

## THE EFFECTS OF FLOW, DEPTH AND SLOPE ON COVER OF SOFT CORAL TAXA AND GROWTH FORMS ON DAVIES REEF, GREAT BARRIER REEF

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## ABSTRACT

A large proportion of variation (9 to 54%) in cover of taxonomic and morphological groups of soft corals on Davies Reef was explained by one to four abiotic environmental variables. Water flow, substratum slope, depth and location all influenced the distribution of 12 genera and 3 families, and were related to colony morphology. The distribution of taxa with soft small capitate colonies was well described by quadratic functions of depth and flow, with maximum cover at intermediate levels of both variables. The abundance of firm small lobate colonies increased linearly with flow. Tall arborescent taxa decreased with increasing substratum slope. Only encrusting taxa displayed a weak relationship to their physical environment, leaving more scope for intrinsic and extrinsic biological parameters to control these persistent and wave-resistant populations.

## INTRODUCTION

For some time, ecologists have discussed the extent to which reef communities are controlled by the abiotic environment (Done 1983), and to what extent biological interactions are a source of community control (Sheppard 1979; Alino et al. 1992). However, only a few studies have quantified either of the two sources, or compared the two alternative views (Bradbury 1988). Community patterns may be more predictable in physical environments that are more predictable (Loya 1972). Moreover, in assessing risks of environmental damage, it seems axiomatic that a strongly abiotically controlled community will be particularly prone to alter when the environment changes. By contrast, a community mostly controlled by biological interaction may be more vulnerable to over-exploitation or other impacts that affect relative abundances without affecting the abiotic environment.

The present study investigates the extent to which soft corals are controlled by their physical environment. It primarily focuses on effect of a few major variables (flow, slope angle, water depth and location) on cover of genera, families and morphological groups of soft corals. Soft corals are an abundant and diverse group of reef benthos on the Great Barrier Reef, and generally cover 5 to 30% of the reefal area (Fabricius 1995). They are passive suspension feeders which filter phytoplankton and other small particulates from the water. Earlier studies have documented the effect of flow on rates of growth, morphology and food intake, and on carbon budgets in soft corals (Fabricius et al. 1995; Patterson 1991). The majority of soft corals are partly phototrophic, in that they contain zooxanthellae and depend on photosynthetically active irradiance for photosynthetic carbon fixation. Thus there is substantial a priori evidence that physical factors should affect the distribution and abundance of soft corals. Here we assess the extent to which this potential is realized.

## METHODS

## Field measurements

Soft coral assemblages were investigated on Davies Reef, a midshelf reef on the central Great Barrier Reef (18°50'S, 147°39'E) which is exposed to predominantly south-easterly wind and tidal induced currents (Pickard 1986). Five sites were surveyed at windward and leeward sides and in the lagoon, and at one site at each of the northern and southern reef flanks (Fig. 1). Communities were censused along depth contours at 5m depth increments as follows: windward side 5 to 30m; leeward 5 to 25m; flanks 5 to 20m; lagoon 5 to 15m. The greatest depth at each location reflected differences in the base of the reef.

Soft corals were identified within belt transects (25 x 0.5m) to genus level, and the longest and shortest diameter of each colony was recorded (Fabricius 1995). Colonies crossing the belt border were treated as follows: The whole area of colonies smaller than 0.5m

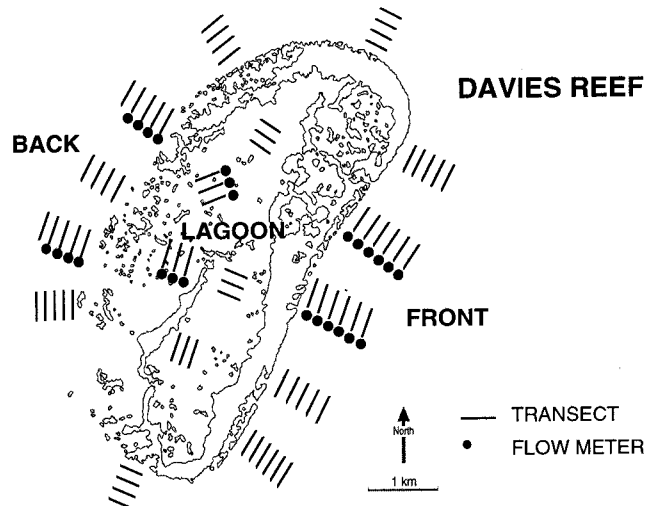


Fig. 1: Position of the survey sites on Davies Reef.

diameter was recorded only when more than 50% of their area was located within the belt, whereas colonies more than 50% outside the belt were not considered. For colonies larger than 0.5m, the actual surface area within the belt was recorded.

Slope angle, irradiance and water flow were recorded at each site by the following methods: The substratum slope was measured every 2m along the transects, and the readings later averaged to one value for each transect. Photo-synthetically active irradiance was determined with a Li-Cor quantum sensor on three cloudless days at each of the locations during noon. However, there were no differences in irradiance between the three locations for any depth (Fabricius and Klumpp 1995). The lagoon values were more variable than those from the front and back of the reef due to changing turbidity and backscattering from the sand on the shallow bottom, but means were similar to those of the remaining locations. Thus, irradiance was confounded with depth, and is not included as separate factor in the present analysis. Dissolution rates of erosive blocks, which are directly proportional to current velocity (Jokiel and Morrissey 1993), were used as indices of water motion at 52 sites. Hemispherical blocks of dental cement with a base diameter of 50mm were dried for 3 days at 60°C, and weighed. Four replicates were placed at 5m intervals between 5 and 30m depth for 24 h at each of the 13 locations on three days with different wind and tidal conditions. The blocks were placed on 10 to 20cm elevated substrata, on the assumption that the flow around the blocks approximated those around medium sized soft coral colonies. After 24 h, the blocks were retrieved, redried, and reweighed. The relationship between weight loss and water flow was calibrated in a flow chamber at flow speeds ranging from 0 to 28cm s<sup>-1</sup> for 24h, and at temperature and salinity as encountered in the field (25°C and 3.5‰).

## Data analysis

Proportions of cover of genera, families and morphological groups were calculated as sum of the colony areas (longest and shortest colony diameter, assumption of ellipsoid colony shapes), divided by the area of hard substrate in the transect (25 x 0.5m, minus the area of loose sand and rubble). Generic data were also pooled into four morphological groups with similar colony morphology:

Small Soft Capitates (SSC): *Efflatounaria*, *Xenia*, (family Xeniidae), *Alcyonium*, *Cespitularia*, *Cladiella*, *Symphodium*; colony height mostly smaller than 5cm, colonies not supported by strong sclerites or tough epidermis, medium to large polyp sizes. In this group, all 3 common families were represented, with the Xeniidae dominating numerically.

Firm Small Lobates (FSL): *Paralemnalia*, *Capnella*, *Lemnalia* (family Nephtheidae); Colony height mostly smaller than 5cm, colonies enforced by sclerites in a tough epidermis, small polyps.

Tall Arborescent Taxa: *Nephthea*, *Stereonephthya*, *Dendronephthya*, *Isis*, *Plexaura* (numerically dominated by Nephtheidae). Tree- or fan-shaped, small polyps.

Encrusting Taxa: *Sinularia*, *Lobophytum* (family Alcyoniidae), *Briareum*, *Parerythropodium*. With or without surface structures (ridges, ledges), all polyp sizes.

The effects of the following four factors on the distribution of genera and morphological groups were investigated: location (back, front, lagoon); depth (5m to 30m); water motion (range: 5 to 35cm s<sup>-1</sup>); slope angle (horizontal - overhang). One major problem in analyzing this data was the confounded character of the environmental factors. Flow, depth and slope all showed uneven distribution over the locations (Fig. 2). For example, flow was consistently lower in the lagoon than at front or back reef sites (see below). The substratum slope was steepest in the lagoon, and very variable on the back reef. Moreover, the deepest depth surveyed varied between locations. The data were thus unbalanced and were therefore analyzed using linear models and type III sums of squares for all tests of significance. This method is suitable to tease apart the effects of the partially confounded explanatory variables. The response variable was proportion of cover (arc-sin square-root transformed). Explanatory variables for an initial model included location as a factor, quadratic polynomials for depth and flow, and linear effects of slope; this form being suggested by exploratory data analysis. The model was simplified by backward elimination of terms of lowest significance, until only variables with significance levels of  $P < 0.05$  were included.

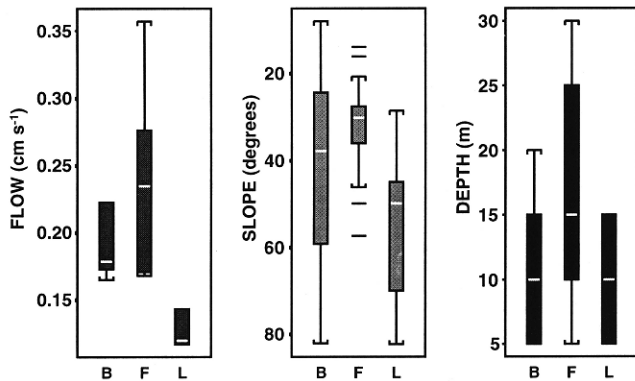


Fig. 2: Flow, slope angle and depth as factors confounded with location (B = back, F = front, L = lagoon) on Davies Reef. y=% erosion; Box-whisker plot, indicating median (white bar), upper and lower quartiles (boxes), the normal range (error bars, and outliers (horizontal lines).

## RESULTS

### Water motion

The weight loss of the erosive blocks decreased with increasing depth at all locations for all three days of measurement, despite the different wind and wave conditions on these days (Fig. 3). The range of flow speeds was 5 - 35cm s<sup>-1</sup>. At 5m depth at the wave-exposed windward side of the reef, weight loss was equivalent to flow rates of around 35cm s<sup>-1</sup>. The corresponding value on the leeward side was around 20cm s<sup>-1</sup>. At 15 to 20m depth, the differences in water movement between the wind- and leeward side were insignificant (mean ≈ 15cm s<sup>-1</sup>). In the lagoon, water movement was lower at all depths than on any part of the outer slope (mean ≈ 5 to 10cm s<sup>-1</sup>).

### Distribution of genera

The physical factors under consideration explained significant proportions of the variation in the distribution of many of the 12 genera (Table 1). Water flow influenced the two most common xeniid taxa (*Efflatounaria* and *Xenia*) and several nephtheid genera. The depth effect was

quadratic for all taxa affected, with highest cover at intermediate depths. Nephtheid taxa varied widely in their responses to the physical environment. The distribution of three nephtheid genera was related to the flow speed: the relationship of *Capnella* and *Paralemnalia* was positive, and that of *Lemnalia* negative. The abundance of *Nephthea* was positively correlated with slope. However, location also had a significant effect on this genus, with relatively low cover on the front reef sites compared to the back and the lagoon. Since location and flow were highly confounded, an alternative model with slope and linear flow as variables explained variation in cover of *Nephthea* almost as well as the slope and location model. The two gorgonian taxa *Isis* and *Plexaura* were strongly affected by substratum slope (decreasing abundance with increasing slope, and absence

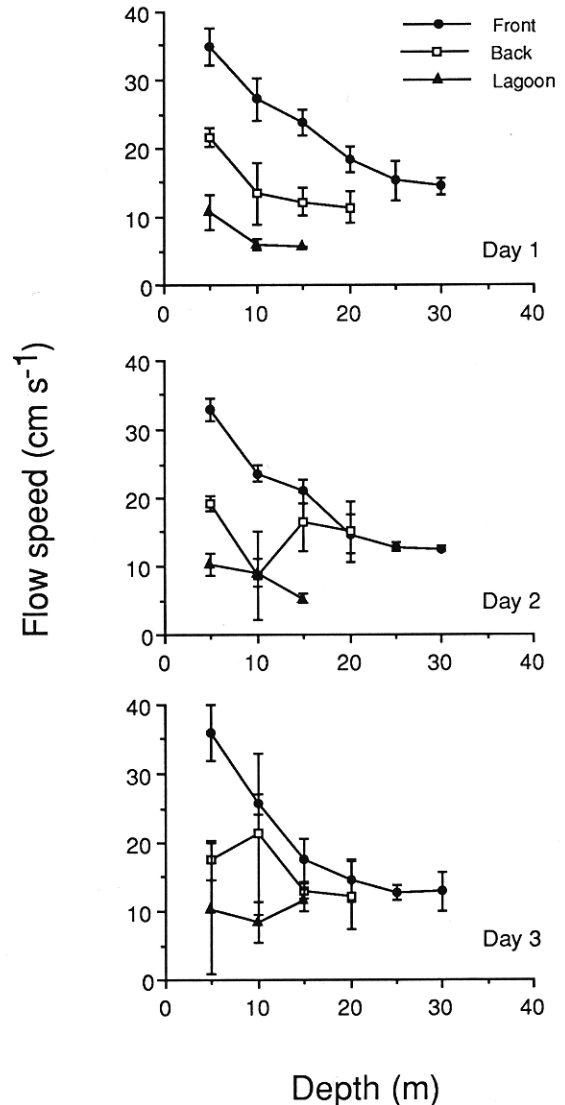


Fig. 3: Relative water movement at Davies Reef, measured by rates of plaster block erosion. Each data point represents the average of 12 measurements (4 sites on each topographic side, 3 replicates per site and depth, see Fig. 1). Filled circles: windward side, open squares: leeward side, filled triangles: lagoon. Bars indicate 1 SD. Measurements were taken on three days with different wind and tidal conditions (16 - 17 October 1992: 12-18km h<sup>-1</sup> wind speed, < 0.3m waves on the windward side of the reef; 21 - 22 October 92: 35-42 km h<sup>-1</sup> wind, 1.5m waves; and 15 - 16 November 1992: 18-27km h<sup>-1</sup> wind, 0.8m waves). Calibration in the flow chamber produced linear correlation function between water flow speed (v, cm s<sup>-1</sup>) and weight loss (%; L):  $v = 5.55 + 1.12 * L$  (n = 72, r<sup>2</sup> = 0.80). Error rate in the flow chamber: 9.2% ± 6.2 SD, in the field 15.1% ± 12.5 SD (n = 3 for each speed).

of the Isidae at slopes steeper than 35°, and of *Plexaura* steeper than 65°). Most Alcyoniidae showed no response to their abiotic environment other than location (Table 1), however depth did affect the cover of *Sarcophyton* (maximum cover at 20m). Overall, 9 to 54% of the overall variation in the genera, and 45% of the variation in total soft coral cover were explained by the models, with flow accounting for 9 to 31%.

Table 1: The most common soft coral genera on Davies Reef between 5 and 30m depth and their relationship to the physical variables flow, slope angle, depth and location. Outcomes of model III analyses of variance on the distribution over 75 transects, and percent of variation in the data explained by the model and by flow (see methods). (lin) = test for linear relationship, (quad) = quadratic polynomial model fitted. \*  $P < 0.05$ , •  $P < 0.005$

| Taxon                 | Flow (lin) | Slope (lin) | Depth (quad) | Locat. (3 levels) | % Var. (model) | % Var. (flow) |
|-----------------------|------------|-------------|--------------|-------------------|----------------|---------------|
| <b>Xeniidae</b>       |            |             |              |                   |                |               |
| <i>Efflatounaria</i>  | •          |             | *            |                   | 18.1           | 10.5          |
| <i>Xenia</i>          | •          |             | *            | *                 | 40.9           | 14.9          |
| <b>Nephtheidae</b>    |            |             |              |                   |                |               |
| <i>Capnella</i>       | •          |             |              |                   | 31.5           | 31.5          |
| <i>Paralemmalia</i>   | *          |             |              | *                 | 23.8           | 9.8           |
| <i>Lemnalia</i>       | *          |             |              |                   | 8.7            | 8.7           |
| <i>Nephthea</i>       |            | •           |              | •                 | 32.3           |               |
| <i>Dendronephthya</i> |            |             | •            |                   | 32.3           |               |
| <b>Gorgonians</b>     |            |             |              |                   |                |               |
| <i>Plexaura</i>       |            | •           | •            |                   | 39.7           |               |
| <i>Isis</i>           |            | •           | •            | •                 | 53.9           |               |
| <b>Alcyoniidae</b>    |            |             |              |                   |                |               |
| <i>Sarcophyton</i>    |            | *           | •            | *                 | 46.6           |               |
| <i>Sinularia</i>      |            |             |              | •                 | 25.9           |               |
| <i>Lobophytum</i>     |            |             |              | •                 | 14.0           |               |
| <b>Xeniidae</b>       |            |             |              |                   |                |               |
|                       | • (quad)   |             | •            |                   | 36.2           | 27.1          |
| <b>Nephtheidae</b>    |            |             |              |                   |                |               |
|                       |            | •           |              | •                 | 35.4           |               |
| <b>Alcyoniidae</b>    |            |             |              |                   |                |               |
|                       |            |             |              | •                 | 28.5           |               |
| <b>All taxa</b>       |            |             |              |                   |                |               |
|                       |            | •           |              | •                 | 45.0           |               |

#### Distribution of morphological groups

Physical factors accounted for substantially more of the variation among some growth forms than it did for the individual taxa. The distribution of soft small capitates (SSC), firm small lobates (FSL) and tall arborescent taxa are highly predictable by physical factors. In contrast, the distribution of the encrusting taxa was related to location only, and even this relationship was weak (Table 2). Response curves (Fig 4) display the nature of the relationships between the morphological groups and the effects of physical variables. A quadratic function of flow and depth best predicted cover of the SSC. Their cover was highest at intermediate flow (ambient flow of around 25-30cm s<sup>-1</sup>) and intermediate depth (15 to 20m) (Fig. 5). As SSCs lie close to the substratum ( $\leq 5$  cm), their optimal flow speed will be somewhat slower than the values 20cm above the substratum, as a result of shelter provided by rugosity at the 5-10cm scale. Only water flow accounted significantly for variation in the distribution of the FSL (Table 2, Fig. 4). Their cover increased linearly with flow, and more than 50% of the sites with  $< 15\text{cm s}^{-1}$  flow were free of FSL (Fig. 5). The cover of tall arborescent taxa decreased linearly with increasing slope angle, and their distribution was also related to location (Figs. 4 and 5). Cover of this group was lowest at the front, and highest at the less wave-exposed back reef and the lagoon. Encrusting taxa had highest cover on the back reef sites (Fig. 4), and their cover showed a weak tendency to increase linearly with increasing flow. However, the abiotic factors explained only 14% of the variation in their distribution, whereas they explained 27 to 38% of the variation in cover of the other three growth forms.

Table 2: The four morphological groups of soft corals, and their relationship to the physical environment. P-values of type III analyses of variance on the distribution over 75 transects on Davies Reef, and percent of variation in the data explained by the model factors and by flow (see methods). \*  $P < 0.05$ , •  $P < 0.005$ ; (+), (-) positive and negative relationship, respectively.

|                   | Soft small capitates (SSC) | Firm small lobates (FSL) | Tall arborescents | Encrusting taxa |
|-------------------|----------------------------|--------------------------|-------------------|-----------------|
| Flow (quad)       | •                          |                          |                   |                 |
| Flow (lin)        |                            | •(+)                     |                   |                 |
| Slope (lin)       |                            |                          | •(-)              |                 |
| Depth (quad)      | •                          |                          |                   |                 |
| Locat. (3 levels) |                            |                          | •                 | *               |
| % Var. (model)    | 37.7                       | 26.9                     | 37.8              | 13.9            |
| % Var. (flow)     | 27.3                       | 26.9                     |                   |                 |

#### DISCUSSION

In the literature, the distribution of organisms has often been related to gradients in single environmental variables. Soft corals on Davies Reef were found to be distributed systematically in relation to physical and topographic variables, and for 7 out of 12 genera the relationship was substantially accounted for by two or more variables. The genus *Nephthea*, for example, showed an apparent depth zonation, with a peak at 15m depth (Fabricius and Klumpp 1995), however, even greater insights in the distribution of this genus were obtained by considering the statistically confounded variables slope and location. Depth *par se* disappeared as a significant variable when slope and location were included in the analysis. This demonstrates the importance of considering the simultaneous effects of multiple factors when modeling and predicting community properties.

This study indicated similar distribution responses of morphologically similar groups of soft corals, suggesting that colony growth forms may be subject to substantial physical control. Sebens and Done (1993) found a similar clustering in the distribution of scleractinian coral growth forms over Davies Reef, but no clear patterns when species were grouped by calyx size. Both studies suggest that valuable information can be gained in rapid surveys carried out on low taxonomic resolution or colony growth forms. This is particularly relevant for groups such as soft corals where for most researchers species level identification in the field is limited to a small proportion of the individuals encountered.

Flow appears to act as a major force in delimiting soft coral distribution and abundance. Optimal flow for particle capture was found to be 8 - 15cm s<sup>-1</sup> in the octocorals so far investigated (Dai and Lin 1993; Fabricius et al. 1995; Fabricius and Sebens: unpublished data from Caribbean gorgonians). This approximates the flow conditions on Davies Reef at 15 to 20m, the depth of highest soft coral cover (Fabricius 1995). Very slow, or very fast flows depress feeding efficiency and growth rates of the suspension-feeding soft coral (Fabricius et al. 1995). In the Red Sea, *in situ* growth rates of the soft coral *Dendronephthya hemprichi* are up to eight times higher at flows of 16 to 20cm s<sup>-1</sup> compared to flows  $< 5\text{cm s}^{-1}$  or  $> 25\text{cm s}^{-1}$ . The species was absent from regions where flow averaged  $< 5\text{cm s}^{-1}$  (Fabricius 1995). It appears likely that the prevailing flow conditions exert a similarly strong control on other soft coral taxa.

Sebens and Done (1993) characterized the hydrographic patterns on Davies Reef with repeated 10min deployments of electromagnetic current meters. These short-term deployments resulted in flow data which resembled in detail those found here with erosive blocks. The electromagnetic current meters provided additional information on the distribution of wave-induced oscillatory flow. A strong bidirectional and oscillatory component occurred to a depth of at least 9m on the windward side, whereas flow was more unidirectional on the leeward

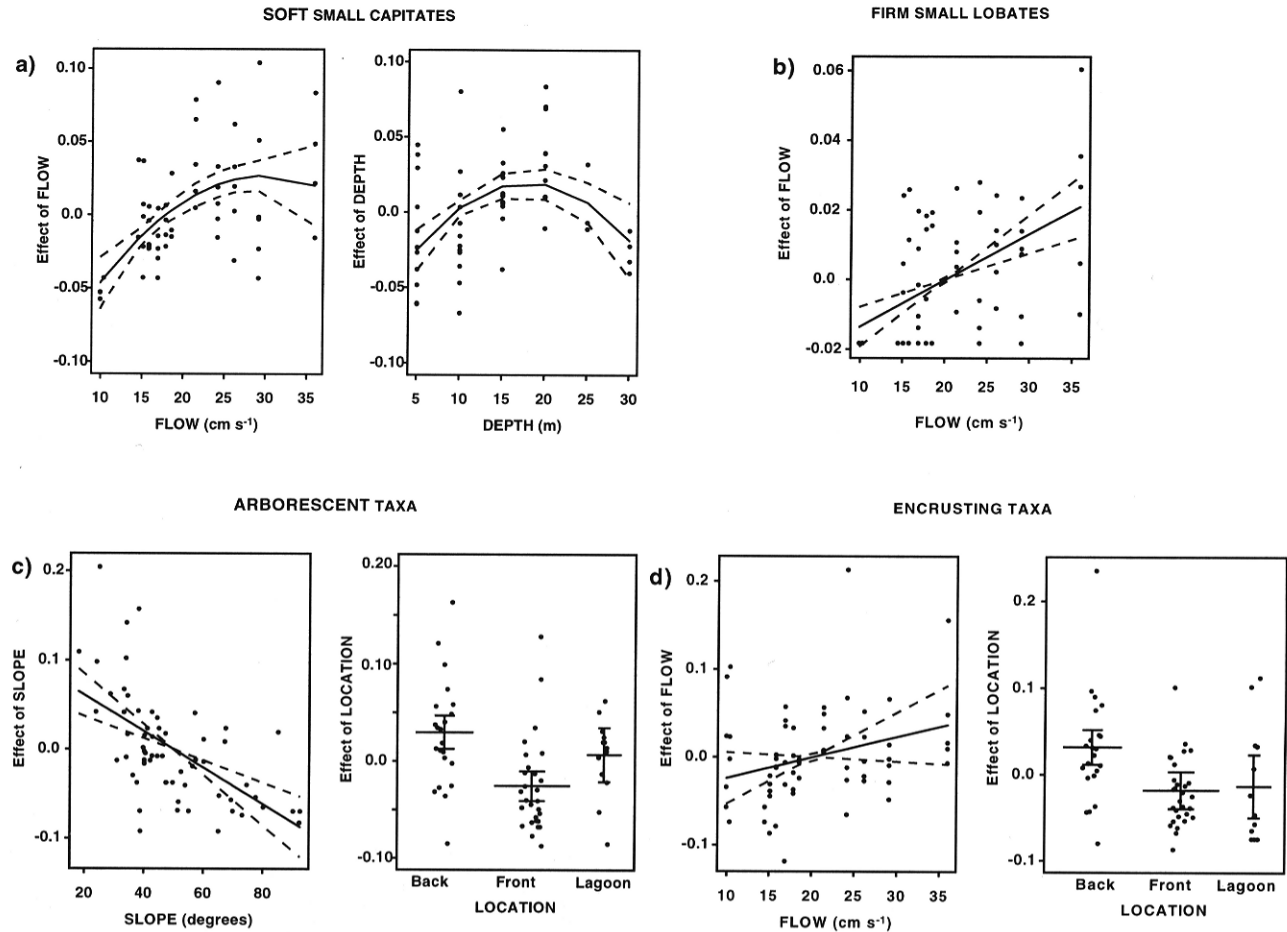


Fig. 4: Response curves of the four morphological groups to factors of their abiotic environment. a) Soft small capitates, b) firm small lobates, c) tall arborescents, d) encrusting morphs. The solid line indicates the response of cover to the physical variable (linear or quadratic function fitted), standardized and adjusted to the other significant factors. Dashed lines: 90% confidence intervals. Data points represent the residuals of individual observations to the predicted response. X-axes: Flow (as % erosion), depth (m), slope angle (degrees), location (B = back, F = front, L = lagoon). Morphological groups: a) Soft small Capitates, b) Soft firm lobates, c) Tall arborescent taxa, d) Encrusting taxa.

side at the same depth, the wave energy having been dissipated on the reef front (Sebens and Done, *ibid*). Most of the arborescent Nephtheidae and the small soft Xenidae were rare in the reef-front zone of wave-induced bidirectional flow. By contrast, the encrusting Alcyoniidae, and the firm small lobate taxa were little affected by flow and wave action.

The mode of action of slope angle on the tall arborescent soft corals is not immediately obvious. One potential cause is that the longer daily period of saturating irradiance on gradual slopes than on shaded steep slopes. This could be of significance in terms of carbon supply, because the photosynthetic efficiency of soft corals is relatively low, and periods of light saturation are limited to a few hours a day in deeper water (Fabricius and Klumpp 1995). Thus, every additional hour of exposure to irradiance enhances the photosynthetic carbon gain in soft corals.

The proportion of variation in total soft coral cover explained (45%) by the variables slope and location appears high, considering the many other physical and biological parameters known to contribute to control population growth in sessile marine invertebrates. Among these are extrinsic biological controls such as intraspecific (density-dependent effects) and interspecific effects (interactions with neighbours, predation and parasites). Interspecific factors appear to be of only moderate influence in soft corals, due to their effective chemical defences against overgrowth and predation (Maida et al. 1995). The few taxa known to feed on soft

corals (such as the egg cowry *Ovula ovum*, and some fish) are grazers rather than predators, but few data exist which actually quantify feeding pressure. The effect of intrinsic biological factors (life history traits, and settlement preferences of larvae) are equally unknown for many soft coral taxa. Furthermore, there are undoubtedly more abiotic parameters which contribute to the variation in taxonomic and growth form distribution than we have considered here. These include differences in microhabitat flow environments, particle load in the water column, and sediment load. Disturbance history, and random events or chance are also known to affect the community composition in complex ecosystems (Connell 1978; Hughes 1994). Notwithstanding the potential contribution of these myriad factors and processes, in this study, they need to be invoked to account for only a relatively small residual variation once the effects of flow, slope and depth have been accounted for.

To summarize, the distribution of soft corals, and in particular of their colony morphs, is fairly predictable on the spatial scales investigated here (geomorphological locations, 25m transects). Growth forms are strongly affected by flow, depth and/or slope angle, and also the cover of many of the genera is forced to considerable extent by the physical environment. The strength and relative simplicity of these relationships provide a good foundation for hypothesis generation and for the development of models to predict soft coral zonation and composition in a variety of environmental setups.

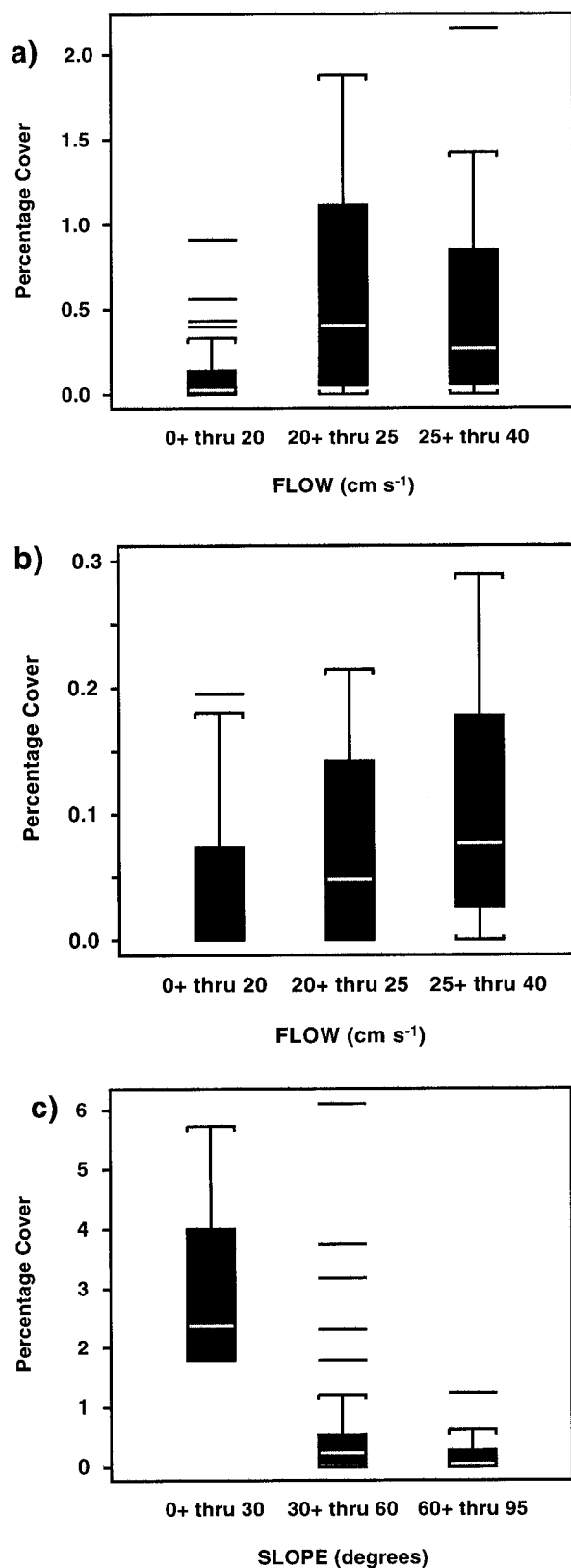


Figure 5: Box-whisker plot of the mean cover of the morphological groups along grouped environmental factors. These plots are not controlled for other significant (and often confounded) parameters, and therefore need to be interpreted with some caution. a) Quadratic response of Soft small capitates to flow. b) Linear response of Firm small lobate taxa to flow. c) Response of tall arborescent taxa to slope angle.

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