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A Long-Term Compartmental Partitioning of Photosynthetically Fixed Carbon in a Symbiotic Reef Coral

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Abstract

Long-term compartmental partitioning of photosynthetic products within and between three main compartments of the coral body (tissue, organic matrix and skeletal carbonate) were followed in the coral *Stylophora pistillata* at Eilat, Red Sea. Corals were labelled *in situ* with $NaH^{14}CO_3$ and periodically sampled up to 12 months after incubation. Three months after incubation, only about 10% of the initial ^{14}C materials in the tissue were retained. After the following 5 months, only 3% to 5% of the initial radioactivity remained. Significant differences in the ^{14}C partitioning between the body compartments as well as between tips and bases were recorded immediately after incubation. Only about 10% of the ^{14}C photosynthates is immediately fixed within the organic matrix either in tips or bases. While the amount of ^{14}C in the skeletal carbonate did not vary during the first month after incubation, translocation of ^{14}C into this compartment was recorded in the following months. No translocation of ^{14}C materials was recorded in the newly formed organic matrix months after incubation. On the other hand, photosynthetically fixed products were found within the newly formed tissue. These materials are used for respiration, energy reservoir for egg production, and for building a new tissue. The results of this study indicate that different fragments along a branch and perhaps different parts of a colony exhibit dissimilar activities, which must be taken into consideration when sampling a colony for a physiological study.

Keywords: compartmentation, coral reef, photosynthesis, *Stylophora pistillata*, symbiosis, translocation, zooxanthellae

1. Introduction

It is now documented that carbon compounds which are synthesized by the symbiotic algae (zooxanthellae) in coral tissue during exposure to light are translocated to the cells of the host (Muscatine and Cernichiari, 1969; Crossland et al., 1980a; Muscatine et al., 1981, 1984; Rinkevich and Loya, 1983, 1984; and literature therein). This daily flux of photosynthetically fixed carbon is employed by the host coral for many uses including maintenance, excretion, synthesis of new cells, skeletal matrix, mucus, deposition of calcium carbonate, as storage of energy rich compounds for coral reproduction and more (Kellogg and Patton, 1983; Muscatine et al., 1984; Stimson, 1987; Rinkevich, 1989). However, experimental studies of the fate of these photosynthetically fixed products have been mainly concerned with short-term observations, from several hours up to a few days. Crossland et al. (1980b) determined the ^{14}C content within *Acropora formosa* colonies for only 5 days after labelling, while Cooksey and Cooksey (1972) followed labelled photosynthetic products in *Montastrea annularis* and *Siderastrea siderea* tissues up to 262 hr (11 days) after incubation. Patton et al. (1983) labelled heads of *Stylophora pistillata* and followed the distribution and loss of radioactive photosynthates for 16 days. In a previous work (Rinkevich and Loya, 1983), we studied the fate of photosynthetic products in *Stylophora pistillata* and followed the fixed carbon for up to one month.

The few studies cited above (all employed the technique of radioactive carbon as a tracer) indicate that labelled materials are lost at a moderate or rapid rate. Cooksey and Cooksey (1972) demonstrated a very rapid loss of ^{14}C materials from two coral species. They found that total radioactivity in the coral tissues fell to about half of its initial value one night after the end of incubation and then to about a third in the next 10 days. They calculated that the half-life of the residual ^{14}C products left after one night's loss was about 2 weeks to one month. Patton et al. (1983) found a rapid loss of radioactivity with time in the ethanol-ether fraction of the tissue. Crossland et al. (1980b) found that 50 to 60% of the photosynthetically fixed ^{14}C was lost from *Acropora* colonies during the first 48 hr after incubation while thereafter the rate of loss gradually decreased. However, Lewis and Smith (1971) found no significant decrease in the total amounts of radioactivity in corals sampled up to 4 hr after incubation. Rinkevich and Loya (1983) found 24 hr after incubation no significant decline in ^{14}C amounts within the tissues of *Stylophora* colonies. Only in one out of seven tested colonies was a significant loss recorded in the following 24 hr. After one month, 20 to 50% of the accumulated ^{14}C products were retained.

By using two different experimental approaches, Muscatine et al. (1984)

and Davies (1984) described and quantified the daily energy budgets for two common reef corals. Both budgets showed that under cloudless conditions in shallow water, the input of the translocated fixed carbon as energy would be in excess of that required by the colony. Moreover, these corals immediately released only 6% of the translocated carbon, which is usually in a surplus of about 143% of the animal maintenance respiration needs (Muscatine et al., 1984). Therefore it is not surprising that large amounts of translocated materials are reserved in shallow water coral tissues as "lipid" or "fat bodies" (Kellogg and Patton, 1983; Stimson, 1987). The fact that a significant portion of a one-day yield of photosynthetic products is accumulated within the coral tissue leads to two questions: (1) In which of the main coral's body compartments (skeletal carbonate, the organic matrix of the skeleton and the tissue) are these products accumulated? (2) What are the pathways and the fate of these photosynthetic products in the long term?

In the present work we discuss the results of long term observations, of up to one year, on the fate of the photosynthetic products within the Red Sea coral *Stylophora pistillata*. Quantitative data of these products are presented by tracing their flow within and between the three major compartments of the coral body.

2. Materials and Methods

General procedures

The study was carried out in front of the Marine Biological Laboratory at Eilat, Red Sea. Sampling regime, incubation procedure and working methodology on tissues are discussed in Rinkevich and Loya (1983). Only mature and healthy specimens of *S. pistillata* were chosen. A hammer and chisel were used to detach the colonies from the substratum. The colonies were carefully transferred underwater and placed in a new site, where they were tied with plastic cords to concrete plates, at the same depth as they had been naturally growing. Specimens which were harmed by this procedure were excluded. All underwater work was carried out by SCUBA diving.

After an acclimation of at least 24 hr in the new site, the corals were covered with plastic bags, and radioactive carbon ($NaH^{14}CO_3$, final concentration of 0.05 μCi/ml) was injected into the bags. In some experiments the hydroquinone dye, Alizarin Red S, was simultaneously added by another injection to a final concentration of $\approx$ 10 mg/l (Lamberts, 1973). The incorporation of this dye into the coral skeleton reflects the calcification activity of the coral so that actively calcifying sites are visibly stained in pink-red. Every colony

was labelled in a separate bag. In all experimental colonies, incubation time always terminated after 24 hr. Branches were sampled in different periods after incubation (up to one year) using wire cutters.

Coral fragments were put into plastic vials and 0.5–0.9 ml of hydrogen peroxide (30%) was slowly added. The addition of the hydrogen peroxide solution immediately after sampling the coral branches causes much frothing. Therefore, the digesting solution was added only after obtaining partial desiccation of the samples (up to 1 hr after sampling). After complete digestion of the tissue, the skeleton was removed and two to three replicates (0.2–0.3 ml each) were placed into separate mini-vials. Thereafter, 0.1 ml of 5 N HCl was added to each replicate to remove all unincorporated [^{14}C]bicarbonate, plus 1 ml of distilled water followed by 2 ml of Instagel (Packard) scintillation cocktail. Activity of ^{14}C was determined by Tri-Carb liquid scintillation counter (Packard).

Five different types of fragments were tested: tips, bases (see Rinkevich and Loya, 1983),old tips, old bases and new branches. We termed as "old tips" the pink-stained areas along the branches which had been marked with alizarin several months previously. "Old bases" refer to the areas below the "old tips." "New branches" refer to the new branches which had grown after the labelling with alizarin.

^{14}C in the skeleton

The ^{14}C is distributed in the skeleton either within the skeletal carbonate or within the organic matrix. Acidification of the coral skeleton releases $^{14}CO_2$ and leaves the labelled organic matrix behind. The separation of ^{14}C found in these two compartments was accomplished using a special apparatus (Fig. 1). This apparatus was made of 2 plastic mini-vials (A and B) connected by a polypropylene duct (C, Fig. 1). This duct is inserted into vial B and ends in a capillary tube. The vials are easily united or removed since the left end of the duct is fixed to a fitted polypropylene cap and the right part passes through a similar cap. Duct connections with caps were sealed by glue and were checked for possible leakage. A syringe (D) containing acid penetrated the left cap while a small hole (usually protected by syringe needle) pierced the right cap.

A coral sample was placed in vial A and 1 ml of distilled water was added to cover it, while 1.5 ml of CO_2-collecting agent (Carbosorb, Packard) was poured into vial B. After fitting and tightening the caps, 0.5 ml of H_3PO_4 (concentrated to 1/3 concentrations, depending on the sample size and the time of sampling after incubation) was injected through the syringe (D) drop

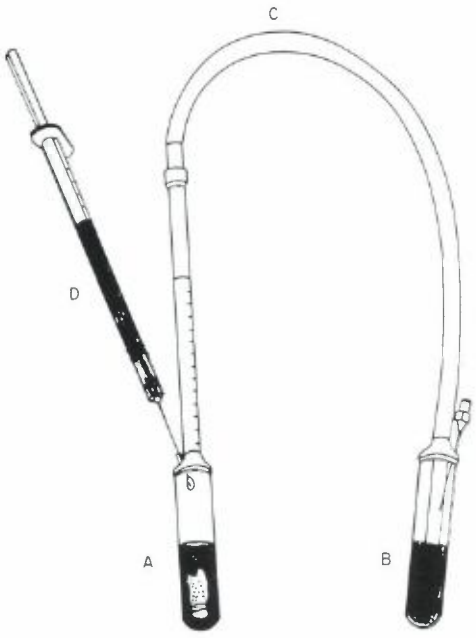

Figure 1. An apparatus for separation between carbonate and organic matrix from small pieces of coral skeletons (see text for further details).

by drop. H_3PO_4 proved to be most useful because it does not cause much frothing or high quenching while counting (Erez, 1977). The evolving CO_2 was collected in vial B. All the $^{14}CO_2$ produced was found to be collected by the carbosorb, since in control experiments, in which vial B was connected in a similar manner to an additional vial containing carbosorb, no radioactivity was recorded in the latter vial. Decalcification was terminated after 6 to 8 hr. At the end of each experiment, two replicates (0.5 ml each) were taken from vial A. One ml of distilled water followed by 2 ml of Instagel were added to each replicant. Into vial B, 2–2.5 ml of Instagel was added. Activity of ^{14}C was determined using Tri-Carb liquid scintillation counter.

3. Results

Retention of photsynthetically fixed carbon in coral tissue

The retention of photosynthetically fixed carbon in *Stylophora* tissue was studied in two sets of experiments (Table 1; Fig. 2a,b). In the first trial (Table 1), 5 mature colonies were marked simultaneously with ^{14}C and alizarin. As a result, the newly formed tips and branches were easily recognizable

Table 1. Average specific activity (dpm/mm^2) in tissue fragments of *S. pistillata* colonies simultaneously marked with alizarin and ^{14}C labelled bicarbonate. B = bases of branches, N = new parts, samples taken above the red marks of alizarin. O = old parts, below the alizarin marks, T = tips. Numbers in parenthesis refer to the sample sizes of tested branch fragments.

Coral no.	Tissue specific activity after labelling (months)											
	1			2			3			4		
1	T	47±15	(10)	T	45±11	(6)	T	12±2	(5)	N	10±1	(5)
	B	66±11	(13)	B	65±10	(11)	B	26±6	(4)	O	16±3	(6)
2	T	46±8	(5)	T	26±1	(3)	T	16±5	(4)	N	11±3	(5)
	B	61±8	(8)	B	41±3	(3)	B	21±4	(3)	O	15±2	(7)
3	T	104±7	(5)	T	49±4	(4)	N	20±5	(3)	N	17±6	(5)
	B	97±9	(9)	B	66±12	(8)	O	29±4	(8)	O	25±2	(9)
4	T	99±28	(3)	T	47±11	(2)	N	29±2	(5)	N	21±3	(6)
	B	103±17	(7)	B	60±9	(4)	O	36±9	(6)	O	26±4	(6)
5	T	45±15	(5)	T	29±3	(3)	T	12±1	(4)	N	11±3	(4)
	B	59±13	(10)	B	47±4	(5)	B	21±6	(5)	O	14±3	(4)

above the red-pink marks, even in the underwater observations. As from three months after labelling, these newly formed fragments were long enough (about 0.5 cm in length), which permitted their individual sampling (N, Table 1), without including "old" parts previously marked with ^{14}C and alizarin (O, Table 1). These colonies were sampled up to 4 months after labelling them when a severe southern storm killed them. In the second trial (Fig. 2a,b), tips and bases of branches were sampled from 6 colonies labelled with ^{14}C alone. In this experiment, colonies were followed up to 8 months after labelling (all results are presented as $\bar{X}\pm$S.D. dpm/mm^2 of coral tissue).

In both sets of experiments (raw data for the second trial, Fig. 2, are presented in Rinkevich, 1982), tips of branches, in most cases, exhibited lower levels of activity (the differences in ^{14}C amounts between sampled fragments along a branch are summarized and discussed in Rinkevich and Loya, 1983). It is interesting to note here that a similar trend was recorded up to 8 months after labelling (Table 1 and Rinkevich, 1982) and even between "new" and "old" fragments (Table 1). It is clear that labelled materials are translocated upward to the newly formed tissue (Table 1).

The loss of photosynthetically fixed carbon from *S. pistillata* tissues during

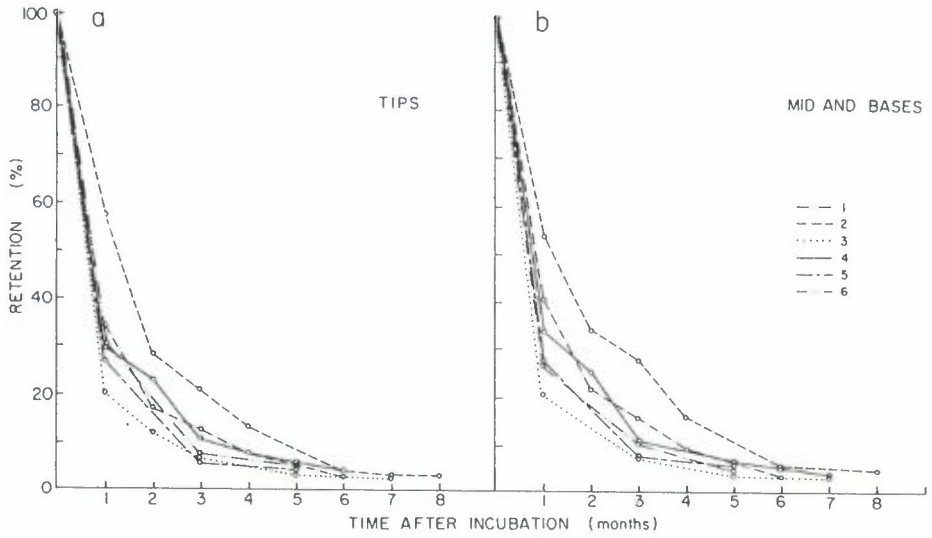

Figure 2. Retention (%) of ^{14}C within branch tips (a) and within base fragments (b) in six *S. pistillata* colonies up to eight months after incubation. The initial activity was recorded 4 to 24 hr after incubation.

8 months of observations is summarized for the tips (Fig. 2a) and for the fragments below the branch tips (Fig. 2b). The great rate of loss of radioactive materials during the first month became moderated and gradually decreased, until 3 months after incubation only about 10% of the initial ^{14}C materials in the tissue were retained. About 3 to 5% of the initial of the radioactivity remained during the following 5 months. In an additional set of experiments (Rinkevich, 1982), we followed the specific activity of one day yield recorded in coral tissues where, in one case, it did not differ from background after one year of observations. It is also demonstrated in Fig. 2a,b that the rate of reduction in photosynthetically fixed carbon in tissues of tips and bases has a similar shape.

Distribution of labelled carbon in tissue, organic matrix and skeletal carbonate

Eight large *S. pistillata* colonies (each more than 10 cm in radius) were labelled with ^{14}C and checked for the content of radioactive carbon within the main three body compartments: the tissue, the skeletal carbonate and the organic matrix of the skeleton. These colonies were divided into 2 groups in accordance with their color morphs:yellow (colonies 1–4, Fig. 3) and purple (colonies 5–8, Fig. 3). No differences were found between the color morphs

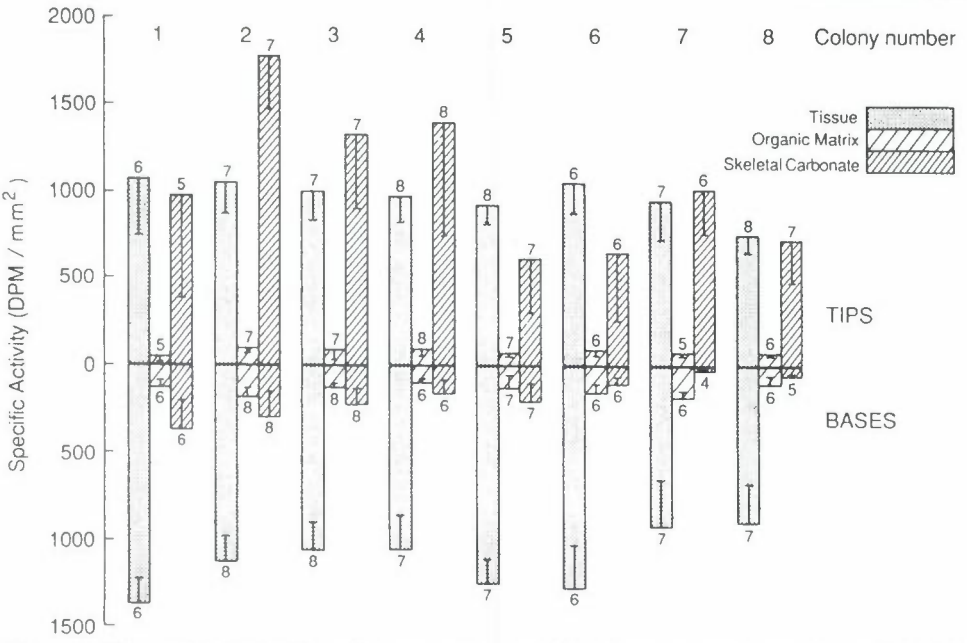

Figure 3. The average specific activity recorded within tissue, organic matrix and skeletal carbonate of tips and bases in eight *Stylophora pistillata* colonies. Colonies were sampled immediately after incubation. Numbers above and below bars represent the sample size of the tested fragments. Vertical lines within bars refer to the SD values.

in the gross amounts of ^{14}C found within the different compartments (Fig. 3, $p > 0.05$, t-test). On the other hand, when comparing between the different fragments along branches, a great dissimilarity was recorded in the ^{14}C partitioning of the tissue, the organic matrix and the skeletal carbonate between tips and bases, irrespective of the color morph. In the tips, 36 to 61% of the total ^{14}C was recorded in the skeletal carbonate (as $Ca^{14}CO_3$, while in the bases only 2 to 28%. Examination of the raw data (dpm/mm^2) revealed differences between 5–10, although it may increase up to 34 times (coral no. 7, Fig. 3). Within the tissue compartment, 36 to 68% of the total counts are recorded within the tips as opposed to 65 to 85% in the bases. The amounts of ^{14}C found in the organic matrix of the skeleton indicate that only a minor portion of the total ^{14}C (in most cases about 6% and less, ranges 3–14%) was recorded within this compartment.

Regarding the organic matrix, significantly more radioactivity is sometimes recorded within the bases than in the tips of a given colony (corals 2, 4 and 6; Fig. 3; $p > 0.05$). However, this is not the general pattern in *S. pistillata*, since in some other experiments (unpublished) and some of those presented here (Table 2), the reverse trend is obtained. These results are surprising since

S. pistillata typically grows by apical accretion and deposition of new organic matrix in tips (see discussion). Examination of the organic ^{14}C separately (the tissue and the organic matrix) demonstrates that only about 10% of the photosynthetically fixed carbon is immediately translocated into the organic matrix of the skeleton, either in tip branches or bases.

Turnover of ^{14}C between compartments — short and long term observations

Table 2 (colony nos. 1–5) provides the results of ^{14}C turnover within the tissue, organic matrix and skeletal carbonate 24, 48, 72 hr and 1 month after labelling in 5 tested colonies. Within these limited post incubation periods, no significant differences ($p > 0.05$; one-way ANOVA) are recorded in the amounts of ^{14}C which were incorporated into the skeletal carbonate or the organic matrix, either in tips or branch bases. it should be noted that the very high variability in the recorded results (50% and more, in spite of the large number of fragments sampled, up to 23; Table 2) could mask a genuine turnover or translocation. Generally, the variability recorded in different fragments within a given colony is higher in the skeletal carbonate values than in tissues. The tissue labelling in colonies 1 and 2 (Table 2) is very low, since these colonies were simultaneously marked with alizarin, which reduces the available light for photosynthesis.

In an additional set, five colonies (not marked with alizarin; colonies 6–10, Table 2) were checked for the gross amounts of ^{14}C in tips and bases, up to 7 months after incubation. During sampling the boundaries between "old" and "new" parts of the branches were unknown.

The results presented in Table 2 indicate differential partitioning of labelled carbon between different compartments along *S. pistillata* branches. High reduction of specific activities is recorded in both the tip and the base tissues (see also Fig. 2a,b). In the skeletal carbonate, on the other hand, no clear trend is found, while in some cases (such as in the tips of colonies 1, 6, 7, 9 and 10; Table 2) a significant reduction in the skeletal specific activity is recorded as from the first month after labelling and thereafter. In other cases, such as in the tips of colony 2 and the bases of colonies 1, 2, 7–10 (Table 2), no reduction in the specific activity of the skeletal carbonate is recorded up to 7 months after labelling. Similarly, in the organic matrix of the branch tips a great reduction in radioactivity is recorded with time, and in some cases (colonies 8 and 9; Table 2) almost no traces of labelled carbons are recorded 5–7 months after incubation. Several colonies (nos. 7–10) exhibited a similar trend in the radioactivity of the organic matrix of branch bases, although the rate of reduction was milder (see discussion). One of the possibilities for this trend

Table 2. Short and long term examinations for compartmental partitioning of labelled carbon in *S. pistillata* branches. Numbers in parenthesis represent the sample size.

Colony no.	Time after incubation	Specific activities of coral compartments (dpm/mm²)											
		Tips						bases					
		Tissue Tissue		Organic matrix		Skeletal carbonate		Tissue Tissue		Organic matrix		Skeletal carbonate	
1	24 hr	50±15	(16)	18±12	(15)	100±55	(12)	48±13	(13)	8±3	(13)	30±17	(13)
	48 hr	28±11	(13)	12±4	(13)	133±64	(10)	41±10	(6)	6±3	(6)	53±24	(5)
	1 month	49±20	(7)	5±2	(7)	83±37	(5)	50±28	(10)	4±3	(10)	41±30	(10)
2	24 hr	42±12	(27)	2±1	(27)	38±19	(23)	52±12	(12)	3±2	(17)	15±7	(14)
	72 hr	39±13	(14)	3±1	(14)	36±27	(11)	55±23	(15)	2±1	(15)	16±16	(12)
	1 month	16±5	(9)	2±1	(9)	52±21	(4)	21±1	(2)	2±0	(2)	9±4	(2)
3	24 hr	290±80	(17)	17±7	(17)	275±95	(10)	–		not done		–	
	48 hr	284±30	(6)	15±3	(6)	332±284	(5)	–		not done		–	
4	24 hr	777±198	(8)	107±29	(8)	1816±579	(6)	817±129	(8)	95±43	(7)	296±128	(7)
	48 hr	696±129	(8)	112±21	(8)	1678±589	(8)	639±105	(8)	93±34	(7)	204±48	(8)
	72 hr	555±136	(8)	83±23	(6)	1525±565	(5)	584±141	(8)	87±59	(6)	285±180	(5)
5	24 hr	624±114	(8)	119±39	(8)	415±197	(7)	893±126	(8)	100±30	(8)	242±145	(6)
	48 hr	592±128	(8)	83±29	(8)	593±143	(8)	791±58	(8)	88±18	(8)	266±102	(7)
	72 hr	469±83	(7)	78±33	(8)	486±216	(8)	756±115	(8)	57±12	(8)	284±113	(8)
6	24 hr	289±70	(23)	16±7	(23)	294±172	(15)	–		not done		–	
	2 months	55±6	(9)	15±9	(8)	144±79	(7)	76±24	(9)	5±2	(9)	99±78	(8)
	3 months	42±6	(8)	4±1	(8)	29±21	(7)	56±13	(10)	3±2	(10)	32±28	(9)

Table 2. Continued

Colony no.	Time after incubation	Specific activities of coral compartments (dpm/mm²)											
		Tips						bases					
		Tissue		Organic matrix		Skeletal carbonate		Tissue		Organic matrix		Skeletal carbonate	
7	24 hr	157±18	(4)	19±7	(4)	149±31	(3)	190±50	(10)	21±3	(9)	40±24	(10)
	2 months	19±2	(5)	2±1	(5)	13±4	(5)	27±2	(8)	3±1	(8)	47±44	(8)
	3 months	11±2	(8)	3±3	(8)	21±18	(6)	14±4	(6)	2±2	(6)	55±60	(6)
	5 months	5±1	(6)	0±1	(6)	12±17	(6)	7±1	(6)	1±0	(6)	52±44	(6)
	7 months	4±1	(7)	0±1	(8)	9±6	(8)	7±1	(8)	2±1	(9)	44±29	(9)
8	24 hr	181±41	(8)	28±5	(8)	227±90	(5)	202±36	(12)	34±10	(12)	83±48	(8)
	1 month	55±9	(8)	11±4	(8)	119±40	(6)	63±8	(13)	6±1	(13)	121±86	(12)
	2 months	43±7	(8)	1±1	(8)	18±14	(7)	50±14	(11)	3±1	(11)	18±11	(9)
	3 months	20±3	(8)	2±1	(7)	31±33	(8)	22±6	(6)	2±1	(6)	73±80	(6)
	5 months	10±1	(6)	2±2	(6)	46±33	(5)	13±2	(5)	1±0	(5)	59±21	(5)
	7 months	6±1	(9)	1±2	(9)	19±27	(9)	8±1	(12)	3±2	(12)	134±96	(12)
9	24 hr	326±63	(6)	25±13	(6)	321±125	(6)	350±71	(8)	29±12	(8)	82±36	(8)
	1 month	86±9	(7)	12±5	(6)	170±113	(6)	98±14	(8)	8±2	(6)	83±75	(4)
	3 months	18±4	(6)	5±2	(5)	50±42	(4)	26±3	(6)	6±3	(6)	75±14	(5)
	5 months	13±3	(10)	1±1	(10)	6±5	(10)	18±2	(10)	4±2	(10)	81±45	(10)
10	24 hr	249±133	(7)	38±9	(7)	336±129	(7)	369±69	(9)	52±11	(9)	70±19	(8)
	1 month	75±14	(8)	11±8	(8)	104±55	(8)	98±14	(8)	14±4	(8)	110±88	(8)
	3 months	19±1	(6)	7±2	(6)	59±33	(4)	39±6	(8)	8±2	(6)	72±28	(5)
	5 months	12±3	(10)	3±3	(10)	26±25	(10)	16±3	(9)	6±3	(9)	139±93	(8)

Table 3. A long term examination of turnover of ^{14}C products within different compartments of alizarin marked coral branches. Percentage numbers below values refer to the relative distribution of ^{14}C materials within different compartments of the branch-fragment. Numbers in parenthesis represent the sample size.

Colony no.	Time after incubation (months)	Average dpm/mm^2 in different fragments and compartments					
		New fragments			Old fragements		
		Tissue	Organic matrix	Skeletal carbonate	Tissue	Organic matrix	Skeletal carbonate
1	3	11 (1)	0 (1)	15 (1)	14±3 (9)	1±1 (9)	32±21 (7)
		42%		58%	30%	2%	68%
2	3	–	not done	–	19±5 (6)	2± 1 (6)	47±22 (6)
					28%	3%	69%
3	4	11±3 (4)	0 (4)	56±56 (4)	13±2 (2)	2±1 (2)	162±10 (2)
		16%		84%	7%	1%	92%
4	5	10±2 (3)	0 (3)	22±16 (3)	15±2 (6)	2±1 (6)	64±41 (5)
		31%		69%	19%	2%	79%
5	5	12±1 (4)	0.5±0.5 (4)	13±7 (4)	16±5 (6)	2±1 (6)	37±22 (6)
		48%		52%	29%	4%	67%
6	7	8±3 (6)	0 (6)	10±12 (6)	14±1 (6)	2±2 (6)	38±16 (6)
		44%		56%	26%	4%	70%
7	7	7±2 (4)	0 (4)	17±11 (4)	11±1 (4)	3±1 (4)	25±12 (3)
		29%		71%	19%	2%	79%

is that the newly formed organic matrix after labelling of the coral branches is not the product of the "old stuff" of labelled carbon found in the coral tissue. This possibility is checked in the next experiment. It should also be noted that even the very low counts in some compartments (1–5 dpm/mm^2) are real. Data were normalized to unit area after the deduction of background. Raw data of several hundred dpm above background (per tip or base of a branch which usually exceeds 120 mm^2 in size) were transformed to this mode of presentation.

Turnover of ^{14}C between compartments — an additional marking with alizarin

In this set of experiments (Table 3), samples were taken from 7 colonies which were marked simultaneously in alizarin and ^{14}C. Fragment samples were taken from new branches (above the red line) and old branches (below the red line). The newly formed organic matrix found above the red line was free of radioactivity, while the old organic matrix was marked with ^{14}C. In contrast, the new tissues and skeletal carbonates, which were formed weeks and months after labelling, contained ^{14}C. Up to 70–80% of the total radioactivity in the new fragments was concentrated within the skeletal carbonates. In the old parts, the skeletal carbonate contains up to 80–90% of the total specific activity.

Discussion

Very little is known about the turnover of photosynthetically fixed carbon, the fate of ^{14}C materials and the distribution of these products within and between the different body compartments of hermatypic corals. In this work we chose to analyze the main three compartments of the coral body: the tissue, the organic matrix of the skeleton and the skeletal carbonate. Tissue can be divided into subcompartments such as algae and animal tissue, storage lipids, structural proteins and others, but without understanding the gross turnover between the major compartments, more specific data on minor translocations lack vital background information.

The limited experimental study which focused on the compartmentation of the photosynthetic products and their transmigration thereafter was mainly concentrated in short-term pathways. In a pioneering study, Muscatine and Cernichiari (1969) examined *Pocillopora damicornis* in the field and in the laboratory for the amounts of fixed carbon translocated into the three compartments immediately after labelling. They found that most of the ^{14}C (87.5 to 89.2%) was recorded in the tissue, much less in the skeletal carbonate (9.6

to 11.5%), while only minor amounts (0.2%) were incorporated within the skeletal organic matrix. Working on the same species, Young et al. (1971) exhibited slightly different distributions of ^{14}C between these compartments. They found that the skeletal organic matrix accumulates about 6 times more, on the average 1.3% (up to 2.1%) of the radioactive carbon. The skeletal carbonate accumulates an average of 9.0% while most of the ^{14}C (87.0 to 94.4%) was found within the tissue. Pearse (1971) demonstrated in *Fungia scutaria* that 90.0 to 95.1% of the ^{14}C was found within the tissue, while the skeletal carbonate and the skeletal organic matrix concentrated 4.3 to 9.3% and 0.6 to 0.7%, respectively. Crossland et al. (1980b) investigated the distributions of ^{14}C materials in the coral *Acropora formosa* within the tissue and skeletal carbonate and followed the dynamic turnover in these compartments during 115 hr after incorporation. Only 4% of the total ^{14}C was recorded after incubation within the skeletal carbonate, but during the next 5 days, more ^{14}C was incorporated there while more than 60% of the fixed ^{14}C within the tissues was lost.

The results of the present work exhibit a similar pattern of short-term partitioning of labelled carbon between the three main body compartments (although characterized by a high variability within and between colonies). Most of the ^{14}C was recorded within the tissue, while the compartment of the skeletal organic matrix contained the lowest amounts. In addition, it is demonstrated that different branch fragments within *S. pistillata* colonies exhibited dissimilar forms of ^{14}C accumulation. In the tips' skeletal organic matrix, only 3 to 5% of the total ^{14}C was found, in comparison to up to 14% within the bases. This unpredictable result may be the outcome of the typical apical accretion of a branch, where huge amounts of ^{14}C are incorporated into the tip's skeletal carbonate (as $Ca^{14}CO_3$), compared to small amounts within the skeletal carbonate of the base-fragments (up to 34 times less). Moreover, within the tip's skeleton, much more labelled carbon (in an order of magnitude, Table 2) is incorporated into the inorganic skeleton than within the skeletal organic matrix. As a result, the relative proportion of the labelled carbon in the organic matrix of the tip seems less significant. However, looking at the raw data (Table 2), it is clear that the specific activity of the tip's organic matrix does not differ from that recorded within the base's organic matrix ($p > 0.05$, one-way ANOVA). This surprising result is therefore in contrast to the widely accepted idea that most of the organic matrix is incorporated simultaneously, together with the inorganic skeletal carbonate of the actively growing tips, and is enriched by photosynthetically fixed carbon (Wainwright, 1963; Pearse and Muscatine, 1971; Young, 1973). On the other hand, the above results fit the

outcome of a previous study (Rinkevich and Loya, 1984), in which the pathways of ^{14}C incorporation into the three major compartments were analyzed by using the "optic glass-fiber" method.

In Table 4, the major changes found during labelling and thereafter are summarized. The results presented in this work, in addition to other studies on *S. pistillata* (Rinkevich, 1982, 1989; Rinkevich and Loya, 1983, 1984), demonstrate that corals use ^{14}C photosynthates for a variety of processes. It seems that only in one compartment, the organic matrix, did the amounts of ^{14}C remain unchanged. During photosynthesis, a minor part of the photosynthetic products accumulates into the organic matrix and stays there constantly. Corals do not use these products again and, on the other hand, the old ^{14}C from other compartments, which is used for other different services, such as growth, metabolism, reproduction, etc., is not found to be a potential source for building a new organic matrix. The non-specific change of carbon between the unlabelled organic matrix and the photosynthetically fixed carbon seems to be unimportant, and the traces introduced into the new organic matrix do not change the results (i.e. in the new organic matrix, the accumulated ^{14}C is less than 1 dpm/mm^2 of surface area). This result, and the above-mentioned outcome of no direct correlation between the amounts of ^{14}C within the organic matrix and in the skeletal carbonate of tips and bases, are in contrast to the findings of Young (1973) in *Pocillopora damicornis.*

In the other two compartments, impressive alterations occur, following the different proportional distributions of ^{14}C in tips and branch bases. During incubation, the tips' skeletal carbonate accumulates higher amounts of ^{14}C than does the base. This phenomenon is connected with the significantly high deposition of $CaCO_3$ in the tips. Thus, the initial deposition of ^{14}C within calcium carbonate is not primarily the result of the photosynthetic process, and the ^{14}C is mostly taken directly from seawater. A similar conclusion was reached by several authors working on photosynbthesis vs. calcification processes in hermatypic corals (Goreau, 1961, 1977; Pearse, 1970, 1971; Erez, 1978). The ^{14}C which is incorporated thereafter into the new skeletal carbonate should be the result of animal respiration. Thus, different levels of metabolism in different parts or fragments within the colony may produce the high variability of ^{14}C found in the skeletal carbonates immediately after incubation. The additional accumulation of ^{14}C within the old skeletal carbonate compartment within the long range, and its appearance within the skeleton of the newly formed tips, are therefore the result of secondary use of ^{14}C photosynthates. it is not known whether the ^{14}C found in the new tips's skeleton originates in the old base's tissue and in some way is deposited within the tips, or whether some photosynthetic products are translocated upward in the tissue, used as energy

Table 4. A short and long-term compartmental partitioning of labelled carbon along *S. pistillata* branch fragments

Time after labelling	Fragment	Compartmental partitioning	Directional movement or utilization*
A short period - within 1 month	tip**	Most of the labelled carbon is accumulated in the skeletal carbonate (36–61%) and in the tissue (35–60%). Low radioactivity in the organic matrix (3–5%). During the first month after labelling, only 18–41% of the original amounts of ^{14}C in the tissue are retained.	From the tissue to respiration, mucus production, synthesis of new cells (algae and coral). New materials are probably translocated from tissue below tips. From the organic matrix and skeleton, no leakage or any utilization. Accumulation of respired $^{14}CO_2$ in skeletal carbonate.
	base**	Most ^{14}C (up to 85%) is accumulated within the tissue. Low specific activity in the organic matrix (7–14%) and skeletal carbonate (2–28%). In comparison with the tips, the tissue of the bases is significantly enriched with ^{14}C materials ($p < 0.05$). In contrast, the tips' skeletal carbonate contains up to 34 times more ^{14}C than that of the bases. During the first month after labelling, a great loss of radioactivity is recorded in the tissue.	From the tissue to respiration, mucus production, synthesis of new cells and reproduction. Translocation of fixed carbon upward. The organic matrix and the skeletal carbonate – as in the tips.
A long period – more than 1 month	old tip	Most of the specific activity in skeletal carbonate (70% and more). Radioactivity in tissue declined to a similar value of the old bases. No changes in organic matrix.	As in "base" above. After one month, the new formed mucus is free of carbon fixed in the past.
	old base	Low radioactivity in all compartments. The relative proportion of the ^{14}C in the skeleton increased due to the great loss of activity from tissue. No changes within the organic matrix.	As in "old tip" above.
	new formed fragment	No activity in the new formed organic matrix. Less radioactivity in the tissue compared to old parts. High variability in the skeleton. Usually more than 50% of total activity is recorded in the skeletal carbonate.	Translocation of materials from fragments below to the new formed tissue. Accumulation of respired $^{14}CO_2$ in skeletal carbonate. New formed organic matrix is free of carbon fixed in the past. Utilization of photosynthates for respiration, synthesis of new cells and probably for reproductive activity

* Based on results of the present study and on Muscatine et al., 1981; Shafir, 1984; Rinkevich and Loya, 1983, 1984; Rinkevich, 1982, 1989.

**These tips and bases are referred to after more than one month as "old tips" and "old bases", respectively.

sources, and their waste product ($^{14}CO_2$) accumulated in the nearest skeleton. It is also possible that the accumulation of ^{14}C within the new skeleton is a combined result of these two processes.

In the tissue, a dramatic decrease of ^{14}C labelled photosynthetic products was recorded. The coral uses the photosynthetically fixed carbon within tissue not only for respiration or in mucus release, which is expressed by the initial great reduction within 1 month, but also for building new tissue (Rinkevich and Loya, 1989), as an energy reservoir for egg production (Rinkevich, 1989) and/or structural elements. It is likely that different coral species or even different colonies of the same species will vary according to their use of the photosynthetic products. For example, Muscatine and Cernichiari (1969) and Muscatine et al. (1981) figured that only 40% of the photosynthetically fixed carbon is translocated to the host. However, Davis (1984) reported a much higher percent translocation of approximately 90%. He also suggested that about 51% of the derived energy is used in respiration, 0.9% in growth and 48% is unaccounted for and presumably lost from the colony. In the present study we found that the photosynthetically fixed products are spread within all tissue fragments, new and old, and it seems that long after incubation, most of the incorporated ^{14}C in the tissue is found within the structural elements (see also Fang et al., 1989). It is of great interest that these products are also heavily invested within the planulae (Rinkevich, 1989).

The results of Rinkevich and Loya (1983, 1989) and the present study indicate that at least in the case of *S. pistillata*, we cannot consider the colony as a uniform animal in which different parts of its body have similar physiological and metabolic levels. Different fragments along a branch, such as tips and bases, reproductive zones, and perhaps different parts of the colony exhibit unlike activities, which must be taken into consideration when sampling part of, or a branch from, a colony for a physiological study.

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