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Intraspecific Competitive Networks in the Red Sea Coral *Sty[ophora pistillata*

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Summary. Intraspecific competItIve interactions were studied underwater in the Red Sea coral *Stylophora pistillata* during 1976-1981, through a series of field observations (FO) and field experiments (FE). The FO series were conducted on more than 200 pairs of colonies (with a gap of 1–3 cm between the nearest branches in a pair), which were checked monthly for possible interactions, during approximately five years. The FE series consisted of allografts, isografts and colony to colony attachments. S. *pistillata* exhibits two basic colour morphs, in which purple colonies are found to be superior to yellow morphs and competitively exclude them, even when they are not physically touching. When differences in size between the competing colonies were in the range of 2-3 orders of magnitude, a significant superiority of big colonies over little ones was recorded, irrespective of colour morphs. Five major schematic routes of intraspecific interactions are drawn and discussed. The outcome of interactions between two competing colonies is the synergistic effect of different aggressive forms, such as nematocyst discharge, overgrowth on branches or basal plates, a "retreat growth" phenomenon (possibly caused by pheromones), formation of border lines, abnormal growth forms and others. SEM observations indicate the existance of a gap (up to 30 μm) between allografts that appeared to be fused in naked-eye observations and the appearance of plasmic (?) filaments immediately above and within the contact zones. In contrast to the FE series the FO were free from any stress caused by experimental procedures and provided the opportunity to record additional forms of aggression, which were not observed in the FE series. In many cases, the duration of processes and the final outcome of interactions were much faster in FE than in FO. It is concluded that intraspecific interactions involve significant energetic expenditures that otherwise would be channelled into other metabolic requirements such as reproduction and growth. Self-recognition mechanisms and the role of immunological processes are discussed. The FO series indicate that in the vast majority of interactions no physical contact (cell to cell) is needed for self-identification.

Introduction

Although intraspecific competition seems to be generally important amongst sedentary animals (Knight-Jones and Moyse 1961), its appearance within coral populations has been poorly recorded. In contrast, interspecific competition between reef-corals has been extensively studied and widely discussed, since the work of Lang (1971, 1973).

So far, a considerable number of studies either demonstrated or indirectly indicated that the intraspecific aggression phenomenon does not take place in madreporarian corals. Ninety years ago, von Koch (1892) first termed the phenomenon of "aggregated colonies" in the Mediterranean coral *Balanophyllia verrucaria.* The designation "aggregated" was termed by him to those colonies which had been formed by secondary fusion of different distinct-polyps (i.e., non-aggressive interactions). He also concluded that in some cases a coral larva settled near an older polyp and the two specimens became fused and produced one bigger colony. This phenomenon of aggregated colonies was also observed in the cases of *Caryophyllia sp.* (Lacaze-Duthiers 1899), *Siderastrea radians* (Duerden 1902a, b), *Manicina areolata* (Boschma 1929), *Pocillopora bulbosa* and *Porites haddoni* (Stephenson 1931), *Fungia actiniformis* (Abe 1937), *Pocillopora damicornis, Stylophora pistillata, Galaxea aspera* and *Seriatopora hystrix* (Atoda 1947a, b, 1951a, b). It is interesting to note Duerden's (1902 b) report of a similar phenomenon of aggregated colonies, in a case of a rugose coral from the Lower Silurian of Ohio. A more advanced form of intraspecific fusion between branches of different big colonies has been reported by Gardiner (1931, p. 45) who noticed that "rough and more irregular twisted branches, some species fine and others an inch or more thick, are charactistic of *Pocillopora,* while smoother branches with rounded ends, often fusing together, form lumps a few feet across, *Stylophora* and *Porites."* More recently Lang (1973) indicated that adjacent tissues and skeletons of two individual corals of the same species, which settle beside one another, subsequently fuse.

Some other observations pointing out indirectly that intraspecific competition is insignificant or does not exist within hermatypic corals can be demonstrated from the literature. Stimson (1974) stressed that intraspecific interactions were not seen in the case of *Pocillopora meandrina.* When colonies of this species had grown one near the other no damage was apparent to either colony. Potts (1976) stated that digestive aggression seems totally unimportant among different forms of *Acropora palifera* and Dana (1976) reported on contagious settling in reef corals but did not mention any intraspecific interactions.

The possible importance of intraspecific competition in hermatypic corals is discussed by Sheppard (1980). He interpreted the bimodal pattern of the population structure of S. *pistillata* in Chagos Atolls as an apparent effect of intraspecific competition. Although he stated that intraspecific competition may be more important than interspecific competition, no experimental data or field observations were brought to support this view.

In the last few years great attention has been given to immunological aspects of intercolony contacts. Hildemann and co-workers (Hildemann et al. 1975a, b; Hildemann 1977; Hildemann et al. 1977a, b, c; Johnston et al. 1981) presented results showing the occurrence of incompatibility reactions in different hermatypic corals and referred to them as immunoincompatibility processes rather than the ecological outcome of competition or aggression (Hildemann et al. 1977 a). The main difference between immunoincompatibility and aggression reactions was suggested by Hildemann et al. (1975b) to be in the time it takes to develop. While the immunorecognition reactions slowly develop over a period of days or weeks, aggression reactions may be instigated promptly within minutes or hours.

The present work attempts to describe a variety of intraspecific interactions within a coral population, emphasizing ecological rather than immunological processes. Experiments and field observations were conducted on the Red Sea branching coral *Stylophora pistillata* indicating the effect of intraspecific competition on the survival of interacting colonies and the variety of outcomes of such interactions.

Material and Methods

All experiments and observations were conducted underwater during 1976-1981 in front of the Marine Biological Laboratory at Eilat, Gulf of Eilat, Red Sea. In this area the shallow reef is dominated by the branching coral *Stylophora pistillata.* In many cases, two or more different colonies are growing one near the other (Fig. 1a), so the possibility of aggressive interactions between different colonies (sensu Lang 1973; Jackson and Buss 1975) is possible.

S. *pistillata* exhibits a wide variety of colour morphs from pale yellow to dark purple (Rinkevich and Loya 1979). In the present work two different sets of morphs were selected for experimentation: yellow morphs (Y) and purple morphs (P). The study was composed of underwater field experiments (FE) and field observations (FO), in which S. *pistlillata* colonies were studied every month.

Field Experiments

Field experiments were performed on three different experimental sets: A. Branch-colony experiments – Branches from different colonies were carefully broken underwater with side cutting pliers. Some of these branches were placed on their original colonies (isografts), whereas the others were grafted to alien colonies belonging to the same species (allografts). All the truncated branches were grafted to the host-colony branches by plastic-locking cable-ties (2 mm wide, Fig. 1b). The grafting procedure was easily and quickly performed underwater producing minimal scrubbing to branches (see discussion). B. Inter-colonial experiments – Pairs of big (> 20 cm in diameter) or little « 5 cm in diameter) colonies of the two colour morphs were brought into contact. The experiments involved series of interactions between pairs of big colonies vs. big colonies or small colonies vs. big ones. In these experiments the little colonies, or only one of the big colonies in a pair, were carefully detached from the substrate by hammer and chisel. Only unharmed colonies were used in the grafting experiments. C. Concrete-plate experiments - Plastic clippers glued on concrete plates were used for holding detached little colonies or broken branches (Fig. 1c). The plates with the corals were covered by plastic bags and later injected with Alizarin Red S dye, producing a final concentration of about 10 mg/1. After 24 h the bags were opened and the dyed colonies and branches were brought into physical contact (branch to branch and colony to colony). In all the cases of yellow colonies or branches, the accumulation of the red dye was most markedly seen in their tips (the acitve sites of calcification) and easily recongnized underwater. The amount of new growth ("white" layer) could be detected and documented in situ above the red parts. Such observations were not possible with the purple colonies or branches. In termination of the experiments the plates with their attached corals were brought to the lab. The coral tissues were removed by a jet of tap water, or by putting the plates in buckets containing solution of NaOH. The variety of growth forms and interactions types in the grafted pairs were recorded.

Field Observations

In the field-observation series, more than 200 pairs of colonies, which grew healthily one near the other (1-3 cm apart and in few cases touched each other) were numbered by plastic tags and were checked monthly until one or the two colonies in the pair died.

SEM Observations

In some cases, allograft branches which appeared to be fused, were taken for SEM examination. The samples were first fixed in 2% glutaraldehyde in filtered seawater for 24 h, then transferred to a buffer solution of sodium cacodylate (0.1 *M),* dyed with buffered OS04 (1%) and dehydratedina series of increasing concentrations of ethanol. Small fragments of branches were coated with gold and examined with Jeol SEM.

Results

Field Experiments

The results of246 interactions of coral branches grafted to big purple or yellow colonies are presented in Table 1. Since the processes involved in the interactions are dynamic and variable, and during the course of recorded events in a single pair several interactions could take place, we decided to present the results recorded six months after grafting. This relatively short time (see discussion) is enough in this case to indicate the general trends of interactions. We divided the interactions into five major categories: Damage observed on the corals, on grafts, reciprocal damage, fusion and no visible damage. The controls are cases in which broken branches were replaced on their original colonies (self).

It can be seen from Table 1 that the purple colonies of S. *pistillata* are significantly more aggressive than yellow colonies ($P < 0.05$, testing equality of two percentages, Sokal and Rohlf 1969). Six months after grafting yellow colonies were damaged by purple branches (Fig. 1d)

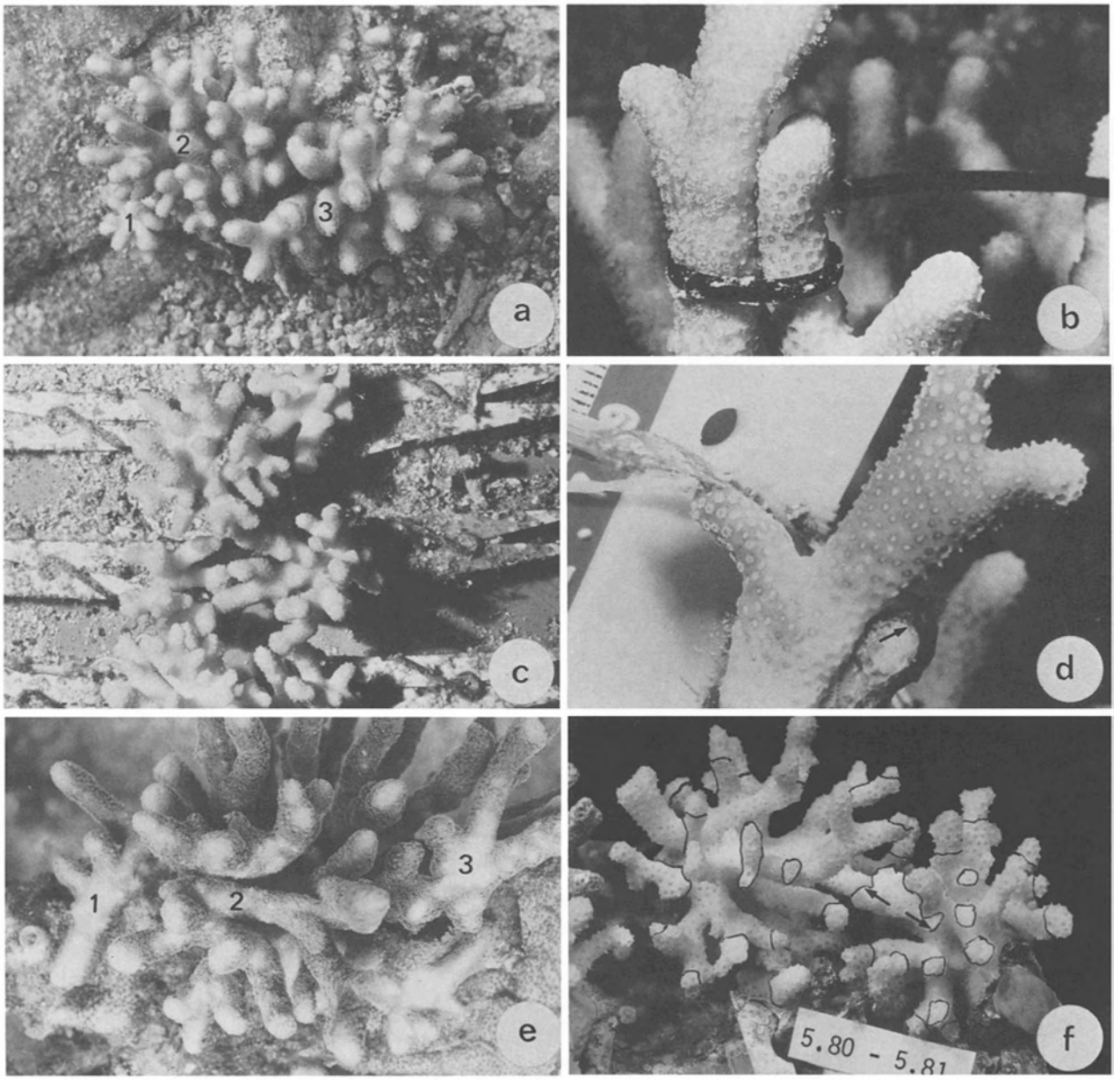

Fig. 1a-f. S. *pistillata:* Field experiments (b, c, d, f) and field observations (a, e). a Three little colonies (No. 1, 2, 3) growing in very close neighborhood on the reef flat. b An alien branch attached to a colony by a plastic locking-cable. c Pairs of little colonies held by plastic clippers on concrete plate. d Allograft - two months after grafting. *Arrow* indicates encrusting algae along and above the grafted branch. e Natural occurring isografts (branches 1, 2, 3). Complete fusion in contact zones. f Overgrowth of a superior purple colony *(left)* on a subordinate yellow colony, in areas of contact. Arrows indicate the amount of overgrowth above the subordinate colony. Black lines refer to the amount of growth above the alizarin marked areas during a year

significantly more than yellow colonies by yellow branches. However, purple colonies were not damaged at all, either by purple or yellow branches. Reciprocal damage was very common immediately after grafting, yet six manths later, less than 10% of this state was recorded.

In all the control experiments complete fusion was observed. This type of self fusion occurs soon after grafting (no more than 1-2 months) and was different from the type offusion found between branches and alien host colonies. In the case of syngeneic grafts (isografts), continuous and uniform layer of tissue connects the graft and the host branches. No border-lines or any other sort of interruption can be seen between the two parties. This self fusion is commonly found in S. *pistillata* especially after storms or breakage inflicted by divers (Fig. 1e), but never occurs in naturally-growing unharmed colonies. In the case of allografts, the contact zone between the parties, even of the same colour morph, is always typified by a border-line, or some sort of longitudinal suture produced by thin skeletal risings from both sides. Later, differential growth of the superior party resulted in overgrowth on the touching branches of the inferior party (Fig. 1f). Table 1 also points out the superiority of big colonies over alien branches of the same colour morph (Y vs. y and P vs. p). This superiority intensified with time and in most of the cases, after one year, most of the branches (p and

y) were killed by the colonies. This phenomenon is further investigated in two other sets of experiments (Tables 2, 3).

In the first experiment, 107 branches broken from different colonies were put on alien colonies (Table 2). These branches were not tied to the colonies, as described in the former experiments, but were carefully put within their branches. This procedure was adopted to minimize the stress produced by using the cable-ties, since the tying procedure fractured the tissues and skeletons of the grafted branches (clearly seen under binocular microscope), although great care was given to prevent any damage. Since equal numbers of colonies and branches were taken from the purple and yellow morphs, the results were grouped without differentiating between the morphs. The differences recorded between the types of interactions, 2 and 12 months after grafting (Table 2), emphasize the dynamic nature of these interactions and demonstrate the superiority of the big colonies over the branches. Moreover, most of the 72% of the branches reported as "damaged" in Table 2, were actually dead. The superiority of the "bigger" is also clear from the experimental series of big colonies vs. little colonies (Table 3). After one year of interactions most of the little colonies were damaged, while big colonies were not harmed. Some of the reciprocal interactions developed after more than one year to a total death of the pairs.

It is of great importance to note that in a case of a big colony vs. a little one, or a branch vs. a colony, we are dealing with differences of 2–3 orders of magnitude (from a few grams to more than 1.5 kg in weight). This phenomenon of the "superiority of the bigger" does not hold in cases where one of the parties is bigger only by one order of magnitude.

The general trend of the superiority of P on Y was also found in big colonies (Table 4). Careful monthly observations on different phases and sequence of events found in 52 coral pairs (Table 4), in addition to 60 other different pairs, are schematically summarised in Fig. 2 and Table 6 and will be discussed later. The results of the experiments dealing with little colonies marked with alizarin are also summarised in Fig. 2 and Table 6.

In the experiments testing branch-to-branch grafted pairs on concrete blocks (more than 200 couples), very fast mortality was evidenced in the majority of the cases (within 1-3 months), although extreme care was taken during the grafting procedures. Numerous field observations on broken branches of S. *pistillata* (as a result of storms or human activities) showed that their survivorship is very low. We have therefore excluded these experiments from the discussion of the problem of intraspecific competition, since there is no way to distinguish between death caused due to stress conditions or competition. We suggest that whenever possible, whole colonies should be used for such experiments, or at least big parts of such colonies.

Field Observations

From more than 200 naturally growing pairs of S. *pistillata* colonies, only 101 cases were followed until at least one of the colonies in the pair died. In other 5 pairs the couples are still alive (in one case we are following the mutual interactions for more than 5 years). The other pairs were excluded from the present results, because their

Table 5. End result of intraspecific interactions within naturally growing pairs of S. *pistillata* in very close neighbourhood

Type of interaction	No. of pairs	Interaction outcome (%)			
		Death of Y	Death of P	Reciprocal killing	"Retreat growth" of branches"
Y vs P	60	66.7	11.6	16.7	5.0
Y vs Y	23	60.9		34.8	4.3
P vs P	23		78.3	17.4	4.3

" In these cases interactions are still in process (see also Fig. 2 and Table 6 for further explanations)

death was caused by external factors, such as human vandalism or strong southern storms. The result of these factors, was the immediate death of at least one of the colonies in the pair. We have also excluded from this study cases in which colonies suffered injuries (partial breakage) as a result of physical factors. Table 5 summarizes the end result of the 106 naturally growing pairs and demonstrates that the general trend of the superiority of purple colonies on yellow colonies also occurs in natural conditions. Purple colonies caused the death of yellow colonies 6 times more than the reverse situation. The end result of the intraspecific interactions is the death of at least one of the colonies in the pair.

Careful examination of the modes of interaction processes points out five major routes schematically drawn in Fig. 2. The duration and time range of interaction types are summarized in Table 6. Figure 2 and Table 6 are based on the results obtained from the field observations (FO) and field experiments (FE). The detailed account of the main routes of interactions shown in Fig.2 and Table 6 is given below:

1. A→C route. A = Physical contact between two colonies. B = Overgrowth in contact zones and very slow growth rate in other parts of the two colonies (Fig. 1f). C = The end result of this interaction: death of the inferior colony. The superior colony overgrows dead parts of its neighbour and is growing faster than before.

During A→B process, minute tissue damages could be found in contact zones. This deleterious effect was recorded in colonies that later died (phase C). Death of inferior colony is evident even if overgrown on small portions. In many cases B phase is characterized by longitudinal suture of tissue and skeleton in the contact zones (Fig. 3a). Tissue destruction is followed by settlement of algae and fouling organisms. The A→C process is more frequent in FE than in FO pairs (31.2% compared with 3.8%, respectively). It should be noted that the 4 cases of FO colonies were selectively chosen in the beginning of the observations, i.e., their real frequency in S. *pistillata* populations is even lower.

2. I or A→D→F, G or H routes. D=Point of injury is evident in the contact zone. E = Death of one branch. F = Complete death of one of the colonies. Fast growth exhibited by the winner (Fig. 3b). G = Partial death (up to 50%) in one colony (Fig. 3c). Fast growth exhibited by the unharmed partner, while slower growth rate is found in living parts of the damaged colony. H = Dead portions of facing branches in competing colonies. Slow growth rate follows in both colonies (Fig. 3d), while in some cases fas-

Table 6. Duration of final (T) and important intermediate (I) processes in field experiments (FE) and field observations (Fa) of S. *pistillata* pairs (see Fig. 2 and text for further explanations)

Type of process	Tested process	Field experiments			Field observations		
		No. of pairs	Average duration of process (months)	Time range of process (months)	No. of pairs	Average duration of process (months)	Time range of process (months)
T	A→C	35	10±5	4-24	4	13± 8	8–25+[a]
	I or A→D→F	67	4±3	1– 9	45	11± 6	2–26
	I or A→D→G	7	10±3	4-14	1	13	13
	I or A→D→H	3	6±2	5– 8	5	15± 7	6-25[a]
	I →J[b]				13[c]	15±11	3–55+[a]
	K→L				17	10± 8	3–29
	K→M or N[b]				15	8± 6	3–21
	K→O[b]				3	12± 1	11–15
	P →R				4	19± 10	6-30
	P →T				7	10± 2	6–12
	A →D	35	1± 1	1- 4			?
	A →B	26	3±6	1- 4			?
	D↔E	12	2±1	1– 4	27	5± 4	1–11
	B↔D	6	5±5	1–14			
	J →D				8	10± 5	3–16+[a]
	Q→R				4	14± 11	3-28
	S →T				7	5± 3	1-10

[a] Observations began when interactions have already been in process, so the average duration and ranges of time could be longer

b In field experiments this process was recorded only in the cases of alizarin marked colonies. No data are available on the duration and time range of this process

[c] Out of the 13 pairs, 8 cases continued to D→F, G or H processes. Hence, the total number of interactions in the Fa cases increases from 106 to 114

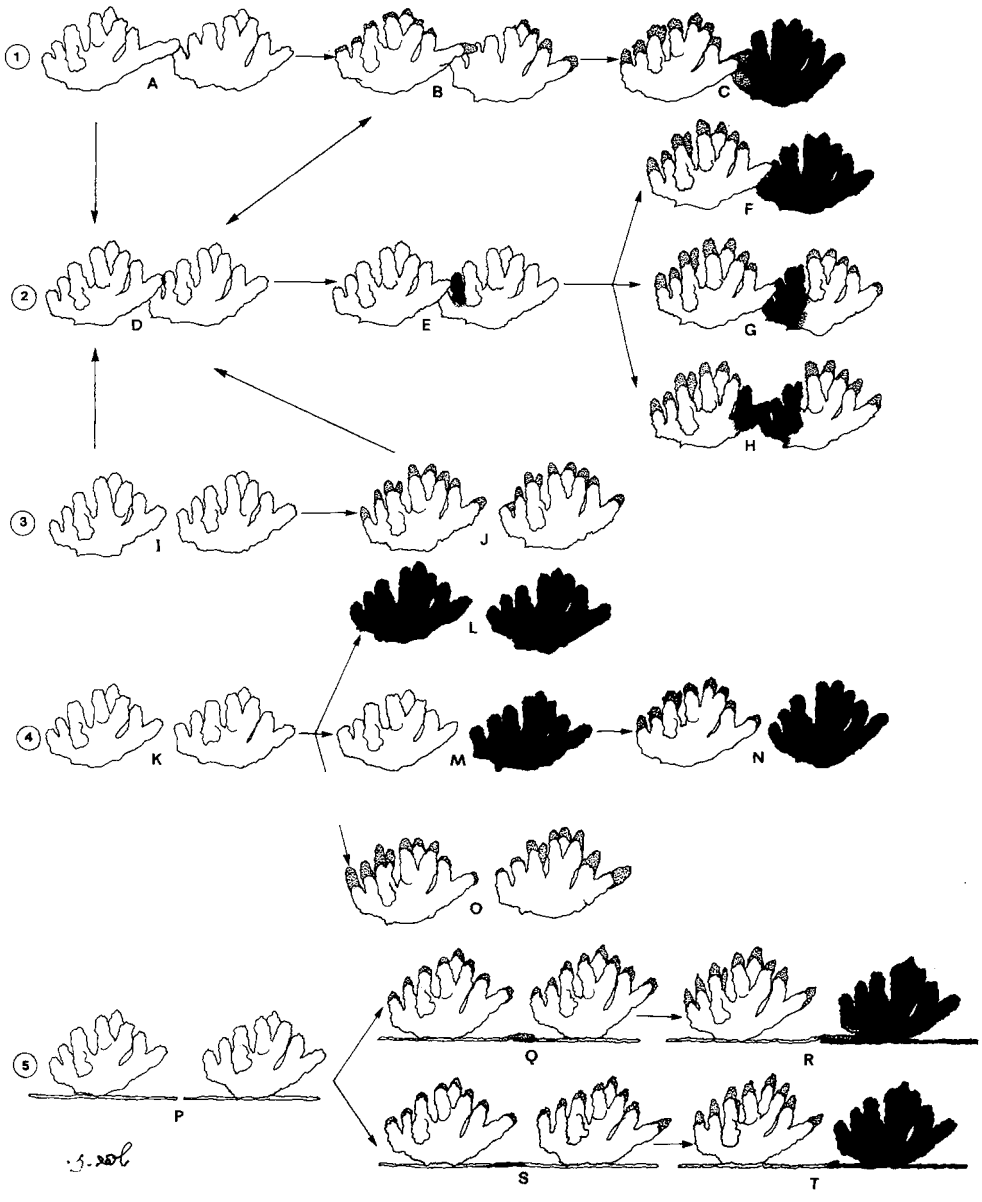

Fig. 2. Major routes of intraspecific interaction in S. *·pistillata. Black parts* represent dead branches or dead colonies, dotted parts represent amount of growth taking place during interactions. *Arrows* indicate different routes of interactions. *Letters* point out to important stages within the course of interactions (see text for further explanations)

ter growth rate of one of the colonies is evident (Fig. 3e). I=Two colonies growing one near the other (1–2 cm apart) without any visible interactions.

These routes started in phase A during FE (68.8% of 112 cases, Table 6) and in phase I during FO (47.7% of 114 cases). Route D→E is significantly slower in FO than in FE and could develop into the reverse situation. The reversed process E→D is very rare in FE and common in FO. Routes D→G and D→H form together 8.9% of the FE colonies and only 5.3% of the FO colonies. Moreover, in all the 6 cases of FO pairs (D→G and D→H) death of at least one of the partners was recorded in the following two months. Thus, situations G and H, in naturally growing colonies are not the end process and the D→F route is the only one, which may be found in nature. The average duration of A→F in FE is up to 3 times faster than in FO. In many cases of FO, injuries (D phases) are reciprocal and repeated: Destruction of tissue in one of the colonies was followed by full regeneration after a short period of time, tissue degeneration of the second colony, and vice versa. This phenomenon usually occurs when the distance between the two competing colonies is approximately 1 cm.

3. I→J route. J = Abnormal growth pattern – "retreat growth" (Figs. 3f, g). A branch or branches of one of the colonies in a pair, sharply change their normal growth direction and are growing upwards, downwards or backwards – away from their competitor. This phenomenon occurs only between very close branches of the two colonies. In the FE colonies this process could be detected only in the alizarin marked colonies, in branches which did not come into physical contact. This result indicates that this phenomenon is most probably much more abundant than what may be recorded in normal field situations (i.e., the 11.2% recorded in FO pairs is an underestimate). The pattern of "retreat growth" develops very slowly (in some cases we followed it for more than 5 years) and in 8 of the 13 cases recorded, it continued in the D→F, G or H routes. Thus, the I→J route acts as a decelerating process. This process is included in the final processes section of

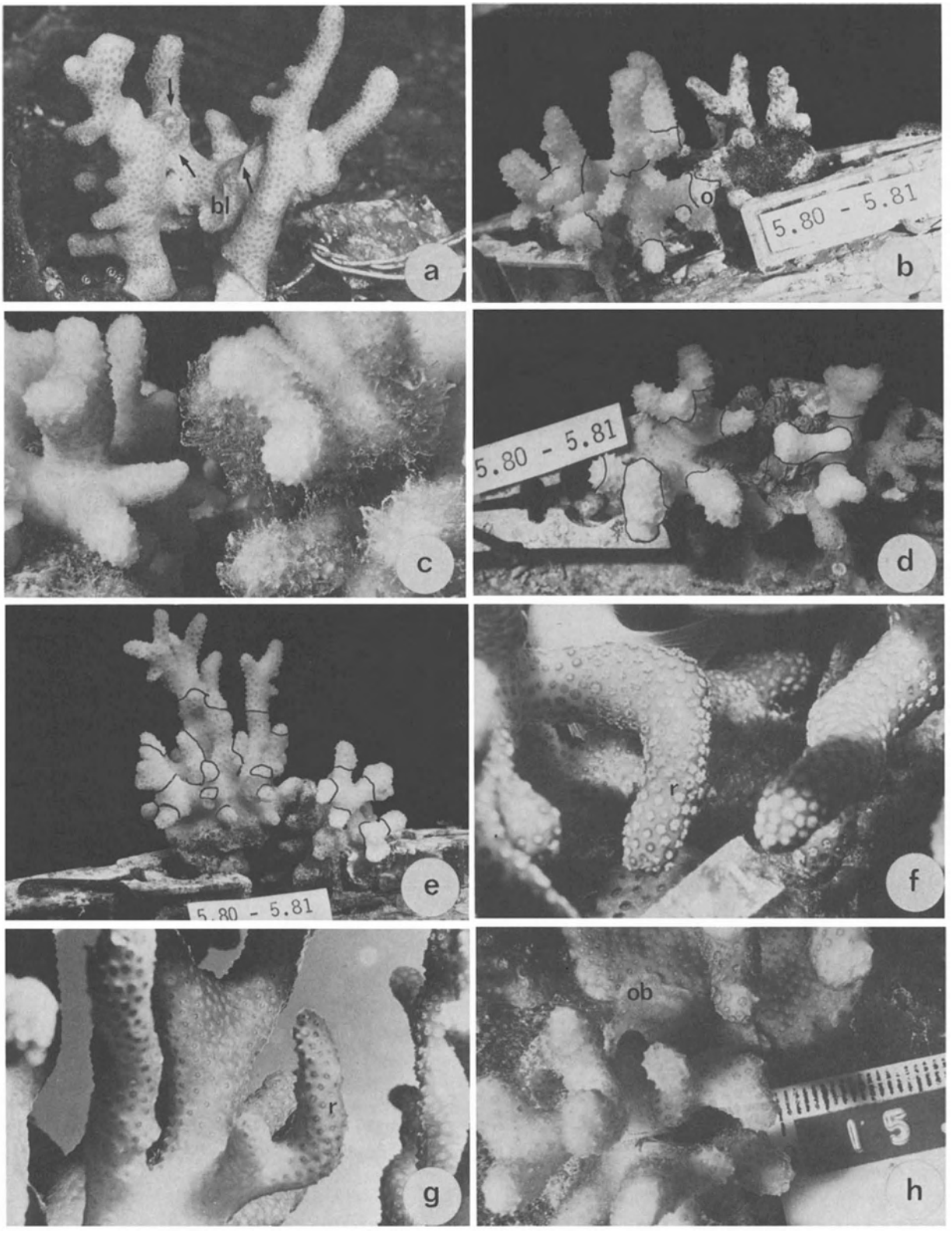

Fig.3a-h. S. *pistillata:* Field experiments (a, **b, d,** e) and field observations (c, C, g, h). a A border-line (*bl*) between branches of two different colonies, one year after attachment. The right branch overgrows the left through slow "advancement" of the border-lines *(arrows).* b Rapid growth rate of a purple colony follows the death of a yellow subordinate colony (phase c, Fig. 2). c Partial death in the right colony. Dead areas are covered rapidly by encrusting algae. d Partial death in facing branches of two competing purple colonies. e Two purple colonies: Unusual fast growth in the superior colony. Facing parts of both colonies are dead. **f,** g "Retreat growth" in facing branches of two different pairs: downwards (**f**) and upwards (g). h Basal plate of superior colony overgrows inferior colony. *o* = overgrowth, *ob* = overgrowth by basal plates, *r* = "retreat growth". *Black lines* refer to the amount of growth above the alizarin marked areas

Table 6, because of its very long duration, which allows external physical conditions (such as storms) to act.

4. K→L, N or 0 routes. K = Same as 1. L = Death of the two colonies. M = Sudden death of only one of the pair. N = Fast growth rate in the surviving colony. 0 = Accelerated growth in further away branches. Obviously, these processes occur only in the FO colonies. **In** the beginning of the study it was hard to decide whether these observations were meaningful and played a role in the intraspecific competition processes, because of the wide gap (1-2 cm) between the two neighbour colonies. The K→L and K→N routes are characterized by fast mortality of the colonies (1-2 months) after the first sign of damage. **In** the K→L route the sudden death of the two colonies is simultaneous after a long period (up to 3 years) of no visible interaction. **In** the K→N route, only after the sudden death of one of the colonies in the pair, fast growth rate was recorded in the surviving colony (supported from the study of the alizarin marked colonies). The K→O process leads to asymmetric shape of each one of the colonies, which form together a general circular shape of "one" big colony (composed of two separate and almost identical halves). A brief survey in the field suggests that the K→O process is more frequent in the reef than what might be concluded from the FO population (only 2.6%). The end results of the K→O process could be observed in anyone of the A→C, A→F or K→L, M processes, if not terminated before by physical factors.

5. P→R or T routes. This category of processes is made unique by the fact that interactions begin and develop through contacts of the basal plates of the colonies. P = Two colonies (usually young) become close to each other by rapid growth of their basal plates. Q = One of the basal plates overgrows the second (Fig. 3h). R = Death of the inferior colony occurs after a long time of overgrowth. Accelerated growth of the winner is evident after the death of its competitor. S = Dead parts in the contact-zones of the basal plates. T = Only after complete death of the inferior colony, the basal plate of the winner overgrows dead areas. **In** many cases the P→R or T processes occur below branches of big colonies (which are in other types of competition processes) and hence are undistinguishable. The P→T process is faster than P→R (almonst twice as much, Table 6) and characterised by the death of the inferiors during initial overgrowth.

It should be stressed that the five main routes illustrated in Fig. 2 are only a schematic representation of the processes occuring in intraspecific interactions. **In** many cases the detailed course of events within a given pair of colonies is too complicated to be schematically expressed by a given series of illustrations. **In** order to demonstrate the complexity and variability of interactions involved, we summarise in Table 7 three examples of representative cases, in which the succession of events is recorded.

SEM Observations

In cases of isografts a complete fusion of the grafted branches is evident. When decalcification procedures were conducted on these branches (more than 50 pairs), in all cases the remaining tissues were absolutely united. No visible signs of any sort of border-line or separation were distinguished. **In** contrast, in cases of allografts (more than 85 pairs), complete separation of the two colonies always occurs during the decalcification process along their contact zones. We therefore conclude that in cases of allografts, real fusion never takes place. To strengthen this conclusion more than 20 pairs of branches (in B phase, Figs. 2, 4a) were taken for SEM examination, 6–20 months after grafting. The SEM observations demonstrate that a narrow gap (from a few microns up to 20-30 μm) exists between the two tissues (Fig. 4b). The width of this gap varies according to the topography of the surface of the contact zones. **In** all the SEM observations true fusion has never been seen. Obviously, cell to cell contact occurs immediately after the grafting procedure. However, this procedure harms both sides, even in the isograft series. Shortly afterwards, the tissue within these contact zones disintegrates. **In** isografts these areas are filled with skeletal deposition covered by a uniform layer of tissue. **In** allografts, however, no such cementation takes place, instead, a narrow gap is formed right above the harmed contact zone. With time, the tissue of the dominant coral overgrows the inferior colony, but the gap continues to exist throughout the process and "moves" with the advancement of the winner's tissue. The nearest areas to the contact zones differ from the further-away "normal" surface-areas, not only by forming the "border-line" but also by exhibiting a smooth surface area (Fig.4a) deficient of cilia (usually surface areas between polyps are covered by cilia). **In** many cases, threads of unknown material (cytoplasmic?) were detected in the SEM observations between the allograft contact-zones (Fig. 4b). These threads were not found in any other parts of the grafted colonies, nor in control colonies growing alone (without interactions with others). We suggest the possibility that these threads are plasmic filaments extruded from one tissue to the other for "self-recognition". **In** some cases the locality of their extrusion can be seen (Fig. 4c) and sometimes, in the distal part of such threads, plate-like structures were found on the alien tissue (Fig.4b). Usually these filaments are 2–5 μm wide and in many cases 1,000-2,000 μm long. The possibility that these threads are an artifact (i.e., mucus filaments) can be excluded, since mucus sheets and threads are wider, irregular, much shorter and found all over the surface area of a colony (Fig.4d).

Often, by applying the slightest force by hand on the grafted branches, or when detaching the grafted branches from their colonies, they instantly separated in the contact zones. This is an additional result that strengthens the conclusion that no real fusion occurred. SEM observations were conducted also at the inner parts of these "opened" contact zones, where such threads were also found (Fig.4e). **In** some cases discharged nematocysts (Fig.4f) were observed in large numbers below the contact zones. They were always found only on the surface areas of the inferior colonies, which suggests a possible aggression mechanism in which nematocysts play as the weapons.

Table 7. Examples of intraspecific interactions in S. *pistillata:* Case history of 3 field-observation pairs (P = purple colony, Y = yellow colony, Big colony = 21–40 cm in diameter, Intermediate = 6-20 cm in diameter, Small = < 5 cm in diameter)

Date	Detailed information
Pair No. 149	
4.78	P vs. P. Big colony (A) and intermediate (B) are 2 cm apart. No visible interactions
5.–11.78	No changes
12.78	Three branches in B and two in A are newly damaged (dead tissues). All damaged branches are the nearest neighbours
1.79	One-third of B facing A is dead and covered by algae. In A one of the damaged branches is covered with algae while the other is only half covered
3.79	One third of B and 1/5 of A (facing parts) are dead covered by encrusting algae
5.79	Two additional branches in B died. Slight regeneration in A
6.-12.79	Same situation in B. Colony A gradually recovers, only one branch is still covered by algae
1.-2.80	More branches in B are dead. Colony A without change
4.80	Colony B is completely dead. Colony A fully regenerated
5.80-5.81	Colony A continues to grow normally, no damage signs
Pair No. 85	
4.78	Y vs. P. Big colonies, about I cm apart. No visible interactions
5.78	Reciprocal points of injury at the tips of 2 facing branches
6.78	Increase of dead areas to approximately 0.5 cm^2 in Y and P
8.78	Two branches in P are damaged. Full regeneration in Y
10.78	Half of Y is dead. Regeneration in P tips. Some other branch bases are damaged
11.78	Y is completely dead. P regenerating (except for one dead branch)
12.78-1.79	Full regeneration in P
2.79-2.80	P continues to grow normally. No damage signs
3.80	P destroyed during a southern storm
Pair No. 142	
4.78	P vs. P. Two intermediate colonies in Q phase (Fig. 2). No visible interactions
5.78	Fast overgrowth of A on basal plate of B
6.-7.78	Colony A completed overgrowing on the facing basal plate of B and continues to overgrow a low branch of B (covers it almost completely)
8.78	Dead interphase of I cm in width covered by encrusing algae is formed along contact zones
9.-10.78	The advance of A on B is halted
11.78	The algal-covered separating-interphase slowly "moves" on B
12.78	Same. Dead areas reduced in some parts to 0.2 mm in width
1.–2.79	Dead areas become thinner, producing border-lines, almost reestablishment of physical contact between A and B
3.-12.79	Wall of cementum appears between A and B. Colony A slowly advances on B. From time to time different dead zones appear, covered by algae and later regenerated
1.–9.80	Accelerated overgrowth of A on B. Less damaged contact zones. Colony A overgrows the facing B main branches No other visible interactions
10.80	Colony B completely dead. Colony A without any visible injury
11.80-5.81	Colony A continues to grow normally. No damage signs

Discussion

Although interspecific competition in coral communities has received increasing attention in the last 10 years, the question of intraspecific competition has been neglected. Only in one case (Sheppard 1980) intraspecific competition was mentioned to play an important role in the ecology of reef corals, but no data were presented to back the conclusions.

In other works some evidence can be found pointing out the existence of intraspecific competition in reef corals, but its consequences have been overlooked. Potts (1976) indicates that Dustan (per comm.) has seen intraspecific digestion in *Montastrea annularis.* In a following work, Potts (1978) describes one rare example of intraspecific extra-coelentric digestion in the case of *Acropora.* Lang (1971) indicates that although individual corals of the same species, which settle beside one another, never attacked each other, in some species adjacent tissues and skeletons of the two corals subsequently fused and in some other cases (Lang 1973) the neighbour-corals stopped growing in the regions of contact. Eighty years ago, Duerden (1902) described the phenomenon of aggregated colonies, in which colonies of *Siderastrea radians* had formed through a second fusion of individuals which were originally distinct, and noted that in this case growth of the aggregated colonies was very slow, compared with that of isolated individuals. Lamberts (1973) concluded that some corals may cause a depression of alizarin uptake in neighbour colonies. He noted that survivorship of *Pocillopora damicornis* heads grown separately in aquaria was much better than when held together. Moreover, when newly settled polyps of *P. damicornis* were grown in overflow of water from aquarium containing large heads of the same species, they often died. He explained his observations as a possible result of metabolites or other substances in the water which have a deleterious effect on other corals of the same species.

Theodor (1976) showed that in allografts of 1479 different segments of the gorgonian *Eunicella stricta* only 0.7% fused completely, 2.7% were considered to be cases of semi-rejection and in 96.6% total rejection was recorded. Bigger and Runyan (1979) found in allografts of the gorgonian *Pseudopterogorgia elisabethae* three cases of overgrowth without fusion and one case of necrosis. Hildemann et al. (1977b) in his work on incompatibility reactions in hermatypic corals pointed *out* the disappearance of zooxanthellae from contact zones of allografts.

Potts (1976) examined the question of tissue connections in allografts using electrical stimulations. Corals were

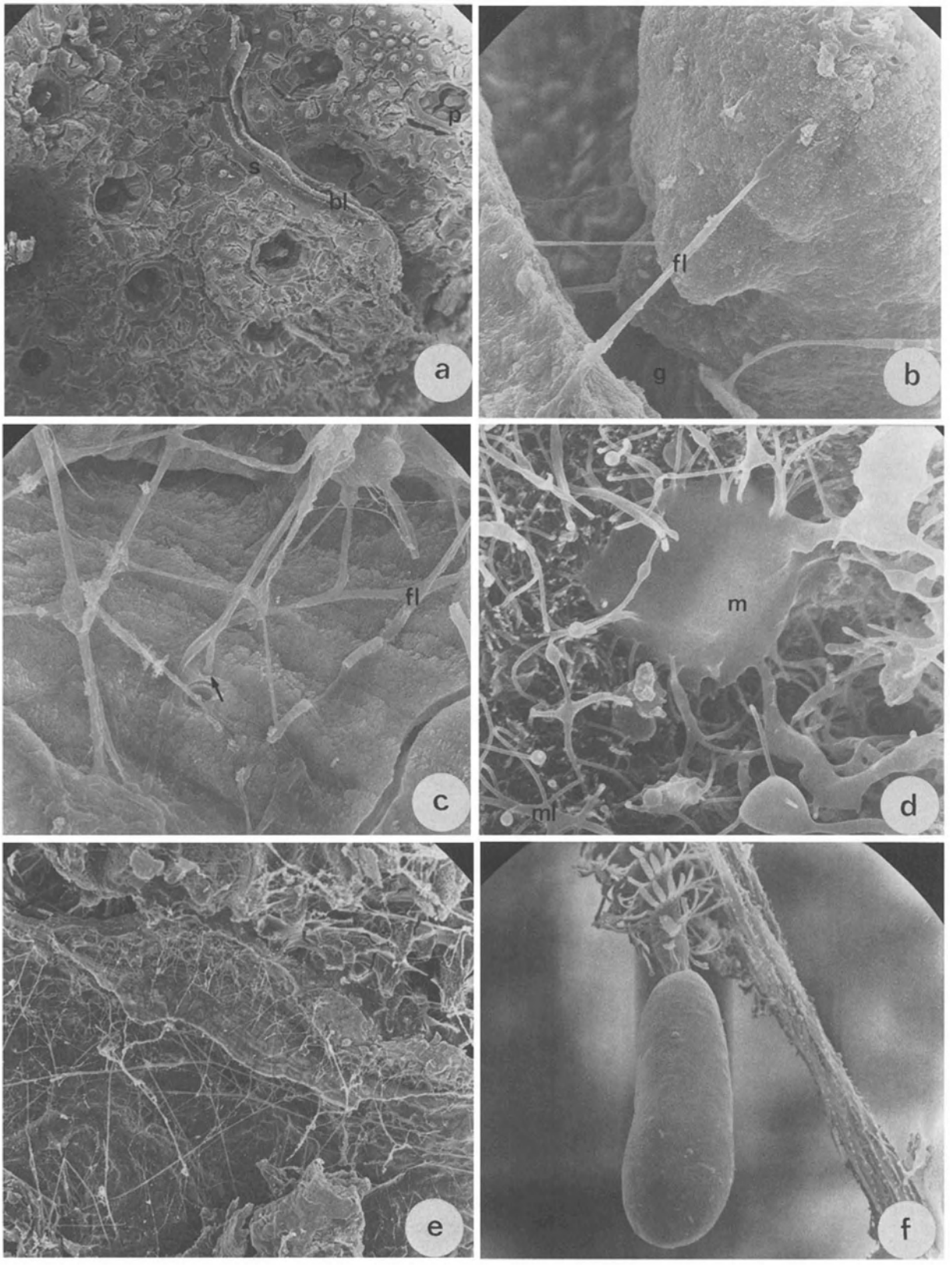

Fig. 4 a-f. SEM observations in contact zones of allografts. a A borderline between two colonies (x 20). b A gap within the border-line. Plasmic filaments are connecting the two different tissues. Note plate-like structure on distal part of one of them (x 1,000). c Filament exit site *(arrow,* x 1,000). d Mucous sheets and mucous filaments on surface area (x 2,000). e Filaments within the borderline (x 50). f Nematocysts found on the surface tissue of the subordinate colony within the contact zone (x 3,200). *bl* = borderline, *fl* = filaments, *g* = gap, *m* = mucus sheet, *mf* = mucus filament, *p* = polyp, *s* = smooth area of border-line lacking cilia

repeatedly stimulated when their polyps were fully expanded. In every set of isografts contractions continued across the boundary between the pieces, with no detectable irregularity in the extent or rate of contractions along the contact zones. Conversely, after 12 months of growth, physiologically functional union of allograft tissues was not present across overgrown boundaries.

Although only a few hints exist in the literature, the results of the present work clearly demonstrate the existence and importance of intraspecific competition in hermatypic corals. It is evident that differences exist between the results obtained from our grafting field-experiments (which are similar to laboratory experimental procedures used in other works) compared with our field observations, which were conducted on intact and undisturbed colonies. Many interactions which could be detected from field observations (I→J, I→D, D⇆E, P→R, P→T, K→L, K→M, K→O and others, Fig. 2), could not be detected from the field experiments. Moreover, although maximal care was given during the grafting procedure, it severely stressed both sides and accelerated interactions, while the naturally occurring interactions developed slowly and their final outcome (complete death of one of the competing colonies) could be detected sometimes only after years of interactions (Table 6). Hildemann et al. (1975 a) stressed the major differences between ecological aggression and immunological reactions in corals, stating that while immunorecognition reactions slowly developed over a period of days or weeks, aggression reactions may be instigated promptly within minutes or hours. However, in the present study we have demonstrated that in S. *pistillata*, intraspecific interactions are variable (Fig. 2, Tables 6, 7) and the vast majority of these different types of interactions develop within years. We have further demonstrated that in comparing similar ecological consequences occurring in field experiments, as well as in field observations (for example A→H, D→F, D⇆E and others, Table 6), the development of natural interactions are remarkably slower (up to 3 times) than the experimental outcome. Some interactions (such as A→G, A→H, Table 6) which are found to be important final stages in the field experimental series, have been found to be only intermediate stages in the field observations. Furthermore, some major routes detected in field observations (such as I→J, K→L, K→Nand K→O, Fig. 2) are not possible in grafting experiments. These three points (stress caused by experimental procedures, different routes or modes of aggression between FO and FE and differences in duration of interactions between FO and FE), must be taken into account when considering intraspecific interactions.

The results presented in this work indicate on several possible mechanisms involved in processes of intraspecific competition. Some of them may be described as behavioural aggression forms, such as nematocyst discharge (Fig.4f), the formation of "border-lines" (Fig.4a), the rapid overgrowth in contact zones (branches or basal plates, Fig. 3h) and perhaps the threads, which appear above and within the contact zones (Fig. 4b, e). It is not clear what is the trigger for these aggression forms; however, they may be found only when physical contact occurs between the competing colonies. We further suggest that the deleterious effects found in subordinate colonies of S. *pistillata*, growing relatively far (1-2 cm) from their dominant couples (K→L, K→M, K→O, Fig. 2) are based on the biochemical level, as allelochemical interactions which are known in benthic organisms (Jackson and Buss 1975). The processes mentioned above and the phenomenon of "retreat growth" (Fig. 3f, g; I→J process, Fig. 2) suggest the possibility that a variety of substances secreted by the corals can affect growth patterns or survivorship of neighbour-colonies. Since we are dealing in intraspecific interactions, the substances involved must be regarded as pheromones rather than allelochemicals (Whittaker and Feeny 1971). It is still possible that the same chemical substance is used for intraspecific interactions, as well as interspecific interactions, but its physiological or behavioural consequences are different. Some of these substances probably have great solubility in sea water and since they are highly diluted, they can only act within very close distances (a few centimeters) around the colony. Other substances can be secreted within the mucous (Lubbock 1979) and thus be transferred to relatively large distances.

During many years of observations and experiments with S. *pistillata* colonies, we have never observed extruded gastric filaments nor sweeper tentacles (Richardson et al. 1979). We therefore exclude these forms of aggression or defence mechanism as factors involved in the intraspecific interactions occurring in S. *pistillata*.

The results which are presented in K→O, K→N, K→L, A→C processes (Fig. 2) suggest active energetic investments in the various competition forms. The sudden collapse of the subordinate colony indicates that in addition to nematocyst discharge, secretion of some substances and abnormal growth patterns, other significant energetic expenditures may be involved. The suggestion of energy channelled into competitive mechanisms rather than other metabolic needs is evident in the marked reduction of growth rates and reproduction in competing colonies (Rinkevich and Loya, in prep.).

The results presented in Fig. 2 and Tables 6, 7 point out the complex network of intraspecific interactions. Careful examination of all the pairs followed in the field observations (three cases of which are presented in Table 7), emphasize the conclusion that the outcome of interactions between two competing colonies of S. *pistillata* is the synergistic combination of different aggressive forms.

The role of immunological responses in S. *pistillata* interactions is very complicated. We have shown that this species exhibits hierarchical aggression of colour-morphs, in which purple colonies are superior to yellow colonies of similar size and competitively exclude them, even when they are not physically touching (Table 7, Fig. 2). Furthermore, when the differences in size between the colonies in a pair were in the range of 2-3 orders of magnitude, a sig-

nificant superiority of the big colony over the little one was evident, irrespective of the colour-morph (Tables 1,3). Hildemann et al. (1977 b) tested the influence of allograft size on the direction, rate of appearance, or degree of severity of cytotoxic reactions using a narrow range of sizes (9 cm^2-72 cm^2). They found that within this size-range, graft size had little or no effect on the direction or timing of allograft reactivity.

Another question to be considered is the mechanism of self recognition in hermatypic corals. Our field observations on S. *pistillata* colonies suggest that in the vast majority of interactions, no physical contact (cell to cell) is needed for self identification (Figs. 2, 3f, 3g). Furthermore, in cases where physical contact is formed through branches (A→C, D→E, Fig.2) or basal plates (P→R, P→T, Fig. 2), a gap of up to 30 µm is evident (Fig. 3b). In other words, the H system of cell mediated immunity (Hildemann et al. 1975b, Hildemann 1977) is avoided. It is possible that the threads (Fig. 4b) found in the narrow gaps between allografts play a role in the self recognition phase, and if so, after the recognition of non-self, a variety of aggression forms follow. Thus, the immunological system might be a trigger or suppressor for different aggressive mechanisms. A more complicated situation is the recognition from a distance, which is the most common case on the reef. If there is indeed any component of recognition in these cases, it must be carried out through allelochemicals or pheromones. In addition, chemical interactions might occur through continous secretion of an array of materials, which do not necessarily require any recognition mechanisms.

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