SESSION 6

Reef connectedness

Habitat optima of soft corals on the central Great Barrier Reef: niche characterisation using regression tree analysis

Katharina E Fabricius[1] *and Glenn De'ath*[2]
[1] *CRC Reef Research Centre and AIMS, PMB No. 3, Townsville Qld 4810*
[2] *CRC Reef Research Centre and TESAG, James Cook University Qld 4811*

ABSTRACT

Soft corals are often cast as the villains that invade unoccupied reef substrata, thereby excluding reef-building corals and retarding reef growth. This study seeks to determine the optimal environmental conditions for soft coral abundance and richness of genera. We demonstrate distinct cross-shelf gradients in soft coral assemblages, and also less pronounced changes in abundance along other environmental gradients. Depth, wave exposure, slope, flow, sediment levels, and interactions between these factors affect abundances of taxa.

We discuss the rapid survey technique as a field method that can detect subtle spatial changes in communities. Regression trees are presented as a statistical technique ideal for revealing the complex interactions between environmental factors which affect the distribution of taxa. Regression trees are easy to use and simple to interpret. They can be used to characterise combinations of environmental variables related to different abundance levels, and thus determine the most favourable (and most avoided) habitats for taxa, and identify patterns of niche separation. Rapid surveys, combined with regression trees, are a powerful and efficient combination for community analyses, well suited to both scientific and managerial application.

INTRODUCTION

Previous studies of soft coral assemblages have demonstrated that distinct assemblages are found in certain types of reefs across the shelf (Dinesen 1983). Distribution and abundance of taxa on Davies Reef, central Great Barrier Reef, were strongly related to the physical environment (Fabricius et al. 1995; Fabricius and De'ath, in press). In contrast, abundances remained unaltered in areas where space availability was enhanced after crown-of-thorns starfish outbreaks (Fabricius, in press). The latter studies were carried out on mid-shelf and outer-shelf reefs using a combination of line intercept and belt transects. In the present investigation, rapid surveys were used to assess soft coral assemblages from near-shore to outer-shelf reefs between Townsville and Innisfail. Belt transects have been used successfully in detailed analyses of relationships between taxa and microscale to mesoscale environmental parameters, whereas the use of rapid surveys for studies other than large-scale studies have not been widely accepted, in spite of successful applications (e.g. Done 1982). Recording a single soft coral belt transect of 25 x 0.5 m takes 20 to 80 minutes. In the same time, rapid surveys covering hundreds of square meters and 5 depth zones can be carried out (personal observation). Moreover, rare taxa are more likely to be observed in rapid surveys than in belt transects, as their probability of occurrence in a small area is low, and thus communities with many rare taxa may be better represented. In this paper, we characterise large-scale and mesoscale patterns in the distribution of soft coral families and individual genera, and we present regression trees as a powerful, yet easily interpretable statistical technique capable of detecting changes in abundances caused by complex interactions between environmental factors.

FIELD METHODS

Rapid surveys were carried out on a total of 278 sites at 71 locations on 22 reefs across the continental shelf. Inner-shelf sites were represented in greatest numbers in order to complement earlier studies (inner-shelf: 165 sites on 15 reefs, mid-shelf: 39 sites on 4 reefs, outer-shelf: 74 sites on 3 reefs). The area surveyed ranged from latitude 17.00°S to 19.20°S,

and longitude 146.00°E to 147.50°E. At each location, the reef was surveyed at the following depth zones: 18–13 m, 13–8 m, 8–3 m, 3–1 m and on the reef flat.

The following data were recorded during swims on scuba of 10–15 min within each site:

- Abundances of all soft coral genera, estimated on a scale of 0 to 5, using the following rating scale: 0 = absent, 1 = one or few colonies (0+ to 0.2% cover), 2 = uncommon (0.2+ to 0.5%), 3 = moderately common (0.5+ to 3%), 4 = common (3+ to 20%), and 5 = dominant (> 20%).
- Per cent total cover of soft corals, hard corals, turf and macro algae, and unconsolidated substratum (sand and rubble).
- Physical variables were estimated during the time of surveys: flow speed (cm s^{-1}), wave exposure (rated on a 5-point scale between 0.0 to 1.0), slope angle (degrees), sediment deposits (rated on a 4-point scale of 0 to 3)

STATISTICAL METHODS

The relationships between abundances of taxonomic groups and regional characteristics (shelf position, reefs, location within reefs), and local physical conditions (flow rates, wave exposure, depth, slope angle, and sediment deposits on the benthos), and their interactions, were analysed with univariate statistics, principal components analysis, and regression trees.

Classification and regression trees are a modern statistical technique which explains the variation of a single response variable in terms of several explanatory variables (Breiman et al. 1985; Chambers and Hastie 1992). The response variable may be either categorical (classification trees) or quantitative (regression trees); we will deal only with the latter. The explanatory variables may be either categorical and/or quantitative. The tree is constructed by repeated binary splitting of the data, each split being based on the value of the explanatory variable which maximises the difference between the two resulting sets of response values. At the end of the procedure the data are partitioned into groups (leaves of the tree), each of which may be simply characterised by the values of the variables which formed the divisions.

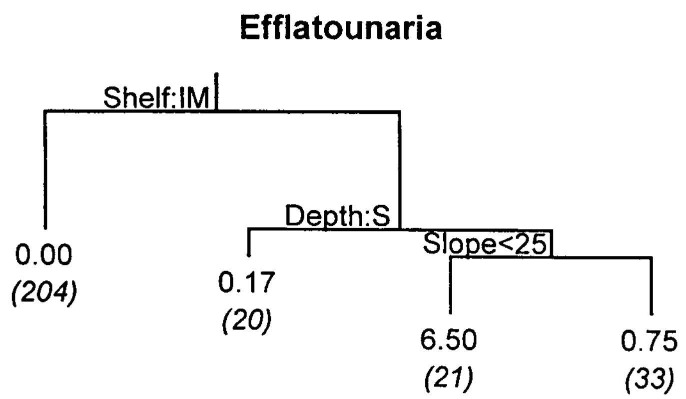

Figure 1. Outcome of a regression tree analysis on the soft coral genus *Efflatounaria*

Consider the simple example in figure 1. The response variable is the percentage cover of *Efflatounaria*, a genus of soft coral. The explanatory variables are cross-shelf position (categories: inner, mid and outer), depth (categories: shallow, medium and deep), and slope (quantitative: range 0–90). The first division is based on shelf, with inner- and mid-reefs in the left branch having a mean cover of 0.0 (n = 204). This group of data is not subsequently divided (all data are 0!) and forms a terminal node or leaf. The right branch, consisting of all outer-reefs, is now divided into shallow depths to the left, and medium and deep depths to the right. This process is repeated until the tree is completed with four leaves as shown.

The four groups can be characterised as follows:

Group	Definition	Mean cover	Size
1	Shelf: inner and mid reefs	0.00	204
2	Shelf: outer reefs; Depth: shallow	0.17	20
3	Shelf: outer reefs; Depth: medium to deep; Slope: < 25	6.50	21
4	Shelf: outer reefs; Depth: medium to deep; Slope: ≥ 25	0.75	33

The advantages of regression trees include:

- Simplicity of interpretation. Each group is characterised by the mean value of the response variable, its size, and its defining variables and their values.
- Detection of complex interactions, often difficult with linear models, is automatic since left and right branches are independent.
- Missing values can be handled easily.

There are some disadvantages:

- The technique has not been widely used in the ecological literature and requires explanation.
- Inference for trees is not as well developed as for more traditional models.

RESULTS

A total of 31 soft coral genera was identified in surveys of 278 sites on the central Great Barrier Reef. Over all reefs, the richness (number of genera) averaged 8.1 per site, with an average of 11.7 on mid-shelf reefs, compared to 7.2 on the inner-shelf and 8.1 on the outer-shelf reefs (figure 2). The soft coral family Alcyoniidae dominated on the inner-shelf reefs, whereas all families, but in particular members of the families Xeniidae and Nephtheidae, were represented on the mid-shelf and outer-shelf reefs (figure 3). Gorgonian abundance was generally low except on some mid-shelf reefs.

Soft coral cover was highest on inner-shelf reefs (20%). It was 12% on mid-shelf reefs, and 13% on outer-shelf reefs. The zone of highest cover within each shelf position shifted downslope with increasing distance from the coast (figure 2). It was highest in shallow water on the inner-shelf sites, and at depths greater than 8 m on the outer-shelf reefs where wave exposure and water clarity are greater. In contrast, mean richness in genera increased at all positions on the shelf with depth.

The proportion of soft corals to total coral cover was greatest on inner-shelf reefs, and independent of depth (figure 2). In contrast, on the outer-shelf reefs this ratio increased with increasing depth, due to the combined effect of a depth-dependent increase in the cover of soft corals and decrease in hard corals.

These summaries of cover and richness values along gradients of depth and distance to the coast served as first insight into patterns of distribution. Naturally, other environmental variables, such as wave action, sediment load, flow and slope angle, contributed to the distribution patterns. However, principal components analysis on the 18 most common taxa displayed a distinct cross-shelf pattern in the assemblages, indicating that changes in communities across the shelf were more consistent than changes due to any other single environmental variable (figure 4). The sites clustered strongly as inner-shelf, mid-shelf and outer-shelf sites.

The distinct cross-shelf pattern was due to the restricted distribution of several taxa (figure 4). Among the 16 most common genera, *Asterospicularia* and *Efflatounaria* were typical outer-shelf genera. In contrast, *Paralemnalia, Lemnalia, Capnella* and *Plexaura* were found on mid- and outer-shelf reefs, but only very rarely on inner-shelf reefs. Whereas *Pachyclavularia, Parerythropodium, Alcyonium* and *Clavularia* were almost exclusively restricted to inner-shelf reefs. Only a few genera occurred in all three shelf positions, these being *Sarcophyton, Sinularia, Nephthea, Lobophytum, Briareum* and *Xenia*. Abundance differences across the shelf in these taxa were also strong (e.g. highest abundances of *Sarcophyton* and *Briareum* on the inner-shelf reefs, and *Nephthea* and *Xenia* on the mid-shelf and outer-shelf). Moreover, two of the most common *Sinularia* species, *S. flexibilis*

and *S. capitalis*, dominated the inner-shelf reefs, but were rarely found on mid-shelf reefs and never occurred on the outer-shelf.

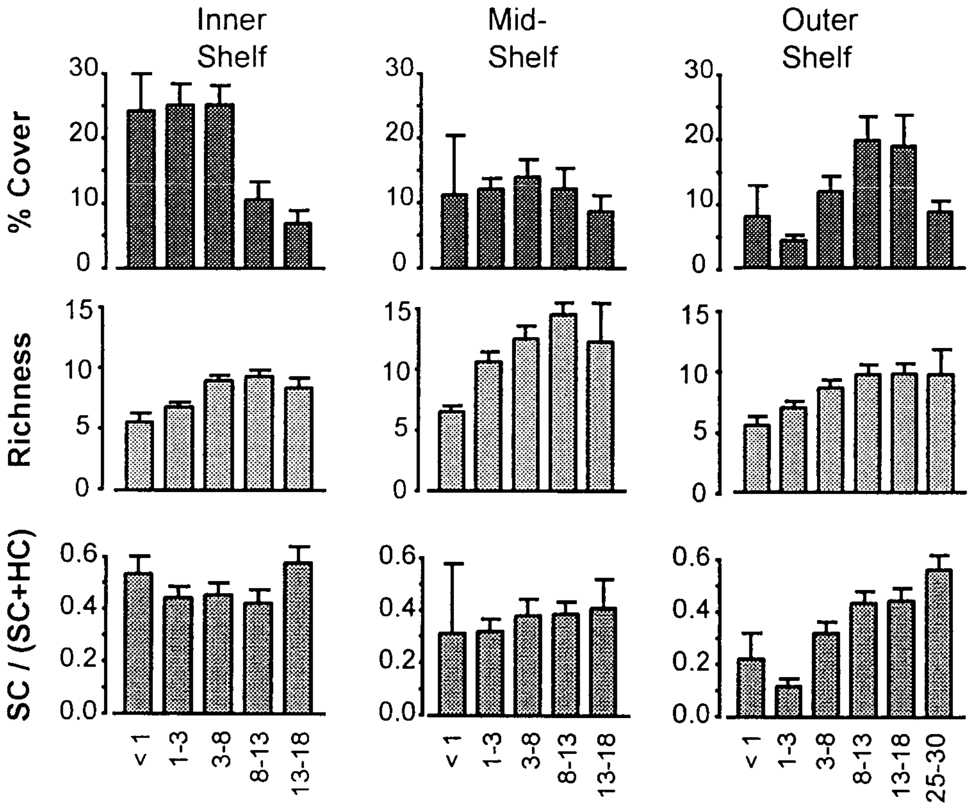

Figure 2. Depth related gradients in soft coral cover, richness in genera and the proportion of soft coral cover to total coral cover (SC/(SC+HC)) across the continental shelf. Error bars indicate 1 SE.

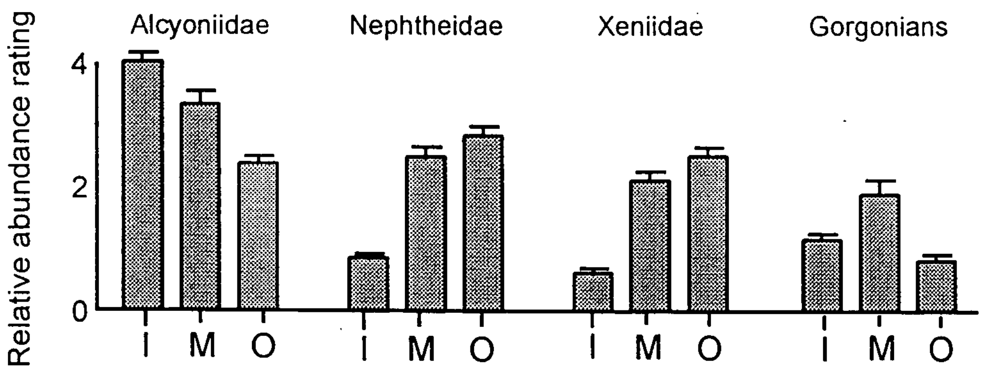

Figure 3. Relative abundance of families on inner-shelf (I), mid-shelf (M) and outer-shelf (O) reefs. Error bars indicate 1 SE.

When inner-shelf sites were analysed separately using the most common inner-shelf taxa, depth gradients were strongly evident (figure 6). Each of the taxa shown in the principal components biplot, favoured a particular depth. For example, *Briareum, Clavularia*, and the alcyoniid genera *Lobophytum* and *Sinularia capitalis* characterised the upper 3 m zone, whereas the greatest abundances of *Alcyonium* and *Pachyclavularia* occurred at 13–18 m. The plot also shows that higher soft coral cover occurred in shallow compared to deeper zones.

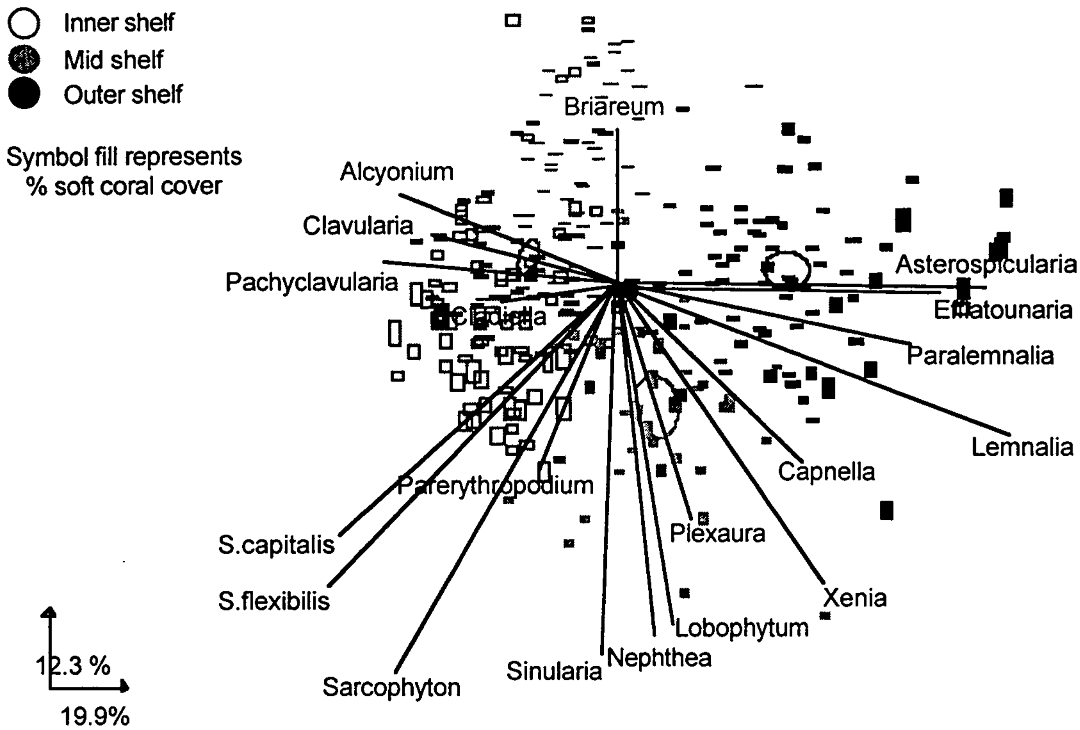

Figure 4. Principal components biplot on the 18 most common soft coral taxa. The sites (rectangles) are arranged according to their similarity in soft coral assemblages. Species vectors point towards the sites with higher abundances. Ellipses indicate 90% CI for the group means.

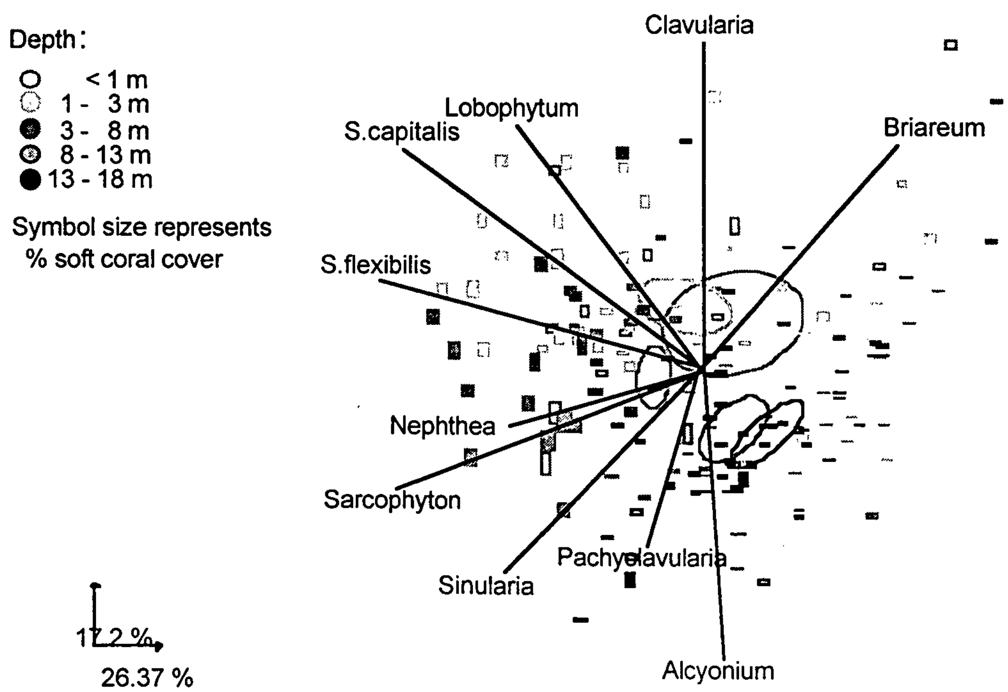

Figure 5. Principal components biplot of near-shore sites on the central Great Barrier Reef, indicating a consistent depth-gradient in terms of composition of the soft coral assemblages (different taxa representing different depth zones) and relative abundances. Ellipses indicate 90% CI for the group means.

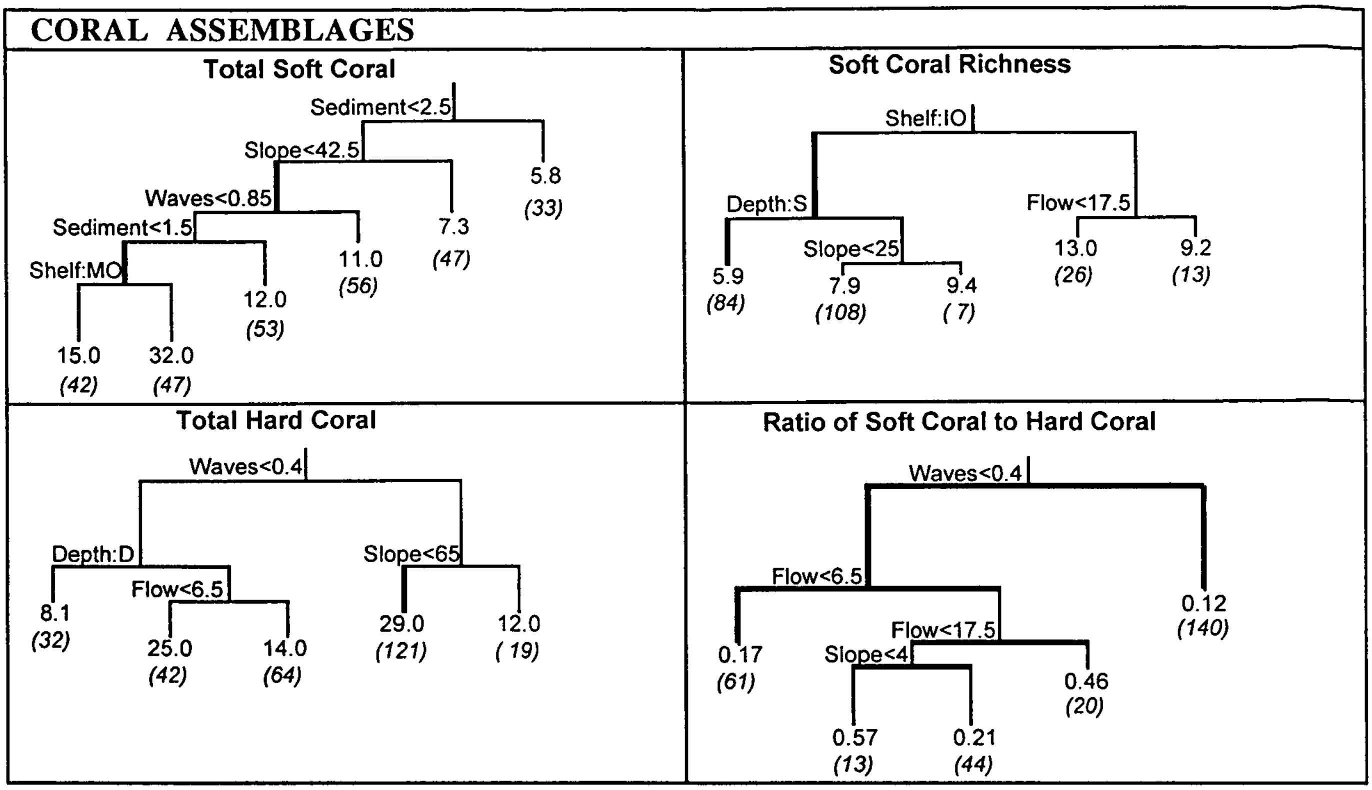

Figure 6. Regression trees of the characteristics of the coral assemblages

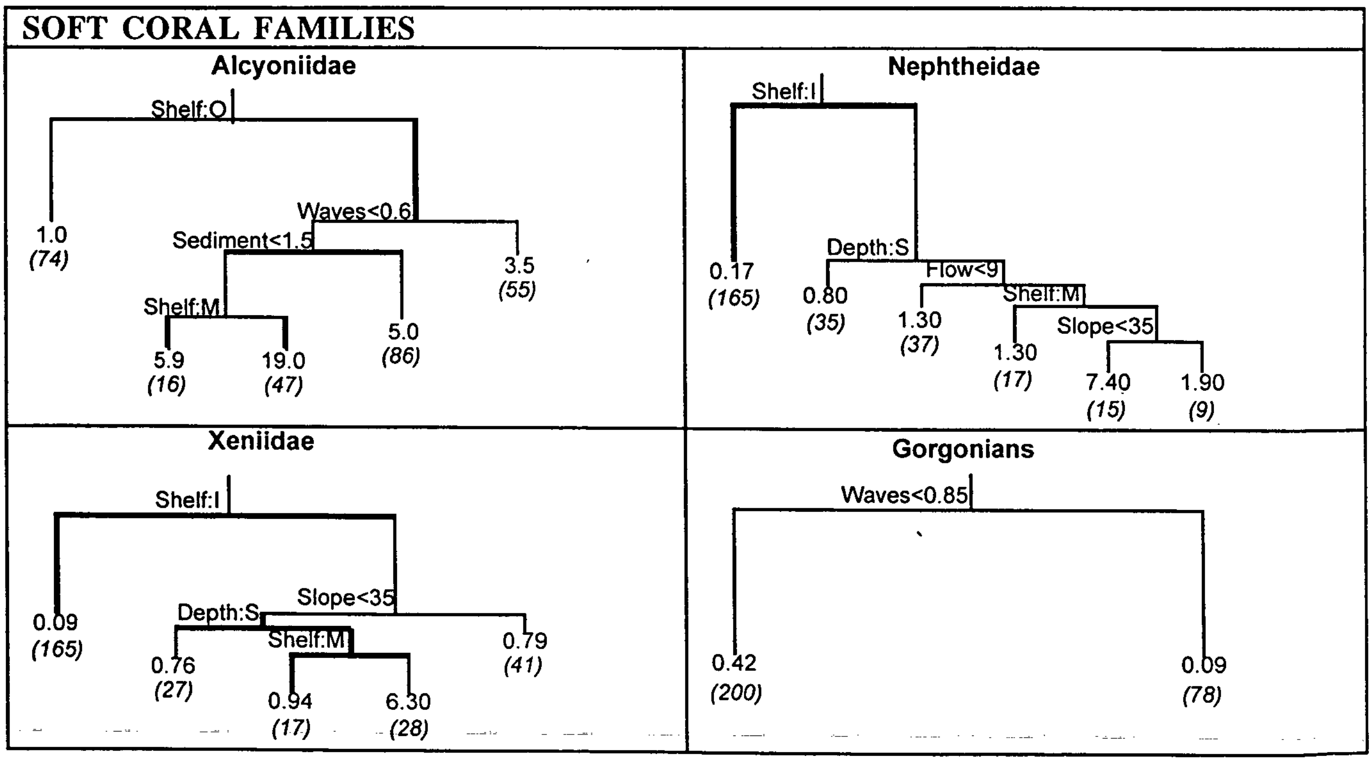

Figure 7. Regression trees of the three most common soft coral families, and of gorgonians

The regression tree analyses of characteristics of coral assemblages (figure 6) revealed the following patterns:

- **Total soft coral cover:** Highest (mean = 32%) on inner-shelf sites with low sediment load, a slope angle of < 42°, and moderate to weak wave exposure.
- **Soft coral richness:** Number of genera per site was highest (13) on mid-shelf sites with moderate to low flow. On inner- and outer-shelf sites, richness was very low at shallow depths, and moderate at depths > 3 m.
- **Total hard coral cover:** On wave-exposed sites, cover was highest (29%) on 121 sites with slopes < 65°. On wave-protected sites, cover was lowest at depth > 13 m and was highest on more shallow sites with low flow.
- **Ratio of soft coral to hard coral cover:** Highest ratio (0.57) on wave-protected sites where flow was moderate and where the reef formed horizontal terraces. Very low in wave-exposed habitats.

For the families, the regression tree analyses (figure 7) showed the following habitat characteristics favoured and avoided by the different families:

- **Alcyoniidae:** Highest abundance (19%) on 47 inner-shelf sites with moderate to low wave exposure and low sediment deposits.
- **Nephtheidae:** Very rare on inner-shelf sites. Most abundant (7.4%) at depth > 3 m with fast flow, on outer-shelf sites where the slope angle was < 35°.
- **Xeniidae:** Very rare on inner-shelf sites. Most abundant (6.3%) on medium to deep depths on outer-shelf sites with gradual slopes.
- **Gorgonians:** Very low abundances on wave-exposed sites, and evenly distributed elsewhere.

DISCUSSION

The composition of soft coral assemblages changed drastically across the continental shelf. The most conspicuous feature was the high proportion of genera with spatially restricted distributions. Almost 70% of the 16 most common genera were only found at one or two of the three cross-shelf positions (6 occurred in one position, 5 were restricted to 2 positions, and only 5 genera occurred at all positions). Highest richness was found on the mid-shelf reefs, as some of the inner-shelf and outer-shelf taxa extended their distribution into this intermediate region. In contrast to the taxonomic composition, the overall soft coral cover changed little across the shelf, due to the varying habitat optima for the different families. The Alcyoniidae dominated the inner-shelf region, whereas the Xeniidae and Nephtheidae were most common on the outer-shelf. For the families, shelf position and not one of the physical factors was the strongest separator of the groups in the regression trees. Within shelf groups, depth, flow, sediment and wave exposure also strongly influenced the distribution of the families, though to a varying extent at different shelf positions. Contrary to earlier assumptions (Dinesen 1983), there was no simple inverse relationship between the cover of soft and hard corals. Instead, the ratio between these two benthic groups was strongly habitat-specific.

The rapid survey technique was able to detect subtle changes in abundances and composition of soft coral assemblages along environmental gradients. This technique enables large areas of reef to be surveyed in a highly cost and time effective manner, particularly so when distributions of taxa are very variable or a large proportion of taxa are rare. In these cases, the more traditional belt and line transect methods are likely to result in data which inadequately represent the reef community. Regression trees, as used in this paper, proved ideal for the detection of complex environmental interactions, which would have been difficult to reveal in the more usual linear model analysis. Another advantage of this method is that findings can be represented in an simple, yet ecologically meaningful way. To conclude, rapid surveys, in combination with regression tree analysis are a powerful procedure for benthos community analyses, well suited to both scientific and managerial application.

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