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Allorecognition responses in the soft coral *Parerythropodium fulvum fulvum* from the Red Sea

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Abstract

Allogeneic encounters were experimentally arranged in Eilat, Red Sea for the first time in the Alcyonacea with the soft coral *Parerythropodium fulvum fulvum*. All possible pairwise combination assays within two groups of five colonies each and one group of three colonies were setup in situ in 2–4 replicates each (a total of 76 assays). Control isogeneic encounters always resulted in complete tissue fusion. Two types of allogeneic responses were documented following tissue-to-tissue contacts. The first was retreat growth, in which contacting allografts started to retreat from each other a few days following direct contact until a bare area of a few mm separated them. In several assays the colonies repeatedly grew into contact and retreated again. The second allogeneic response was unilateral or reciprocal tissue overgrowth. In this type of response one colony overgrew the conspecific partner by several mm and then stopped. The underlying tissue of the overgrown partner died. No cytotoxicity was observed in allogeneic contacts either in growing parts or when assays were established between cut surface areas. Repeated assays of the same pair-combination were not consistent in terms of type and directionality of responses. We propose that effector mechanisms elicited following allogeneic encounters in *P. f. fulvum* may be affected by biological as well as non-biological parameters and are not specific to the type of allogeneic challenge. However, colony specificity in this species is restricted only to the level of self- and non-self discrimination.

Keywords: Coral; Alcyonacea; Intraspecific competition; Histocompatibility

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1. Introduction

Allorecognition, the capacity to discriminate between 'self' and 'nonself' is already documented for more than 40 species of colonial cnidarians (Leddy and Green, 1991). The recognition of self is always followed by operational compatibility in the form of tissue fusion (Bak and Criens, 1982; Rinkevich and Loya, 1983; Chadwick-Furman and Rinkevich, 1994; Frank and Rinkevich, 1994; Rinkevich et al., 1994), while recognition of nonself is usually characterized by the expression of antagonistic responses of various types between allogeneic counterparts (Hildemann et al., 1977; Lang and Chornesky, 1990; Leddy and Green, 1991). True tissue fusions between allogeneic adult colonies are not common in the Cnidaria, although they have been documented in the Hydrozoa (Hauenschild, 1954, 1956; Buss et al., 1985; Shenk, 1991; Frank and Rinkevich, 1994).

Most histocompatibility related studies in the Cnidaria (reviewed by Leddy and Green, 1991) have been carried out on scleractinian corals (Potts, 1976; Hildemann et al., 1977; Bak and Criens, 1982 Rinkevich and Loya, 1983; Lang and Chornesky, 1990; Chadwick-Furman and Rinkevich, 1994; Rinkevich et al., 1994), hydrozoans (Hauenschild, 1954, 1956; Ivker, 1972; Müller et al., 1983; Buss et al., 1984, 1985; Bosch and David, 1986; Lange et al., 1989; Frank and Rinkevich, 1994) and gorgonians (Theodor, 1970; Theodor and Senelar, 1975; Theodor, 1976; Bigger and Runyan, 1979; Lasker and Coffroth, 1985; Salter-Cid and Bigger, 1991). Little is known, however, about allogeneic responses in soft bodied alcyonaceans. This is surprising in view of the many published studies on allelopathy in this group during xenogeneic encounters (e.g., Coll et al., 1982; Sammarco et al., 1983; La Bare et al., 1986).

In the field, many soft corals grow in direct contact with conspecifics, apparently without eliciting any visible allogeneic responses (pers. observ.). In addition, no experimental documentation on the existence of isogeneic and/or allogeneic tissue fusion in the Alcyonacea is yet available. The aims of this study are to find out if soft corals distinguish between self and nonself and how the integrity of self is maintained in this group. We describe in detail, for the first time in the Alcyonacea, the existence of historecognition in the encrusting Red Sea soft coral *Parerythropodium fulvum fulvum*, as expressed by allogeneic responses to conspecifics.

2. Methods

2.1. Location of study and experimental organism

All underwater work was carried out at the fringing coral reef in front of the H. Steinitz Marine Biology Laboratory, Eilat, Red Sea (29°N, 35°E), at a depth of 5–20 m using SCUBA.

The octocoral *Parerythropodium fulvum fulvum* (Forskål) is a common encrusting species in the coral reefs of the northern Gulf of Eilat (Benayahu and Loya, 1977). It occurs in two color morphs, brown-yellow and gray, which exhibit the same reproductive patterns and growth forms and are thus considered to comprise a single species

(Verseveldt, 1969; Benayahu and Loya, 1983). Allogeneic contacts in the field are frequent in this species (pers. observ.).

2.2. Experimental setup

We chose 13 large *Parerythropodium fulvum fulvum* colonies (assigned letters A–M), three of the gray morph (A–C) and ten of the yellow-brown morph (D–M). The colonies were encrusting on metallic or concrete artificial substrata. In a preliminary study we found that peeling colonies from artificial substrata was relatively easy, less stressful to the sampled colonies or subclones and provided clean fragments without attached substratum remnants. Small, approximately square pieces (ca. 4 × 4 cm), were cut from the periphery of the colonies with sharp scalpel blades, in such a way that resulted in two cut surfaces and two natural growing edges for each subclone. They were carefully peeled off the substrata and immediately attached in pairs to 5 × 7.5 cm glass slides by 5–10 wraps of cotton sewing thread per colony fragment. The colonies were put in direct contact at the same plane, both well attached to the glass slide, or one overlying the other by < 1 mm. The slides were hung vertically in situ by plastic clips from horizontally stretched nylon cords at a depth of 7–10 m. All assays were observed in situ daily for the first 3–4 days and thereafter every 10–15 days for up to 10 weeks.

The 13 colonies were divided into three groups: Group 1 (effects of cut vs. growing edges; colonies A–E), Group 2 (effect of overlay; colonies F–J) and Group 3 (effect of secondary contact; colonies K–M). All possible pairwise combinations of colonies within each group were assayed (allogeneic assays of colonies from different groups were not carried out). In Group 1, each allogeneic pair combination was set up at the same plane in four morphological positions: cut surface vs. growing edge (and the opposite position), cut vs. cut surfaces and growing edge vs. growing edge (one replicate for each position, total of 40 assays). In Group 2, colonies were set up in 3 replicates of each allogeneic combination (cut surfaces vs. cut surface: 30 assays): in two replicates of each combination in this group, the cut surface of one colony was overlaying the other colony, respectively and in the third, both fragments were at the same plane. In Group 3, two replicates of each pair combination (6 assays) were put in contact at the same plane (cut surface vs cut surface) and after retreating from each other, they were brought again into tissue-to-tissue contact. Five pairs of isografts were set up, one replicate each from colonies of Group 1: Two cut surface isografts (colonies A, B), cut surface vs. growing edge (colony C) and growing edge vs. growing edge (colonies E, F). An additional 15 isografts were established from other colonies.

2.3. Histology

Contacting tissues from pairs on the glass slides were fixed in 2.5% glutaraldehyde in filtered sea water for 3–4 hours at room temperature. Samples were then rinsed in running tap water for about 30 min and decalcified in a formic acid/sodium citrate solution (Rinkevich and Loya, 1979). After the completion of decalcification, samples were rinsed in double distilled water, dehydrated by ethanol and embedded in glycol

methacrylate plastic. Thin sections (1–2 μm) were prepared using glass knives and stained with hematoxylin and eosin (Bancroft et al., 1990).

3. Results

3.1. Effects of experimental manipulations

The two exposed cut surfaces on each *Parerythropodium fulvum fulvum* subclone, in both isogeneic and allogeneic encounters, healed completely within 1–2 days. They could no longer be distinguished from the other two uncut growing edges. The cutting wounds were sealed within 12 hours following their removal from the 'parent' colony. Allogeneic pairs of *P. f. fulvum* revealed two types of effector mechanisms (see below). No visible effects on the outcomes of interaction, in terms of time scale, type of response or directionality, were observed between different setup positions of cut surfaces vs. uncut growing edges in repeated assays of the same colony combinations (Table 1). The cotton threads, which held the subclones to the glass slides, were found to be covered by the coral tissue within several days (Fig. 1). Fastening of coral tissue by cotton threads, therefore, did not appear to have any visible detrimental effect on the colonies. However, when the threads were put very close to each other (< 3 mm) they caused local tissue degeneration and necroses.

3.2. Isogeneic encounters

All 20 isograft assays resulted in complete fusion within 2–3 weeks following tissue to tissue contact (Fig. 2). The first evidence for fusion appeared within several days as thin tissue filaments connecting the two isogeneic subclones. This was succeeded by the development of a connecting, light-coloured (due to the fewer numbers of zooxanthella

Table 1
Allogeneic responses in ten colony combinations (colonies A–E) two weeks after first contact

Allogeneic combination	Setup position of allogeneic partner			
	CS vs CS	GE vs GE	CS vs GE	GE vs CS
A vs B	A < > B	A < > B	A < > B	A < > B
A vs C	A > C	A < > C	A < > C	A < > C
A vs D	A*D	A*D	A > D	A > D
A vs E	A < E	A*E	A*E	A < E
B vs C	B < C	B > C	B < C	B > C
B vs D	B < D	B < D	B < D	B < D
B vs E	B < > E	B < > E	B < > E	B > E
C vs D	C < D	C > D	C*D	C*D
C vs E	C > E	C > E	C > E	C < E
D vs E	D*E	D > E	D < E	D > E

Colonies were aligned in the same plane. CS = cut surface position; GE = growing edge position; < or > = overgrowth directionality; < > = reciprocal overgrowth; * = retreat growth
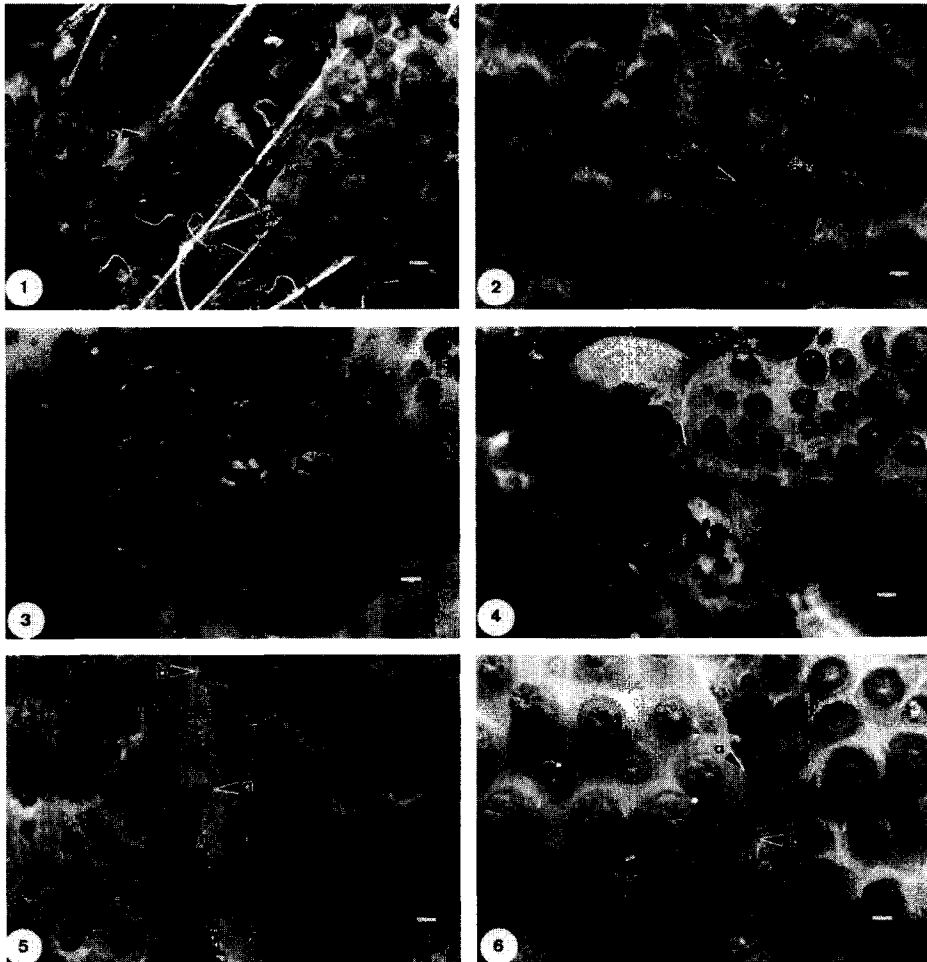
Fig. 1. A retreat growth phenomenon between two *Parerythropodium fulvum fulvum* colonies two weeks after first contact. Cotton threads which were used for fastening the colonies are (a) exposed in retreated areas or (b) covered by coral tissue. Scale bar approximately 2 mm.

Fig. 2. Fusion between isogeneic subclones two weeks following contact. Arrowhead points to the original contact area. Scale bar approximately 2 mm.

Fig. 3. Allelopathic interaction. *P. f. fulvum* growing around *Xenia macrospiculata*. Scale bar approximately 2 mm.

Fig. 4. Unilateral overgrowth of one colony over another. Arrowhead points to the edge of the overgrowing colony. Scale bar approximately 2 mm.

Fig. 5. Reciprocal overgrowth of two allogeneic colonies. Right colony overgrowing the left one (a) and vice versa (b). Scale bar approximately 2 mm.

Fig. 6. Unilateral overgrowth followed by retreat growth. Arrowheads point to (a) the edge of the overgrowing colony and (b) the damaged tissue of the overgrown colony. Scale bar approximately 1 mm.

Table 2
Allogeneic responses in ten colony combinations (colonies F–J) two weeks after first contact

Allogeneic combination	Setup position of allogeneic partners		
	Left over right	Right over Left	Same plane
F vs G	F > G	F < G	F*G
F vs H	F > H	F < H	F < H
F vs I	F > I	F < I	F*I
F vs J	F > J	F < J	F < J
G vs H	G > H	G > H	G > H
G vs I	G > I	G < I	G > I
G vs J	G > J	G < J	G > J
H vs I	H > I	H < I	H > I
H vs J	H > J	H < J	H*J
I vs J	I > J	I < J	I*J

Each combination was set up in three morphological positions: Left partner overgrowing right partner, right overgrowing left, and both at the same plane. < or > = overgrowth directionality; * = retreat growth

cells in the growing edges), layer of tissue within 10–14 days. Polyps within the fused area appeared only 1–2 weeks later when the borderlines demarcating the two subclones had vanished. Additionally, we observed > 100 naturally occurring isogeneic contacts of *P. f. fulvum* colonies growing on flat surfaces. Encrusting colonies usually bypass other encountered organisms (such as the branching coral *Stylophora pistillata*; Rinkevich et al., 1993) or other upright obstacles by growing around them (Fig. 3). The growing edges, when in contact, always fuse, forming a continuous and homogeneous layer of coral tissue.

3.3. Allogeneic encounters

In contrast to the outcomes of the isogeneic assays, no fusion was recorded within the 76 allogeneic pairs (Table 1, Table 2 and Table 3). Two types of allogeneic responses were observed following allogeneic contacts. The first was the retreat growth phenomenon in which contacting colonies withdrew from each other until a bare area of several mm separated between them (Fig. 1). This situation was usually static for at least several weeks. In some cases other parts of the same subclones grew again towards each other

Table 3
Allogeneic responses between colonies K–M two weeks after first contact, and after manually recontacting following retreat growth (second contact)

Allogeneic combination	Allogeneic response following	
	First contact	Second contact
K vs L	K*L (2)	K*L (2)
K vs M	K*M (2)	K*M (2)
L vs M	L*M (2)	K < M (2)

until new tissue contacts were formed. All new contacts retreated again as before or overgrew each other. No visible sign of tissue mortality was observed in this type of response. The retreat growth phenomenon was documented as a primary response in 14 pairs out of 76 (18.4%) distributed between 11 allogeneic combinations out of 23 (48%) (Table 1, Table 2 and Table 3). In all other combinations, retreat growths were documented as a secondary response following overgrowth (data not shown). The retreat growth phenomenon was not influenced by the setup position of allogeneic partners (Table 1). However, when one of the partners was in overlaying position, neither one of the allogeneic colonies retreated (0% out of 20 pairs as compared to 22% out of 50 pairs positioned on the same plane; Table 1, Table 2).

The second type of allogeneic response was an overgrowth response (Fig. 4, Fig. 5 and Fig. 6), which was not consistent in directionality between most given pair combination. We documented reciprocal overgrowths between different replicate pairs of the same combination and even within the same assays (Fig. 5; Table 1, Table 2). A reproducible overgrowth directionality of one colony over its counterpart was observed only in two allogeneic combinations (BD and GH; Table 1, Table 2). In Group 2 (20 assays), where the colonies were set up in overlying positions, in 19 cases (95%; Table 2) the directionality of the overgrowths continued to be the same as the initial setup position, irrespective of the allogeneic combination. In all assays that resulted in overgrowth, tissue advanced to a distance of 3–5 mm over the other partner within the first 10–15 days and then stopped for a period lasting from several days to two weeks. The overgrown tissue degraded during this period, leaving behind dead tissue remnants and exposed spicules under the overgrowing tissue (Fig. 6, Fig. 7). Thereafter, the overgrowing colony retreated or remained in close contact with the living tissue of the other partner without any further visible response. After a period of static retreat growth, which varied from 1–3 weeks, we observed several cases of secondary contacts that were formed between the two colonies by other advancing growing edges. In these secondary contacts, the directionality of overgrowth was sometimes inverted. Colonies of Group 3 all expressed the retreat growth phenomenon (Table 3). Several days after they had retreated, they were brought into secondary contact by manipulation on the slide. Two assays again developed the retreat growth, while one (LM) resulted in overgrowth (M over L). We also observed naturally occurring overgrowths between *P. f. fulvum* colonies in situ. In these cases the overgrowing colonies advanced up to 15 mm but all other outcomes were the same, i.e., the overgrowing colony retreated leaving behind dead tissue of the overgrown partner (data not shown).

Histological sections revealed gradual tissue degeneration in the overgrown parts (Fig. 8 and Fig. 9). Tissue death first started at the original contact area (which was the first to be overgrown) and spread posteriorly. No sign of cell death was found in non-overgrown parts of the same subclones, even in close proximity to the overgrowing tissue. In several assays the two colonies overgrew each other reciprocally, leaving scars of dead tissues and exposed spicules on the overgrown parts.

None of the two common colour morphs of *P. f. fulvum* (the brown-yellow and the grey; Benayahu and Loya, 1983) was found to be consistently superior over the other in terms of overgrowth directionality. This result contradicts the outcome of color-morph superiority in the scleractinian coral *Stylophora pistillata* (Rinkevich and Loya, 1983).
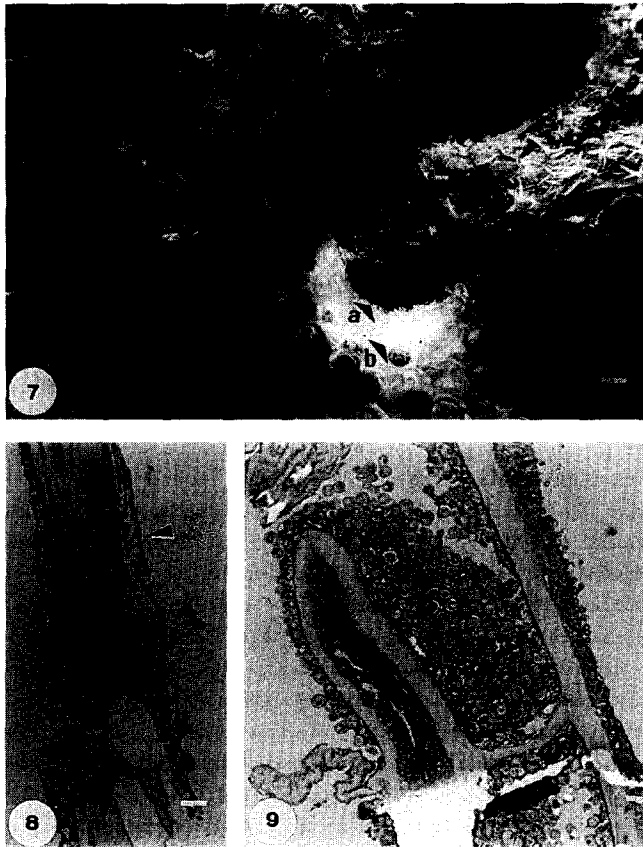
Fig. 7. Overgrown degenerated tissue after removal of the overgrowing colony; (a) indicates the site of cross section shown in Fig. 8; (b) the site of cross section shown in Fig. 9. Scale bar approximately 2 mm.

Fig. 8. Cross sections through overgrown colony showing gradual tissue degradation. The area shown in Fig. 8 (sectioned at area (a) in Fig. 7) was overgrown before the area shown in Fig. 9 (sectioned at area (b) in Fig. 7). The degraded area (Fig. 8) is much thinner, lacking the ectodermal layer (arrow) with reduced numbers of zooxanthellae. The overgrown tissue in this area will disappear shortly thereafter. Scale bars 20 μm.

Fig. 9.

4. Discussion

4.1. Self-nonself recognition in Parerythropodium fulvum fulvum

We have demonstrated here that the alcyonacean coral *Parerythropodium fulvum fulvum* possesses a self-nonself discrimination system, similar to all other studied colonial cnidarians. Tissue contacts between isogeneic colonies in this species always led to complete fusion between them. In contrast, allogeneic colonies of *P. fulvum fulvum* that were put in direct tissue to tissue contact, always failed to fuse and expressed either a retreat growth phenomenon or an overgrowth phenomenon followed

by tissue death and retreat growth. These results are in line with historecognition responses in other anthozoan cnidarians (Leddy and Green, 1991), but differ from studies in the Hydrozoa, where fusion between allogeneic colonies was revealed (Shenk, 1991; Frank and Rinkevich, 1994). We did not document combination-specific effector mechanisms in allogeneic encounters in this species, as pair replicates of the same colonies often resulted in different outcomes.

The two clear effector mechanisms recorded in *Parerythropodium fulvum fulvum* allogeneic encounters were the retreat growth and overgrowth phenomena. Tissue degeneration was observed only when one colony overgrew the other colony and only in the overgrown areas. We do not know yet if the dislodged tissues under the overgrowing areas were the result of the expression of an additional specific effector mechanism (such as nematocyst discharge or allelopathy), or a nonspecific outcome of physical cover of one colony by the other colony's tissue, resulting in the reduction of light and/or nutrient supply (cf. Ivker, 1972). Tissue necroses in other parts of the colonies were not documented here in any allogeneic interaction.

4.2. Effect of extrinsic parameters

Each colony combination in Group 1 was assayed in the four possible positions between natural growing edges and cut surfaces of two interacting conspecifics. However, due to the rapid regeneration recorded in *Parerythropodium fulvum fulvum*, it appeared that the wounds at the cut surfaces healed before the series of events primed by the allogeneic contacts were developed. This experimental manipulation therefore had no affect on the outcome in terms of the type of response, time scale or directionality. This issue should be taken into consideration since in other colonial invertebrates (e.g., ascidians), allogeneic colonies that reject each other when contacted through their growing edges, fuse when confronted by their cut surface areas (Hirose et al., 1994).

Allogeneic encounters between *Parerythtopodium fulvum fulvum* colonies did not show any pattern of hierarchy or transitivity. Overgrowth directionality in Group 2, for instance, was clearly associated with the physical position of the interacting colonies. These outcomes are unlike the results obtained for allogeneic encounters in other colonial cnidarians (Rinkevich and Loya, 1983; Chadwick-Furman and Rinkevich, 1994; Rinkevich et al., 1994; Frank and Rinkevich, 1994). It is possible that the expression of specific allogeneic effector mechanisms in *P. f. fulvum* is affected by biological as well as non-biological parameters such as the appearance of symbionts, seasonality, the physical setup of the interaction and more (Bak et al., 1982; Chornesky, 1989). In that case, colony specificity in *P. f. fulvum* is conferred on the level of self-nonself discrimination alone and the expression of the effector mechnisms are not specific in terms of type and directionality.Uncited ReferenceChornesky, 1991

done in the MINERVA Center for Marine Invertebrate Immunology and Developmental Biology.

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