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Nutrition of the temperate Australian soft coral *Capnella gaboensis*

II. The role of zooxanthellae and feeding

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Abstract

We examined the ability of *Capnella gaboensis* Verseveldt, 1977 (Coelenterata: Octocorallia: Alcyonacea: Nephtheidae) to utilize heterotrophic food sources, and the importance of heterotrophic nutrition and photosynthesis in its diet, by using preserved material and histological sections of field-collected specimens and by means of laboratory experiments in which coral branches were fed with ^{14}C-labelled food of different sizes. The study was conducted from April 1982 to August 1984. *C. gaboensis* receives nutrition from the photosynthesis of its symbiotic zooxanthellae, *Symbiodinium* sp., and from heterotrophic sources. Up to 10% of the algal photosynthate was translocated to the animal-host tissues. The contribution of translocated carbon from the zooxanthellae to the daily respiratory carbon requirement of the animal was estimated to be well below 50% in all seasons except in the summer of 1983–1984, indicating that the coral must rely on additional sources of nutrition (i.e., heterotrophy) for most, if not all, of the year. Field (Sydney Harbour: 33°50′S; 151°15′E) and laboratory observations and experiments indicated that this coral probably feeds upon zooplankton, small particulate matter and dissolved organic matter.

Introduction

Corals which contain zooxanthellae may belong to several different trophic levels simultaneously, with individual colonies perhaps specializing in the type of nutrition appropriate to their habitat at any one time (Drew, 1973). The relative dependence of coral colonies upon endosymbiont photosynthesis and other sources of nutrition has received a great deal of attention during the past century. Such studies have established that most octocorals which contain zooxanthellae are capable of feeding heterotrophically. This is true even for members of the Xeniidae (Lewis, 1982), which lack the structural adaptations associated with plankton-feeding and which, for a long time, were thought to depend entirely upon their zooxanthellae for nutrition.

There have been few comprehensive studies of nutrition in individual species of soft corals. The most important studies are those on *Heteroxenia fuscescens* (Schlichter, 1982; Schlichter *et al.*, 1983) and on the ahermatypic *Alcyonium siderium* (Sebens and Koehl, 1984). Lewis (1982) has shown that the tropical soft coral *Capnella lacertiliensis* was able to feed on ground fish, brine shrimp and live plankton. Nutrition of the northern-hemisphere cool-temperate hard coral *Astrangia danae* has also been studied (e.g. Szmant-Froelich, 1981). Colonies of this species occur with and without zooxanthellae in the same habitat. Well-fed colonies used less of the carbon from ingested food or translocated algal photosynthate for immediate metabolism and stored more as lipid than starved colonies; the presence of zooxanthellae did not significantly affect the amount of ^{14}C assimilated from brine shrimp (Szmant-Froelich, 1981).

This study investigates the ability of *Capnella gaboensis* to utilize heterotrophic food sources, and the importance of heterotrophic nutrition and photosynthesis for this species. Using the photosynthetic rates, respiratory rates, and translocation rates of Farrant *et al.* (1987), the contribution of the translocated carbon produced by the zooxanthellae to the daily respiratory requirement of the animal was calculated for each season.

Materials and methods

Feeding ability

Preserved material and histological sections of field-collected *Capnella gaboensis* Verseveldt, 1977 (Coelenterata:

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Octocorallia: Alcyonacea: Nephtheidae) were examined for the presence of prey items or other gastrovascular contents. In the field (Sydney Harbour: 33°50'S; 151°15'E), *C. gaboensis* polyps were observed closely by divers (from about 10 to 20 cm distance, or closer using an underwater magnifying glass), at hourly intervals on one day and at 2 h intervals on one night, as well as on every other possible occasion, to see whether they were able to capture "prey". Expansion and contraction of colonies and polyps were monitored from 10.00 to 21.00 hrs Wednesday 21 April, 1982 and from 23.00 hrs Saturday 24 April, 1982, to 9.00 hrs Sunday 25 April, 1982. In the laboratory, freshly collected whole coral colonies, branches of colonies, juvenile colonies, and laboratory-reared settled recruits of *C. gaboensis,* were tested for their ability to feed upon various types of food, including living brine shrimp nauplii (*Artemia* sp., hatched from eggs collected in Western Australia), fresh fish homogenate, and ground, rehydrated, freeze-dried zooplankton.

^{14}C-labelled foods

Artemia sp. (Expt A)

Approximately 2 000 freshly hatched brine shrimp nauplii were fed with labelled algae (*Pyramimonas* sp.) for 36 h. The nauplii were washed on to filter paper and rinsed several times with sterile seawater, then resuspended in 25 ml sterile seawater and stored at 4 °C until use the same day. For each treatment, 5 ml of the suspension was added to the 25 ml seawater containing the coral-branch tips. The remaining 5 ml was used for counts of the animals and for determination of specific activity (dis/min/nauplius) by extraction of replicate 1 ml aliquots in KOH. The carbon content of the *Artemia* sp. was not determined.

Algae (Expt B)

Marine flagellates (*Pyramimonas* sp., Chlorophyta), were labelled with 14.8 MBq $NaHC^{14}O_3$ (specific activity 2.21 GBq mmol^{-1}, 25.7 MBq mg^{-1}, Amersham) for 20 h in the light. Half of the suspension was used for feeding to *Artemia* sp., and the other half was stored in a refrigerator for 36 h. The algae were concentrated by centrifugation and resuspended in 25 ml sterile seawater. For each treatment, 5 ml of the suspension was added to the 25 ml seawater containing the coral-branch tips. Algal cells from the remaining 5 ml were counted with a haemocytometer and their specific activity was determined by extraction of replicate 0.5 ml aliquots in methanol-chloroform-water (MCW) and KOH as described by Farrant *et al.* (1987: preceding paper in this issue). The carbon content of the algae was not determined.

Bacteria (Expt C)

A subculture of nonpathogenic marine bacteria (*Vibrio* DW1) was incubated at 30 °C for 2 d on a slope of nutrient Moritas medium (Humphrey *et al.,* 1983), then inoculated into a broth of the same medium, to which 1.85 MBq ^{14}C-glucose (specific activity 9.98 GBq mmol^{-1}, 52.54 MBq mg^{-1}, Amersham) was added. This was incubated at 30 °C, with occasional agitation, for 2 d. The broth was centrifuged to sediment the bacteria, which were then resuspended in 25 ml sterile seawater. For each treatment, 5 ml of the suspension was added to the 25 ml seawater containing the coral-branch tips. The remaining 5 ml of suspension was used for bacterial counts with a haemocytometer, and measurement of specific activity determined by extraction of 0.5 ml aliquots in MCW.

Glycerol, glucose, and sodium bicarbonate (photosynthesis) (Expt D–F)

With filtered seawater, we mixed 1.85 MBq ^{14}C glycerol (specific activity 6.33 GBq mmol^{-1}, 64.6 MBq mg^{-1}, Amersham), 1.85 MBq ^{14}C glucose (specific activity 9.98 GBq mmol^{-1}, 52.54 MBq mg^{-1}, Amersham), and 1.85 MBq $NaH^{14}CO_3$ (specific activity 2.21 GBq mmol^{-1}, 25.7 MBq mg^{-1}, Amersham) to make up 20 ml, 5 ml of which was added to each treatment (coral pieces in 25 ml filtered seawater) at Time zero, to give a total volume of 30 ml during incubation.

Capnella gaboensis colonies (one male, one female) were collected 2 d prior to the day of the experiments from the study site at Fairlight in Sydney Harbour (Farrant *et al.,* 1987). Branch tips were cut off and kept at ambient laboratory light and temperature in seawater which had been filtered through 1 μm pore-size Millipore filters. The water was changed daily and was aerated continuously. All tips appeared to remain healthy and the polyps were continuously expanded at the time the experiments were commenced. Experiments were conducted during daylight hours (11.00 to 16.00 hrs) of 13 May, 1984, and during the night 23.00 to 4.00 hrs). Sampling at night was done under red light. The photon-flux density for daytime experiments was 100 μE m^{-2} s^{-1}. In all experiments the water temperature was 18 °C, the same as that at the site of collection. In all treatments the water was gently aerated throughout the experiment.

Four branch tips (2 males, 2 females) were incubated day and night for each experimental feeding regime in 30 ml seawater containing the labelled "food". Two tips (male, female) were removed 20 min after addition of the "food", and the other two after 100 min. After removal, they were washed several times with filtered seawater and kept in aerated filtered seawater for 30 min before grinding, separating and extracting. Samples for specific-activity determination of the seawater in which the tips were incubated for Experiments D, E and F, were taken at 0, 20 and 100 min. The particulate and/or dissolved organic ^{14}C (P/DOC) in the medium was determined only in Treatment F, i.e., the photosynthesis experiments. MCW extraction (including separation of algae and animal tissues, separation of methanol and chloroform fractions, and chlo-

rophyll *a* determinations), KOH extraction, P/DOC determination (Experiment F) and specific-activity (Experiments D–F) determinations were used to determine the amount of ^{14}C which had been incorporated by the coral and the classes of compounds labelled; these procedures were all carried out as described by Farrant *et al.*, (1987). The translocation rate was assessed by subtracting the dark (heterotrophic) fixation rate for the animal tissues from the rate of ^{14}C incorporation into the animal tissues in the light. Liquid nuclear-emulsion autoradiographic techniques were also employed, using 2 μm sections of coral-branch tips which had been incubated separately from those used for counting. The coral tips were fixed in 3% glutaraldehyde in 0.1 *M* cacodylate buffer for 12 h, decalcified in 0.1 *M* cacodylate buffer, pH 7.1, containing 3% EDTA, and embedded in glycol methacrylate (Cole and Sykes, 1974). The autoradiographic procedures of Bogoroch (1972) were followed.

Photosynthesis

Since the photosynthesis experiment (^{14}C-Feeding Regime F) was done in one season only, the photosynthetic and respiratory rates obtained by Farrant *et al.* (1987) for different seasons were used to estimate the ratios between total daily photosynthesis and respiration (*P:R*). The *P:R* ratio is equivalent to that proportion of the total carbon required over 24 h by the animal tissue which can potentially be supplied by the zooxanthellae (*Symbiodinium* sp.), and was calculated using the following relationship:

$$P{:}R = P_z \text{ net}/R_a,$$

where P_z net = net photosynthesis of zooxanthellae during 24 h, and R_a = respiration of the animal tissues over 24 h (Muscatine, 1980). R_a was calculated for *Capnella gaboensis* using respiration rates (ml O_2 mg^{-1} chlorophyll *a* h^{-1}) from oxygen-electrode experiments, converted to mg C mg^{-1} chl *a* h^{-1} by assuming a respiratory quotient of 1.0 and using the formula of McCloskey *et al.* (1978) for conversion of ml oxygen to mg carbon. The proportions of the total respiration due to the algae and animal tissue were assumed to be equivalent to their respective contributions to the total protein of the whole coral. The ratio of algal to animal protein in *C. gaboensis* was estimated by the method of Lowry *et al.* (1951). P_z net was estimated by subtraction of R_a, the respiration of the zooxanthellae over 24 h, from the gross photosynthetic rate of the zooxanthellae, P_z gross, measures as the rate of ^{14}C fixation (mg C mg^{-1} chlorophyll *a* h^{-1}) and converted to 12 h.

The contribution of translocated carbon produced by the zooxanthellae to the animal's daily requirement for substrates for respiration (CZAR) was calculated for *Capnella gaboensis* for each season by the following formula (Muscatine, 1980):

$$\text{CZAR} = \frac{P_z \text{ net(day)} \times T}{R_a},$$

where P_z net (day) = net photosynthesis of the zooxanthellae during a 12 h day, R_a = respiration of the animal tissues over 24 h, and T = translocation rate.

The values for daily photosynthesis, respiration, and translocation used in the above calculations were extrapolated from short-term laboratory measurements. Ideally, these values should be obtained in the animals' habitat over 24 h in order to take into account the different photon-flux densities and day lengths in each season.

Results

Feeding ability

Capnella gaboensis polyps were seldom observed to catch zooplankton in the field. In the laboratory, small colonies offered living *Artemia* sp. nauplii and eggs did not actively catch them. However, the polyps were capable of grasping nauplii which happened to swim into their tentacles. Sometimes the nauplii were grasped and held by tentacles and pinnules then released a few minutes later, and on one occasion a polyp ingested one of the nauplii but discharged it about 5 min later. Polyps sometimes ingested and retained up to four or five nauplii. Only small colonies were observed to take *Artemia* sp. nauplii. No other types of particulate foods were accepted by *C. gaboensis* polyps and no mucus nets or strands were ever observed on polyps. Fixed *C. gaboensis* colonies rarely contained any type of recognizable food material in the coelentera of polyps.

Observations of the behaviour of colonies in the field over a 24 h period (and in general) showed that the polyps and coenenchyme of most *Capnella gaboensis* colonies are expanded during daylight hours and, to a lesser extent, at night. The increase of colony surface area due to expansion of the coenenchyme was estimated to be 300% for one colony. The increase in surface area due to expansion of the polyps would add to this.

^{14}C-labelled foods

Labelling of "prey" items (Expt A–C)

Artemia sp., *Pyramimonas* sp. and *Vibrio* DW1 incorporated 13.7, 12 and 4.6%, respectively, of the ^{14}C offered to them (Table 1).

Uptake of ^{14}C food items by corals

Only in Experiment F (photosynthesis) was there a significant difference (chi-square, $p \ll 0.05$) between uptake of ^{14}C-labelled food during the day and during the night (Fig. 1). The greatest uptake in terms of percentage of the labelled food provided to the corals that was recovered in the whole corals, was in Experiments C (bacteria, day and night) and F (photosynthesis, day). The lowest uptake was

Table 1. *Capnella gaboensis.* Uptake of ^{14}C-labelled foods by branches; 20 and 100 min samples combined

		Experiment:					
		(A) *Artemia* sp.	(B) Algae	(C) Bacteria	(D) Glycerol	(E) Glucose	(F) $NaHCO_3$
Total radioactivity (kBq) per treatment		23	186	17	462	462	370
% of label taken up by prey		13.7	12.0	4.6	–	–	–
% labelled food taken up by coral	Day	2.2	1.6	8.8	3.0	2.7	10.1
	Night	3.8	1.4	9.4	2.8	2.7	0.6
Total dis/min digested by coral, $\times 10^{-4}$, and (equivalent number of prey digested)	Day	3.1 (27)	18.3 (406)	8.8 (293 000)	117.4	96.7	223.2
	Night	5.7 (48)	15.5 (345)	9.4 (313 000)	103.5	93.9	12.2

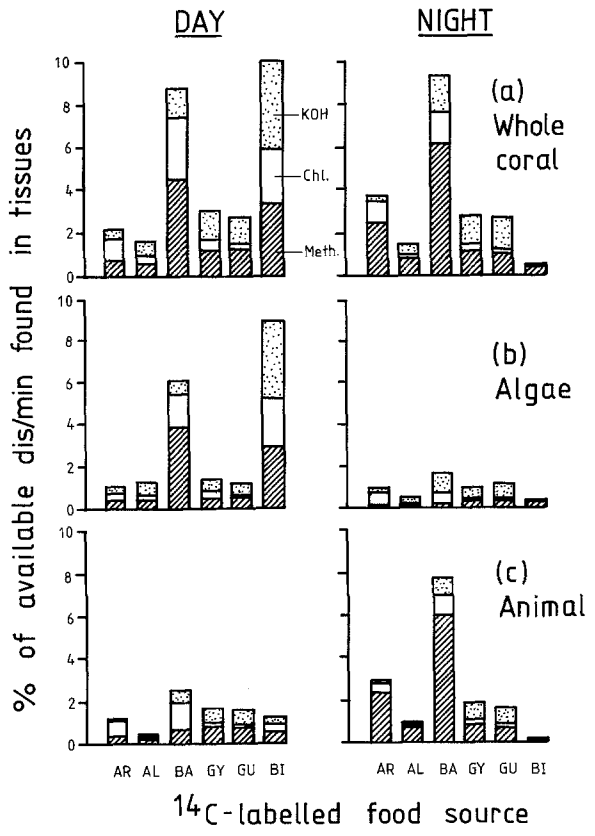

Fig. 1. *Capnella gaboensis.* Percentage of available dis/min incorporated into methanol (Meth.), chloroform (Chl.) and KOH fractions during day and night incubations with different ^{14}C-labelled foods. "Whole coral" includes algae and animal tissues. Twenty and 100 min samples combined; experiments carried out at 18 °C and at a photon-flux density of 100 μE m^{-2} s^{-1} for day experiments. AR: *Artemia* sp.; AL: algae; BA: bacteria; GY: glycerol; GU: glucose; BI: sodium bicarbonate (= photosynthesis expt)

recorded for Experiment B (day and night), in which algae were provided as a food source (Table 1).

Number of ^{14}C prey items taken up by corals

The total radioactivity (dis/min) and calculated number of prey taken up by corals during these experiments are listed in Table 1. The results indicate uptake of all types of food. Autoradiographs of histological sections did not show the presence of any prey items (brine shrimp, algae, or bacteria) in the coelentera of polyps, although the washing and chasing treatments might have removed those still present at the time when the corals were removed from the food source. However, the probability of encountering one of the larger food items in a section would be low.

Distribution of fixed ^{14}C into algae and animal tissues

For some of the day experiments, and most of the night experiments, more label was recovered from the animal fraction than from the algal fraction (Fig. 1). The results suggest that these foods are being utilized by the animal, with subsequent transfer of metabolites to the algae.

Compounds formed after carbon-dioxide fixation

The proportions of label recovered in the methanol (amino acids, organic acids, sugars and other neutral compounds), the chloroform (lipids), and the KOH (structural compounds) fractions, for whole coral, algae, and for animal tissues, for each experiment, are shown in Fig. 1. The slightly different patterns of ^{14}C recovery in the fractions for the day and night experiments may be due in part to photosynthetic refixation of respired $^{14}CO_2$ by the zooxanthellae during the day, and in part to the different uses of carbon from food in the presence of freshly synthesized photosynthetic products (i.e., less glycerol might be synthesized from products of digestion when photosynthesis is also occurring).

Photosynthesis

Results for photosynthesis (i.e., Experimental Feeding Regime F) were consistent with the experiments reported in the preceding study (Farrant *et al.*, 1987), although dark fixation (as a percentage of light fixation) was considerably

lower than the mean value of 13.5% for the previous experiments. The following fixation rates were found in the light and in the dark – light: 22.41 μmol C mg^{-1} chlorophyll *a* h^{-1}; dark: 0.160 μmol C mg^{-1} chlorophyll *a* h^{-1} (0.72% of light fixation).

Translocation of photosynthate

The rate of incorporation of ^{14}C into animal tissues (I_a) between 20 and 100 min incubation in Experiment F during the day was 10.3% of the ^{14}C incorporation rate for whole-coral tissues (Table 2, legend). Since less than half of the dark (heterotrophic) fixation rate (0.72% of light fixation) may be attributable to the animal tissues (Fig. 1), approximately 10% of the total ^{14}C fixation represents translocation of photosynthetic products from the zooxanthellae to the animal tissues (Table 2, legend).

Photosynthesis:respiration (P:R) ratio and CZAR values

The ratio of algal to animal protein for *Capnella gaboensis* was 1:1.13 ($n=3$). The *P:R* ratios calculated for *C. gaboensis* branches in different seasons (Table 2) are greater than one in all cases. When translocation to the animal tissues was taken into account, the contribution of translocated carbon from the zooxanthellae to the daily carbon requirement for respiration by the animal (CZAR) was estimated to be less than 50% for all seasons except for the summer of 1983–1984; the latter result is unreliable, however, due to electrode problems. The CZAR values for winter, spring and autumn (around 11%) are well below the summer value (34%), despite the level of translocation being approximately the same in all seasons (Table 2). The CZAR estimates, however, were based upon translocation rates obtained using ^{14}C-fixation methods which may underestimate translocation (Muscatine, 1983), and the translocation rates were based upon the relatively high levels of dark fixation (13.5% of light fixation) obtained for experiments in the preceding study which may have been lower if experiments had been done at night rather than during the day using covered treatments. Both the *P:R* ratios and CZAR estimates must be regarded as tentative, since they are based upon respiration values derived from oxygen-electrode experiments and photosynthesis values derived from ^{14}C experiments; since the corals were not expanded to the same extent in the oxygen-electrode experiments as in the ^{14}C experiments, *P:R* ratios and CZAR estimates may be overestimates (Farrant *et al.*, 1987).

Table 2. *Capnella gaboensis.* Rate of incorporation of ^{14}C into animal tissues between 20 and 100 min, as percent of total rate, I_a; translocation rate (I_a – dark fixation by animal tissues), T; photosynthesis rate, measured by ^{14}C methods, P_z net (day); respiration rate measured by oxygen electrode methods, R_a 24; photosynthesis:respiration, P:R ratio; and CZAR (contribution of translocated carbon produced by zooxanthellae to animal's daily requirement for respiration) value for branches in different seasons: winter 1983, spring 1983, summer 1982–1983 (1983–1984 in parentheses), and autumn 1984. Values of 10.3 and 10% were obtained for I_a and T, respectively, for Experimental Feeding Regime F in the present study (autumn 1984)

Season	I_a (%)	T (%)	P_z net (day) (mg C mg^{-1} chl *a* h^{-1})	R_a 24	P:R ratio	CZAR (%)
Winter	14	7.7	0.95	0.70	1.2	10.5
Spring	13	6.7	1.07	0.65	1.5	11.0
Summer	16	9.7	1.98 (6.30)	0.56	3.4 (11.1)	34.3 (109)
Autumn	11	4.7	1.59	0.61	2.5	12.3

Discussion and conclusions

Capnella gaboensis is selective about its sources of heterotrophic nutrition. Brine shrimp, bacteria and dissolved substances were accepted. Field observations and the results of experiments with ^{14}C-labelled food suggest that *C. gaboensis* can feed upon and digest zooplankton. This may be an important food source, since one brine shrimp is estimated to be equal to 35×10^6 bacteria in terms of carbon content [based on Szmant-Froehlich's (1981) value for the carbon content of *Artemia* sp., and applying bacterial dimensions to Strathman's (1967) equation for the carbon content of phytoplankton]. *C. gaboensis* polyps, despite their relatively small size, are capable of catching, holding and ingesting larger particulate prey. They are not, however, active predators, and do not always accept *Artemia* sp. nauplii, indicating that only a few *Artemia* sp. are necessary to satisfy the coral, or that *Artemia* sp. may not be the most suitable type of prey, or that other smaller "foods" might be preferred. *C. gaboensis* polyps use tentacles, pinnules and nematocysts in prey capture, but the nematocysts are small and appear to function only slowly in paralysing large prey; they possess short glandular lateral and ventral mesenterial filaments, which may be used for extracellular coelenteric digestion; they have few external cilia and flagella (i.e., apart from the flagellar region of the pharynx); they can increase their surface area by expansion; they have abundant microvilli in the ectoderm; and the endoderm cells usually show extensive folding and vesicle formation in their outer membranes (Farrant, unpublished data). These features suggest that the polyps might be able to take up dissolved organic matter by pinocytosis (although the reverse process of secretion cannot be ruled out).

Capnella gaboensis colonies do not readily accept planktonic algae as food, and in general there is little evidence for corals being able to feed upon or digest plant material. The results, however, suggest that *C. gaboensis* take up and digest labelled bacteria. Many hard corals are able to feed upon bacterioplankton (Sorokin, 1973), and the soft coral *Alcyonium siderium* is known to capture small non-motile prey, such as foraminiferans and ascidian larvae (Sebens and Koehl, 1984). *C. gaboensis* also appears to be able to assimilate dissolved organic matter from seawater (glucose, glycerol, and probably various labelled compounds excreted by the *Artemia* sp., algae, and bacter-

ia used in the experiments), as can the soft coral *Heteroxenia fuscescens* (Schlichter, 1982).

For experiments with brine shrimp, algae and bacteria, the percentage of the total ^{14}C absorbed by the whole association which was found in the animal tissues was generally lower during the day. Since all the incubations and the washes were carried out under identical conditions (except that they were in the light for day experiments, in the dark for night experiments), these results suggest that photosynthetic re-fixation by the zooxanthellae of $^{14}CO_2$ produced during respiration by the food organisms or by the *Capnella gaboensis* association occurs in the light in addition to the uptake of labelled food by the coral.

After uptake of ^{14}C-glycerol by *Capnella gaboensis*, more organic ^{14}C was recovered from the methanol-soluble fraction than from the chloroform-soluble fraction, in both day and night experiments. A similar distribution of label has been reported by Battey and Patton (1984) for the anemone *Condylactis gigantea* after feeding with ^{14}C-glycerol. It therefore appears that neither the zooxanthellae nor the animal tissues in these two organisms rapidly convert glycerol into lipids. During photosynthesis the zooxanthellae may produce free glycerol as well as lipids for translocation to the animal tissues. The host would not need to be able to rapidly convert glycerol into lipid if the zooxanthellae produce sufficient lipid during photosynthesis and translocate it directly to the host.

There is evidence for the translocation of photosynthetic products from the zooxanthellae of *Capnella gaboensis* to the animal tissues. The proportion of fixed ^{14}C translocated to the animal partner of *C. gaboensis* (approximately 10%) is consistent with translocation rates obtained previously in different seasons (Farrant *et al.*, 1987), which ranged from 4.7% (autumn) to 9.7% (summer) (Table 2). However, the dark fixation (as a percentage of light fixation) was considerably lower in the present study than in the previous experiments. The reason for this is not known: leakage of light in the previous experiments may provide an explanation; in the earlier study, experiments were conducted during the day (using black plastic to cover dark treatments), whereas in the present study the dark experiments were conducted at night. However, although the proportion of fixed ^{14}C in algae and animal tissues in the dark was quite different from that in the light (in the dark approximately 40% was found in the animal tissues), the total amount of ^{14}C fixed in the dark was much lower than the amount of ^{14}C fixed in the light (Fig. 1). The values for translocation in the light (4.7 to 10.0%) are below the range of published values for other symbiotic associations (Trench, 1971, for a zoanthid and an anemone; Muscatine and Cernichiari, 1969, for a hard coral; Von Holt and Von Holt, 1968, for a zoanthid, two jellyfish, and a hard coral), but are similar to the 17% reported by Schlichter *et al.* (1983) for the soft coral *Heteroxenia fuscescens*. New methods devised by Muscatine (1983), which have yet to be applied to temperate corals in general, and to soft corals (Muscatine, personal communication), indicate that the traditional ^{14}C methods may underestimate translocation by 50% or more. The contribution of the zooxanthellae to the daily carbon requirement of the animal (CZAR) for *C. gaboensis* may, therefore, be considerably higher than suggested by the values obtained for translocation in this study. The CZAR estimates in this study, based upon conventional ^{14}C methods, indicate that photosynthesis probably cannot satisfy the requirements of the coral, even in summer.

The exact nutritional requirements of *Capnella gaboensis* are difficult to ascertain. Metabolic studies indicate that the zooxanthellae are able to contribute sufficient carbon to satisfy the respiratory requirements of the animal tissue only in summer, and that for most of the time the animal tissues must rely on additional sources of nutrition. During the summer months, photosynthesis may be sufficient to provide for other energy requirements (maintenance, growth and reproduction) as well as for respiration. However, the extent of these requirements is not known. *C. gaboensis* shows distinct and regular responses to light, and photosynthesis is the most likely cause of the need for light. The ability of *C. gaboensis* colonies to survive in the laboratory without a food supply implies that photosynthesis is an important source of nutrition for the species, although the poor condition of colonies kept in aquaria suggests that both light and food are required for normal maintenance and growth. The nocturnal expansion behaviour of colonies, together with the results of ^{14}C-feeding experiments, indicate that other sources of nutrition are also important for *C. gaboensis*. Future studies should be directed towards ascertaining the types and quantities of foods available in the habitat of *C. gaboensis*. Comprehensive feeding experiments could then be done in all seasons, and using natural foods, with a view to obtaining a carbon budget for the species. Estimates of the carbon content of each type of food need to be made in order to establish the value of each to the nutrition of the coral.

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