Coral Reefs

The cnidom: an index of aggressive proficiency in scleractinian corals

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Abstract. This study of ten Indo-Pacific and Caribbean scleractinian corals explains their relative aggressive proficiencies in terms of their cnidoms. Species ranging from aggressive to subordinate, on an established hierarchy, were studied. Size, number and distribution of each cnida type were quantified. A marked relationship between number of nematocysts per polyp and aggressive proficiency was demonstrated. The recorded differences in aggressive proficiency between the Indo-Pacific and Caribbean corals are discussed in terms of cnidom differences. In two species a significant trend in linear distribution of nematocysts along mesenterial filaments was recorded, with a distinct zonation of the different nematocyst types along the length of the filament.

Introduction

Interspecific aggression between scleractinian corals was first mentioned in studies by Gravier (1910, cited in Sheppard 1979), although it was not until the work of Lang (1970, 1971 and 1973) that interactions between corals were described in detail. Since this work the phenomenon has been observed occurring between many species, in both laboratory and field studies (Connell 1973; Potts 1976, 1978; Sheppard 1979; Cope 1981; Chornesky and Williams 1983; Ohlhorst 1984; Logan 1984).

Aggression hierarchies have been formulated for both the Atlantic (Lang 1973; Logan 1984) and Indo-Pacific reef corals (Sheppard 1979; Cope 1981). These authors propose that certain species are highly proficient at aggressive competition and others inefficient, with some species intermediate between the two extremes.

Aggression does not necessarily result in the death of the subordinate colony (unless <3 cm in diameter, Lang 1970), nor in competitive exclusion by a single species (Wellington 1980). A balance is maintained between aggressive proficiency and various other factors, such as: interspecific growth rate differences (Lang 1973); sweeper tentacle development by either of the interacting corals

(den Hartog 1977; Richardson et al. 1979; Wellington 1980; Chornesky and Williams 1983; Hidaka and Yamazato 1984); depth of interaction (Lang 1973; Sheppard 1981; Logan 1984); initial mode of contact and "reach" of either antagonist (Sheppard 1981; Bak et al. 1982); reaction to interspecific cytotoxicity or allelopathy (Hildemann et al. 1977); faunal interactions (Bak et al. 1982; Suchaneck et al. 1983; Olhorst 1984); lesion colonisation (Bak et al. 1977) and adverse environmental conditions (Connell 1976; Bak et al. 1977; Cope 1981; Logan 1984).

Despite attempts to quantify the importance of coral aggression in reef community structuring, its role still remains unclear. Aggression has been described as of only minor importance by some workers (Bradbury and Young 1981, 1983) while others (Richardson et al. 1979; Sheppard 1979; Bothwell 1983; Ohlhorst 1984) suggest that the phenomenon may have a significant influence on community structure.

The aim of this study was to quantify the cnidom (cnida complement) of a range of scleractinian corals, from both the Caribbean and Indo-Pacific hierarchies, and attempt to establish a basis upon which to explain their relative aggressive proficiencies.

Materials and methods

Material studied

Ten species of coral were studied, seven Indo-Pacific species: *Fungia fungites* (Linnaeus), *Galaxea fascicularis* Edwards and Haime, *Goniopora lobata* Edwards and Haime, *Acropora aspera* (Dana), *Lobophyllia hemprichii* (Ehrenberg), *Montipora digitata* (Dana), *Porites lutea* Edwards and Haime, and three Caribbean species: *Isophyllia sinuosa* (Ellis and Solander), *Montastrea annularis* (Ellis and Solander) and *Porites astreoides* Lamarck. The Indo-Pacific species were collected from the fringing reefs at Ko Phuket, Thailand and the Caribbean species from Teague Bay, St. Croix, U.S. Virgin Islands. Specimens were transported to the laboratory in seawater, contained in plastic bags. Handling was kept to a minimum.

Fixation and squash methods. All the corals were treated with a 0.1% (w/v) solution of reduced glutathione (in seawater), to induce rapid polyp

expansion (Lenhoff 1971) This was followed by anaesthetisation with 3.5% (w/v) magnesium chloride in seawater (Johnston 1977), fixation in formalin [7% (v/v) in seawater], followed by storage in 70% (v/v) alcohol at 4 °C. Pieces of each corallum, containing up to 25 small polyps (e.g., *Acropora*) or one large polyp (e.g. *Lobophyllia*) were subsampled with a rotary diamond saw or fine hacksaw. Decalcification was carried out in 1:1 10% (v/v) formic acid and 5% (v/v) formalin (Gooding and Stewart cited in Gray 1954; Harriot 1983). Selected tissues, i.e., tentacle, pharynx, mesenterial filament, tubercle, were dissected out from the large polyped species, while whole polyps were dissected out from the other specimens. In the case of *Galaxea* and *Lobophyllia* it was possible to divide the mesenterial filaments into thirds or quarters. Orientation of the filaments (oral-aboral) was recorded. Five samples of each tissue (large polyped corals) or five whole polyps (small polyped corals) per species were used for quantitative analysis of cnidae. The whole polyp quantitative samples were supported by qualitative observations on selected tissues dissected out of the same subsample.

Prior to squashing the samples were macerated in 5% (v/v) potassium hydroxide (KOH) overnight at 4 °C (after Gray 1954). The samples were squashed in 5% KOH, and observed using phase-contrast optics. Cnidae present were identified according to Manuel (1981), adapted from Carlgren 1940; Schmidt 1969, 1972, 1974). Five measurements, of length along longest axis, from each cnida type present in the squash were made using a calibrated ocular graticule. In this way, twenty-five lengths were recorded for each cnida type per tissue or polyp squashed. The number of each cnida type was counted directly where practical (i.e. when present in a relatively low quantity) by sequential scanning with a micrometer stage. If this was impractical because of large numbers of cnidae, one of two estimators was used:

(a) the number of each cnida type present in half or quarter of the squash (by area) was counted and then multiplied by two or four, respectively, to give an estimation for the whole area.

(b) Counts were made of the number of cnidae in five unit areas in the field of view of the X100 oil-immersion objective, these combined areas being equivalent to between 5–20% of the total squash area. The estimated total number of cnidae in the squash was then calculated. The percentage frequency of each cnidae type was derived from a count of a random sample of 100–200 cnidae in the squash. An estimated total number of each type was then calculated from these results.

Each of the estimator techniques was compared with direct counts of spirocysts in *Isophyllia* tubercles. For each technique, five different tubercle samples were quantified.

Evaluation of the effects of fixation and squash methods on cnida size and number. A live colony of *Goniopora stokesi* Edwards and Haime was purchased from a local aquarist supplier and maintained in an artificial seawater aquarium. Five tentacle samples were squashed in seawater and length measurements taken (as described) and numbers of each cnida type counted directly. Further samples were taken post glutathione and post glutathione/magnesium chloride treatments. Fixed and fixed/decalcified samples were also squashed and quantified, after maceration.

Results

Evaluation of fixation/squash and estimation methods

95% confidence intervals are plotted, for both cnida size and number, for the *Goniopora stokesi* control in Figs. 1 and 2. The results show that the techniques had no overall effect ($p < 0.05$) on either cnida counts or sizes (see Burnett et al. 1963).

The results from the *Isophyllia* control, for each of the estimators used (Fig. 3), indicate that all of the counts are comparable, whatever the estimator method used. These data also show the high variation in the cnida counts. This was found in all of the species studied (Table 1). The
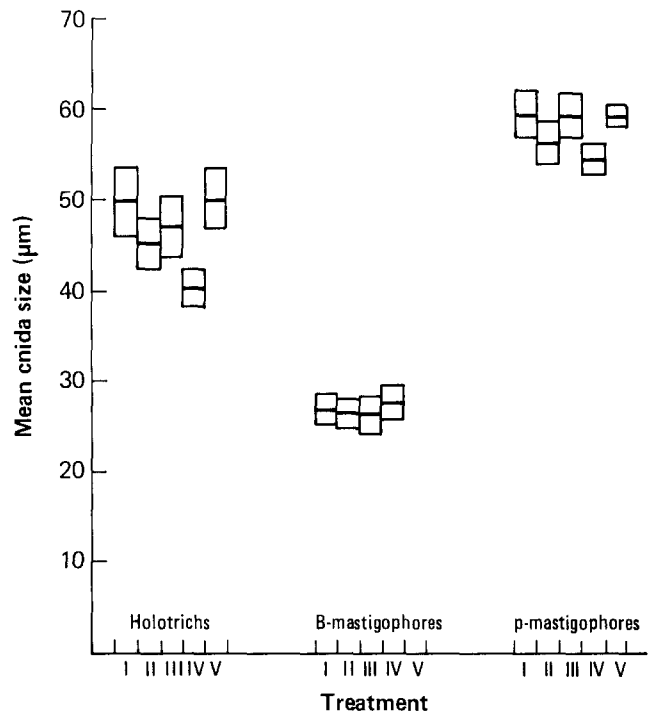

Fig. 1. The sample mean and 95% confidence intervals for the length of each nematocyst type in *Goniopora stokesi* control samples. Heavy horizontal bar indicates sample mean. Treatment key: I = fresh; II = post glutathione; III = post glutathione/MgCl$_2$; IV = fixed/KOH; V = fixed/decalcified/KOH
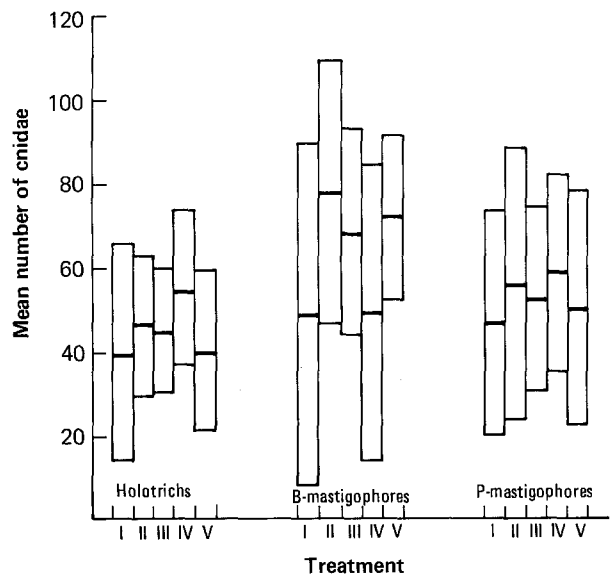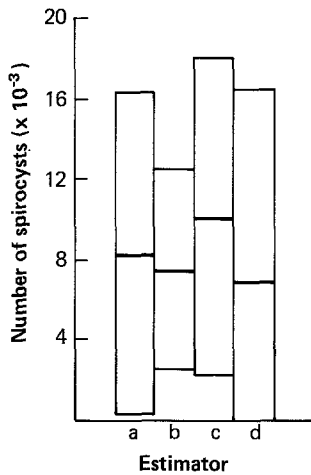

Fig. 2. The sample mean and 95% confidence intervals for the number of each nematocyst type in *Goniopora stokesi* control samples. Heavy horizontal bar indicates sample mean. Treatment key: I = fresh; II = post glutathione; III = post glutathione/MgCl$_2$; IV = fixed/KOH; V = fixed/decalcified/KOH

effect of sample size on the large cnida count variation was tested by sampling ten small radial polyps of *Acropora*. Standard errors remained large (Table 1).

Cnidom characteristics of the Indo-Pacific and Caribbean corals. The length measurement and count data for each

Fig. 3. The mean number and 95% confidence intervals for spirocysts in *Isophyllia sinuosa* control samples. Heavy horizontal bar indicates sample mean. Estimator key: a = counted directly; b = estimated by 'halves'; c = estimated by 'quarters'; d = estimated by 'unit areas'

cnida type per tissue/polyp were summed separately and a sample mean and standard error calculated. These results are shown in Table 1. Spirocysts (Fig. 4) were found in all species. Three types of nematocyst were recorded (Fig. 4): holotrichs; microbasic P-mastigophores; microbasic B-mastigophores. Not all species contained all three nematocyst types, e.g., *Montipora* possessed only P-mastigophores, whereas some species, such as *Montastrea*, possessed not only several types of nematocyst, but two or three morphological variants of one type as well.

Three general variants of P-mastigophore were recognised, hereafter termed types I, II, III (Type I, shaft relatively long compared to capsule. Types II and III both with relatively short shafts, though type II with capsule similar in proportions to type I. Type III with a long thin capsule – see Fig. 4).

No general distinctions were made within the other nematocyst types, but where two variants were found in one tissue, they were labelled I or II, for convenience.

Table 1. The data for the cnidom of each coral studied. "Tissue" indicates where the cnidae were found in each coral. "Size" is mean length of 25 measurements along the longest axis in μm. "No." is mean number of cnidae in 5 samples. Size and No. both ±1 standard error. "*" indicates only 1 sample taken, therefore no standard error calculated. "I" indicates 10 samples taken, all included in the means and standard errors. "Type" refers to the morphological variants within single cnida types. A horizontal dash means "not found", a question-mark "uncertain". The Indo-Pacific and Caribbean species are ranked from top to bottom in order of decreasing aggressive proficiency, according to Sheppard (1979) and Lang (1973), respectively

Indo-Pacific species	Tissue	Holotrichs			P-Mastigophores			B-Mastigophores		Spirocysts	
		Size	No.	Type	Size	No.	Type	Size	No.	Size	No.
Fungia fungites	Filament	63.76 (±0.76)	662.40 (±184.61)		66.29 (±0.94)	20.00 (±9.12)	II	–	–	22.48 (±0.89)	74.40 (±27.90)
					28.09 (±0.75)	48.80 (±26.04)	II				
	Tentacle	–	–		48.40 (±0.93)	96.60 (±17.39)	II	22.16 (±0.52)	22.40 (±9.00)	21.68 (±0.61)	2235.20 (±1013.32)
					35.44 (±0.47)	312.40 (±150.43)	II				
	Pharynx	40.32 (±0.66)	224 (*)		17.83 (±0.40)	248 (*)	I	30.28 (±0.48)	336 (*)	–	–
Galaxea fascicularis	Filament	24.25 (±0.47)	182.40 (±54.28)		41.45 (±1.76)	27.27 (±12.36)	I	20.16 (±0.58)	263.40 (±31.53)	15.97 (±0.52)	65.60 (±159.19)
	Tentacle	20.84 (±0.42)	193.20 (±46.45)		60.56 (±0.90)	180.65 (±80.79)	III	34.43 (±1.88)	88.20 (±83.72)	17.92 (±0.84)	154.00 (±38.55)
Goniopora lobata	Filament	–	–		–	–		–	–	–	–
	Tentacle	49.28 (±1.00)	1003.00 (±323.92)		72.58 (±1.21)	255.80 (±116.10)	II	–	–	13.17 (±1.27)	22.60 (±12.56)
Lobophyllia hemprichii	Filament	58.05 (±1.44)	126.87 (±41.86)		61.19 (±1.96)	25.80 (±10.42)	I	–	–	15.72 (±0.87)	156.40 (±40.36)
					30.24 (±2.60)	21.33 (±8.94)	II				
	Tentacle	–	–		51.00 (±1.70)	1.40 (±0.93)	III	–	–	23.24 (±0.62)	563.00 (±87.72)
	Pharynx	53 (*)	16 (*)		21.86 (±1.57)	56 (*)	II	32.44 (±0.65)	312 (*)	20.16 (±0.60)	133 (*)
					66.25 (±2.06)	56 (*)	III				
	Tubercle	–	–		–	–		–	–	14.75 (±0.69)	6.40 (±3.09)
Acropora aspera	*Axial polyp* Filament	–	–		18.91 (±0.41)	270.60 (±121.15)	I	–	–	–	–

Table 1 (continued)

Indo-Pacific species	Tissue	Holotrichs			P-Mastigophores			B-Mastigophores		Spirocysts	
		Size	No.	Type	Size	No.	Type	Size	No.	Size	No.
	Tentacle	–	–					17.16 (±0.57)	417.80 (±62.25)	17.36 (±0.39)	852.80 (±167.76)
	Small radial polyp										
	Filament	–	–		19.14 (±0.44)	54.96 (±56.64)	I	–	–	–	–
	Tentacle	–	–		~	–		13.10 (±0.41)	3.30 (±2.20)	15.76 (±0.42)	28.70 (±9.67)
	Large radial polyp										
	Filament	–	–		18.47 (±0.42)	32.60 (±12.36)	I	–	–	–	–
	Tentacle	–	–		~	–		14.77 (±0.39)	47.60 (±20.79)	17.82 (±0.36)	213.20 (±50.58)
Montipora digitata	Filament	–	–		92.88 (±1.41) 25.80 (±0.86)	240.40 (±58.32) 7.00 (±2.90)	I I	–	–	–	–
	Tentacle	–	–		~	–		–	–	11.20 (±0.38)	40.80 (±25.65)
Porites lutea	Filament	65.76 (±0.88) 23.76 (±0.72)	303.20 (±28.60) 158.40 (±43.73)	I II	29.32 (±1.00)	86.40 (±22.37)	I	–	–		
	Tentacle							–	–	11.40 (±0.62)	40.80 (±25.63)

Caribbean species

Caribbean species	Tissue	Holotrichs			P-Mastigophores			B-Mastigophores		Spirocysts	
		Size	No.	Type	Size	No.	Type	Size	No.	Size	No.
Isophyllia	Filament	134.24 (±2.05)	?		49.28 (±0.01)	?	I	–	–	24.84 (±0.92)	?
	Tentacle	–	–		71.09 (±1.89)	401.20 (±165.70)	I	–	–	37.72 (±2.15)	14462.60 (±2404.05)
	Pharynx	59.91 (±0.65)	480 (*)		21.92 (±0.59)	272 (*)	II	35.05 (±0.64)	4496 (*)	20.20 (±0.66)	960 (*)
	Tubercle	–	–		20.56 (±0.59)	2.20 (±1.24)	II	–	–	20.28 (±0.56)	841.20 (±289.32)
Montastrea annularis	Filament	62.48 (±1.36) 34.80 (±0.93)	290.60 (±98.32) 48.00 (±5.66)	I II	33.04 (±1.30) 69.33 (±1.04)	960.00 (±74.40) 87.80 (±26.88)	I III	14.70? (±0.47)?	56? ?	–	–
	Tentacle	–	–		42.92 (±0.86)	241.60 (±23.79)	II	–	–	17.80 (±0.64)	4354.40 (±1156.75)
Porites astreoides	Filament	45.08 (±0.54)	195.20 (±28.60)	I							
	Tentacle	33.13 (±1.33)	64.00 (±31.32)	II	28.52 (±1.21)	559.20 (±131.39)	I	20.00 (±0.85)	47.20 (±42.30)	14.26 (±0.44)	371.20 (±225.86)

In Fig. 5, the total number of nematocysts per polyp for each of the Indo-Pacific and Caribbean corals is shown. For data derived from specific tissue samples, the total was calculated by multiplying the data against observed number of tentacles, filaments, etc., and then summing each result.

Figure 6 shows the total number of nematocysts per polyp plotted against calyx area. There is no obvious relationship between calyx area and nematocyst number. Figure 7 shows the number of tentacles per polyp, observed in each of the species studied, plotted against its recorded position in an aggression hierarchy. No relationship between these factors is apparent.

Spatial distribution of cnidae within certain tissues and between polyps. The distribution of cnida types along me-
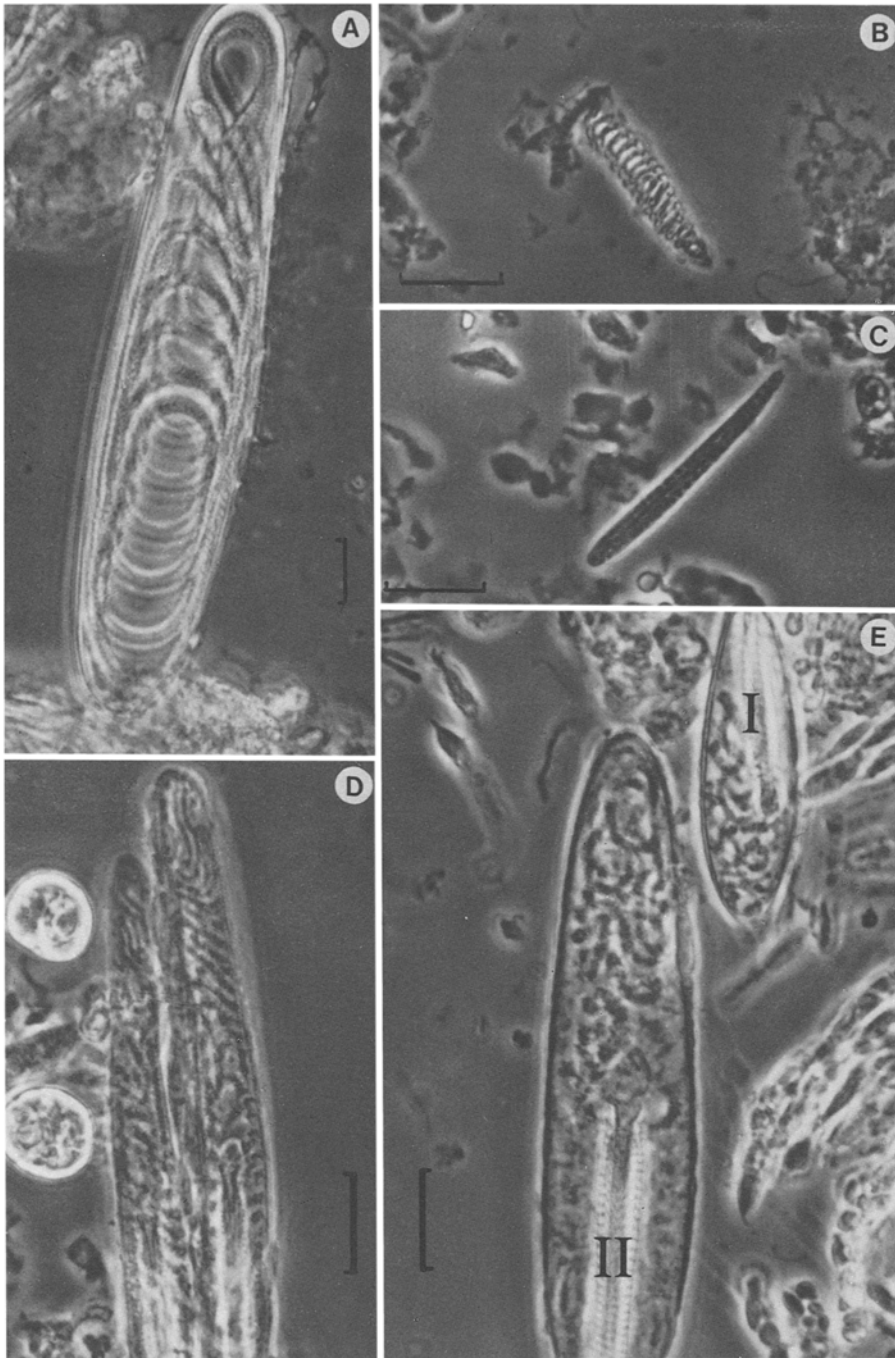
Fig. 4. Typical cnida types found in the coral species studied.
A Large holotrich from *Isophyllia sinuosa* mesenterial filament.
B Spirocyst from *Fungia fungites* mesenterial filament.
C B-mastigophore from *Galaxea fascicularis* tentacle.
D Type III P-mastigophore from *G. fascicularis* tentacle.
E Type I (I) and type II (II) P-mastigophores from *Montastrea annularis* mesenterial filament.
All photomicrographs were taken using phase contrast optics. Scale bat represents 10 μm

senterial filaments in *Galaxea* and *Lobophyllia* is given in Figs. 8 and 9. These data show a significant trend in linear distribution along a filament in both species, for each cnida type, with the exception of B-mastigophores in *Galaxea* (arcsine transformed data, G-test, $p<0.05$; Sokal and Rohlf 1981). If data for the aboral quarter of the filament from *Lobophyllia* is excluded (this region being composed almost entirely of granulous columnar cells) then there is no significant trend in linear distribution of P-mastigophores. In both these species the number of spirocysts decreases along the length (oral –

aboral) of the filament. In contrast, the number of holotrichs in both species increases along the length of the filament. In *Galaxea*, the number of P-mastigophores decreases along the length of the filament.

It is possible to distinguish three polyp morphs in *Acropora aspera*, namely: axial; large (lipped) radial; small radial (see Wallace 1978). Samples were taken from each of the three morphs and the data treated separately. There are differences between the cnidom of each morph, both in cnida type, size and distribution within the polyp. *Acropora* also differs from the other corals, in having
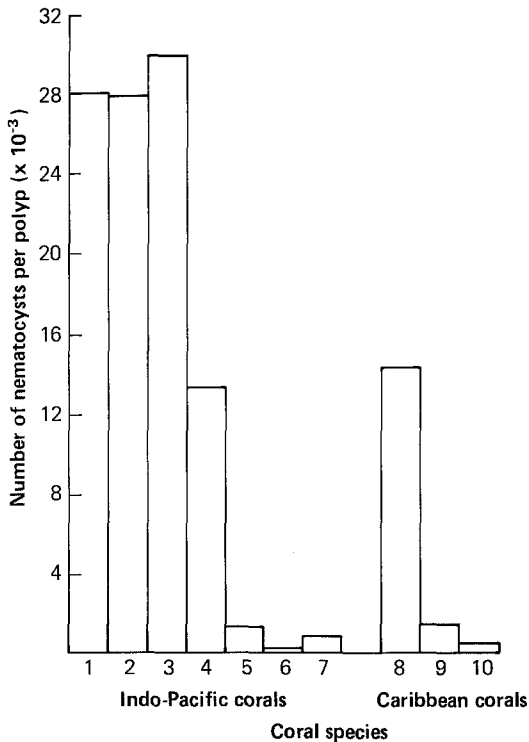
Fig. 5. The total number of nematocysts per polyp for each species studied ±1 standard error. Each group of species is ranked in order of aggressive proficiency; Indo-Pacific corals according to Sheppard (1979), Caribbean corals according to Lang (1973). Key to species: 1 = *Fungia fungites*; 2 = *Galaxea fascicularis*; 3 = *Goniopora lobata*; 4 = *Lobophyllia hemprichii*; 5 = *Acropora aspera*; 6 = *Montipora digitata*; 7 = *Porites lutea*; 8 = *Isophyllia sinuosa*; 9 = *Montastrea annularis*; 10 = *Porites astreoides*

Fig. 6. The total number of nematocysts per polyp for each species studied, plotted against their respective calyx areas. Key to species: 1 = *Fungia fungites*; 2 = *Galaxea fascicularis*; 3 = *Goniopora lobata*; 4 = *Lobophyllia hemprichii*; 5 = *Acropora aspera*; 6 = *Montipora digitata*; 7 = *Porites lutea*; 8 = *Isophyllia sinuosa*; 9 = *Montastrea annularis*; 10 = *Porites astreoides*

only very small nematocysts (three times smaller than the maximum nematocyst size in any other species; Table 1).

Discussion

Lang (1973) described *Isophyllia sinuosa* as very aggressive, *Montastrea annularis* as moderately aggressive and *Porites* spp to be weakly aggressive. With the exception of *Montastrea*, these characteristics correspond with the total number of nematocysts per polyp, as found in this study. However, Bak et al. (1982) noted that although *Montastrea* was initially dominant in an interaction, it suffered an increasing degree of mortality as the time span of the interaction increased. Within *Montastrea* there is an unequal distribution of nematocysts between the tissues, with the majority of the nematocysts being found in the mesenterial filaments (Table 1). The use of such heavily armed mesenterial filaments, in an aggressive interaction, may account for the initial dominance by *Montastrea*. Subsequent lesion colonisation by the xanthid crab *Domecia acanthophora* (Desbonne & Scham), and/or development of sweeper tentacles by the subordinate species account for the subsequent reversal of the interaction (Bak et al. 1982).

Likewise, Sheppard (1979) placed the Indo-Pacific corals in the following categories:
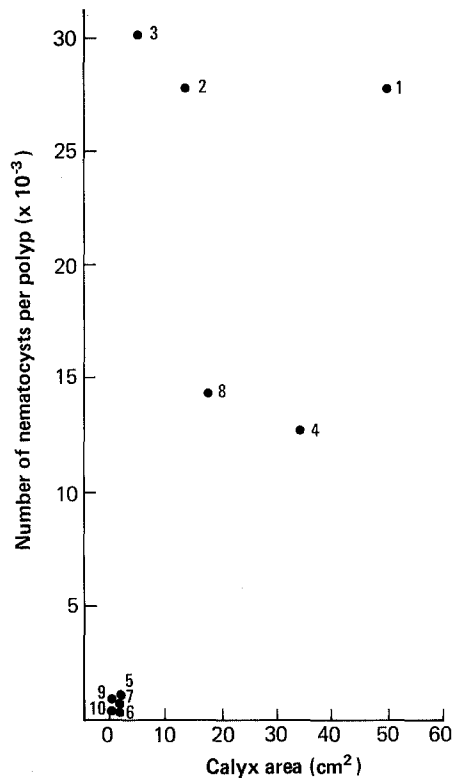
Aggressive: *Fungia* spp; *Goniopora* spp; *Galaxea clavus*. Intermediate: *Lobophyllia corymbosa*. Subordinate: *Montipora* spp; *Porites lutea*. *Acropora* spp were either aggressive (*A. palifera, A. hyacinthus*) or intermediate (*A. humilis*). Again the results in the present study follow this pattern (assuming *G. clavus* and *L. corymbosa* to have similar aggressive proficiencies as *G. fascicularis* and *L. hemprichii*, respectively), except for *Acropora* which falls into the subordinate group. However, Sheppard (1979) did not record the aggressive proficiency of *Acropora aspera*, used in the present study. Also, a competitive strategy based on overtopping (Randall 1981) and asexual reproduction by fragmentation (Bothwell 1981, 1983) is probably more important to this *Acropora* species than direct tissue contact, and any tissue lesions caused by *Acropora* in contact with another coral, may be due to only cytotoxic reactions (e.g. Hildemann et al. 1977). The small size of the nematocysts found in the *Acropora* polyps supports this hypothesis.

The total number of nematocysts per polyp does not appear to be related to polyp size (calyx area being used in the present study as a rough indication of polyp size). In addition, results also indicate that aggressive proficiency is not related to the number of tentacles or mesenterial filaments. An earlier study (Sheppard 1981) also suggested that aggressive proficiency of corals was not related to polyp size.
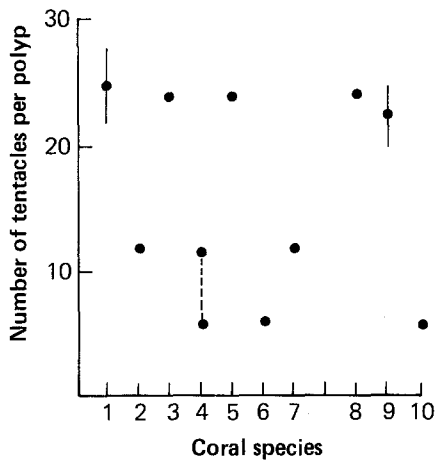
Fig. 7. The number of tentacles per polyp for each species studied. Each group of species is ranked in order of aggressive proficiency; Indo-Pacific corals according to Sheppard (1979), Caribbean corals according to Lang (1973). Heavy vertical bar indicates a variation in tentacle number was found between polyps sampled. Dashed vertical line connects the two values for *Acropora* radial and axial polyps. Key to species: 1 = *Fungia fungites*; 2 = *Galaxea fascicularis*; 3 = *Goniopora lobata*; 4 = *Lobophyllia hemprichii*; 5 = *Acropora aspera*; 6 = *Montipora digitata*; 7 = *Porites lutea*; 8 = *Isophyllia sinuosa*; 9 = *Montastrea annularis*; 10 = *Porites astreoides*
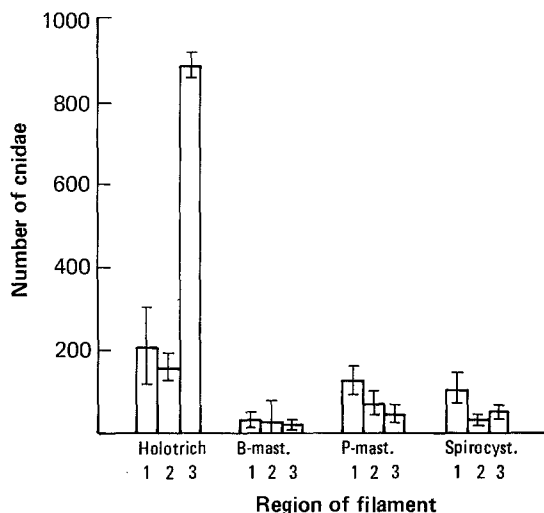

Fig. 9. Sample means (± 1 standard error) of cnida numbers per quarter of a mesenterial filament in *Lobophyllia hemperichii*. 1 = oral quarter; 2 = oral median quarter; 3 = aboral median quarter; P-mast.I = P-mastigophores type I; P-mast.II = P-mastigophores type II

Fig. 8. Sample means (± 1 standard error) of cnida numbers per third of a mesenterial filament in *Galaxea fascicularis*. 1 = oral third; 2 = median third; 3 = aboral third; B-mast. = B-mastigophores; P-mast. = P-mastigophores

These results may also provide some evidence to explain the differences between the Caribbean and Indo-Pacific hierarchies, viz the Caribbean is dominated by *Isophyllia* and other species of Mussidae, whereas the fungiids, *Goniopora* ssp and *Galaxea* are dominant in the Indo-Pacific hierarchy (Lang 1973; Sheppard 1979). From data in the present study, *Lobophyllia* would also be at the top of the Caribbean hierarchy. However, it is the presence of the "super-aggressive" species in the Indo-Pacific that place it in an intermediate position. Conversely, the "super-aggressors" would put the Caribbean mussids into an intermediate position (with no
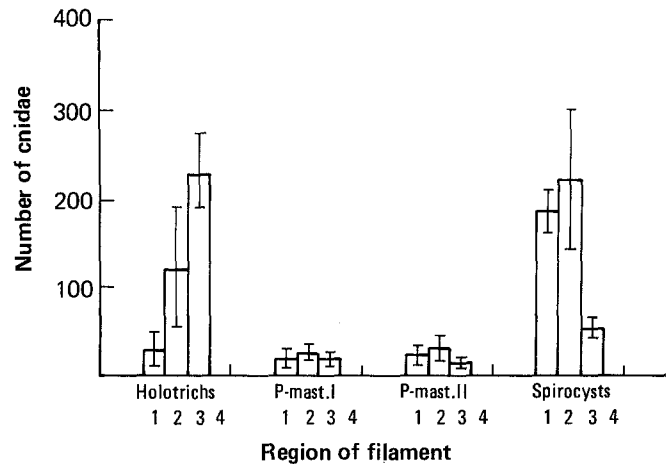
allowances for other factors complicating the interactions – see Bak et al. 1982). The evolution of a more effective means of interaction in the Indo-Pacific, than in the Caribbean, is logical in view of the higher diversity (Rosen 1975), theoretically smaller spatial niches and hence a greater probability of interspecific spatial competition (May 1973) encountered in the Indo-Pacific province. This suggests that competitive interactions can be important to an individual coral, but may not necessarily be a primary influence on coral reef community structure.

Generally, the cnida types and their distribution within these species agrees with previous work on scleractinian cnidoms (e.g., Schmidt 1974; den Hartog 1977). The data showing a significant trend in linear distribution along both *Galaxea* and *Lobophyllia* mesenterial filaments give quantitative support to previous observations that cnidae are not evenly distributed along a filament (Hyman 1940; Goreau 1956; Muscatine 1973; Schmidt 1974). Although the heteroscedasticity of the data precludes any generalised statistical analyses, a rough comparison of the data for numbers of cnidae in either the mesenterial filaments or tentacles of each species (Table 1) reveals some interesting trends. Firstly, all species have few spirocysts in the mesenterial filaments, most being located in the tentacles. Assuming, for the present, spirocysts to be only adhesive in function (and not toxic – Mariscal et al. 1977), this distribution of spirocysts is indicative of the specialisation of the tentacles for particulate feeding (Muscatine 1973). The very high numbers of spirocysts in the tentacles of the three species with large polyps (i.e. *Fungia, Lobophyllia* and *Isophyllia*) is possibly related to their raptorial feeding behaviour (Muscatine 1973). The trend towards higher numbers of nematocysts in the mesenterial filaments of all species (except *Goniopora*), than in the tentacles, can be related to the use of the filaments for intra- or extracoelenteric subduing and digestion of prey (Muscatine 1973), or for interspecific

aggression. The particularly high number of nematocysts in the filaments of *Montastrea* has already been discussed. The lack of nematocysts in the filaments of *Goniopora* (and high number in the tentacles) may be owing to the unusual morphology and behaviour of the polyps of this species, viz their very extendable column and sweeping behaviour in both feeding and defence.

Cnidom alterations have been noted in the development of sweeper tentacles, from normal tentacles, in scleractinians (den Hartog 1977; Hidaka and Yamazato 1984). Wallace (1978) described the morphological change of any radial polyp into an axial polyp, during branch formation in *Acropora aspera*. In conjunction with the morphological changes the cnidom must also change (see Table 1). This sustains a hypothesis of a change in role (in respect of feeding and defence) as the polyp morphology changes.

In conclusion, there appears to be a basis upon which to explain scleractinian aggressive proficiencies and differences between the Caribbean and Indo-Pacific hierarchies. Little insight, however, can be gained about the functional morphology of different nematocyst types from this study. Earlier workers have attributed a defensive/aggressive role to holotrichs (Ewer 1947; Francis 1973; den Hartog 1977; Purcell 1977), or to B-mastigophores (Wellington 1980). More evidence is needed to clarify their precise roles during aggression, feeding, etc. Currently work is in progress to help resolve this problem by investigating the relationship between specific nematocyst types and the toxin they contain.

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