Interspecific Aggression in Hermatypic Corals from Panjang Island

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Abstrak

Penelitian terhadap agresi interspesifik antara koral hermatipik dari Pulau Panjang dilakukan di akuarium antara bulan September – Desember 2000 di Laboratorium Kelautan Teluk Awur Jepara. Resultan hirarki dibuat dengan melakukan rangking terhadap kemampuan suatu spesies untuk 'merusak' kompetitor. Studi lapangan dilakukan untuk mekonfirmasi apakah spesies paling agresif merupakan spesies yang mendominasi. Hasil meunjukkan ditemukannya proses fusi terhadap semua pasangan dari koloni yang sama. Histoinkompatibilitas ditemukan setelah seminggu waktu kontak dengan adanya respon penolakan. Hal ini menunjukkan bahwa digesti oleh filamen mesenterial merupakan mekanisme paling penting dalam proses agresi, diikuti dengan overgrowth, dan unindirectional woundings yang diakhiri dengan rekasi penolakan. Stylophora pistillata merupakan spesies paling agresif, diikuti oleh Pectinia sp. Dan Pocillopora damicornis. Sedangkan Montipora dan Acropora memiliki sifat agresif lemah. Hasil ini menunjukkan bahwa karakteristik morfologi berperan penting dalam interaksi kompetitif. Tidak ditemukan interaksi intransitif pada hirarki yang ada. Namun studi lapangan menunjukkan bahwa spesies paling agresif tidak selalu merupakan spesies yang mendominasi. Agresifitas diduga bukan merupakan satu-satunya factor yang menentukan distribusi dan zonasi karang di Pulau Panjang.

Kata kunci: *agreasi interspesifik, karang, Pulau Panjang*

Abstract

Interspecific aggression between hermatypic corals on Panjang Island reef has been investigated by aquarium study. This study was performed between September and December 2000 at Marine Station Research Center, Kampus Teluk Awur Jepara. Resultant hierarchy was constructed by ranking the abilities of species to damage competitors. Field study was conducted to check whether the most highly aggressive species are those occupying the greatest area of sea floor. Fusion was observed in all same colony pairs by the end of experiment, regardless duration after initial contact. Histoincompatibility was visible after a week of contact with rejection was the most common response. It suggest that digestion by mesenterial filaments is the most important mechanism of aggression followed by overgrowth and unidirectional woundings that ended as a stand-offs reaction. Stylophora pistillata being the most highly aggressive species in Panjang Island followed by Pectinia sp and Pocillopora damicornis while Montipora and Acropora are weakly aggressive. This result confirmed that differences in morphological characteristics play an important role during competitive interactions. No intransitive interaction was observed from the present hierarchy. Field study revealed that the most highly aggressive species is not necessary to those occupying the greatest area of sea floor. Aggression may not the single factor which influence spatial distribution and zonation of coral reefs in Panjang Island.

Key words: *interspecific anggression, corals, Panjang Island*

Introduction

The spatial distribution of hermatypic corals on a reef is governed by a complex interplay of physical and biological factors; of the latter, interspecific competition may play a significant role direct interaction. Indirect mechanism of competition would include overgrowth and overtopping (Connell, 1976).

The significance of interspecific competition in scleractinian corals has been discussed by various authors (Lang, 1973; Sheppard, 1982; Logan, 1984;

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Lang and Chornesky, 1990; Van Veghel *et al.*, 1996) and still remains much in question (Logan, 1984; Lang and Chornesky, 1990; Van Veghel *et al.*, 1996, Frank *et al.*, 1997). Although it is believed that the importance of interspecific interactions increases in areas with high coral density and diversity (Bak and Povel, 1988), the effect and ecological consequences of interspecific interactions on the structure and evolution of reef communities are not well understood (Van Veghel *et al.*, 1996).

This study examines aggressive interactions among Panjang Island corals, Jepara in the aquarium with addition of observation in the field. The reefs of Panjang Island are at the northern of Java Island support a depauperate fauna of about 19 hermatypic coral genera that are readily distinguishable in the field (Munasik *et al.*, 2000). This relatively small number allows experiments to be performed from which an aquarium hierarchy can be established.

This study documents the frequency of interactions of various species of hermatypic corals. A model of aquarium hierarchy, derived from grafting assayed observation was established. The mechanism and possible role of interspecific aggression in influencing the diversity and spatial distribution of corals on Panjang Island reefs are briefly discussed.

Materials and Methods

This study was performed between September and December 2000 at Marine Station Research Center, Kampus Teluk Awur Jepara.

Experiments

We selected Ten frequently occurring coral species, which were most abundance species in Panjang Island based on preliminary survey using line transect method (Loya, 1972) were selected on conducted at the middle of September 2000. Those are *Montipora digitata; Acropora sp; Pocillopora damicornis; Acropora aspera; Porites* sp; *Stylophora* pistillata; *Goniastrea* sp.; *Pectinia* sp; *Montipora hispida* and *Pavona decussata* (Veron, 1986; Suharsono, 1996). All corals colonies were kept in indoor tank aquaria (1 x 2 x 1.5 meter) supplied with running seawater at ambient temperature for 1-week acclimatization before grafting experiment was done. Experimental grafts were performed as follows: branch segments were made from donor colonies using cutting pliers; 5 cm long for branching corals or 5 x 5 cm for massive corals. They were then tied onto recipient colonies with nylon monofilament line. Each experimental graft was labeled with a tag of plastic sheet. Grafts were then hanged on wooden strip using a small fishhook connected with nylon monofilament line (Neigel and Avise, 1985). Each graft was allowed to hang freely in the seawater.

The number of possible pairings between colonies of different species is N (N-1)/2, where N is the number of species (Logan, 1984). In this study, 10 species were used, resulting in 45 possible interactions; in addition, a piece of the recipient colony was grafted to itself, acting as an isogenic control. There were 10 pairs of isogenic control. Three replications were made for each possible interaction between the same (isografts) or different species (xenograft). A total of 165 pairs were made for grafting experiment. Each graft was observed weekly using dissecting microscope (NIKON SMZ-2T) for consecutive 2 months. During observation every reactions and development were recorded and classified. Once a month each graft was photographed (Contax 167 MT). During experiment, all pairing species were cleaned once a week to avoid sedimentation and to remove algal competitor.

Interpretation of the outcome of each graft was based on the condition of tissue at the graft interface and skeletal morphology with reference to the control graft. The results of all interactions were recorded as follows:

(1) Fusion (2) rejection (3) non-fusion (4) incompatible fusion (5) stand-offs (6) tissue rejection to overgrowth (Table 1). The results would be classified based on the reactions of each graft. Hierarchy model would be established based on the out comes of grafting experiment. The hierarchy model would be used for predicting the structure of hermatypic corals of Panjang Island.

Field transect

At the end of grafting experiments, a field transect using Line transect method (Loya, 1972) was conducted to check whether the positions of each species in hierarchy model based on the aquarium data related to their percentages of coral cover of species in nature by counting *Simpson* domination index (English *et al.*, 1994).

Results and Discussion

Pairings of controls (Isografts)

At the end of grafts experiments from a total of 30 pairs between isografts most all control colonies fused (Table 2). Only in isografts of *Montipora* *digitata* and *M. hispida* both showed a stand offs reaction without any lesions. In fused pairs of *Pocillopora damicornis, S. pistillata* and *Pectinia sp.*, fusion occurred within 2 weeks after contact the tissue of the grafts become continuous (Fig. 2A). In *Goniastrea sp.* fusion occurred within 3 weeks after contact. Four pairs of *Acropora sp., A. aspera, Porites sp.* and *Pavona decussata* fusion occurred between 5 to 7 weeks after contact. One replicate of *Pavona decussata* pair showed no reaction until the end of experiment. Non-fusion reaction was not observed in pairs within species. Incompatible fusion reaction apparently occurs in one replicate of *A. aspera* pair since a white gap was observed in the contact area (Fig. 2B), but such fusion never changed to other reaction until the end of observation.

Pairings between colonies of different species (xenografts).

Different types of response are observed in contacts between 10 hermatypic corals. At the end of grafts experiments, from a total of 135 experimental pairings between different species in the aquaria 16 pairs (11.85%) resulted in overgrowth reaction; 2 pairs (1.48%) resulted in conclusive one-way results where digestion of tissue of the subordinate species by mesenterial filaments from the dominant coral resulted in an area of bare skeleton. There were 25 (18.51%) cases of rejection that both corals suffered from necrosis (tissue lesions) probably due to mesenterial digestion or sweeper tentacle contact. While there were 59 (43.19%) cases demonstrated the most frequent reaction; the subordinate species was death and their opponent--the dominant species stayed alive until the end of experiment; though the dominant species showed different reactions. There were 38 (28.14%) dominant species suffered from tissue lesions while 21 (15.56%) dominant species stayed alive without any damage on their tissues (Table 3)

Grafts between *Montipora digitata* with its 9 opponents demonstrated almost the same results. From 27 grafts, *M. digitata* never showed as a dominant species. At the end of the experiment, all *M. digitata* branch segments were death, though two opponents suffered from tissue lesions. i.e. *Pocillopora damicornis* and *Acropora aspera* and three were death : i.e. *Acropora sp, M. hispida* and *Pavona decussata*. More over two species; *Goniastrea sp* and *Pectinia sp* tended to overgrowth the bare skeleton of *M. digitata* (Fig. 2C) while two other species; *Porites sp* and *Stylophora pistillata* stayed alive without any lesions. Most of grafts between *Acropora sp* and *A. aspera* ended at the same results. Nor *Acropora sp* or *A. aspera* could act as a dominant species. *S. pistillata* and *Pectinia sp* showed overgrowth reaction on the necrosis area or the bare skeleton of *A. aspera*, but in case of *Pectinia sp*, a small lesions was also observed during contact with *A. aspera* (Fig. 2D). *Porites sp.* also revealed not too aggressive to their competitors. At the end of the experiments, most branch segments of *Porites sp.* were death.

Different reaction was demonstrated by *Stylophora pistillata*. This species mostly dominated its opponents and only that in pairing with *Pectinia sp.* resulted in stand-offs with mutual damage while in pairing with *Pavona decussata* both contestants were death at the end of the experiments. Similar results were found on pairings between *Pectinia sp.* and its opponents. *Pectinia sp* mostly dominated its opponents except when it paired with *Goniastrea sp* and *S. pistillata*, both resulted in stand-offs reaction. The colonies of *Pectinia sp* tend to overgrowth its opponent's death tissues. While in *Montipora hispida* and *Pavona decussata* both corals could not reveal their dominance to their opponents (Table 4).

From these experiments (Table 4) an aquarium hierarchy was established (Fig. 1), based on interaction results and number of subordinate species. *S. pistillata* being the most highly aggressive in Panjang Island and then followed by *Pectinia sp.* and *P. damicornis* while *Porites sp., Goniastrea sp.*, and *P. decussata* are moderately aggressive. Both *Montipora* and *Acropora* species are weakly aggressive. No intransitive interactions occurred from the present hierarchy. It has generally been assumed that coral interactions under normal conditions conform to a strict linier hierarchy with few exceptions (Lang, 1973; Connell, 1976).

Field study

Field occurrences of interspecific interactions are common between most abundant species in Panjang Island. Fourteen genera were observed with Acropora as the greatest genus occupying the sea floor (Table 5). Simpson domination index shows no domination in Panjang Island coral species since the index value is merely zero (Table 5). These results were similar to preview worth reported by Munasik *et al.* (2000).

Control pairs (Isografts)

Fusion was observed in almost all controls (isografts) 2 to 6 weeks after contact. Since those branch segments were taken from the same colony, it can be assumed that they are genetically identical. Contact between conspecific coral colonies usually ended in partial or complete fusion, depending upon their genetic relationship (Rinkevich and Loya, 1983a).

However, both in isogenic experiments of *Montipora digitata* and *M. hispida* fusion was not observed after 8 weeks of contact. This may mean that although those pair was compatible enough to fuse there were minor differences and recognition for fusibility took longer (William, 1997). Fusion may occur only when individuals share all histocompatibility alleles, but histocompatibility loci may be only moderately polymorphic. Alternatively, fusion may occur for pairs of individuals which share only a proportion of their histocom-patibility alleles or between pairs of genetically distinct individuals if the immune response is surpressed by periods of prior contact (Willis and Ayre, 1985) as described in primary polyps of the coral *Pocillopora damicornis* (Hidaka, 1985).

Despite initial abrasion in the area of contact (Rinkevich and Loya, 1983a), fusion of soft tissues generally has been thought to benefit both reef corals, rather than being a form of competition. Fusion appears to be limited to intraspecific encounters; while within a given genotype it is common both in nature and during grafting experiments (Hildemann *et al.*, 1975). Fusion sometimes occurs between juveniles or its aggregated and established reef corals in the field (Sammarco, 1982). Newly metamorphosed polyps known to have the same or different maternal parents (Hidaka, 1985), have been observed to fuse in the laboratory. Fusion also occurs at certain allograft interfaces (Rinkevich and Loya, 1983b), including some in which the parabionts have been shown to be electrophoretically distinct (Heyward and Stoddart, 1985; Resing and Ayre, 1985: Willis and Ayre, 1985). However, recent experiment demonstrated, that those derived from different colonies some showed incompatible fusion; tissues were continuous but a white zone without zooxanthellae was observed at the interface (Hidaka *et al.*, 1997). Incompatible fusion appears to be a distinct histoincompatible response which later transforms into non-fusion (Hidaka *et al.*, 1997).

Reef corals gaining increased physical stability by fusing (Hildemann *et al.*, 1975) will benefit from this interaction, but some possible deleterious side effect for their soft tissues still occur. Eventually border-line gaps may develop at the graft interfaces which in *Stylophora pistillata* are up to 30 mm wide (Rinkevich and Loya, 1983a). A restricted growth may occur when fusion of soft tissues is followed by contiguity of the underlying skeletons. Branches of certain reef corals, when they are separated *in situ* by distances of about 1 cm or less, change either their direction or rates of skeletal growth, rather than growing into direct contact (Rinkevich and Loya, 1983a; Rinkevich and Loya, 1985). In some species, natural contact avoidance (*sensu* Hildemann *et al.*, 1975) may regulate interbranch spacings within colonies. When individuals which are genetically different fuse, it is believe that one genotype will suffer as a result of being paratised by the other (Buss, 1982). Such effects which may occur in reef corals (Rinkevich and Weissmann, 1987; 1992) have been reported in somatic and germ cell lines in chimeras of the colonial urochordate *Botryllus schlosseri* (Pancer *et al.*, 1995).

Pairings between colonies of different species (Xenografts)

When physical contact occurs during direct encounters, many reef corals utilize one or more competitive structures or secretions to injure the soft tissues of certain opponents. However, not all reef corals are damaged equally by any given neighbour; those having fleshy polyps with relatively strong, ciliary. cleaning currents (Lang, 1970 *in* Lang and Chornesky, 1990) or thick layers of mucus (Bigger and Hildemann, 1982: Chadwick, 1988) perhaps are better protected from direct attack by competitors. Results of the present grafting experiment between xenografts show *Stylophora pistillata* as being the most aggressive-dominant species followed by *Pectinia sp* and *Pocillopora damicornis.* It is likely that the results consistent with the above statements. Both *S. pistillata* and *P. damicornis* which belong to family Pocilloporidae have submassive, ramose or arborescent colonies with thick or sturdy branches, while *Pectinia sp* as the member of Pectiniidae has fleshy polyps with thick layers of mucus (Veron, 1986). On the other hand, Montipora as the weak aggressive contestants has character as submassive, laminar, foliceous, encrusting or branching colonies with very small corallites that are found either immersed in the coenosteum or situated at the base of tunnel-shaped depressions (Veron, 1986); while most Acropora species usually have light skeletons which allow them to grow quickly and overcome their neighbours. So they are usually powerful in indirect contact (Veron, 1986) by forming the large, delicately engineered plates and tables that are common in most reef slopes.

Goniastrea and Porites as moderately aggressive contestant have massive or encrusting colonies (Veron, 1986). Most digestively dominant reef corals are usually slow growing, massive or encrusting as in the family of Faviina (Lang, 1973), which

Goniastrea belong to. It is likely that differences morphological characteristic among species play an important role during competitive interactions (Van Veghel *et al.*, 1996). Bumpy morph of *Montastrea annularis* that has relatively fleshy polyps and thicker layers of mucus created larger lesions to its opponent; massive and columnar morph of the same species (Van Veghel *et al.*, 1996).

Histoincompatibility reactions appearing in parabiotic grafts generally are visible within days to weeks after initial contact, and tend to occur more rapidly in xenografts than in allografts (Hildemann *et al.*, 1975). Histoincompatibility in the present study appeared within a week after contact experiment. Lesions observed in the tissues of subordinat species. Lesions at parabiotic graft interfaces commonly are attributed to induced cytotoxic effects resulting from contact with the soft tissues of another reef coral (Hildemann, 1977). The underlying biochemical basis of the presumed cytotoxicity is not understood (Bigger and Hildemann, 1982).

Most previous works on competitive-interactions in reef building corals have been demonstrated that the common mechanisms involved are the extracoelenteric digestion by mesenterial filaments and the extent of sweeper tentacle development (see Lang and Chornesky, 1990). In the present study, it is likely that the dominant species directly damages the subordinat species by mesenterial filaments. Mesenterial filaments were occasionally observed in *P. damicornis*, *Goniastrea sp* and *Pectinia sp* especially during the night while histoincompatibility mechanism was shown in parabioticgrafts of *Pavona decussata, S. pistillata and Porites sp.* Overgrowth mechanism mostly was shown by *Pectinia sp.* The tissue of *Pectinia sp.* grown over the exposed skeletons of its opponents whose soft tissues have injured previously as shown in pairs of *Pectinia sp* with *M. digitata*. Some experiments grafts showed unidirectional woundings where the sizes approximately equal on both reef corals as in pairs of *P. damicornis* and *Goniastrea sp; P. damicornis* and *Porites sp; Porites sp* and *Goniastrea sp; S. pistillata* and *Pectinia sp; Goniastrea sp* and *Pectinia sp*; *Goniastrea* and *M. hispida*. All that pairs showed a stand-offs reaction until the end of experiment without any domination from one contestant to their encounter (Table 4). None of the contestant showed an ultimate domination. It probably the answer why the circular interaction (intransitive) was not observed in this present study.

Compare to the study of interspecific aggression in hermatypic corals from Bermuda (Lang, 1984) which also based on an aquarium dominance hierarchy, members of the families Mussidae, Meandrinidae and Faviidae were moderately to highly aggre-ssive while those from the Astrocoeniidae, Pocilloporidae, Agariciidae, Siderastreidae, Poritidae and Oculinidae were weakly aggressive. While outcomes of this present study showed that the members of the families Pocilloporidae and Pectiniidae being the most aggressive while those from Faviidae, Poritidae and Agariciidae are moderately aggressive. In Bermudian aquarium hierarchy most of the circular interactions occurred within a network of weakly aggressive species as the same as the result of a coral hierarchy of 16 species in Hongkong (Cope, 1981) while in this study a hierarchy of circular interaction was not observed. Differences in ranking of the coral species are thought to be a product of geographic variation, species composition and species diversity differences (Sheppard, 1982; Lang, 1984).

It may be argued that a digestive hierarchy of coral aggression derived solely from experiments where coral colonies are artificially brought into direct contact over a short period of time in an aquarium except where periodic low-level disturbance brings coral colonies into similar contact under natural conditions. Such disturbances are common on the pinnacle reefs in Panjang Island, where branches of Pocilloporidae and Acroporidae are often dislodged, but much less common amongst the more massive corals. Nevertheless, because the mechanism of aggression appears mostly by extracoelenteric digestion by mesenterial filaments, result interaction results do have value in suggesting the predominant mechanism responsible in the field.

Research over the last decade has revealed the potential complexity of competition between reef corals. Recent opinion seems to favour either a minor role for aggression in structuring coral reefs or one which is impossible to delimit because of the unpredictable nature of interactions (Lang and Chornesky, 1990). As in Bermuda, the most highly aggressive species in Panjang Island are not those occupying the greatest area of sea floor (Table 5). Other biological factors affecting corals such as reproductive mechanisms and rates, larval ecology, growth rates and susceptibility to predation and diseases must all be taken into account, while physical factors, such as wave action, seasonal water temperature variation and turbidity doubtless play an important disturbance role in the distribution of corals. Aggression not only the single factor which influence the spatial distribution, and zonation of coral reefs in Bermuda, achieving greatest importance in areas of high coral density and diversity.

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Tabel 1. Categories of Grafts Observed responses

Reaction	Definition
Fusion	The tissue of pairs becomes continuous, there is no sign of junction and zooxanthellae are uniformly distributed through the contact area (Hidaka, 1985).
Rejection	Tissue destruction in one or both components of the pair extending up to a few millimeters from the contact point (Hidaka et al., 1997)
Non-fusion	A response in which tissues of paired corals are demarcated by a borderline without any tissue necrosis (Hildemann et al., 1975; Rinkevich and Loya, 1983; Chadwick-Furman and Rinkevich, 1994). A skeletal ridge or suture is usually formed at the interface
Incompatible fusion	Tissue appeared continuous, but zooxanthellae were not evenly distributed across the interface area, creating a while zone. Skeleton was not continuous (Hidaka et al., 1997).
Stand off	When two reef corals appear to stop growing a long a common margin without obvious damage to their soft tissues (Connell, 1976). Areas of mutual, soft-tissue damage which lack evidence of current competitive activity (Lang and Chornesky, 1990).
Overgrowth	Skeletal ridges extend vertically at first but latter, in most cases, lean towards one of the pair members resulting in overgrowth of one of the pair (Chadwick-Furman and Rinkevich, 1994).

Table 2. Reaction observed in controls pairs (isografts) after 8 weeks of contact, Numbers of different type of responses are shown. The letter indicates the name of the species *Montipora digitata* (A), *Acropora sp.* (B), *Pocillopora damicornis* (C), *Acropora aspera* (D), *Porites sp.* (E), *Stylophora pistillata* (F), *Goniastrea sp.* (G), *Pectinia sp. (Physophyllia sp.*) (H), *Montipora hispida* (I), *Pavona decussata* (J). NR = No Reaction, F = Fusion, D = Death

No	Pairs	Replication	Reaction	Duration of contact (Weeks)
1	A-A	1	NR	8
		2	NR	8
		3	NR	8
2	B-B	1	F	5
		2	F	6
		3	F	6
3	C-C	1	F	2
		2	F	2
		3	F	2
4	D-D	1	F	7
		2	F	7
		3	F	6
5	E-E	1	F	7
		2	F	4
		3	F	5
6	F-F	1	F	2
		2	F	2
		3	F	2
7	G-G	1	F	3
		2	D	3
		3	F	3
8	H-H	1	F	2
		2	D	2
		3	F	2
9	I-I	1	NR	8
		2	NR	8
		3	NR	8
10	J-J	1	NR	8
		2	F	6
		3	F	7

Table 3. The outcomes of grafting experiments between different colonies (xenografts) after 8 weeks of contact. Type of responses, number of xenografts and their percentation are shown.

Type of responses	Number of Pairs	Percent
Overgrowth	16	11.85
Rejection in stay alive pairs		
- subordinate species suffered from tissue lesions	2	1.48
- both contestants suffered from tissue lesions	25	18.51
Rejection in pairs which only one contestant stay alive		
- alive opponent suffered from tissue lesion	38	28.14
- alive opponent did not suffer from tissue lesion	21	15.5
Both contestant death	33	24.44

Table 4. Table of domination of Panjang Island corals in grafting experiments. Minus lines indicate control pairs. Horizontal arrows indicate consensus of dominance of species in left-handed column over those in top column, Vertical arrows indicate the opposite. Asterisk indicate no domination.

	M. digitata	*Acropora sp.*	*P. damicornis*	*A. aspera*	*Porites sp.*	*S. pistillata*	*Goniastrea sp.*	*Pectinia sp.*	*M. hispida*	*p. decussata*
Montipora digitata	-	*	↓	↓	↓	↓	↓	↓	*	*
Acropora sp.	*	-	↓	*	↓	↓	*	↓	↓	*
Pocillopora damicornis	→	→	-	→	*	↓	*	*	→	→
Acropora aspera	→	*	↓	-	↓	↓	↓	↓	→	*
Porites sp.	→	→	*	→	-	↓	*	↓	*	↓
Stylophora pistillata	→	→	→	→	→	-	→	*	→	*
Goniastrea sp.	→	*	*	→	*	↓	-	*	*	*
Pectinia sp.	→	→	*	→	→	*	*	-	→	→
Montipora hispida	*	→	↓	↓	*	↓	*	↓	-	*
Pavona decussata	*	*	↓	*	→	*	→	↓	*	-

Table 5. Summary of line transect data on coral coverage which shown in percent cover and domination (D) of Panjang Island population based on their life form. Panjang Island was divided into 4 station respectively (AA= algal assemblages; DC= death corals; DCA=death coral algae; HA= halimeda; RB= rubble; RCK= rock; SD=sediment)

Life Form/ Genus	Station				Total	% Cover	D
	1	2	3	4			
Acropota	128	231	2260	2804	5423	10.846	0.011763572
Favia	197	64	286		547	1.094	0.000119684
Favites	45	150	906	39	1140	2.28	0.00051984
Galaxea	301	133	85	53	572	1.144	0.000130874
Goniastrea	542	180	360	198	1280	2.56	0.00065536
Goniopora	50	109	257	1961	2377	4.754	0.002260052
Lobophylia			175	104	279	0.558	3.11364E-05
Montipora	*295*	*191*	*66*	*1304*	*1856*	*3.712*	*0.001377894*
Pavona	351	121			472	0.944	8.91136E-05
Pectinia	508				508	1.016	0.000103226
Platygyra	102	262	807	101	1272	2.544	0.000647194
Pocillopora	178	59	22	99	358	0.716	5.12656E-05
Porites	1050	1299	5097	1109	8555	17.11	0.02927521
Stylophora	587	109		127	823	1.646	0.000270932
AA	59	145	52	121	377	0.754	5.68516E-05
DC	956	840	646	41	2483	4.966	0.002466116
DCA	998	3411	759	1175	6343	12.686	0.01609346
HA			105		105	0.21	0.00000441
RB	2854	5609	1845	1749	12057	24.114	0.0581485
RCK	799	1087	272	332	2490	4.98	0.00248004
SD				683	683	1.366	0.000186596
	10000	14000	14000	12000	50000	100	0.126731323

Fig. 1. Hierarchy of dominance for Panjang Island corals based on an aquarium experiment after 8 weeks of contact. *Lines with arrow head* indicate direction of contact, ranking based on interactions and number of subordinates, *parallel lines with arrow head* indicate mutual damage within a pair, *lines without arrow head* indicate both contestant died. Number of subordinates in parentheses.

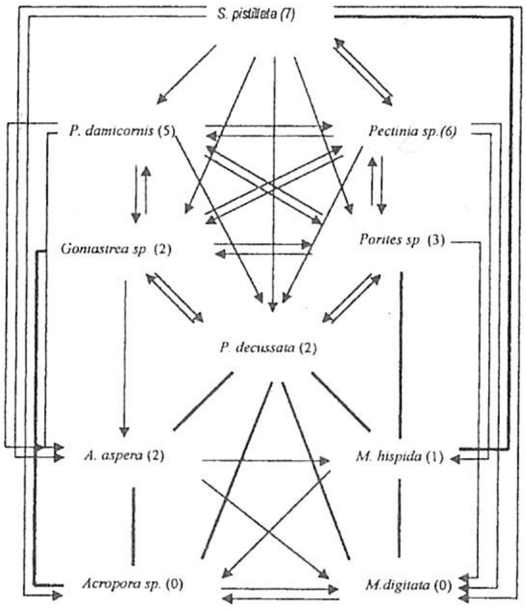

Fig. 2. A — B. Fusion response of isografts pairs.

A. Fusion of colonies of *Pocillopora damicornis* after 2 weeks of grafting experiment. Tissue of pairs become continuous, there is no sign of junction through the contact area. (magnified 10 x)

B. Fusion of colonies of *Acropora aspera* after 6 weeks of grafting experiment. Tissue appeared continuous, but zooxanthellae were not evenly distributed across the interface area of contact, creating a white zone. (magnified 10 x) (CA=area of contact; WZ=white zone)

C – D. Nonfusion response of xenograftpairs

C. A colony *A. aspera* (mid-bellow) which had been injured (white area of exposed skeletal tissues) by *Pectinia sp* (mid – above) but somehow the tissue of *Pectinia sp* revealed a small lesions through the contact area (after 8 weeks of contact).

D. The *Pectinia sp* (to left) which is digestively dominant to *Montipora digitata* (to right) during experimental manipulation, also appeared to be overgrowing this colony in the area of contact (after 6 weeks of contact) (ca = area of contact, p= *Pectnia sp*, a= *Acropora aspera*, sl= small lesions, m= *Montipora digitata*, og= overgrowth, both photos are magnified for 10x)