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Energy integration between the solitary polyps of the clonal coral *Lobophyllia corymbosa*

Itzchak Brickner[1], Uri Oren[1], Uri Frank[2] and Yossi Loya[1,*]

[1]*Department of Zoology, Tel Aviv University, Tel Aviv, Israel and* [2]*Department of Zoology and The Martin Ryan Marine Science Institute, National University of Ireland, Galway, Ireland*

*Author for correspondence (e-mail: yosiloya@post.tau.ac.il)

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Summary

Clonal integration in the coral *Lobophyllia corymbosa* was studied from two perspectives: transfer of carbon among clonemates and allorecognition. This coral forms colonies in the early post-metamorphic stages. In later ontogeny, the tissues interconnecting polyps die, transforming the colony into a clone of solitary polyps. These polyps continue to live in close proximity but without tissue continuity. Isolated polyps labeled with radioactive carbon in the light showed oriented transfer of assimilates towards adjacent, injured polyps. No significant transfer of carbon was observed towards intact, isogeneic polyps or allogeneic polyps. Grafting of coral tissues resulted in intra-clonal fusion, but only when polyps were previously sectioned. Allogeneic sectioned grafts were always rejected. Intact polyps were unresponsive towards isogeneic and allogeneic counterparts when grafted. Our results show that isolated *Lobophyllia* polyps not only recognize their clonemates as such, but also help them when necessary, although no tissue continuity exists between them.

Key words: *Lobophyllia*, integration, injury, allorecognition, ^{14}C-labeling.

Introduction

Marine clonal organisms are composed of repeated, genetically identical building blocks (e.g. polyps in cnidarians, zooids in bryozoans and colonial ascidians), which are asexually derived from a single, sexually derived founder polyp/zooid (Hughes, 1989; Hughes et al., 1992). Traditionally, two morphologically based growth forms are distinguished in clonal organisms: solitary and colonial. Solitary clonal organisms are morphologically discrete and physiologically independent. They are not interconnected by tissue. A colony, by contrast, is a physiologically united clone in which the individual modules (polyps/zooids) maintain prolonged tissue continuity, enabling them to exchange metabolites and cells through common tissues.

The within-colony degree of integration in hermatypic corals, the main tropical reef constructors, has long been the focus of scientific interest. Connell reported that large colonies have a better capacity to heal injuries than smaller ones of the same species (Connell, 1973). Loya found that skeletal regeneration restores the symmetry of the original colony shape (Loya, 1976). Wallace noted that in some coral species fertile polyps are distributed unevenly within the colony (Wallace, 1985). Kojis and Quinn (Kojis and Quinn, 1985) and Szmant-Froelich (Szmant-Froelich, 1985) showed that the number of polyps in a colony, rather than colony age, is the primary threshold determining reproductive stage in many colonial corals. Shelton documented that polyp retraction is coordinated within colonies in some corals (Shelton, 1982). Oren and coworkers found that regeneration of injury in *Porites* colonies activates an extended magnitude of energy integration throughout the colony and that the extent of this integration is regulated by the colony, in accordance with lesion characteristics (Oren et al., 2001).

Carbon transfer between sources and sinks within colonies has been documented (Pearse and Muscatine, 1971; Rinkevich and Loya, 1983a; Rinkevich and Loya, 1983b). Taylor hypothesized that soluble organic compounds and Ca^{2+} are translocated among polyps, probably towards regions of maximal demand (Taylor, 1977). This early idea has since been experimentally confirmed by Oren and coworkers, who demonstrated an oriented intra-colonial transport of ^{14}C-labeled photosynthetic products towards regeneration areas in the hermatypic corals *Favia favus*, *Platygyra lamellina* and *Porites* sp. (Oren et al., 1997; Oren et al., 1998), and by Fine and coworkers in the encrusting stony coral *Oculina patagonica* from the Mediterranean (Fine et al., 2002).

Another aspect of colony integration is that of histocompatibility: in colonial coral species, separated clonemates fuse when recontacted even after being isolated for

years. Allogeneic (interclonal) grafts, by contrast, always fail to fuse (Hildemann et al., 1977).

The above studies provide evidence that colonial corals show a certain degree of recognition and cooperation among the individual polyps that may outweigh the 'interest' of a single polyp. The situation in solitary corals is less clear. Integration among solitary clonal cnidarians has been studied in the sea anemone *Anthopleura elegantissima*, which often remains associated as dense aggregations. Within-clone polymorphism and division of labor have been demonstrated in this species (Ayre and Grosberg, 1996). Histocompatibility or other forms of clonal recognition are well documented in solitary clonal cnidarians (e.g. Jokiel and Bigger, 1994). However, translocation of energetic products between clonemates in solitary forms has not, as yet, been studied.

Lobophyllia corymbosa Forskål is a common inhabitant of shallow-water coral reefs in the northern Red Sea. This clonal coral starts its post-metamorphic life as a colony (Fig. 1a). Later, the tissues connecting individual polyps die, transforming the colony into a clone of solitary polyps (Fig. 1b,c). Clonemates, previously belonging to a single colony, usually remain associated, occupying the numerous extremities of one skeleton (corallum). Although separated, occasional, temporal tissue contact between the individual polyps may occur during the night, when polyp body columns expand (i.e. broaden). These contacts do not result in tissue fusion (Fig. 1d).

This transformation from a colony to a clone of solitary polyps represents a unique model system to study aspects of integration in clonal organisms, to which we addressed the following question: do *Lobophyllia* polyps undergo only a morphological, or also a functional, change following separation? In order to answer this question we studied allorecognition and translocation of photosynthetic products between isolated *Lobophyllia corymbosa* polyps.

Materials and methods

Study site

The study was carried out on the shallow-water coral reef (3–5 m) in front of the Interuniversity Institute of Marine Science at Eilat (Red Sea). In the course of the study we tagged 15 intact *Lobophyllia* clones *in situ*.

Allorecognition assays

Fifty-two polyps from 14 clones whose polyps have already undergone tissue separation were removed from their original corallum. Fourteen intact polyp pairs were prepared: seven isografts and seven allografts. They were pair-wise fastened by insulated copper threads, bringing them into direct and permanent tissue-to-tissue contact. We then longitudinally sectioned 24 polyps, ensuring that each section contained a portion of the original mouth. Pair-wise grafts were then prepared from sections of the same polyp (autografts) (*N*=4), clonemates (isografts) (*N*=6) and non-clonemates (allografts) (*N*=14). Graft terminology was adopted from Jokiel and Bigger's work on the solitary mushroom coral *Fungia* (Jokiel and Bigger, 1994). The results of all grafting experiments were evaluated after 6 weeks and documented in terms of tissue fusion, skeleton fusion, no response, cytotoxic rejection and tissue overgrowth. Two isografts and two autografts were fixed in 4% formalin in seawater (24 h) for histological examination. Following fixation, samples were rinsed in tapwater, decalcified in formic acid/sodium citrate solution, dehydrated in ethanol

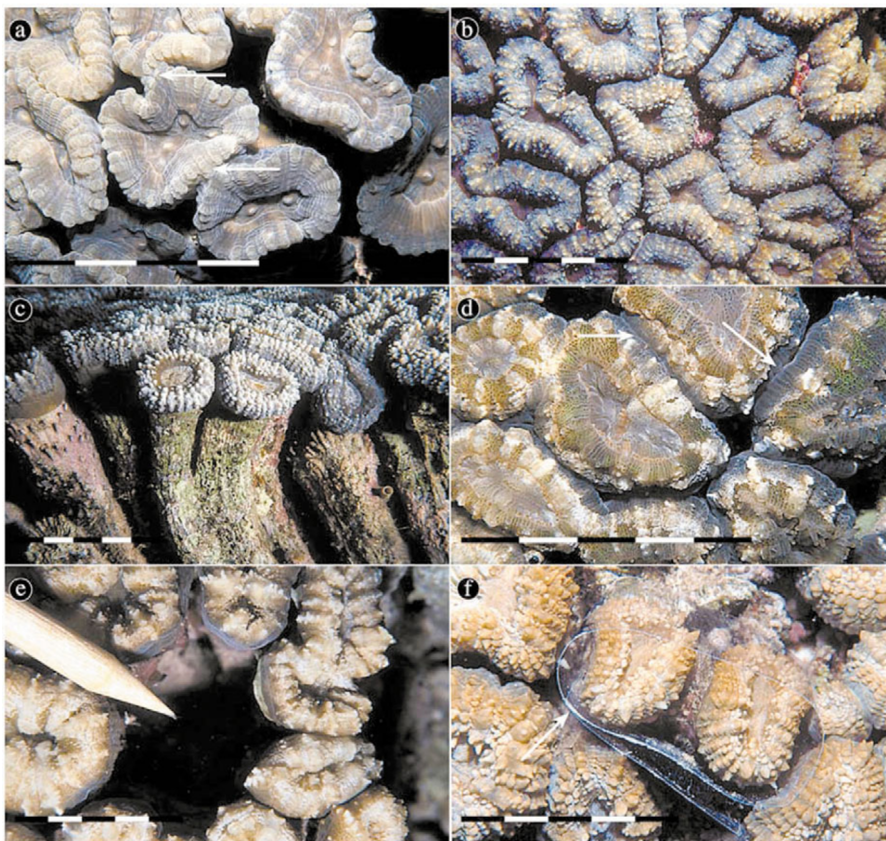

Fig. 1. *Lobophyllia corymbosa* clones. (a) Post-budding stage characterized by tissues connecting between individual polyps (see white arrows); these connecting tissues later die, transforming the colony into a clone of solitary polyps (b,c). (d) During the night, polyp body columns expand, causing intra-clonal contacts between individual polyps (see white arrows). (e) The center of a clone from which an intact polyp was removed for ^{14}C-labeling. (f) 'Hot' polyps wrapped with a plastic collar, reattached in their original clone. Scale bars, 5 cm.

series, embedded in paraffin, sectioned and stained with hematoxylin and eosin using standard protocols.

Energy integration

In order to examine possible energy integration within clones of *Lobophyllia corymbosa*, we conducted three different ^{14}C-labeling treatments as follows. For isogeneic experiments, one intact polyp was removed from the center of seven different *Lobophyllia* clones (Fig. 1e). These polyps were brought to the laboratory for a period of 24 h during which they were labeled with ^{14}C (see protocol below). After this period, each 'hot' polyp was returned to the sea and fixed back into its original spot in its original corallum. For allogeneic experiments, one intact polyp was taken from the center of six other *Lobophyllia* clones. After 24 h of ^{14}C-labeling, these hot polyps too were returned to the sea; however, in contrast to the first treatment, each polyp was reallocated into a different, allogeneic corallum (i.e. hot polyps were switched between the clones). Additionally, two central polyps from two different *Lobophyllia* clones were removed, labeled with ^{14}C and returned to the sea, where they were fixed back into their original spot in their original corallum. In contrast to the first treatment, however, both these hot polyps were wrapped with a plastic collar that prevented any tissue contact with neighboring polyps in the clone (Fig. 1f).

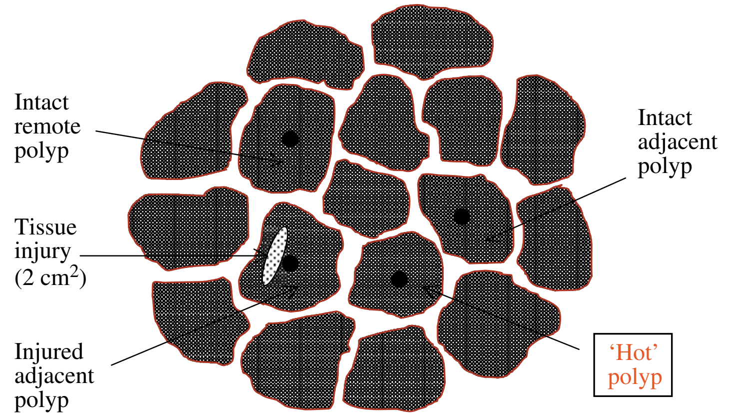

Fig. 2. A schematic diagram of the ^{14}C-labeling and sampling locations in *Lobophyllia corymbosa* clones. Forty-eight hours after reattachment of the 'hot' polyp to the experimental clones, we sampled four fragments (marked as black circles) from each clone, using a round stainless-steel corer that enabled collection of similar-sized fragments (1 cm^2 each). One fragment was taken from the 'hot' polyp, one from the injured polyp adjacent to the hot polyp (injury size, 2 cm^2), one from an intact polyp also adjacent to the hot polyp, and one from an intact remote polyp. ^{14}C activity in the tissues of each fragment was determined by liquid scintillation counting.

^{14}C-labeling of the polyps was conducted in 4-liter aquaria placed in a radioactive hood. The aquaria were illuminated for a period of 20 h (400–700 nm) to enable active photosynthesis and high ^{14}C incorporation (final concentration of the radioactive carbon in the aquaria was 0.2 μCi ml^{-1}). Following this labeling procedure, the polyps were transferred to another similar sized aquarium in which they were washed with seawater for a period of four hours.

Recent studies have shown that oriented transport of photosynthetic products within colonial corals is initiated following tissue injuries (Oren et al., 1997; Oren et al., 1998; Fine et al., 2002), already detectable 48 h post-injury. Therefore, after attaching each hot polyp to its appropriate corallum, we injured one of its adjacent polyps. These small tissue lesions (projected area of approximately 2 cm^2) were inflicted by air-pick (i.e. an air tube connected to the SCUBA regulator enabling a strong accurate air jet, which locally removes the tissue, causing only minor damage to the skeleton beneath). A schematic representation of the experimental setup is given in Fig. 2. In addition to the above treatments, three polyps from three different clones were similarly labeled with ^{14}C. These polyps were kept in the lab for an additional period of 48 h and thereafter used to determine ^{14}C activity in their released mucus.

Forty-eight hours after reattachment of the hot polyp to the experimental clones, we sampled four fragments (tissue + skeleton) from each clone using a round stainless-steel corer, enabling collection of similar sized fragments (1 cm^2 each, presuming similar tissue thickness in all polyps). One fragment was taken from the hot polyp, one from the injured polyp adjacent to the hot polyp, one from an intact polyp also adjacent to the hot polyp, and one from an intact remote polyp (for sampling locations, see Fig. 2). The fragments were placed individually in plastic vials and brought to the lab. The seawater was drained from each vial and 8 ml of 30% hydrogen peroxide was added in order to digest the tissues. After complete digestion (24 h), the remaining skeletons were removed and two replicates of 0.5 ml from each vial were sampled. Five milliliters of Biodegradable Counting Scintillation cocktail (BCS; Amersham, Bucks, UK) were added to each sample. Activity of ^{14}C in the tissues (c.p.m. cm^{-2}) was determined by a liquid scintillation counter (Tri-Carb 1500; Packard, Bowners Grove, IL, USA). Examination of ^{14}C activity in the mucus was performed by attaching a filter paper to the lateral side of the labeled polyps for a period of 30 s. The filter papers were added to 5 ml of Biodegradable Counting Scintillation cocktail and their ^{14}C activity (c.p.m. cm^{-2}) was determined by a liquid scintillation counter.

Results

Allorecognition assays

No visible response was observed in any of the 28 grafted intact polyps. These polyps neither fused with nor rejected their isogeneic or allogeneic counterparts. Following removal of the copper threads, the grafts fell apart, with only slight signs of mechanical damage at points of contact.

The results from the grafting experiments involving sectioned polyps showed different patterns, as follows: all auto- and isografts had fused completely by tissue and skeleton

Table 1. ^{14}*C activity in Lobophyllia tissues*

	^{14}C activity (c.p.m. cm^{-2})			
Experiment	Labeled polyps	Injured adjacent	Intact adjacent	Intact remote
Isogeneic (*N*=7)	17688.5±9657	433.64±459.76	35.42±12.06	23.285±2.49
Allogeneic (*N*=6)	4835±2343.61	26.66±6.21	25.66±7.21	23.833±7.09
Isogeneic + plastic (*N*=2)	2552.75±297.09	24.5±7.54	28.75±10.30	23.75±5.73

Values are means ± s.d.

Labeled, isogeneic polyps were placed back into their original corallum; labeled, allogeneic polyps were placed into allogeneic corallum; labeled + plastic polyps were wrapped with a plastic collar and placed back into their original corallum.

within the 6-week study period. Histological sections of fused partners confirmed the continuity of their tissues across the original contact area. By contrast, none of the allografts had fused. Instead, they either remained in a non-responsive state, healing the wounds caused by the sectioning, or cytotoxically rejected their allogeneic confreres using an unknown effector mechanism.

Energy integration

Forty-eight hours after reattaching the ^{14}C-labeled polyps to their original clone, the hot polyps showed high ^{14}C activity (>2000 c.p.m. cm^{-2}; Table 1). Tissues taken from the injured adjacent polyps demonstrated significantly higher ^{14}C activity compared with tissues taken from intact control clones (1-way ANOVA, $P<0.01$). By contrast, tissues taken from adjacent, healthy polyps (Fig. 2) exhibited ^{14}C activity similar to the control tissues (1-way ANOVA, $P>0.05$).

When hot polyps were wrapped with a plastic collar before being reattached to their original clones (i.e. treatment 3; Fig. 1) they demonstrated no significant translocation to any of their adjacent polyps (i.e. both healthy and injured) (Table 1).

When hot polyps were introduced into allogeneic *Lobophyllia* colonies, the ^{14}C activity of the tissues sampled from injured adjacent, healthy adjacent and healthy remote polyps indicated insignificant shifts of photosynthetic products towards them (1-way ANOVA, Scheffe *F*-test, $P>0.05$). That is, their tissues exhibited ^{14}C activity similar to tissues taken from intact control clones. High ^{14}C activity was recorded in the mucus of the labeled polyps 48 h after labeling.

Discussion

We have studied clonal integration in the phaceloid reef-building coral *Lobophyllia corymbosa* from two perspectives: (1) the ability of isolated polyps to recognize their clonemates' tissues as 'self' and (2) the translocation of metabolites towards areas of high demand (here, injured polyps). The results of the two sets of experiments clearly show that, although growing separately, *Lobophyllia* polyps not only recognize their clonemates as such (known from other solitary corals too) but also directly 'help' them when necessary despite the lack of a common coenosarc. The latter finding has not been documented in any other solitary clonal organism and is especially surprising.

Allorecognition assays showed that *Lobophyllia* does not differ from other clonal invertebrates in this regard: genetically identical animals repeatedly recognize their clonemates as 'self', while allogeneic individuals are treated as foreign and rejected. The results of the transplantation experiments resemble those of experiments done with the solitary clonal coral *Fungia* (Jokiel and Bigger, 1994). Contact between intact polyps usually resulted in no visible response (independent of the genetic identity of the counterparts), while cut polyps fused only with (cut) clonemates, rejecting allografts. These results also indicate that the separation of polyps during ontogeny is genetically programmed rather than environmentally induced, since intact polyps 'insisted' on maintaining their solitary state rather than fusing with clonemates and re-forming a colony. Contact between cut polyps may be interpreted as regeneration, in which only clonemates' tissues are accepted as 'tissue donors'.

The results of the radioactive experiments showed a significant and oriented translocation of photosynthetic products from the labeled polyps towards the adjacent injured polyps in *Lobophyllia* clones. These results resemble previous studies done on 'genuine' colonial corals with developed coenosarc, such as the massive stony corals *Favia favus, Platygyra lamellina* (Oren et al., 1997) and *Porites* sp. (Oren et al., 1998) and the encrusting stony coral *Oculina patagonica* (Fine et al., 2002). *Lobophyllia* forms a colony only in early ontogeny and directly following budding, whereas the adult coral constituted a cluster of separated polyps without interconnecting tissue (I.B., personal observation). Nonetheless, *Lobophyllia* clonemates displayed here a typical 'colonial' behavior in regard to energetic collaboration.

One of the questions arising from our results is that of the mechanism of transfer of photosynthetic materials among these separated polyps. Translocation of organic compounds between polyps could result from diffusion down a concentration gradient (Murdoch, 1978; Fang et al., 1989) or from active (i.e. oriented) transport (Rinkevich and Loya, 1983a; Fang et al., 1989; Oren et al., 1997). In the present study, active, oriented transport was evident, as significantly less labeled material was transferred to healthy clonemates and to injured allogeneic polyps, compared with translocation to

injured clonemates. How are the metabolites transferred in an oriented way without an existing tissue bridge? We suggest two possibilities, which may apply to *Lobophyllia*. (1) The material is transferred in the form of mucus. As can be seen from the results, part of the photosynthetic production was channeled toward mucus production, and coral mucus has recently been shown to have a significant role in the carbon household in coral reefs (Wild et al., 2004). Mucus may be moved across the coral's surface by ciliary beat, which, in turn, could be oriented. (2) The material is transferred in living, migrating cells when polyp body columns touch at night (Fig. 1). A combination of the two modes, i.e. transfer of cell-containing mucus, is also possible. Mucus alone would constitute rather a 'poor aid' due to its low nutritional value. Cells offer a more complete resource for regeneration. Migratory cells may be transferred through mucus when body columns contact at night. Indeed, preventing physical contact by means of the plastic collar eliminated the transfer of radioactivity and fits both modes of transfer.

Interestingly, in the coral *Stylophora pistillata*, Rinkevich and Loya documented oriented translocation of photosynthetic metabolites among allogeneic, incompatible colonies, also without a tissue bridge between source and sink tissues (Rinkevich and Loya, 1983a). These authors interpreted their results as competition, with the direction of transport being from the inferior colony towards the dominant one. Although transport of energy *via* cells is possible also in this case, there is a basic difference in our study as follows. Movement of cells among clonemates enables incorporation of living cells in the recipient's soma. This would not be possible among distinct genotypes since allogeneic cells would have likely been rejected by the recipient's allorecognition system. Hence, among allogeneic partners, donor cells could only be used as 'food' following phagocytosis by the recipient's cells. Olano and Bigger have reported that phagocytic activity increases following wounding in the gorgonial coral *Swiftia exserta* (Olano and Bigger, 2000). Allogeneic interaction may be interpreted as 'stress', similar to wounding, which could stimulate phagocytosis of allogeneic cells.

Previous workers have attempted to make connections between the colony structure, pattern of vegetative reproduction and degree of integration existing in a colony. Branching structures, polymorphic polyps, perforations in walls and well-developed coenosarc are among the morphological characters that indicate integration in coral colonies (Ryland and Warner, 1986; Soong and Lang, 1992). In the present study, a high degree of integration was found in *Lobophyllia* clones, as revealed by the translocation of photosynthetic products towards injured clonemates only, despite no tissue bridge existing between the polyps and the lack of any other morphological indication for integration.

Why should a coral colony select to transform into a clone of solitary polyps? 'True' colonial growth form may offer better physical conditions for transfer of metabolites and cells (we could only demonstrate translocation to adjacent polyps, in contrast to long-distance transfer in colonial species). A continuous tissue may also facilitate communication between clonemates. A solitary life strategy, by contrast, may offer a better protection against pathogens, which cannot (or can less easily) infect clonemate polyps living without tissue bridges. Furthermore, the formation of a clone of disconnected polyps also facilitates the dispersal of the genotype in space. This has also been shown in fungiid mushroom corals, where the detachment of polyps from the colony occurs earlier in ontogeny. *Lobophyllia corymbosa* seems to combine the two strategies: in early post-metamorphic stages, a high degree of integration is necessary to increase survival chances (see also Shenk and Buss, 1991). In line with this, *Lobophyllia* indeed forms colonies at this stage. Later on, survival of polyps (and of the whole clone) is less dependent on common tissues and the coral takes advantage of its solitary growth form as a better protection against pathogens and more efficient dispersal. As demonstrated here, however, intra-clonal aid is still possible among morphologically isolated clonemates.

Taken together, our results show that integration among clonal marine invertebrates does not necessarily depend on structure but can also be maintained between separated clonemates. Examining the structure of coral reef communities from this point of view may provide a new perspective regarding energy shifts within this highly complex ecosystem.

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