp. 273–284.

- BEYERS, R. J., 1970. A pH-carbon dioxide method for measuring aquatic primary productivity. *Bull. Georgia Acad. Sci.*, Vol. 28, pp. 55–68.
- BREYER, A., 1981. Observations on the reproduction, feeding and ecology of the wentletrap *Epitonium tinctum* (Gastropoda : Mesogastropoda). M.S. thesis, Sonoma State Univ., 50 pp.
- BURRIS, J. E., 1981. The effects of oxygen and inorganic carbon concentrations on the photosynthetic quotients of marine algae. *Mar. Biol.*, Vol. 65, pp. 215–219.
- CHALKER, B. E., 1981. Simulating light-saturating curves for photosynthesis and calcification by reefbuilding corals. *Mar. Biol.*, Vol. 63, pp. 135–141.
- CHALKER, B. E. & D. L. TAYLOR, 1978. Rhythmic variations in calcification and photosynthesis associated with the coral *Acropora cervicornis* (Lamarck). *Proc. R. Soc. London*, Vol. 201, pp. 179–189.
- CROSSLAND, C. T. & B. J. BARNES, 1977. Gas exchange studies with the staghorn coral *Acropora acuminata* and its zooxanthellae. *Mar. Biol.*, Vol. 40, pp. 185–194.
- DAYTON, P. K., 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.*, Vol. 45, pp. 137–159.
- ENDEAN, R., 1973. Population explosions of *Acanthaster planci* and associated destruction of hermatypic corals in the Indo-west Pacific region. In *Biology and geology of coral reefs*, edited by O. A. Jones & R. Endean, Academic Press, New York, Vol. II, pp. 389–438.
- FITT, W. K. & R. L. PARDY, 1981. Effects of starvation, and light and dark on the energy metabolism of symbiotic and aposymbiotic sea anemones, *Anthopleura elegantissima*. *Mar. Biol.*, Vol. 61, pp. 199–205.
- FOGG, G. E., 1959. Nitrogen nutrition and metabolic patterns in algae. *Symp. Soc. Exp. Biol.*, Vol. 13, pp. 106–125.
- FOGG, G. E., 1965. *Algal cultures and phytoplankton ecology*. University of Wisconsin Press, Madison, 126 pp.
- FRANCIS, L., 1979. Contrast between solitary and clonal lifestyles in the sea anemone *Anthopleura elegantissima*. *Am. Zool.*, Vol. 19, pp. 669–682.
- FRANZISKET, L., 1969. Riffcorallen können autroph leben. *Naturwissenschaften*, Vol. 56, p. 144.
- FRANZISKET, L., 1970. The autotrophy of hermatypic reef corals maintained in darkness and their subsequent regeneration in light. *Int. Rev. Hydrobiol.*, Vol. 55, pp. 1–12.
- GLYNN, P. W., 1974. The impact of *Acanthaster* on corals and coral reefs in the Eastern Pacific. *Environ. Conserv.*, Vol. 1, pp. 295–304.
- GLYNN, P. W., R. H. STEWART & J. E. MCCLOSKER, 1972. Pacific coral reefs of Panama: structure, distribution and predators. *Geol. Rundschau*, Vol. 61, pp. 483–519.
- GLYNN, P. W., G. M. WELLINGTON & C. BIRKLAND, 1979. Coral reef growth in the Galapagos: limitation by sea urchins. *Science*, Vol. 203, pp. 47–49.
- GOULD, S. J., 1966. Allometry and size in ontogeny and phylogeny. *Biol. Rev.*, Vol. 41, pp. 587–640.
- HADFIELD, M. G., 1976. Molluscs associated with living tropical corals. *Micronesica*, Vol. 12, pp. 133–148.
- HAND, C., 1955. The sea anemones of Central California. Part II. The endomyarian and mesomyarian anemones. *Wasmann J. Biol.*, Vol. 13, pp. 37–99.
- HODGSON, L. M., 1980. Control of the intertidal distribution of *Gastroclonium coulteri* in Monterey Bay, Calif. U.S.A. *Mar. Biol.*, Vol. 57, pp. 121–126.
- JACQUES, T. G., M. E. Q. PILSON, C. CUMMINGS & N. MARSHALL, 1977. Laboratory observations on respiration, photosynthesis and factors affecting calcification in the temperate coral *Astrangia danae*. *Proc. 3rd Int. Coral Reef Symp.*, Vol. 2, pp. 455–461.
- JEFFREY, S. W. & G. F. HUMPHREY, 1975. New spectrophotometric equations for determining chlorophylls *a*, *b* and *c* in higher plants, algae and natural phytoplankton. *Biochem. Physiol. Pflanz.*, Vol. 167, pp. 191–194.
- JOHANNES, A. E., 1974. Sources of nutritional energy for reef corals. *Proc. 2nd Int. Coral Reef Symp.*, pp. 133–137.
- KANWISHER, J., 1966. Photosynthesis and respiration in some seaweeds. In *Some contemporary studies in marine science*, edited by H. Barnes, George Allen & Unwin Ltd., London, pp. 407–420.
- KAWAGUTI, S., 1965. An electron microscopic proof for a path of nutritive substances from zooxanthellae to the reef coral tissue. *Proc. Jpn. Acad. Sci.*, Vol. 40, pp. 832–835.
- KEVIN, K. M. & R. C. L. HUDSON, 1979. The rôle of zooxanthellae in the hermatypic coral *Plesiastrea urvillei* (Milne Edwards and Haime) from cold waters. *J. Exp. Mar. Biol. Ecol.*, Vol. 36, pp. 157–170.
- KING, R. J. & W. SHRAMM, 1976. Photosynthetic rates of benthic marine algae in relation to light intensity and seasonal variations. *Mar. Biol.*, Vol. 37, pp. 215–222.
- KITTING, C. L., 1980. Herbivore-plant interactions of individual limpets maintaining a mixed diet of intertidal marine algae. *Ecol. Monogr.*, Vol. 50, pp. 527–550.

- KLEIBER, M., 1932. Body size and metabolism. *Hilgardia*, Vol. 6, pp. 315–353.
- LEWIS, D.H., 1973. The relevance of symbiosis to taxonomy and ecology, with particular reference to mutualistic symbiosis and the exploitation of marginal habitats. In, *Taxonomy and ecology*, Vol. 5, edited by V.H. Heywood, Academic Press, London, pp. 151–172.
- LEWIS, W.M. JR., 1974. Primary production in the plankton community of a tropical lake. *Ecol. Monogr.*, Vol. 44, pp. 377–409.
- LITTLER, M.M., 1977. Spatial and temporal variations in the distribution and abundance of rocky intertidal and tidepool biotas in the Southern California Bight. *Southern California baseline study, year one*, Vol. III, 2.1. Bureau of Land Management, Washington, D.C., U.S.A.
- LITTLER, M.M., 1979. The distribution, abundance, and community structure of rocky intertidal and tidepool biotas in the Southern California Bight. *Southern California baseline study, year three*, Vol. II, 1.0., Bureau of Land Management, Washington, D.C., U.S.A.
- LITTLER, M.M., 1980a. Southern California rocky intertidal ecosystems: methods, community structure and variability. In, *The shore environment. Vol. 2, Ecosystems*, edited by J.H. Price, D.E.G. Irvine & W.F. Farnham, Academic Press, New York, pp. 565–608.
- LITTLER, M.M., 1980b. Morphological form and photosynthetic performances of marine macroalgae: tests of a functional/form hypothesis. *Bot. Mar.*, Vol. 22, pp. 161–165.
- LITTLER, M.M. & S.N. MURRAY, 1974a. The primary productivity of marine macrophytes from a rocky intertidal community. *Mar. Biol.*, Vol. 27, pp. 131–135.
- LITTLER, M.M. & S.N. MURRAY, 1974b. Primary productivity of macrophytes. In, *Biological features of intertidal communities near the U.S. Navy sewage outfall, Wilson Cove, San Clemente Island, California*, edited by S.N. Murray & M.M. Littler, U.S. Navy NUC TP 396, 85 pp.
- MCCLOSKEY, L.R., D.S. WETHEY & J.W. PORTER, 1978. Measurement and interpretation of photosyntheses and respiration in reef corals. *Monogr. Oceanogr. Methodol. UNESCO*, Vol. 5, pp. 379–396.
- MCKINNEY, D.M., 1978. The percent contribution of carbon from zooxanthellae to the nutrition of the sea anemone *Anthopleura elegantissima* (Coelenterata: Anthozoa). M.S. thesis, Walla Walla College, Washington, 45 pp.
- MUSCATINE, L., 1961. Symbiosis in marine and fresh water coelenterates. In, *Biology of Hydra*, edited by H.M. Lenhoff & L. Muscatine, University of Miami Press, pp. 255–268.
- MUSCATINE, L., 1971. Experiments on green algae coexistent with zooxanthellae in sea anemones. *Pac. Sci.*, Vol. 25, pp. 13–21.
- MUSCATINE, L., 1973. Nutrition of corals. In, *Biology and geology of coral reefs*, edited by O.A. Jones & R. Endean, Academic Press, New York, Vol. 2, pp. 77–115.
- MUSCATINE, L., 1974. Endosymbiosis of cnidarians and algae. In, *Coelenterate biology*, edited by L. Muscatine & H.M. Lenhoff, Academic Press, New York, pp. 359–389.
- MUSCATINE, L., 1980. Productivity of zooxanthellae. In, *Primary productivity in the sea*, edited by P.G. Falkowski, Plenum Publishing Corp., New York, pp. 381–402.
- MUSCATINE, L. & E. CERNICHIARI, 1969. Assimilation of photosynthetic products of zooxanthellae by a reef coral. *Biol. Bull. (Woods Hole, Mass.)*, Vol. 137, pp. 506–523.
- MUSCATINE, L. & J.W. PORTER, 1977. Reef corals: mutualistic symbioses adapted to nutrient-poor environments. *Bioscience*, Vol. 27, pp. 454–460.
- MUSCATINE, L., L.R. MCCLOSKEY & R.E. MARIAN, 1981. Estimating the daily contribution of carbon from zooxanthellae to coral animal respiration. *Limnol. Oceanogr.*, Vol. 26, pp. 601–611.
- MYERS, J., 1949. The patterns of photosynthesis in *Chlorella*. In, *Photosynthesis in plants*, edited by J. Franck & W.E. Loomis, Ames, Iowa, pp. 349–364.
- NEUDECKER, S., 1979. Effects of grazing and browsing fishes on the zonation of corals in Guam. *Ecology*, Vol. 60, pp. 666–672.
- NEWELL, R.C. & H.R. NORTHCROFT, 1967. A re-interpretation of the effects of temperature on the metabolism of certain marine invertebrates. *J. Zool.*, Vol. 151, pp. 277–298.
- O'BRIEN, T.L., 1978. An ultrastructure study of zoochlorellae in a marine coelenterate. *Trans. Am. Microsc. Soc.*, Vol. 97, pp. 320–329.
- O'BRIEN, T.L., 1980. The symbiotic association between intracellular zoochlorellae (Chlorophyceae) and the coelenterate *Anthopleura xanthogrammica*. *J. Exp. Zool.*, Vol. 211, pp. 343–355.
- PAINE, R.T., 1966. Food web complexity and species diversity. *Am. Nat.*, Vol. 100, pp. 65–75.
- PAINE, R.T. & R.L. VADAS, 1969. The effects of grazing by sea urchins *Strongylocentrotus* spp., on benthic algal populations. *Limnol. Oceanogr.*, Vol. 14, pp. 710–719.

- PARDY, R. L. & B. N. WHITE, 1977. Metabolic relationships between green hydra and its symbiotic algae. *Biol. Bull. (Woods Hole, Mass.)*, Vol. 153, pp. 228–236.
- RAMUS, J., F. LEMONS & C. ZIMMERMAN, 1977. Adaptation of light-harvesting pigments to downwelling light and the consequent photosynthetic performance of the eulittoral rockweeds *Ascophyllum nodosum* and *Fucus vesiculosus*. *Mar. Biol.*, Vol. 42, pp. 293–303.
- RANDALL, J. E., 1974. The effect of fishes on coral reefs. *Proc. 2nd Int. Coral Reef Symp.*, Vol. 1, pp. 159–166.
- ROBERTSON, R., 1970. Review of the predators and parasites of stony corals, with special reference to symbiotic prosobranch gastropods. *Pac. Sci.*, Vol. 24, pp. 43–54.
- SASSAMAN, C. & C. P. MANGUM, 1970. Patterns of temperature adaptation in North American Atlantic coastal actinians. *Mar. Biol.*, Vol. 7, pp. 123–130.
- SCHMIDT-NIELSEN, K., 1974. Scaling in biology: the consequences of size. *J. Exp. Zool.*, Vol. 194, pp. 287–308.
- SEBENS, K. P., 1977. Habitat suitability, reproductive ecology, and the plasticity of body size in two sea anemone populations. Ph.D. thesis, University of Washington, Seattle, 255 pp.
- SEBENS, K. P., 1980. The control of asexual reproduction and indeterminate body size in the sea anemone, *Anthopleura elegantissima* (Brandt). *Biol. Bull. (Woods Hole, Mass.)*, Vol. 158, pp. 370–382.
- SEBENS, K. P., 1981. The allometry of feeding, energetics, and body size in three sea anemone species. *Biol. Bull. (Woods Hole, Mass.)*, Vol. 161, pp. 152–171.
- SHICK, J. M., W. I. BROWN, E. G. DOLLIVER & S. R. KAYAR, 1979. Oxygen uptake in sea anemones: effects of expansion, contraction, and exposure to air and the limitations of diffusion. *Physiol. Zool.*, Vol. 52, pp. 60–62.
- SMITH, D., L. MUSCATINE & D. LEWIS, 1969. Carbohydrate movement from autotrophs to heterotrophs in parasitic and mutualistic symbiosis. *Biol. Rev.*, Vol. 44, pp. 17–90.
- SMITH, S. V., 1974. Coral reef carbon dioxide flux. *Proc. 2nd Int. Coral Reef Symp.*, pp. 77–85.
- STRICKLAND, J. D. H. & T. R. PARSONS, 1972. *A practical handbook of seawater analysis*. Fish. Res. Board Can., 310 pp.
- SVOBODA, A., 1978. *In situ* monitoring of oxygen production and respiration in Cnidaria with and without zooxanthellae. In, *Physiology and behavior of marine organisms*, edited by D. S. McLusky & A. J. Berry, Pergamon Press, Oxford, pp. 75–82.
- SVOBODA, A. & T. PORRMANN, 1980. Oxygen production and uptake by symbiotic *Aiptasia diaphana* (Rapp), (Anthozoa, Coelenterata) adapted to different light intensities. In, *Nutrition in lower metazoa, I*, edited by D. C. Smith & Y. Tiffen, Pergamon Press, Oxford, pp. 87–99.
- SZMANT-FROELICH, A. & M. E. Q. PILSON, 1980. The effects of feeding frequency and symbiosis with zooxanthellae on the biochemical composition of *Astrangia danae* Milne Edwards & Haime 1849. *J. Exp. Mar. Biol. Ecol.*, Vol. 48, pp. 85–97.
- TAYLOR, D. L., 1968. *In situ* studies on the cytochemistry and ultrastructure of a symbiotic marine dinoflagellate. *J. Mar. Biol. Ass. U.K.*, Vol. 48, pp. 349–366.
- TAYLOR, D. L., 1973. Symbiotic pathways of carbon in coral reef ecosystems. *Helgol. Wiss. Meeresunters.*, Vol. 24, pp. 276–283.
- TAYLOR, P. R. & M. M. LITTLER, in press. Compensatory mortality, physical disturbance and retention of substrate in a rocky-intertidal community: the roles of *Anthopleura elegantissima*, *Phragmatopoma californica* and macroalgae in community development and organization. *Ecology*.
- TRENCH, R. K., 1971a. 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. London*, Vol. 177, pp. 225–235.
- TRENCH, R. K., 1971b. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. II. Liberation of fixed C by zooxanthellae *in vitro*. *Proc. R. Soc. London*, Vol. 177, pp. 237–250.
- TRENCH, R. K., 1971c. The physiology and biochemistry of zooxanthellae symbiotic with marine coelenterates. III. The effect of homogenates of host tissues on the excretion of photosynthetic products *in vitro* by zooxanthellae from two marine coelenterates. *Proc. R. Soc. London*, Vol. 177, pp. 251–264.
- TRENCH, R. K., D. S. WETHEY & J. W. PORTER, 1981. Some observations on the symbiosis with zooxanthellae among the Tridacnidae (Mollusca, Bivalvia). *Biol. Bull. (Woods Hole, Mass.)*, Vol. 161, pp. 180–198.
- WALSH, P. J. & G. N. SOMERO, 1981. Temperature adaptation in sea anemones: physiological and biochemical variability in geographically separate populations of *Metridium senile*. *Mar. Biol.*, Vol. 62, pp. 25–34.

- WETHEY, D.S. & J.W. PORTER, 1976. Sun and shade differences in productivity of reef corals. *Nature (London)*, Vol. 262, pp. 281–282.
- WIDDOWS, J., 1978. Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. *J. Mar. Biol. Ass. U.K.*, Vol. 58, pp. 109–124.
- YENTSCH, C.S. & R.W. LEE, 1966. A study of photosynthetic light reactions, and a new interpretation of sun and shade phytoplankton. *J. Mar. Res.*, Vol. 24, pp. 319–327.
- ZEUTHEN, E., 1953. Oxygen uptake as related to body size in organisms. *Q. Rev. Biol.*, Vol. 28, pp. 1–12.

Fitt W. K., Pardy R. L. & Littler M. M. 1982.

Photosynthesis, respiration, and contribution to community productivity of the symbiotic sea anemone *Anthopleura elegantissima* (Brandt, 1835).
Journal of Experimental Marine Biology and Ecology, 61: 213-232.