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Oriented intra-colonial transport of ^{14}C labeled materials during coral regeneration

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ABSTRACT: Here we document for the first time an oriented intra-colonial translocation of photosynthetic products towards regenerating areas in 2 scleractinian corals, *Favia favus* (n = 5) and *Platygyra lamellina* (n = 3) in Eilat (Red Sea). ^{14}C bicarbonate was injected into round stainless-steel cylinders (10 h daylight incubation period) enabling labeling of a restricted tissue area of 20 cm^2 in each colony center. Three tissue lesion sizes (small, intermediate and large) were inflicted simultaneously on each colony at a distance of 10 cm from and at different angles to the labeled area. After 3 wk, tissue and skeletal samples were taken from various locations on the coral colonies, and ^{14}C activity was determined. In *F. favus* a significant labeling of tissues was recorded in areas bordering the recuperating large lesions and along the axis connecting these lesions with the labeled centers. This pattern of labeling was not found in the smaller lesions. In *P. lamellina* ^{14}C incorporation was recorded in the tissues bordering large as well as intermediate sized lesions. The skeletal samples from *F. favus* showed significant ^{14}C deposition in areas bordering the large lesions, indicating the use of translocated ^{14}C materials for skeletogenesis in large lesion regeneration. Our results indicate that ^{14}C labeled materials originating in distant areas of the coral colony are translocated towards large regenerating lesions. Furthermore, the size of the coral lesion is shown to affect the magnitude of this translocation.

KEY WORDS: Regeneration · Translocation · Photosynthetic products · Scleractinian corals · Red Sea · *Favia favus* · *Platygyra lamellina*

INTRODUCTION

In hermatypic corals, photosynthetic products are continuously translocated from the symbiotic zooxanthellae to the host tissue and thereby contribute to a variety of nutritional requirements such as maintenance, synthesis of new cells, skeletal matrix and mucus, deposition of calcium carbonate, and storage of energy rich compounds for coral reproduction (Muscatine & Cernichiari 1969, Crossland et al. 1980a, b, Muscatine et al. 1981, 1984, Kellogg & Patton 1983, Rinkevich & Loya 1983, 1984, Stimson 1987, Rinkevich 1989). These daily fluxes of photosynthates may also contribute to specific biochemical-physiological needs away from sites of algae-coral translocation (Rinkevich 1989). In a pioneering study on coral-algae symbiosis, Pearse & Muscatine (1971) documented in *Acropora cervicornis* that organic products (mainly in the forms of lipids, glycerol and glucose) are translocated from the base of branches to the tips, contributing to coral calcification. They found that both ethanol-methanol-chloroform soluble and insoluble tissue fractions were translocated upwards from the lower parts of the branches. Taylor (1977) further confirmed a strong preferential movement and accumulation of ^{14}C labeled compounds towards the tips in *A. cervicornis*. In addition, he recorded an analogous pattern of photosynthate translocation in flat colonies of *Montastrea annularis*, where ^{14}C labeled compounds were found at the forward growing edges up to 9 cm away from the incubation area. Working on the branching species *Stylophora pistillata*, Rinkevich (1989) found that plan-

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ula-larvae collected up to 7 mo after coral tissue was labeled with ^{14}C contained significant amounts of ^{14}C labeled photosynthates. These results show that planula production is supported by translocation of products from algal photosynthesis.

The energy resources available to an organism are often limited and are differentially exploited among a variety of biological demands, such as maintenance, somatic growth, reproduction and regeneration (Kozlowski & Wiegert 1986). Sexual reproduction, growth and regeneration in corals are regarded as energy dependent processes (Loya 1976, Rinkevich & Loya 1989, Harrison & Wallace 1990) and several field studies have already documented that damaged corals have lower fecundity during regeneration as compared to intact colonies (Rinkevich & Loya 1989, Harrison & Wallace 1990, Meesters et al. 1994, Van Veghel & Bak 1994, Ward 1995). Such a notion of energetic constraint between regeneration and reproduction has been suggested for several coral species, including *Stylophora pistillata* (Loya 1976, Rinkevich & Loya 1989), *Fungia granulosa* (Chadwick & Loya 1990), *Montastrea annularis* (Van Veghel & Bak 1994), *Pocillopora damicornis* (Ward 1995), *Acropora hyacinthus*, *A. gemmifera* and *Goniastrea retiformis* (Hall in press).

To date no studies have experimentally evaluated the possible allocation of energy resources towards regenerating parts in corals. Several studies (Bak et al. 1977, Bak & Steward-Van Es 1980, Bak 1983, Meesters et al. 1994, Hall in press) have suggested that such a translocation occurs only from polyps directly bordering the lesions. Recently we followed the recovery rates of lesions differing in size and shape in the hermatypic coral *Favia favus*, and found that the lesion perimeter has an important role in regulating the regeneration process (Oren et al. 1997). We further proposed that for the regeneration of large injuries, some of the energy resources should translocate from distant portions of the colony (Oren et al. 1997). The objective of the present study was to test this hypothesis. This was examined by studying the intra-colonial transport of ^{14}C labeled photosynthetic products during regeneration of lesions differing in size and shape in 2 massive hermatypic corals in Eilat (Red Sea).

MATERIALS AND METHODS

The study was carried out in the shallow reef (2 to 3 m) in front of the Marine Biological Laboratory at Eilat (Red Sea) during October to December 1996. Large (>40 cm in diameter) and healthy massive colonies of *Favia favus* (n = 5) and *Platygyra lamellina* (n = 3) were chosen. All underwater work was carried out by SCUBA diving.

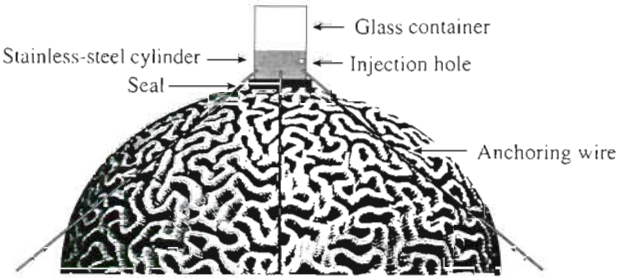

Fig. 1. Schematic illustration of the cylinder used for labeling a restricted tissue area, 20 cm^2, with radioactive bicarbonate

Round stainless-steel cylinders (4 cm long, 5 cm diameter) were constructed for labeling small restricted tissue areas in the center of the examined colonies with radioactive bicarbonate. One end of each cylinder was glued to an artificial sponge material in order to achieve a firm sealing contact between it and the coral tissue (Fig. 1), providing an internal free area of 20 cm^2 for tissue labeling. The other opening was designed to fit hermetically to a 250 ml glass container. Each cylinder was tightly attached to the surface of the colony by 3 steel wires that ran from the sides of the cylinder, anchoring it to a firm hard substrate near the colony. After sealing the apparatus, a 3 mm hole (Fig. 1), covered with rubber, enabled the injection of radioactive bicarbonate. Radioactive carbon (final concentration 0.2 $\mu Ci\ ml^{-1}$) was injected into the sealed glass container, leaving a volume of 50 ml of air for water stirring and gas exchange. Colonies were labeled at 07:00 h in order to enable 10 h of daylight active photosynthesis.

Three different types of tissue lesions were inflicted using a regulator air-pick on each colony, each at a distance of 10 cm from the labeled center: (1) small (S, area = 103 ± 14 mm^2, perimeter = 42 ± 7 mm, n = 6); (2) intermediate (I, area = 259 ± 28 mm^2, perimeter = 97 ± 11 mm, n = 6); and (3) large (L, area = 522 ± 73 mm^2, perimeter = 171 ± 13 mm, n = 6). The lesions were experimentally created immediately after the injection of the radioactive material into the sealed glass containers. One control colony for both species was labeled with ^{14}C in a similar way but without inflicting injuries.

We have previously recorded that the fastest regeneration rates of tissue lesions in *Favia favus* are achieved during the first month after injuries (Oren et al. 1997). Therefore, coral samples (tissue and skeleton) were taken here 3 wk after labeling and lesion infliction, using a round stainless-steel corer, enabling collection of similar sized fragments (1 cm^2). We sampled 32 fragments from each colony (sampling locations are presented in Fig. 2). The sampled fragments were placed individually in plastic vials and brought to

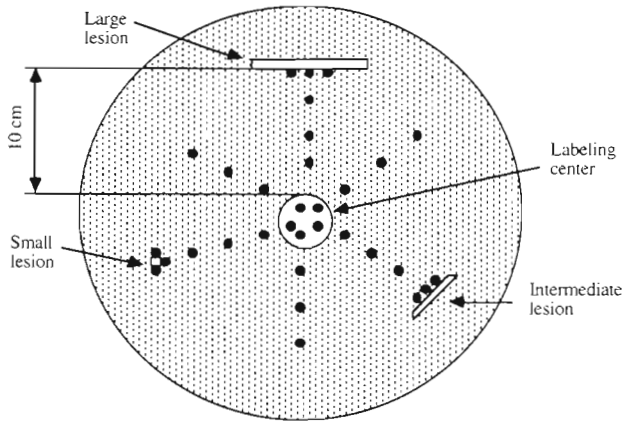

Fig. 2. Locations of the small, intermediate and large tissue lesions inflicted on the coral head, each at a distance of 10 cm from the ^{14}C labeled center. Black circles indicate sampling points

the lab. The sea water from each vial was drained and 8 ml of hydrogen peroxide (30%) were added in order to digest the tissues. After complete digestion of the tissues (24 h), the remaining skeletons were removed and 2 replicates of 0.5 ml from each vial were sampled. Five ml of Biodegradable Counting Scintillation cocktail (BCS; Amersham) were added to each sample. Activity of ^{14}C in the tissues was determined using a liquid scintillation counter (Tri-Carb 1500, Packard). The remaining skeletons from 1 control and 3 experimental colonies of *F. favus* were further used to determine the possible incorporation of ^{14}C into the calcium carbonate (see Rinkevich 1991). Skeletons were decalcified with H_3PO_4 and the released $^{14}CO_2$ was collected by a CO_2-collecting agent (Carbosorb, Packard). Decalcification was terminated after 8 h. Two replicates of 0.5 ml were removed from each vial, 5 ml of BCS were added and ^{14}C activity was counted using a liquid scintillation counter.

RESULTS

The average activity [disintegrations per minute (DPM) cm^{-2} ± SD] of tissue samples from 5 ^{14}C labeled *Favia favus* colonies and 3 *Platygyra lamellina* colonies are presented in Table 1. In both studied species, 3 wk after labeling, the experimentally labeled centers of the colonies (zones C) retained significant levels of ^{14}C activities with high intra-colonial variations. All 27 tissue samples taken from each control colony of the 2 species outside of zone C did not reveal any translocation of labeled ^{14}C away from the labeled centers

Table 1. Average activity of ^{14}C [disintegrations per minute (DPM) cm^{-2} above background] in tissue fragments taken from various locations on the surface of *Favia favus* (n = 5) and *Platygyra lamellina* (n = 3). Tissues were taken from: S = area bordering small lesions, I = area bordering intermediate lesions, L = area bordering large lesions, C--S = axis between labeled center (C) and small lesions, C--I = axis between C and intermediate lesions, C--L = axis between C and large lesions, C--S/I = axis between C and area located between small and intermediate lesions, C--S/L = axis between C and area located between small and large lesions, C--I/L = axis between C and area located between intermediate and large lesions. Numbers in parentheses refer to sample sizes

Sample location	Coral no. 1	Coral no. 2	Coral no. 3	Coral no. 4	Control
***Favia favus* colonies**					
C	2807 ± 1295 (5)	417 ± 52 (5)	230 ± 139 (5)	4739 ± 1696 (5)	2819 ± 375 (5)
S	4 ± 2 (3)	9 ± 3 (3)	9 ± 3 (3)	6 ± 3 (3)	7 ± 1 (3)
I	4 ± 3 (3)	7 ± 4 (3)	5 ± 3 (3)	5 ± 3 (3)	7 ± 3 (3)
L	4132 ± 1702 (3)	126 ± 44 (3)	156 ± 78 (3)	2463 ± 931 (3)	8 ± 1 (3)
C--S	3 ± 2 (3)	6 ± 1 (3)	6 ± 1 (3)	7 ± 1 (3)	7 ± 1 (3)
C--I	7 ± 6 (3)	8 ± 2 (3)	3 ± 4 (3)	6 ± 6 (3)	7 ± 2 (3)
C--L	5078 ± 1935 (3)	219 ± 216 (3)	192 ± 7 (3)	5300 ± 2240 (3)	9 ± 2 (3)
C--S/I	5 ± 2 (3)	8 ± 4 (3)	5 ± 3 (3)	6 ± 3 (3)	10 ± 3 (3)
C--S/L	3 ± 3 (3)	9 ± 4 (3)	3 ± 2 (3)	5 ± 4 (3)	6 ± 2 (3)
C--I/L	5 ± 3 (3)	7 ± 1 (3)	2 ± 1 (3)	7 ± 2 (3)	7 ± 4 (3)
***Platygyra lamellina* colonies**					
C	286 ± 107 (5)	126 ± 76 (5)			1068 ± 409 (5)
S	4 ± 4 (3)	7 ± 5 (3)			3 ± 3 (3)
I	91 ± 31 (3)	174 ± 58 (3)			4 ± 3 (3)
L	303 ± 61 (3)	490 ± 253 (3)			2 ± 4 (3)
C--S	9 ± 8 (3)	3 ± 4 (3)			5 ± 2 (3)
C--I	1 ± 1 (3)	4 ± 4 (3)			7 ± 3 (3)
C--L	115 ± 32 (3)	178 ± 7 (3)			2 ± 3 (3)
C--S/I	3 ± 2 (3)	4 ± 2 (3)			6 ± 2 (3)
C--S/L	5 ± 2 (3)	3 ± 2 (3)			4 ± 2 (3)
C--I/L	5 ± 3 (3)	3 ± 2 (3)			5 ± 1 (3)

Table 2. Average ^{14}C activity (DPM cm^{-2} above background) in skeletons taken from various locations on the surface of *Favia favus* colonies. Coral numbers and sampled areas are as referred to in Table 1

Sample location	Coral no. 1	Coral no. 3	Coral no. 4	Control
C	24 ± 16 (4)	26 ± 18 (4)	21 ± 15 (4)	23 ± 20 (5)
S	2 ± 3 (3)	4 ± 3 (3)	6 ± 4 (3)	6 ± 3 (3)
I	3 ± 3 (3)	5 ± 3 (3)	4 ± 3 (3)	3 ± 2 (3)
L	2964 ± 40 (3)	492 ± 124 (3)	1970 ± 751 (3)	5 ± 3 (3)
C--S	4 ± 3 (3)	5 ± 2 (3)	5 ± 2 (3)	6 ± 3 (3)
C--I	5 ± 2 (3)	2 ± 3 (3)	5 ± 3 (3)	4 ± 2 (3)
C--L	4 ± 1 (3)	6 ± 2 (3)	2 ± 2 (3)	5 ± 2 (3)
C--S/I	3 ± 4 (3)	4 ± 2 (3)	5 ± 4 (3)	4 ± 3 (3)
C--S/L	5 ± 2 (3)	2 ± 1 (3)	6 ± 3 (3)	6 ± 3 (3)
C--I/L	2 ± 1 (3)	7 ± 4 (3)	4 ± 2 (3)	4 ± 2 (3)

(Table 1). On the other hand, tissues sampled from the injured colonies (*F. favus*, Coral nos. 1 to 4 and *P. lamellina*, Coral nos. 1 and 2; Table 1) demonstrated a significant ^{14}C labeling translocation towards tissues bordering the large lesion types (L, Table 1; ANOVA with repeated measures, $p < 0.001$). In addition, significant activity was recorded in the tissues sampled from the axis connecting the labeled centers (C) to the large lesions (C--L, Table 1; $p < 0.001$). In *P. lamellina*, in addition, significant activity was recorded in the tissues bordering the intermediate lesions (I, Table 1; $p < 0.001$) but insignificant activity was recorded along the corresponding axis connecting them with the centers (C--I, Table 1; $p > 0.05$).

The average activity (DPM cm^{-2} ± SD) of the skeletons, sampled from 4 ^{14}C labeled colonies of *Favia favus* are presented in Table 2. A technical problem prevented examination of the skeletons taken from the *Platygyra lamellina* colonies and from *F. favus* Coral no. 2. We recorded in all colony centers similar low amounts of ^{14}C activities (21 to 26 DPM cm^{-2}), yet statistically significant above backgrounds (Table 2; ANOVA with repeated measures, $p < 0.01$). In the control colony no deposition of ^{14}C was detected in any of the 27 skeletal samples taken from outside the labeled center. On the other hand, skeletal samples taken from the injured colonies (Corals no. 1, 3, and 4; Table 2) revealed ^{14}C incorporation into the skeleton bordering the largest lesion area (L, Table 2, ANOVA with repeated measures, $p < 0.001$). No ^{14}C deposition was recorded in any skeletal sample taken from the other locations (Table 2; for the specific locations see Fig. 2).

DISCUSSION

The paradigm for intra-colonial transport of organic compounds within hermatypic corals is not new (Pearse & Muscatine 1971, Taylor 1977), and Pearse & Muscatine (1971) have already proposed that symbiont photosynthates are translocated through the animal tissue and utilized in the region of maximal demand. Here, however, we document for the first time an oriented intra-colonial transport of ^{14}C labeled materials towards regenerating areas in corals. Since both examined coral species, *Favia favus* and *Platygyra lamellina*, exhibited the same pattern of oriented translocation towards the large lesions, it may be suggested that this is a ubiquitous phenomenon for regeneration in scleractinian corals. This supports Oren et al.'s (1997) hypothesis that the products required for recovery may be supplied by polyps located away from the injured area. Furthermore, the results presented here demonstrate the impact of the lesion size on the oriented translocation.

Despite a widespread recognition that some biological aspects of modular organisms differ from those of unitary organisms (Jackson et al. 1985, Harper et al. 1986), many fundamental aspects in modular organization are poorly understood. These aspects include the physiological integration of colonial invertebrates and the rate of interaction on the zooid as well as the colony level (Soong & Lang 1992, Harvell & Helling 1993). One aspect deals with colonial life history traits which may constrain phenotypic expressions, such as energy allocation during regeneration. Several studies (Bak et al. 1977, Bak & Steward-Van Es 1980, Bak 1983, Meesters et al. 1994, 1997) have suggested that energy for regeneration in hermatypic corals is mainly obtained from the polyps directly bordering the lesion area. We did not check this possibility directly. However, when small and large injuries were simultaneously inflicted, translocation of ^{14}C materials from a distance was recorded only for the large injuries, indicating that regeneration in the small lesions was supported by local resources.

In the areas of regeneration the translocated ^{14}C labeled materials are used metabolically, and part of the released ^{14}C is trapped into the newly deposited skeleton. *Favia favus* in Eilat is a massive slow growing coral (Shlesinger 1985), which might explain why only low amounts of ^{14}C were incorporated in the skeletons underneath the labeled centers 3 wk after labeling (Table 2). More interestingly, the outcome of high ^{14}C incorporation in the skeleton during regeneration, and hence high calcification rates during tissue regeneration, may indicate a need for calcium carbonate deposition at any time that new tissue is formed above a

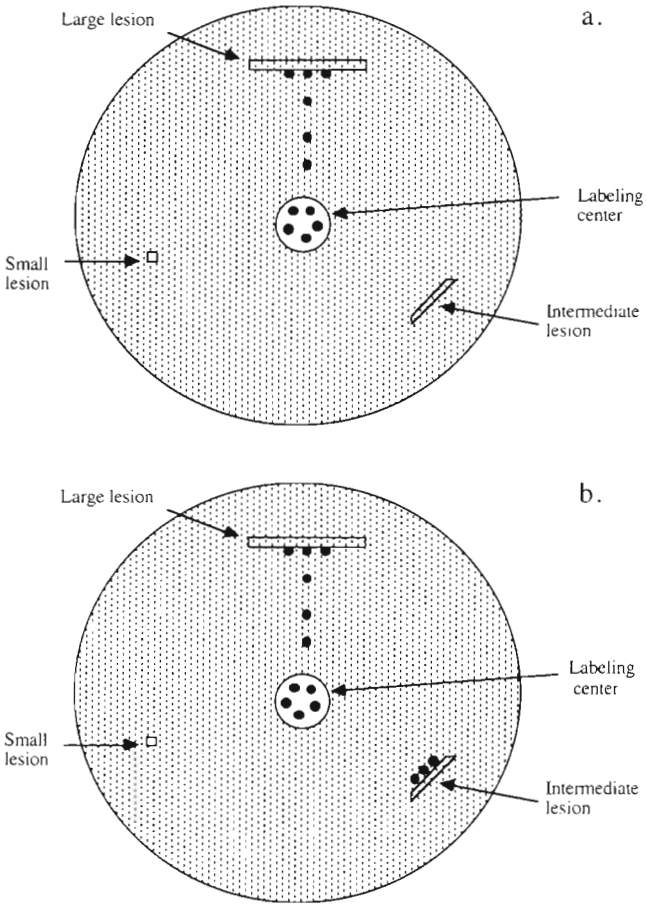

Fig. 3. Occurrence of ^{14}C materials in tissue samples taken from injured colonies of (a) *Favia favus* and (b) *Platygyra lamellina* 3 wk after labeling. (●) Locations where activity above background was recorded

bare skeleton area. The injuries imposed on experimental coral heads were created with the use of an air-pick fueled by the regulator, which clears the tissue causing minor skeleton damage. However, the large regenerating areas were also characterized by a significant skeleton deposition (Table 2).

Both examined species demonstrated a similar mode for ^{14}C material translocation in an oriented way, along an axis towards large lesions (Fig. 3a, b). Injured *Platygyra lamellina* colonies simultaneously translocated ^{14}C materials to a second locality, that of the intermediate lesion (Fig. 3b). This second axis of ^{14}C translocation differs from the first by the absence of ^{14}C materials in the tissue connecting the labeled center and the area of injury (Fig. 3b). It is possible that this route is secondary and only surplus materials are channeled to it. It is also possible that the different results for *P. lamellina* and *Favia favus* reflect 2 species-specific regeneration abilities (Bak et al. 1977, Bak & Steward-Van Es 1980, Bak 1983, Meesters et al. 1992) or 2 types of regeneration strategies in corals as suggested by Ruesink (1997).

The degree of integration of colonial animals has long been the focus of scientific interest (Hubbard 1973, Sandberg 1973, Rosen 1979, Ryland 1979, Chapman 1981, Harvell 1991, Soong & Lang 1992). The control (uninjured) colonies of both species did not translocate any labeled materials outside the labeled centers (Table 1). A similar result was previously recorded also in a branching coral (Rinkevich & Loya 1984). This may indicate that polyps in healthy colonies, under normal conditions, have enough energy resources for daily requirements. However, when injuries are significant, polyps from remote parts of the colony may be recruited to aid in the recovery process. Similar processes may occur as a response to a variety of environmental stresses.

Although this study provides evidence for the existence of an oriented translocation process towards regenerating lesions in corals, the triggers for this process, its mechanism and its dynamics remain unknown. In order to learn more about this intra-colonial translocation process follow up experiments testing for additional time scales and other labeling materials are required. Furthermore, we assume that by inflicting more lesion types at differing distances from the labeled centers we will be able to expand our knowledge on the magnitude of colony involvement during regeneration.

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