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Interspecific competition in Taiwanese corals with special reference to interactions between alcyonaceans and scleractinians

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ABSTRACT: Naturally occurring interspecific competition in scleractinian and alcyonacean corals was studied on the reefs of southern Taiwan. A total of 1168 pairwise interactions were recorded and analysis of the data, using a competitive index, led to classification of corals into 5 categories. Three major conclusions can be drawn. (1) The ranking of competitive ability shown by a species bears little apparent relationship to its systematic position, and the most aggressive corals such as *Merulina ampliata, Echinophyllia asper,* and *Mycedium elephantotus* are often most abundant on the reefs. (2) Alcyonaceans are generally subordinate when in contact with scleractinians; the former are often subjected to mesenterial digestion by the latter. The position of contact is probably an important determinant in interactions between soft and hard corals. (3) Coral interspecific interactions on the reefs of southern Taiwan show some evidence of competitive networks.

INTRODUCTION

Competition for space between corals on a reef is generally understood to be intense. Although coral competition had been noted much earlier (e.g. Darwin 1842) in the sense that corals sometimes killed their neighbors and overgrew them, its possible ecological significance was not investigated further until the studies by Lang (1971, 1973) on the aggressive hierarchy of Atlantic corals. Since then, competition for space among corals has been intensively investigated (e.g. Sheppard 1979, 1980, Wellington 1980, Cope 1981, Bak et al. 1982, Chornesky 1983, Logan 1984).

In comparison to the Caribbean, the interactions of corals on Indo-Pacific reefs are less studied, in part due to the enormous diversity of Indo-Pacific faunas. Scleractinian and alcyonacean corals are abundant sessile invertebrates on Indo-Pacific reefs (Cary 1931, Crossland 1938) in terms of the amount of substratum covered. However, the interactions between these 2 groups have been studied only very recently (e.g. Sammarco et al. 1983, 1985, 1987, La Barre et al. 1986). Previous studies on the interactions between alcyonacean and scleractinian corals found that alcyonacean corals always win conflicts with scleractinian corals (Benayahu & Loya 1977, 1981, Sheppard 1979, Nishihira 1981, Coll et al. 1982, Sammarco et al. 1983). Sammarco et al. (1985), however, have provided contradictory evidence that some alcyonacean corals may suffer tissue necrosis when in contact with scleractinian corals. The complexity of the interactions between these 2 groups of organisms indicates that more studies are necessary to clarify their competitive interactions before we can understand the influence on their distribution and relative abundance on coral reefs.

Coral competitive interactions were originally conceived as consistent and hierarchical (Lang 1973, Connell 1976). However, Sheppard (1979) and Bak et al. (1982) have shown that coral interspecific interactions are not completely hierarchical and several factors such as environmental conditions, colony size, position of contact, the development of sweeper tentacles, and the presence of epifauna may alter the result of interactions. The reversal of digestive interactions when sweeper tentacles develop (Wellington 1980) and the inconsistent competitive relationships among coral interactions imply that interspecific competition on a coral reef may be intransitive (Buss & Jackson 1979, Lang & Chornesky unpubl.).

The purpose of this study is to investigate the pattern

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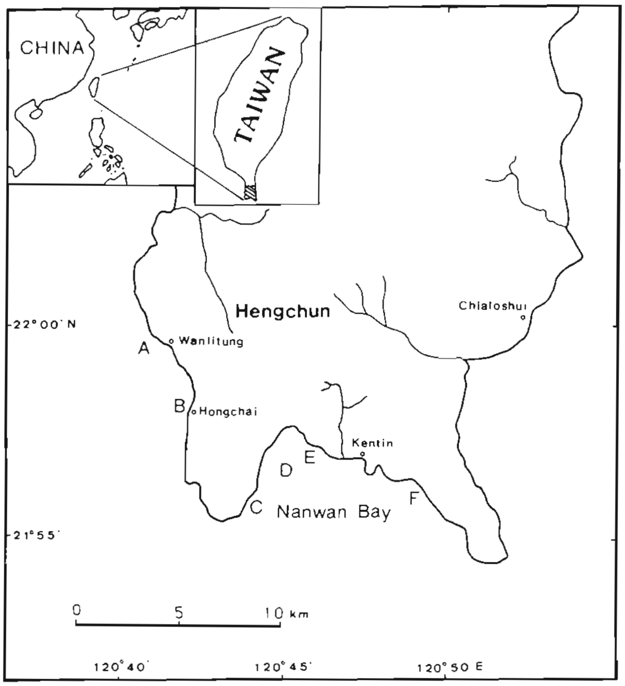

Fig. 1. Study area showing the 6 (A to F) field observation sites

of coral interspecific interactions on the reefs of southern Taiwan. The study surveyed pairwise, naturally-occurring interactions between any 2 species of scleractinian, alcyonacean, and hydrozoan, with an emphasis on interactions between species of alcyonaceans and scleractinians. The mechanisms and possible effects of interspecific interactions in species diversity and distribution of corals are discussed.

MATERIALS AND METHODS

Study site. Observations were made at depths between 1 and 30 m on the fringing reefs of southern Taiwan (21° 55′ to 22° 00′ N, 120° 40′ to 120° 52′ E; Fig. 1). Southern Taiwan is located in the middle of the West Pacific Island Arcs. A moderately well-developed fringing reef and relatively high diversity of corals occur in the study area (Jones et al. 1972). Previous work at Hengchun Peninsula has recorded 245 scleractinian coral species and 15 species of alcyonacean corals. A recent systematic study reviewed 218 species of scleractinians and 36 species of alcyonacean corals (Dai 1986). The alcyonacean corals are mainly distributed on both sides of the Peninsula, near the 2 tips, where they often comprise more than half on the surface area covered by coral tissues (Jones et al. 1972, Dai 1988).

Field observations. Since there are about 250 species of scleractinian and alcyonacean corals on the reefs of southern Taiwan and several thousand pairs of interaction are possible, I restricted this study to naturally occurring interactions. Field observations were made in June to August 1986 and February to April 1987.

Coral colonies that abutted, touched, or were in close proximity (< 8 cm in distance) to those of another species were recorded along 6 transects. Three types of interactions were recognized: direct interaction, overgrowth, and stand-off. A direct interaction was recognized when a dead margin was observed on one specimen of the pair (Connell 1976). Such scars serve as records of presumed interactions and are easily discernible in the field. Direct interactions may have involved mesenterial digestion, as described by Lang (1973), or sweeper tentacles, as described by Richardson et al. (1979) and Wellington (1980). Since the present study was mainly based on static observations at one particular moment, no effort was made to dinstinguish these or any other presumed mechanisms. Overgrowth was recognized when one specimen grew, physically in contact, over its neighbor but no tissue damage on the contact area was discernible. Many cases of overgrowth accompanied by direct interactions were excluded from this category and classified as direct interactions, since the latter mechanism was perceived to precede the former one. Stand-off represents 2 coral colonies in close contact but with no evidence of tissue damage or overgrowth (Connell 1976, Sheppard 1979).

Data analysis. In order to compare the relative competitive ability of coral species, an index (CI) was calculated for each species based on observations of direct interactions and overgrowth, where

$$CI = \frac{\text{No. of wins} - \text{No. of losses}}{\text{Total no. of interactions}}$$

The calculated CI for each species can range from −1 for a species which loses all interactions, to +1 for a species which wins all interactions. Species with more than 6 recorded interactions were then grouped into 5 categories according to their competitive abilities (CI). The criteria for this grouping were: aggressive, 1 to 0.6; moderately aggressive, 0.59 to 0.2; intermediate, 0.19 to −0.2; moderately subordinate, −0.21 to −0.6; and subordinate, −0.61 to −1.

RESULTS

A total of 1168 interactions involving 138 species were recorded. Among these interactions, 533 (45.6 %) of them were direct, 443 cases (37.9 %) involved simple overgrowth, and 184 cases (15.8 %) were stand-offs. The remaining 8 cases were suspected as being caused

by allelopathic chemicals. The recorded interactions between major species, with particular reference to alcyonacean/scleractinian interactions, are summarized in Table 1. The results of grouping of corals based on CI are listed in Table 2.

The relative competitive ability of coral species does not have a relationship with their systematic position (Table 2). Species of several large genera, such as *Acropora* and *Montipora*, have a wide spread of competitive abilities. Since these genera include species with a variety of growth forms and growth rates which are important in determining the outcome of interspecific interactions, it is reasonable that they may have different competitive abilities. In general, species of Pectiniidae, Merulinidae and Oculinidae are the most aggressive; species of Mussidae are moderately aggressive; species of Agariciidae and Dendrophylliidae are intermediate; and species of Poritidae (*Goniopora* excluded) and Alcyoniidae are generally subordinate. The Faviidae display 2 extremes of competitive ability: species of *Hydnophora*, *Platygyra*, *Favia* and *Echinopora* are aggressive and those of *Plesiastrea* and *Cyphastrea* are subordinate. Among the common non-scleractinian reef builders, hydro-

Table 1. Data from field observations on interspecific interactions of corals. Solid arrows indicate direct interactions, dotted arrows indicate overgrowth, double lines indicate stand-off, and wavy arrows indicate possible allelopathic effect. Arrow points toward the winner of an interaction. Each interaction is based on 2 or more repetitive observations. ACHY: *Acropora hyacinthus*, MOVR: *Montipora verrucosa*, MOUN: *Montipora undata*, PCVR: *Pocillopora verrucosa*, SEHY: *Seriatopora hystrix*, STPI: *Stylophora pistillata*, PRAU: *Porites australiensis*, PRLI: *Porites lichen*, PRLU: *Porites lutea*, PSSP: *Pachyseris speciosa*, FASP: *Favia speciosa*, FTAB: *Favites abdita*, PTLA: *Platygyra lamellina*, MEAM: *Merulina ampliata*, ECAS: *Echinophyllia aspera*, MYEL: *Mycedium elephantotus*, GAFA: *Galaxea fascicularis*, ACEC: *Acanthastrea echinata*, SYRA: *Symphyllia radians*, SACR: *Sarcophyton crassocaule*, SATR: *Sarcophyton trocheliophorum*, LOSA: *Lobophytum sarcophytoides*, LOPA: *Lobophytum pauciflorum*, SIEX: *Sinularia exilis*, SIFA: *Sinularia facile*, SINU: *Sinularia numerosa*, SIPO: *Sinularia polydactyla*, SISC: *Sinularia scabra*

	ACHY	MOVR	MOUN	PCVR	SEHY	STPI	PRAU	PRLI	PRLU	PSSP	FASP	FTAB	PTLA	MEAM	ECAS	MYEL	GAFA	ACEC	SYRA	SACR	SATR	LOSA	LOPA	SIEX	SIFA	SINU	SIPO	SISC
ACHY																												
MOVR	⇠⇡																											
MOUN	⇠⇡	↑																										
PCVR	⇠↑																											
SEHY	⇠	↑	⇠↑	↑																								
STPI	⇠⇡			↑	=																							
PRAU	↑	⇠⇡	←↑	↑	←																							
PRLI	↑	=	⇡	⇡		⇡	=⇡																					
PRLU	↑		↑	⇡		⇡	↑																					
PSSP	=⇡					⇡		=																				
FASP	←	←		←⇡		⇡		←	←																			
FTAB	←	←		=	←⇡	←		←	←	=	=																	
PTLA	←=	←		⇡	⇡	←	←⇡	←	←	⇡																		
MEAM	←	←	←	←	←	←	←	←	←	←	←	←	←															
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GAFA	←	←		←	←	←	←	←	←	←	←			←↑	←↑													
ACEC	←	←		←	←		←	←	←		←	←		↑		=↑	↑											
SYRA	←	←‖			←	←	←‖	←	←		←‖	←↑		=↑	=	↑	↑	=										
SACR	⇠↑	↑	⇠↑	↑	↑	↑	↑		⇠	⇠	⇠↑	↑	↑	↑	↑	⇠↑	↑	=↑	=↑									
SATR	↑	⇠	↑		⇠↑	↑	⇠	⇠	⇠		⇠				⇠	↑	↑	=↑	↑									
LOSA	↑	↑		↑	↑	↑	⇠		⇠	⇠	⇠↑	⇠↑		↑	↑	⇠↑	↑	⇠↑	↑									
LOPA	⇠↑				↑		⇠	⇠	⇠		⇠↑	=	↑	↑			⇠		↑									
SIEX	←↑	⇡		↑	↑	↑	↜↑		⇠	⇠↑	⇠↑	⇠↑	⇠		↑	↑	↑	↑										
SIFA	⇠↑			=	↑	↑	⇠⇡	↑		↑		⇠↑		↑	↑	↑			↑					⇡				
SINU	⇡		⇡		↑		⇡	↑					⇠↑		↑		↑	↑	↑		⇠							
SIPO	⇡	↑		↜	↑	↑			⇠	↑	⇠↑	⇠	↜↑	↑			↑	⇠	↑			↜						
SISC	⇠↑	↑		↑	⇠↑	↑	⇠↑		⇠			↑	⇠↑	⇠	↑	↑									⇠			

Table 2. Coral species studied, arranged in 5 categories of relative competitive ability

Family	Aggressive	Moderately aggressive	Intermediate	Moderately subordinate	Subordinate
Acroporidae	*Acropora aspera*	*A. humilis*	*A. hyacinthus*	*M. informis*	*M. venosa*
	A. palifera	*A. nana*	*A. monticulosa*	*M. foveolata*	*M. monasteriata*
		A. tenuis	*A. gemmifera*	*M. peltiformis*	*Astreopora listeri*
		Montipora foliosa	*M. grisea*	*M. ehrenbergi*	
		M. undata	*M. tuberculosa*		
		M. verrucosa	*M. aequituberculosa*		
		M. spumosa			
Pocilloporidae		*Pocillopora verrucosa*	*Seriatopora hystrix*	*P. eydouxi*	*P. damicornis*
			Stylophora pistillata		
Poritidae			*Porites australiensis*	*P. lichen*	*P. lutea*
			P. (Synaraea) rus	*P. cylindrica*	
				P. nigrescens	
Agariciidae		*Pavona varians*	*Pachyseris rugosa*		
			P. speciosa		
			Coeloseris mayeri		
Faviidae	*Hydnophora exesa*	*Favia speciosa*	*Montastrea valence innesi*	*Leptastrea purpurea*	*Cyphastrea chalcidicum*
	Favia favus	*F. pallida*	*Favites flexuosa*		*Plesiastrea versipora*
		Echinopora lamellosa			
		Goniastrea pectinata			
		Platygyra daedalea			
		P. lamellina			
		P. sinensis			
Merulinidae	*Merulina ampliata*				
Pectiniidae	*Echinophyllia aspera*				
	Mycedium elephantotus				
Oculinidae	*Galaxea fascicularis*				
Mussidae		*Symphyllia radians*			
		S. recta			
		S. agaricia			
		Lobophyllia corymbosa			
		Acanthastrea echinata			
Dendrophylliidae			*Turbinaria frondens*		
			T. reniformis		
			T. immersa		
Milleporidae	*Millepora platyphylla*				
Helioporidae					*Heliopora coerulea*
Alcyoniidae			*Sarcophyton trocheliophorum*	*Lobophytum sarcophytoides*	*S. crassocaule*
			L. pauciflorum	*Sinularia compacta*	*S. glaucum*
			Sinularia polydactyla	*Sinularia facile*	*Sinularia granosa*
			Sinularia scabra	*Sinularia gibberosa*	*Sinularia exilis*
					Sinularia numerosa

zoans such as *Millepora platyphylla* are highly aggressive, and the blue alcyonarian *Heliopora coerulea*, which is killed by all corals encountered, is the most subordinate.

Species of Mussidae, Oculinidae, Pectiniidae, Merulinidae and Faviidae often cause severe tissue damage and create a broad polyp-free band on the subordinate species in contact with them. Such polyp-free bands might range up to 5 cm wide and are frequently colonized by filamentous algae or macroalgae.

Interactions between alcyonacean and scleractinian corals included colony movement in addition to direct interaction, overgrowth, and stand-off.

In direct interactions, alcyonacean corals are subordinate and frequently suffer from the attacks of scleractinian corals (Table 1). The most abundant species of alcyonaceans in the study area, such as *Sarcophyton trocheliophorum*, *S. crassocaule*, *Lobophytum sarcophytoides*, *Sinularia exilis* and *S. facile*, often suffer severe tissue damage when in contact with scleractinian corals. Even the least aggressive species of scleractinians such as *Porites* spp. and *Montipora* spp. sometimes can inflict tissue damage on these alcyonaceans. The most aggressive scleractinians such as *Galaxea fascicularis* and *Goniopora* sp. often extrude sweeper tentacles or sweeper polyps to attack adjacent alcyonaceans (Fig. 2).

Alcyonaceans sometimes overgrow scleractinians, especially the less aggressive species and massive or encrusting forms. In all cases of overgrowth, alcyonacean polyp-bearing capitula lie above the scleractinians and the sterile stalks of the former abut against the scleractinian colonies.

Interactions mediated by presumed allelochemicals were difficult to detect in field observations. In 8 interactions, significant tissue necrosis in scleractinians was observed and this was suspected to be caused by allelopathic chemicals.

Five cases of colony movement of alcyonaceans over scleractinians (La Barre & Coll 1982) were recorded when colonies of *Nephthea erecta* moved across the surface of *Acropora hyacinthus* by continuous colony division (Fig. 3).

DISCUSSION

Since more than 100 species of scleractinians and alcyonaceans were involved in this study and the interactions are highly complicated, it is not possible to establish a clear-cut hierarchy as achieved by Lang (1973) and Cope (1981). The grouping of Taiwanese scleractinian corals according to their competitive abilities (Table 2) is mostly in agreement with Sheppard (1979) and Cope (1981) but includes many more species. Sheppard (1979) concluded that *Seriatopora hystrix* was very subordinate and *Acropora hyacinthus* was highly aggressive. In this study, however, they

Fig. 2. *Goniopora* sp. (Poritidae: Scleractinia) extends its 'sweeper polyps' attacking an alcyonacean coral, *Sinularia* sp. (× 0.3)

Fig. 3. *Nephthea erecta* (Nephtheidae: Octocorallia) colonies overgrowing a scleractinian coral, *Acropora hyacinthus*, by continuous colony division. Note the trails of *N. erecta* (× 0.6)

were intermediate and won about half of the interactions.

The alcyonacean corals on the reefs of southern Taiwan are generally subordinate when in contact with scleractinian corals. Previous studies on competitive strategies of alcyonacean corals have emphasized the effects of allelopathic chemicals (Coll et al. 1982, Sammarco et al. 1983, 1985) and their ability to overgrow opponents (Benayahu & Loya 1977, 1981, Nishihira 1981) in competition for space on corals reefs. Since the deleterious effects demonstrated by Sammarco et al. (1983) were rarely observed in this study, chemicals may not be of great importance for alcyonaceans in competition for space on the reefs of southern Taiwan.

In the Caribbean, the most aggressive species (Mussidae, Meandrinidae, and Faviidae) are often massive. Since they grow relatively slowly, they are not good space competitors and they are minor components of coral communities (Lang 1973). On the other hand, in the Indo-Pacific, the most aggressive species (Merulinidae, Pectiniidae) often have a better ability to overgrow other species. Hence, they are efficient space competitors and are major components of coral communities (Sheppard 1982).

Since several mechanisms are involved in coral interactions and a number of factors may influence the outcome of these interactions, scleractinian and alcyonacean coral interspecific interactions on a reef are likely intransitive. The competitive networks are likely to be formed by interactions between alcyonacean and scleractinian corals. Since alcyonaceans are among the major sessile organisms on Indo-Pacific reefs, the significance of competitive networks should not be neglected.

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