THE INFLUENCE OF SUBSTRATE STRUCTURE ON THE LOCAL ABUNDANCE AND DIVERSITY OF PHILIPPINE REEF FISHES*

By

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ABSTRACT

Four Philippine fringing reefs were surveyed, each along eight transects, which compose a continuum of an average of 47, 2 m x 2m quadrats. Fishes were censused and substrate characteristics surveyed in each quadrat. Data were analyzed using rank, multiple, and canonical correlations. Fish abundance was increasingly correlated with greater complexity of susbstrate type. Strong consistent positive correlations were evident in fish abudance and diversity with living coral cover and, in fish biomass, with an index of surface complexity. An analysis of substrate correlations with fish abundance in different activity-range categories lends quantitative evidence to the hypothesis that shelter space is more important than food availability in determining abundance of reef fishes.

INTRODUCTION

Coral reefs are highly productive communities which are important to the fisheries of tropical Indo-Pacific countries (Langham and Mathias, 1974; Stevenson and Marshall, 1974; Carpenter, 1977; Marshall, 1979). In the Philippines, corals are being eliminated from reef communities by siltation, dynamite fishing, collection for ornamental and construction purposes, and other destructive fishing techniques (Carpenter, 1977; Carpenter and Alcala, 1977; Gomez, 1977; McManus, 1980). Because of the many alterations of the coastal zone by man, it has become important to clarify the relationship of reef fish diversity and abundance to habitat characteristics for fisheries management purposes.

The mechanisms maintaining the high density and diversity typical of coral reef fish communities are not clearly understood. The obvious resources most probably limiting for reef fishes are food and shelter space. Both of these resources are expected to be heavily influenced by spatial complexity

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of the substrate and types of bottom cover. Complexity of bottom cover both on a small and large scale would influence area of aggregation for food types and suitable shelter for predator avoidance. Depending on its characteristics, bottom cover could influence suitable attachment sites for forage items, interstitial spaces for prey organisms, or in the case of corals, it may serve as a source of food itself. Sheltering space can be described as hiding places so small that predators cannot enter or, simply as a form of visual interference. In terms of piscivore foraging energetics, the many visual obstructions on a reef result in an increase in search and handling time. Therefore, the greater the sculpturing of the reef the higher the densities of prey items that are necessary to maintain an energetically favorable encounter frequency and probability of capture upon encounter. An obvious corollary to this hypothesis is that greater densities of prey items (fishes) are possible on more complex reefs, if predation is the key limiting factor.

There are many reports qualitatively relating reef fishes distribution to types and configuration of bottom cover (Hiatt and Strasburg, 1960; Vivien, 1973; Fishelson et al., 1974; Hobson, 1974; Nagelkerken, 1974; Harmelin-Vivien, 1977). In addition, there is a growing body of literature which supports a suggestion that space, rather than food, is the primary limiting factor of reef fish abundance (Randall, 1963; Sale, 1978; Smith, 1978; and others). Attempts to quantitatively correlate substrate characteristics with reef fish parameters have yielded a variety of results which are sometimes nebulous and largely inconsistent between studies (Talbot, 1965; Risk, 1972; Talbot and Goldman, 1972; Nolan, 1975; Sale and Dybdahl, 1975; Luckhurst and Luckhurst, 1978). However, some consistency has been found among correlations of fish diversity with a gross index of substrate complexity (Risk, 1972, Luckhurst and Luckhurst, 1978; Gladfelter et al., 1980).

The purpose of this study was to see if any meaningful associations can be drawn between reef fish abundance and diversity, and substrate types and complexity. Attempts were also made to distinguish which habitat characteristics could most influence the resources, either directly or indirectly, which allow these communities to persist.

METHODS

A detailed description of the study areas and the methods used will be given elsewhere (Carpenter et al, in preparation). For completeness, however, these will be briefly described below.

Four fringing reefs in the central Philippines were studied. These included two areas in the Hilutangan Channel near Cebu: Buyong Beach on Mactan Island, and the SW tip of Olango Island. The other reefs surveyed were in the Bohol Strait in the Sumilon Island marine reserve and on the opposite non-reserve side of Sumilon Island. The Sumilon reserve and Buyong reefs have shallow flats bordered by steep submarine cliffs. The Olango and non-reserve Sumilon reefs have shallow flats with more gently sloping reef faces. There were widely differing states of general habitat disturbance and fishing pressure among the reefs studied, but each reef studied was fairly consistent in this regard within the area studied.

Biases and restrictions are inherent in the methods currently used to quantitatively sample reef fishes (see Russel et al., 1978 for a review). Daytime visual censusing along a transect was the primary means of data collection in this study. Eight transects averaging 94 meters long by two meters wide were surveyed in each of the four study areas. A double transect line was used to eliminate confusion as to which fish belonged in the transect area. (This is opposed to using a single line and estimating 1 meter to either side of the transect). Successive transects in each area were located at approximately 50-meter intervals from the previous transect, parallel to one another. Transects were oriented perpendicular to the reef front in order to sample a profile of the reef to a depth of 20 meters.

The Buyong Beach and Olango Island areas were surveyed in March 1978; Sumilon Island in August 1978. Fish censusing was carried out in late morning and early afternoon to avoid the diurnal-nocturnal changeover periods (*sensu* Hobson, 1972).

The same diver censused fishes in all transects with the use of an underwater tape recorder. Surveys began at the deep end of the transect, approximately 20 minutes after the transect lines were laid down. Fishes appeared to resume normal behavior shortly after the transect lines were set and they did not appear attracted to the lines. The transect was marked every two meters such that it could be visually subdivided into a continuum of 4-meter square quadrats. From a distance of 2 to 4 meters, the marker which corresponded to the quadrat being censused, fish species identity, number of each species, and estimated fork length of fishes within each quadrat were recorded. From these were calculated biomass (gm/meter-square), abundance (number of individuals/meter-square), species density (number of species/4 meter-square) (to avoid redundancy this variable was excluded in the canonical correlation analysis described below), and Shannon-Wiener diversity (H') based on biomass (see Pielou, 1975). The diversity index is based on biomass rather than numbers to reduce bias toward the more numerous smaller species. Biomass estimates were calculated from the estimates of fork lengths of fishes with the use of species-specific length-weight conversion factors (*sensu* Grovhoung and Evans, 1974).

The estimation of fish lengths underwater is difficult due to size and distance distortions when using a face mask, and is potentially a major source of observer error. Prior to each set of transects, the censuser utilized a series of visual cues to enhance perception of the actual sizes of fishes on the reef.

This was accomplished by suspending a graded series of labeled bamboo strips close to the substrate and comparing the relative sizes of fishes to these known lengths.

Two levels of spatial heterogeneity were examined. The first level concerned large-scale incongruities in vertical relief and was measured by a surface area index (SAI). The SAI was obtained by measuring surface contours along one side of the transect line. Directly underneath each 2-meter subdivision of the transect line, a thin nylon rope was forced to conform to the bottom contours. The line was then straightened and measured. This length was then divided by 2 meters to obtain the SAI for each quadrat.

The second level of spatial heterogeneity considered involved small-scale surface characteristics due to different substrate types. The choice of substrate categories was based on generalities of relative surface heterogeneity. Unconsolidated sediments (mostly carbonate sand and hereafter referred to as SAND) is clearly the least complex of the substrate types. Non-living consolidated substrate (ROCK) typically consisted of eroded coralline ROCK. Although variously encrusted with algae and invertebrates, ROCK was on the average a less complex substrate in terms of interstices and surface irregularities than living coral. In the areas studied, living coral (CORAL) was the most complex substrate present. In the Sumilon study areas, stony coral was distinguished from soft coral in collection of bottom cover data. The soft coral category is generally less complex than stony coral although still more complex than rock.

Bottom cover characteristics were recorded within each 4-meter-square quadrat. In the Buyong and Olango areas, the proportion of ROCK, CORAL (both scleractinian and other anthozoans), and SAND cover in the entire 4-meter square quadrat, projected horizontally on the bottom, was visually estimated. (Some transects entered grass flats in these 2 areas and these quadrats were deleted from the data set and analyzed only when considered as a separate zone.) In the Sumilon Island areas, a 1-meter-square quadrat divided into 10 cm-squares was placed in one corner of the quadrat. Predominant cover in each of the squares was recorded as stony coral (scleractinian), soft coral (mostly alcyonarian but some other soft anthozoans also occurred and were recorded in this category) ROCK, or SAND.

Superimposed on and related to the above spatial environmental factors are effects due to zonation. Within each study area depth and slope of the reef would be expected to reflect zonation-related environmental factors. These include wave exposure, temperature variation and volume of water available for movement and zooplankton or nekton foraging. Depth was recorded at each 2-meter mark and slope was calculated from these positions.

Spearman's rank correlation coefficient (a non-parametric statistic) was used for all correlation comparisons between two variables. A multivariate parametric technique, canonical correlation (using the 'CANCORR' procedure in the Statistical Analysis System) was used to test the relationships between the groups of fish and substrate variables (bottom cover proportions were transformed using an arcsine transformation). Canonical correlation attempts to define the primary independent dimension which relate one set of variables to another set of variables. Multiple correlations were also performed on each of the fish community variables against the array of habitat variables. Multiple correlation is the same technique as canonical correlation except there is only one variable in the criterion group (Thorndike, 1978). In this study, canonical correlation and multiple correlation indicate which substrate variable is most correlated with the fish variables. They also indicate if any remaining substrate variables explain a significant amount of variability in the fish variables after the effects of the most strongly correlated substrate variables have been accounted for. The overall significance of canonical and multiple correlations can be tested with a chi-square statistic. However, the interpretation of significance of the relative degree of correlation of each fish-substrate comparison is somewhat subjective. Therefore, the recurrence of strong relationships in the analyses is taken to be the most reliable correlation.

To investigate the relative importance of the fishes' daily activity-range habits to associations with habitat variables, each species was assigned an activity-range designation. Three designations were based on field observations of fishes' normal position in the water column and short-term movements around the reef: (1) all types of activity-ranges (all calculations in this paper use this total set of observations unless otherwise indicated); (2) all fishes excluding those with very far ranging habits (abbreviated as WIRAN) i.e., excluding schooling species such as caesionids, wide ranging predators such as carangids, species usually more pelagic in habits, and the few nocturnal species seen in the transect (this exclusion is based on eliminating variability due to these more chance encounters rather than ranging habits);and, (3) only those species with fairly short ranging habits which are usually found close to the substrate (SHRAN) e.g., most pomacentrids, parapercids, cirrhitids, some pomacanthids, small serranids, scorpaenids, gobiids, bleniids, etc. The fish community variables were recalculated for each quadrat based on only those species categorized as to the range designation of interest. Subsequent correlation analyses were carried out the same as above.

RESULTS AND DISCUSSIONS

Significant Spearman rank correlations relating all variables are listed in Table 1 for the four study areas. With the exception of the non-reserve Sumilon area, large proportions of the variables were significantly correlated with each other. Since there are many significant correlations between pairs of substrate variables and between pairs of fish variables, it is difficult to infer which fish-substrate correlations are casually related. This result prompted the use of the more robust multivariate statistics.

Canonical correlations between the sets of habitat and fish variables from each of the study areas showed significant associations on at least, two canonical variables (Table 2). (In the following discussion of results, correlations with SAND are negative and all others are positive.) Consistent strong associations from these analyses are: fish biomass with the SAI; fish abundance with SAND and CORAL; and fish diversity with CORAL and SAND.

Multiple correlations analyses yielded similar results to the canonical correlations (Table 3). Consistent strong associations evident are: fish biomass with the SAI, depth, and slope; fish abundances with SAND, CORAL, and depth; fish diversity with CORAL and SAND; and species density with SAND, CORAL, and depth.

In the above multivariate analyses, a considerable amount of correlation was present between the fish variables and the zonation effects, depth and slope. Separate analyses of each zone was performed to minimize the effects of these two variables. Zones were determined by clustering techniques, factor analyses, and some degree of subjectivity.

Table 4 presents the results of canonical correlation analyses on the Buyong and Olango zones. With the effects of depth and slope minimized, these results corroborate those of the above multivariate analyses emphasizing the influences of the substrate types. Recurrent strong correlations from the zonation analyses were: fish biomass with the SAI, and abundance and diversity with CORAL and SAND.

The negative influence of sand cover on the fish variables should not be suprising to any biologist who has spent time diving on coral reefs. Where sand flats are encountered, there is typically a sharp decrease in frequency of occurrence of fishes. However, the reef often presents a variegated bottom cover of ROCK, CORAL and SAND. Most of the quadrats samples were composed of a combination of the bottom types. To separate the effects of sand cover in a mixed bottom cover quadrat as opposed to areas predominantly sand, all quadrats containing greater than 50% sand cover were deleted from the data set and multivariate analysis performed. Results obtained were only slightly different from those in Table 4 (i.e., SAND continues to exert a strong negative effect on fish abundance and diversity), which infers that even on a very local scale, small patches of sand between hard substrate profoundly affects densities of reef fishes. This could be due to increased predation pressure and/or reduced food availability over sand bottoms. A fish venturing over a fairly uniform, light substrate would present a distinct outline for predators to detect. The relative availability of food items on sand

versus coral and other hard substrate must be clarified before the importance of food availability in this relationship can be determined.

Multivariate analyses showed consistent strong correlations of coral cover with fish abundance and diversity. Although not adequately quantified, a cause-and-effect relationship between these factors has long been suspected by reef fish ecologists. This result is more interesting when compared to correlations with ROCK. ROCK comprised a substantial portion of the bottom cover in all four areas (range of average coverage in the four areas: 26-44%). Yet, in almost all cases it was insignificantly or only weakly correlated to the fish variables; CORAL was always much more highly correlated to the fish variables than ROCK. In these study areas CORAL had on the average a much greater surface complexity. This greater surface complexity may provide relatively greater food or shelter availability.

One strong relationship which consistently occurred in all four areas studied was that of fish biomass and the SAI. This positive correlation supports previous speculation that reef fish distributions will be strongly tied to topographical complexity (*sensu* Randal, 1963). A curious aspect of this result is the lack of consistent relationships of the SAI with numbers of fishes. Larger fishes, "weighted" more in the biomass variable, appear most closely tied to topographical complexity on the scale that the SAI can reflect.

The high frequency and degree of significant correlations of fish variables to substrate characteristics in this study contrast with results of other researchers attempting to statistically quantify this relationship. The bottom cover and/or bottom topography indices used by Risk (1972), Talbot and Goldman 1972), and Luckhurst and Luckhurst (1978), are similar or more detailed than the indices used in this study. The differences in occurrence of significant correlations may perhaps be due to differences in sampling regimes and means of analysis rather than gross inequalities of ecological relationships from different areas. Gladfelter et al (1980) have shown similar relationships of reef fishes to environmental parameters between western Atlantic and central Pacific coral reefs. Sample size in the present study was much larger ($n > 1,500$) than those studies mentioned above (n=16, 60 and 16 respectively), and the unit sample area was smaller (except in Risk's 1972 study). A large sample size with an appropriate unit sample area appears to be a necessity to adequately reflect fish-substrate relationships given generalized substrate indices and the inherent mobility of fishes. The high frequency of significant rank correlations among all variables obtained in this study indicates that simple univariate statistics may not reliably elucidate which of the many complex fish-habitat associations are casually related.

A variety of methods has been used to quantify the relationships of spatial environmental characteristics to spatial variations in density and diversity of animals (MacArthur, 1962; Pianka, 1966; Rozensweig and Winakur, 1969; Murdoch et al., 1972; Roth, 1976; and others). In this study, spatial environmental variation was considered through substrate categories ranked according to complexity of surface irregularities and an index of complexity of topographical relief (the SAI). Factors not directly related to substrate complexity were considered through the variables of depth and slope in multivariate analyses. Based on the magnitude and direction of correlations of fish variables with the substrate types, density and diversity of fishes increase as the proportion of the more complex substrate types increases. On a larger complexity scale, abundance of larger fishes is also significantly influenced by complexity of topographical relief.

The correlations between the SAI and the bottom cover categories reflected the relative spatial complexity of the substrate categories in the same manner that the substrates were ranked *a priori* according to surface irregularities. For all comparisons of correlations coefficients within each area, CORAL was most correlated with the SAI, ROCK was less correlated, and SAND was strongly negatively correlated with the SAI. This pattern is consistent within all areas studied. In the Sumilon study areas, results showed that correlations of the SAI with stony corals was highest, while correlations of the SAI with soft coral ranked between stony coral cover and rock cover. Correlations of all fish variables with stony coral were highly significant. Correlations of fish variables with soft coral were either insignificant or much less correlated than with stony corals. However, soft corals were typically more highly correlated than with stony corals. However, soft corals were typically more highly correlated with fish variables than rock cover.

Evidence supports the hypothesis that reef fishes are generally more abundant in areas of greater complexity. However, it is still unclear whether it is the availability of food or the availability of shelter in more complex substrate that allows these higher densities. Table 5 shows the Spearman rank correlations of habitat characteristics with fish abundance of the three diurnal activity-range categories considered. There is little apparent change in patterns of influences of the substrate variables on fish occurrence of the different ranging types. In almost all cases there was no significant increase or decrease of correlation coefficients within a habitat variable category between the ranging types (t-test, $P > 0.05$). This occurs in spite of significant differences in abundances between the wide activity-range and short activity-range categories in all zones tested (t-test, $P < 0.05$) except the Olango reef flat. Thorough multivariate analyses also failed to show consistent patterns of effects of substrate characteristics on fish abundance from the different activity-range categories. In other words, the relative occurrence of short ranging fishes usually found close to the substrate (i.e., territorial pomacentrids, syndontids, blennies, parapercids, cirrhitids, etc.) is approximately equally influenced by substrate types as those fishes more mobile or less closely tied to the substrate (i.e., zooplanktivores usually found high in the water column, many labrids, etc.). This indicates that availability of shelter is the most important influence on occurrrence of reef fishes. If food was the most important determinant in how reef fishes aligned themselves with substrate types, it would be expected that the wider ranging fishes would be more randomly associated and therefore less correlated with substrate types than the shorter ranging fishes. The shorter ranging fishes would, by definition, be expected to spend a greater part of their time closer to a food source that was tied to substrate type. Food for the wider ranging fishes is less associated with immediate substrate. Their food is often found higher in the water column or the fishes could range over a variety of substrate types in search of food. However, if proximity to adequate shelter was more important than proximity to food, both wide ranging and short ranging fishes would approximately equally align themselves to proper shelter sites. In visualizing the adaptive mechanism for this, it is important not to restrict the concept of shelter as being simply holes in the reef. As pointed out in the introduction, "shelter" could be any visual or mechanical obstruction which could include a means to simply break up the outline of a fish.

Using multivariate statistics on a large sample size, consistent strong correlations of fish abundance and diversity with substrate type and complexity have been demonstrated. Evidence from correlation of substrate type with fishes of different activity-range categories indicates that substrate complexity is more important in providing shelter space than food in determining reef fish abundance.

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Table 1. Significant Spearman rank correlations relating all variables for the four study areas.

(n=230) BUYONG

	DEPTH	SAI	ROCK	CORAL	SAND	SLOPE	ABUN	BIOM	DIV1	DIV2
DEPTH		**	**		**	**	**	**	**	
SAI	**			*	**	**	**	*	*	
ROCK	**	**		**	**	**				
CORAL	**	**	**		**		**	**	**	**
SAND	**	**	**		**	**	**	**	**	*
SLOPE	**	**	**	**		**	*	**	**	
ABUN	*	**	**	**	**	**		**	**	**
BIOM		**	**	**	**	**	**		**	**
DIV 1	**	**	**	**	**	**	**	**		**
DIV 2		**	**	**	**	**	**	**	**	

OLANGO (n = 362)

(n = 361) SUMILON RESERVE

	DEPTH	SAI	ROCK	CORAL	SAND	SLOPE	ABUN	BIOM	DIV 1	DIV 2
DEPTH		**	**	**	**	**	**	**	**	**
SAI			**	**	**	**	**	**	**	**
ROCK				**	**	*	**	**	**	**
CORAL		**	*		**	**	**	**	**	**
SAND		**	**	**		**	**	**	**	**
SLOPE	**						**	**	**	**
ABUN		**		**				**	**	**
BIOM	*	**		*			**		**	**
DIV 1		**		**	**		**	**		**
DIV 2		*		**	**		**	**	**	

NON-RESERVE SUMILON (n = 396)

**Chi-square 0.05 > p >0.001. **Chi-square p < 0.001. SAI = Surface area index; ROCK = proportion of rock cover; CORAL = proportion- of total coral cover; SAND = proportion of sand cover; ABUN = numbers of fishes/meter-square; BIOM- biomass of fishes/meter-square; DIV 1 = number of species/quadrat; DIV 2 = diversity (H') based on biomass, n's are numbers of 2m x 2m quadrat.*

Table 2. Canonical correlation analyses relating fish community variables with substrate variables for the four study areas.

	BUYONG		OLANGO			SUMILON RESERVE		NON-RESERVE SUMILON	
Canonical Variable	I	II	I	II	III	I	II	I	II
Fish Variables									
BIOM	*	*			***		**	**	
ABUN	***		**	*		***		***	
DIV 1		*	***						**
Substrate Variables									
SAI		*			**		*	**	
ROCK									
CORAL		*	**			*		**	
SAND	*		***						
DEPTH	**			*		**			*
SLOPE						**			

**** very high loadings on canonical variable, ** high loadings, * -scorable loadings.*
All correlations with SAND are negative.
All canonical variables presented are significant (Prob > Chi-square < 0.05).
See Table 1 for an explanation of abbrevations.
Interpretations are made within each canonical variable e.g., on the second canonical variable of Buyong, biomass and diversity were most correlated with the SAI and CORAL.

Table 3. Multiple correlation relating each fish variable and the array of habitat variables for the Buyong study area.

Area	Fish Variables	Substrate Variables With Highest Loadings		
Buyong				
	BIOM	SAI***	DEPTH***	SLOPE*
	ABUN	SAND*	DEPTH*	CORAL*
	DIV 1	SAND*	DEPTH*	CORAL*
	DIV 2	CORAL**	SAND*	
Olango				
	BIOM	SAND**	SAI**	SLOPE*
	ABUN	SAND***	CORAL**	DEPTH**
	DIV 1	SAND***	CORAL***	ROCK*
	DIV 2	SAND***	CORAL***	ROCK*
Sumilon Reserve				
	BIOM	DEPTH***	SAI***	SLOPE*
	ABUN	DEPTH**	SLOPE*	SAI*
	DIV 1	DEPTH**	SLOPE**	CORAL*
	DIV 2	CORAL**	DEPTH**	SLOPE*
Non-reserve Sumilon				
	BIOM	DEPTH*	SLOPE*	SAI*
	ABUN	CORAL*	SAI*	
	DIV 1	CORAL*	SAND*	SAI*
	DIV 2	CORAL*	SAND*	SAI*

****= Very high loadings on canonical variable, ** high loadings, * scorable loadings.*
All correlations with SAND are negative.
Overall mutiple correlations were all significant (Prob > Chi-square < 0.001).
See Table 1 for an explanation of abbreviations.

Table 4. Canonical correlation analysis relating fish community variables to habitat variables for each zone in the Buyong and Olango study areas.

Area Zone	Canonical Variables	Variables With Highest Loadings: Fish	Substrate		Canonical R	(Prob > Chi-sq)
BUYONG*						
FRONT	I	BIOM	SAI	DEPTH	0.6127	(.0001)
	II	ABUN	CORAL		0.4394	(.0209)
RIM	I	ABUN	CORAL	-SAND	0.6343	(.0001)
FLAT	I	ABUN	-SAND	CORAL	0.6813	(.0001)
	II	BIOM	DEPTH		0.5154	(.0004)
GR FLAT	I	ABUN	CORAL	-SAND	0.6693	(.0001)
	II	DIV 2	SAI		0.3048	(.0106)
OLANGO						
FRONT	I	DIV 2	-SAND	CORAL	0.6152	(.0004)
RIM	I	ABUN	-SAND	CORAL	0.8151	(.0001)
	II	BIOM	SAI		0.6163	(.0001)
FLAT A	I	DIV 2	CORAL	-SAN	0.7351	(.0001)
	II	BIOM	SAI		0.4146	(.0001)
FLAT B	I	BIOM	CORAL	SAI	0.7087	(.0001)

BUYONG: FRONT, n = 67; RIM, n = 82; FLAT, n = 92; GR FLAT = grass flat, n = 136; OLANGO; FRONT, n = 80 RIM, n = 86; FLAT = deep flat, n = 133; FLAT B = Shallow flat, n = 71.
See Table 1 for an explanation of other abbreviations.

Table 5. Spearman rank correlations of substrate variable with fish abundance in the different activity-range categories.

		Correlation with Abundance of Fishes					
		Buyong			Olango		
Reef Zone	Substrate Variable	TOTAL	WIRAN	SHRAN	TOTAL	WIRAN	SHRAN
Front	ROCK	0.346	0.340	0.337	0.253	0.302	0.357
	CORAL	0.388	0.407	0.428	0.514	0.549	0.513
	SAND	0.258	0.258	0.18+	0.511	0.522	0.513
Rim	ROCK	0.268	0.266	0.359	0.538	0.528	0.555
	CORAL	0.535	0.526	0.534	0.733	0.737	0.714
	SAND	0.560	0.553	0.476	0.733	0.731	0.720
Flat	ROCK	0.13+	0.14+	0.07+	0.359	0.363	0.346
	CORAL	0.310	0.309	0.371	0.630	0.626	0.597
	SAND	0.279	0.281	0.311	0.631	0.626	0.608

All correlations with SAND, and correlations with ROCK in the Buyong Front and RIM zones are negative.
All correlations are significant ($P < 0.05$) except where marked with a '+'.
$n = 67\text{-}133$
See Methods for an explanation of TOTAL, WIRAN, SHRAN.

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