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7 Coral Zonation: Its Nature and Significance

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Of the many definitions of the word ‘zone’, three are of great interest to reef ecologists. The first definition, listed in the Concise Oxford Dictionary, is ‘belt or girdle worn round the body . . . symbol of virginity’ — an evocative reflection on the webbing and lead belts worn by diving ecologists. Another definition is ‘any well-defined tract of more or less belt-like form’ and another, in reference to coral (Wells 1954, p. 396), ‘an area where local ecological differences are reflected in the species association and signalized by one or more dominant species’. These definitions provide the basis for the discussion below.

A large part of the ‘ecological differences’ referred to in Wells’ (1954) definition is physical; the range of physical environments in any one reef may be considerable. The physical environment on a coral reef represents both a resource to be partitioned. and a stress to be endured. Light provides’ energy’ but ultra-violet light damages living organisms. Water motion brings food and removes waste but it can also destroy corals. Sediment builds substrate but it also abrades and smothers benthic organisms. Evolutionary subdivision of resources and adaptation to stresses bring together different species associations in different places. Finer subdivision of a habitat may result from the inability of some species to live in close proximity to others. One result of this interaction between organisms and environment is zonation of corals and associated communities. A zonation pattern may be unique to a particular reef slope, or may be characteristic of entire reef systems. It is important to distinguish between these because the general body of ecological knowledge about coral reefs at present is built almost exclusively from studies of small areas.

The nature and causes of benthic zonation on reefs have been reviewed by Wells (1954, 1957), Yonge (1963), Stoddart (1969), and Glynn (1973). Recent ecological research has continued in a number of broad areas.

ZONATION OF GROWTH FORMS

The observation that growth forms of corals show a clearer zonation than do species distributions is longstanding (e.g. Wood-Jones 1910; Marshall 1931; Vaughan & Wells 1943). A world wide pattern in growth form zonation has been described by Pichon

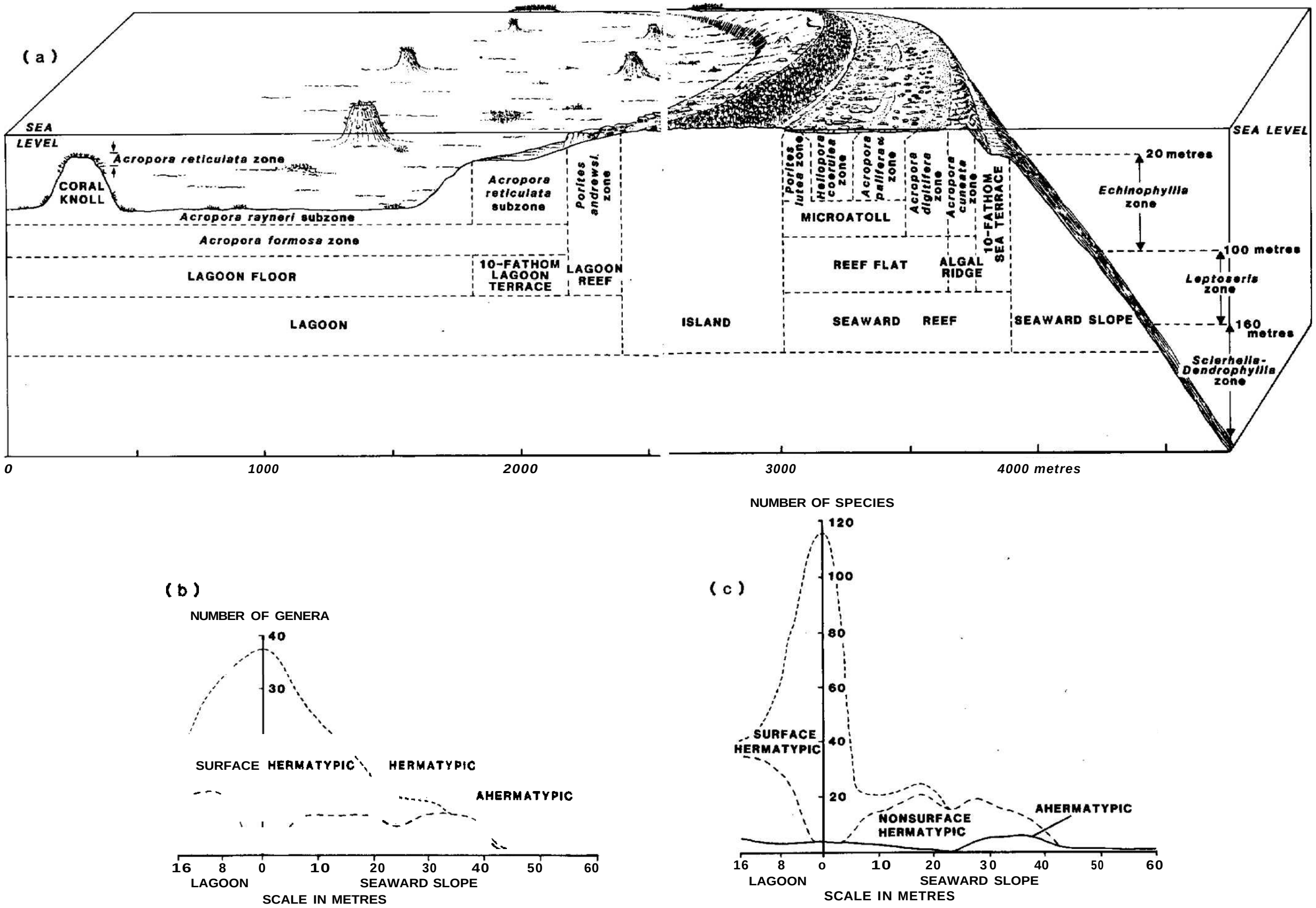


Figure Zonal analysis of Bikini Atoll (redrawn from Wells 1954).
(a) Zonal subdivisions. Note broadly inclusive zones further subdivided on the basis of localized dominance of species.
(b) Bathymetric distribution of surface and nonsurface genera.
(c) Bathymetric distribution of surface and nonsurface species

ZONAL PATTERNS AND ENVIRONMENTAL GRADIENTS

Gradients in water movement (waves, currents) and light (with depth and turbidity) have long been seen as determinants of zonation. Ecologists have continued to schematize zonation (of taxa and growth forms) in terms of gradients in water movement and light but have not progressed far in quantifying the gradient-zone relationship, or in identifying causal pathways.

ZONATION, COMMUNITY STRUCTURE AND BIOLOGICAL INTERACTIONS

Community structure (total cover, intra-zonal spatial organization, diversity and dominance, size class distribution) varies between zones in response to a combination of physical controls and biological interactions. At the time of Stoddart's major review (1969), the importance of biological interactions was recognized but had been little studied. Lessons learnt from terrestrial and intertidal ecology suggest that patterns in community structure and zonation may not be a simple summation of the independent responses of species to environmental tolerances and preferences (Connell 1972; Whittaker 1975). The 'realized zone' of a species may, as a result of competition and predation, be a significant contraction of the 'fundamental zone' (Pielou 1977).

TRANSIENCE OF CORAL COMMUNITIES

Recent work raises questions regarding community succession and climax, and the degree to which community composition is a response to prevailing conditions on the one hand and aperiodic, episodic events on the other (Stoddart 1963, 1974; Loya 1976a; Connell 1978; Chappell 1980; Woodley 1980; Woodley & Porter 1980; Pearson, 1981).

Each of these areas is discussed below, with particular emphasis on zonation in scleractinian corals. Also included are sections on zonation schemes, numerical methods of study, environmental zonation and synthetic analyses. It is hoped that works referred to will direct readers to useful sources. A more comprehensive bibliography in the area of coral distribution studies is provided by Sheppard (1982).

NATURE OF CORAL ZONATION

This discussion of coral zonation requires some passing reference to the physical environment: a more detailed consideration of reef environment follows below.

Zonation of Species

Corals and other benthic species distribute themselves in different segments of a reef environment hyperspace which is both broad ranging and stratified. The result is their zonation on the reef, i.e., the occurrence in given reef habitats of predictable but overlapping subsets of the total species complement (see fig. la). For logistic reasons, coral zonation has been most often described on intertidal reef flats; for ecological reasons it is most clearly manifested there.

REEF FLATS

Reef flats support belt-like tracts of corals, frequently of low cover and/or diversity and often dominated by one or two characteristic species (Mayer 1918; Stephenson *et al.* 1933; Wells 1954, 1957; Spencer-Davies *et al.* 1971; Morrisey 1980). In this habitat, which is uniformly exposed to high light levels, these tracts reflect zonally-distributed

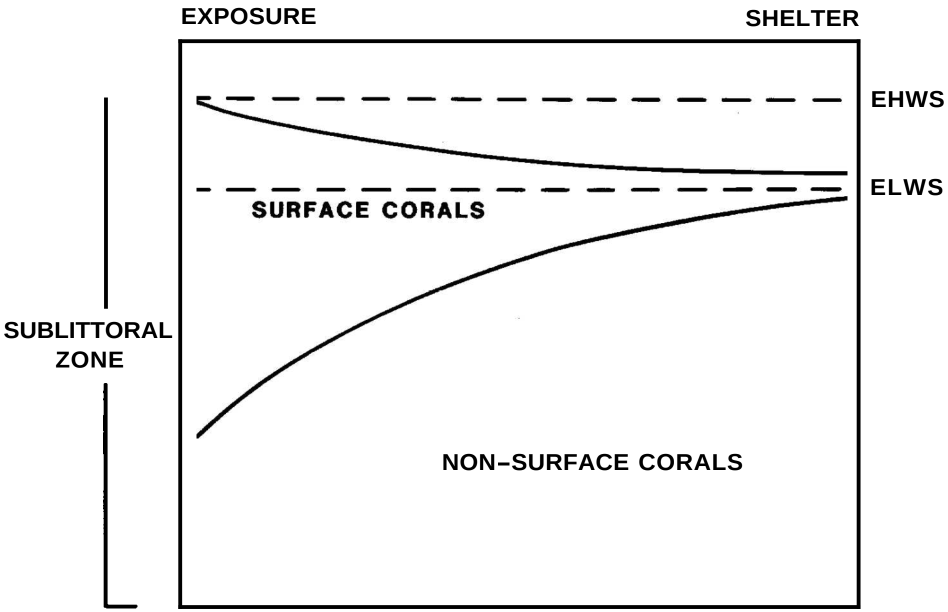


Figure 2 The effect of wave exposure on the bathymetric distribution of surface and nonsurface species. Nonsurface species, which are restricted to depths below the wave base, extend their distributions into shallower depths in sheltered habitats

differences in substrate type, elevation (and thus frequency and duration of subaerial exposure and/or high temperature stress) and exposure to surf, currents or relatively stationary water. It is a habitat wherein an elevational difference of only a few centimetres, or a lateral distance of just a few metres, may be accompanied by major differences in substrate or hydrodynamic regime, and where associated changes in species composition or dominance are marked.

REEF SLOPES

On reef slopes (subjected to gradients of both light and water movement) coral zonation is usually more subtle than on reef flats. The corals are divisible into two suites of species of which the bathymetric distributions, although broadly overlapping, characterize opposite ends of a depth and exposure-related environment gradient. These suites have variously been referred to as 'surface' and 'nonsurface' (Wells 1954), 'reef and 'subreef (Pichon 1972, 1978a) and A and B (Sheppard 1981a). The distribution of these suites at Bikini Atoll is indicated in figures lb and lc.

The shallower suite of species (of which the reef flat corals are a more or less depauperate subset) has its maximum diversity at various depths depending upon wave exposure, slope and illumination. Wells (1954) noted that the downward extent of the shallower suite was limited by the normal wave base; as a corollary, the upper limit of the deeper suite extends into shallower water on reef slopes with sheltered aspect (see fig. 2).

The deeper suite is less diverse than the shallower, and contains both hermatypic and ahermatypic species. By and large, these species do not have sufficient morphological plasticity to enable them to survive the high mechanical stresses associated with shallower wave-affected areas (except in sheltered refuges).

ZONAL COMMUNITIES

Zonal communities are subdivisions of these suites, particularly of the shallower suite. Subdivision is frequently based on the localized predominance of one or more species (or genera) following Wells' (1954) definition (e.g. Goreau 1959; Loya & Slobodkin 1971; Rosen 1971,1975; Sheppard 1980a) and the zones may be named after the dominant(s). Alternatively, subdivision may be made on the basis **of:**

1. the absence of dominant species ('indominate' zones, Sheppard 1980a),
2. quantitatively unimportant but nonetheless 'characteristic' or 'differential' species (Scheer 1978),
3. predominance of characteristic growth forms (Pichon 1972, 1978a; Rosen 1971),
4. the total species complement, using multivariate techniques (e.g. Loya 1972; van den Hoek et al. 1975, 1978; Done 1977; Veron & Done 1979; Bradbury & Young, 1981).

These alternative devices for differentiation of zonal communities are particularly applicable on reef slopes, where single species dominance is frequently less marked. The intergrading nature of zonal communities may be seen in the following example.

SPECIES ZONATION: AN EXAMPLE

Zonal subdivision of some Great Barrier Reef ribbon reefs is presented in table **1.** The table was derived from a multivariate classification described by Done & Pichon (in prep.) and includes only 'constant' species (*sensu* Sheer 1978); that is, tabulated species are also from time to time found as 'accidentals' in zones other than those indicated.

Single species and groups of species show varying degrees of fidelity to topographic and environmental zones. Species with patterns A, B and E (table **1)** by and large have high fidelity to circumscribed sections of the reef (the outer **surf,** inner surf and back-reef slope respectively). Pattern D demonstrates a low fidelity to any single bathymetric or topographic zone but a high fidelity to a single broad environmental zone (moderate wave energy) found on fore-reef, reef flat and back-reef. Species with pattern C are so ubiquitous that neither individually nor collectively are they indicative of any particular bathymetric, topographic or environmental zone. Pattern C species extend from the calm, poorly illuminated depths (25 to 40 m) to the highly illuminated and surf beaten sections of the reef flat. However, all of group C are extremely polymorphic, and in several cases, there is a strong fidelity of growth form to a particular zone.

In this and many other examples, the high degree of species overlap between topographic zones makes zonal delineation on the basis of species composition difficult. By contrast, growth ***forms*** of corals are more distinctly zonal in their distribution.

Ecomorph Zonation

Ubiquitous species tend to adopt different growth forms in different zones. Individual species thus exhibit 'ecomorph zonation'; the ecomorphs differing from each other in colony and/or corallite shape and/or size (Veron & Pichon 1976, Chapter 2). The diverse hydrodynamic, photic and sedimentary environments in the different reef zones each favour different morphologies (Morton 1974) and a characteristic sequence of growth forms across reef profiles has been described (Pichon 1972, 1978a; see also below).

	TOPOGRAPHICZONE	1	2	3	4	5	6	7	8	9	10
	Acropora palmerae				·	++					
	Acropora sp 1.				+	++					
	Acropora rotumana			*	++	++	+				
A	*Acropora variabilis*			++	+	++					
	Pocillopora eydouxi		+	++	++	+			·	·	·
	Acropora digitifera		·	·	++	++	++	·	+	·	
	Acropora robusta		·	·	++	+	+	+	+		
B	*Gonistrea* c.f. *favulus*					·	++	++			
	Acropora millepora				·	·	++	++	++	+	·
	Pocillopora verrucosa	++	++	++	++	++	++	++	+	+	+
	Acropora humilis	·	++	++	++	++	++	++	++	+	+
	Acropora palifera	+	++	++	++	++	++	++	++	++	++
C	*Porites* (massive spp.)	++	++	++	++	++	++	++	++	++	++
	Stylophora pistillata	++	++	++	++	+	+	++	++	++	++
	Acropora hyacinthus	+	+	++	++	++	+	+	++	+	·
	Millipora platyphylla	++	++	++	+	++	·	+	+·	·	+
	Platygyra pini	+	+	·	·	·	+	+	+	+	++
	Acropora cerealis		++	++	·	+		++	++	·	++
	Pocillopora damicornis	+	+	·	·			+	+	++	++
	Favia pallida	++	+	·		·	++	++	+	+	+
	Astreopora listeri	++	+				+	++	+	++	+
	Seriatorpora hystrix	++	++	+	·				+	++	++
D	*Cyphastrea serailia*	+	·	+				++	·	+	+
	Goniastrea pectinata	++	+	·					·	+	++
	Acropora squarrosa	+	+						+	++	++
	Montipora verrucosa	++					·	·	·	·	+
	Favia favus	+							·	++	++
	Fungia spp.		+	·					·	+	++
	Millepora tenera		+						·	+	++
	Tubastrea nigrescens	+									
	Goniastrea edwardsi	·	·			·		·	+	+ +	+
	Echinopora mammiformis									·	++
	Lobophyllia pachysepta									·	+
E	*Fungia echinara*	·	·							·	+
	Acropora carduus										+
	Montastrea magnistellata								·	++	·
	Rumphella sp.									++	++

Key: blank = absent or present as 'accidental' only
· present up to 0.3 ave cover grade
+ = present between 0.3 and 1.0 ave cover grade
++ = ave cover grade 1.0 or greater
1, lower slope; 2.3, mid slope; 4, upper slope; 5, shoulder and outer reef flat; 6, mid reef flat; 7, back reef flat; 8, back reef margin; 9, shallow pinnacle slopes and floor; 10, deep pinnacle slopes and floor.

Table 1 Patterns in the distribution of species on a wave beaten reef of the Great Barrier Reef. For explanation see text

In wave-affected areas, corals exhibit morphological adaptation to mechanical stress (see Shinn 1966; Wainwright *et al.* 1976; Graus *et al.* 1977; Vosburgh 1977). As may be expected, encrusting and streamlined morphs of massive species (e.g. Faviids, Porites spp. and, to a lesser extent, Mussiids) are found in surf areas. However, more predominant on both Indo-Pacific and Atlantic reefs are surf resistant ecomorphs of branching species (e.g. Mayer 1918; Wells 1954; Goreau 1959; Rosen 1971, 1975; Giester 1977). In the Caribbean, *Acropora palmata* maintains an open habit in the surf zone and survives mechanical stresses by branch-thickening and by adopting an orientation in which hydrodynamic forces are directed along rather than across the branches (Shinn 1966; Graus *et al.* 1977). Coral branches have low tensile strength but high compressive strength (Wainwright *et al.* 1976; Tunnicliffe 1979).

In the Indo-Pacific, the branching genera *Acropora*, *Pocillopora* and *Stylophora* are dominant in surf areas (Wells 1954; Rosen 1971, 1975). The strategy of orientation with respect to hydrodynamic forces is dramatically demonstrated by *Acropora palifera*. In calm waters, this species presents several branching growth forms (columns, knobs, micro-atolls). In strong surf it grows as low, ridged colonies with the ridges orientated parallel to water movement. The species dominates this zone (fig. 3). In the Pocilloporidae, compact branching varieties (previously described as separate species) have been shown to be wave-adapted ecomorphs of species which are elsewhere open-branching and fragile (Veron & Pichon 1976). Perhaps the most extreme example of adaptation to the surf zone will prove to be *Acropora palmerae* (Wells 1954), an entirely encrusting coral, which may in fact be a surf ecomorph of one of the ramose *Acropora robusta* group (Wallace 1978; Veron & Wallace, in prep.). It is enigmatic that one of the most delicate *Acroporu* species, with fine, close-packed, fragile vertical branches, thrives in most Great Barrier Reef surf zones (fig. 4).

In more sheltered areas, where there is less mechanical stress, colony shapes are more diverse than in surf zones. Patterns of colony shape distributions in such areas may be understood in terms of species-specific nutritional requirements (Porter 1976; Jaubert 1977; Spencer-Davies 1977; Porter *et al.* 1980), competitive abilities (Lang 1973; Porter 1976; Sheppard 1979) and sediment-removing ability (Hubbard & Pocock 1972; Hubbard 1974; Dodge *et al.* 1974; Loya 1976b; Bak 1978).

Many species have been shown to adopt a more flattened habit with increasing depth, thereby maximizing the interceptions of light, e.g. *Montastrea annularis* (Barnes 1973) and many *Acropora* species (Wallace 1978). However, because a flattened surface also accumulates sediment, many other shapes (including branching, massive, bracket and vase) occur in sheltered habitats (Vaughan & Wells 1943; Morton 1974; Porter 1976).

Micro-atolls (Scoffin & Stoddart 1978) form the best known of all zones defined on the basis of coral growth form. In these zones, the tops of colonies die off due to emersion and, except where water is moated, indicate the level of extreme low spring tides (Scoffin & Stoddart 1978). Instances of single colonies covering hundreds of square metres have been described (e.g. the *Heliopora coerulea* micro-atoll zone, Wells 1954). Forty-three Indo-Pacific species have been recorded as micro-atolls (Rosen 1978) although most never attaip the size of Wells' *Heliopora*.

Zonation in community structure

Reefs exhibit zonation in coral species diversity, area of cover, colony size, crowding and spatial pattern -- those non-taxonomic community attributes on which a great deal of synecological interpretation is based. With few exceptions (e.g. Mayer 1918). the quantitative field work providing these types of data has been published since Stoddart's (1969) observation that 'quantitative work so far has added little to qualitative zonation studies'.

Foremost among recent quantitative studies is that of Loya (1972) at Eilat. Statistical analysis of a large and thorough data base derived from line transects indicated the following trends:

1. a general increase in species richness and diversity with increasing depth to 30 m, even though illumination at 30 m was less than five percent of the surface value,

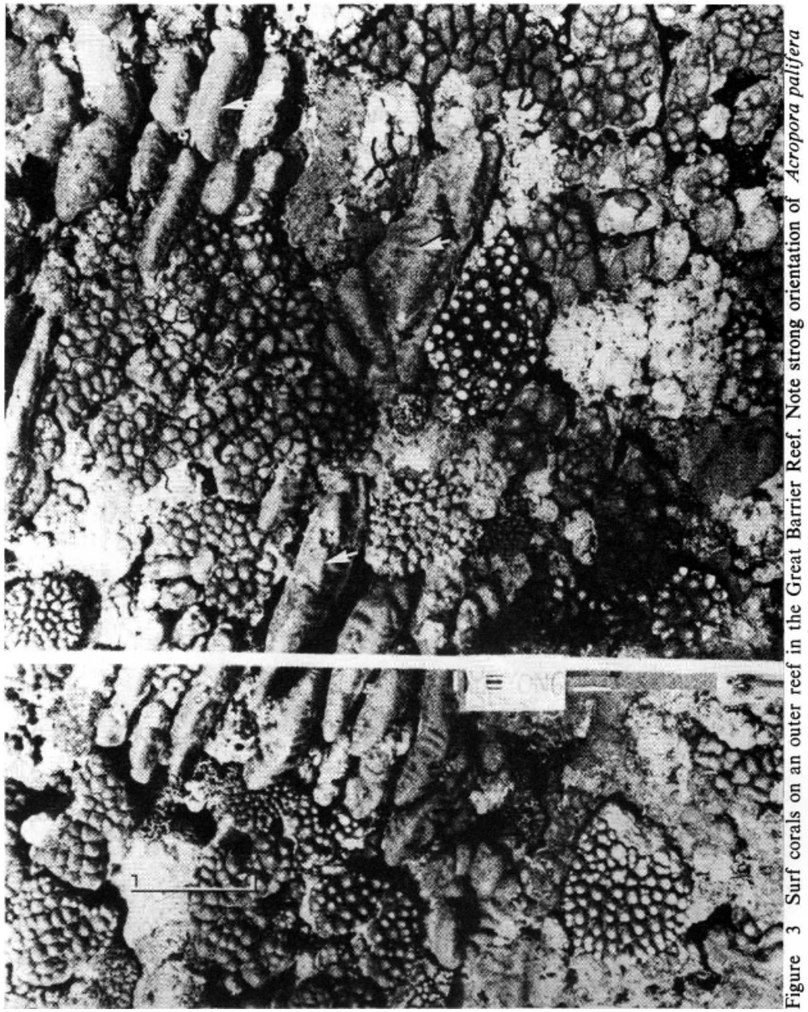


Figure 3 Surf corals on an outer reef in the Great Barrier Reef. Note strong orientation of *Acropora palifera* colonies (see arrows). Scale bar indicates 10 cm

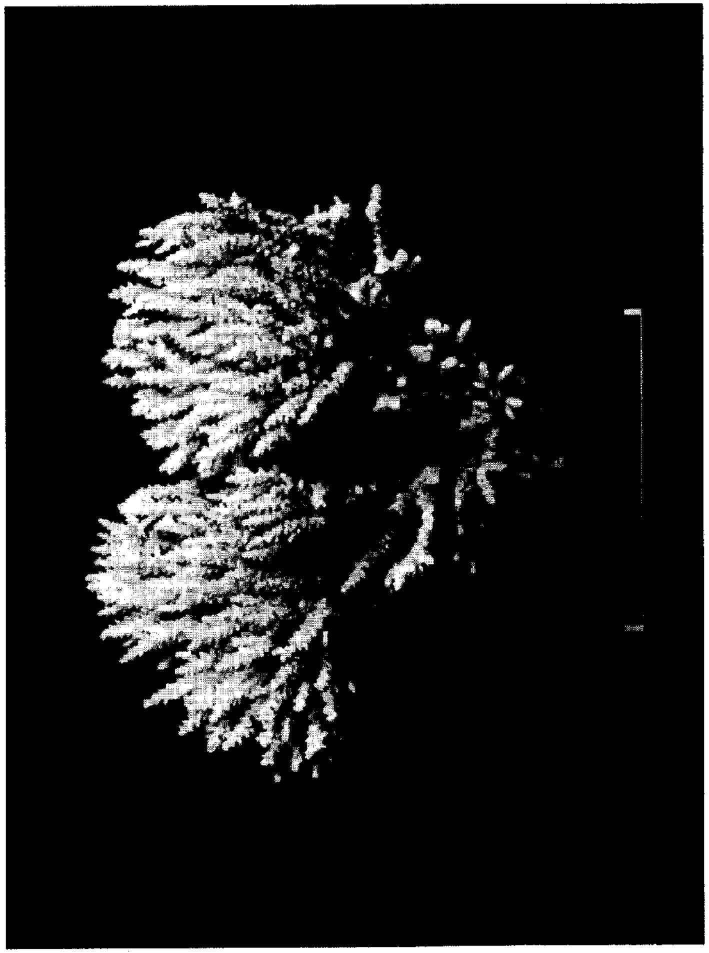


Figure 4 This delicate *Acropora* which is common in surf zones on outer reefs in the Great Barrier Reef resists mechanical damages despite its fragile structure. Scale bar indicates 10 cm. Photograph courtesy of Dr. J. E. N. Veron

2. a smaller average colony size in reef flat and deeper zones than at intermediate depths,
3. a correlation between colony size and light intensity down the slope,
4. absence of correlation between species richness and light attenuation,
5. a greater coverage and diversity of living coral on steeper slopes, compared with flat areas.

These trends were attributed to a combination of local factors, especially differential settlement of sediment. The study also led to conclusions about community structure and biotic zonation; to zonal patterns of environmental ‘severity’ and ‘predictability’, and of ‘physical control’ and ‘biological accommodation’. These concepts, established in the ecological literature by Sanders (1969), Slobodkin & Sanders (1969) and others, were also developed in relation to reef community structure by Porter (1972a), Connell(1978) and Dana (1979).

Further quantitative studies concerned with zonal patterns in community structure have been provided by Glynn (1976), van den Hoek *et al.* (1975,1978) Bradbury & Loya (1976), Goodwin *et al.* (1976), Bull (1977), Wallace & Lovell (1977), Ditlev (1978), Morrisey (1980) and Sheppard (1980). Interpretations have been as diverse as the localities in which the studies took place. Gradients and discontinuities in various abiotic factors (such as tides, waves, light, substrate and sediment) and biotic factors (especially grazing pressure and spatial competition) have been suggested as the proximal causes of their observations. Two syntheses concerned with community structure (namely Connell 1978 and Chappell 1980) are considered below.

Zonation in community function

Zonal communities have been shown to differ considerably in their capacity for photosynthesis and calcification (see methods papers by Kinsey 1978; Maragos 1978; Marsh & Smith 1978). The annual mean productivity of zones on One Tree Island reef flat varies twenty-fold (Kinsey 1979) and in four of the five zones studied, mean annual calcification was between 11% to 20% of productivity; in the fifth it reached 60%. These disparities in production and calcification have lead to the concept of upstream ‘producer’ and downstream ‘consumer’ zones (LIMER 1976; Kinsey 1979). Overall reef morphology itself is ultimately determined by the rates of carbonate consolidation into the reef framework. rates of dispersion and accumulation as sediment, and in particular, the differences in these rates between zones.

Zonation schemes

Various authors have created schemes to provide synoptic regional views of the ways taxa and growth forms are distributed with respect to reef structure and environment. The schemes are usually presented as subjective ordinations of assemblages against two or three spatio-environmental axes. The assemblages are generally loosely defined and many encompass allied subgroupings with a dominant taxon (or growth form) in common, but with differences at subordinate levels (see fig. 13 and Veron & Done 1979). They thus correspond to the ‘alliance’ of Beale & Costin (1952) and Scheer (1978) and, since they indicate broader environmental ranges than the more fundamental ‘association’, they are appropriate for regional synopses.

The authors of the schemes use subjective, ordinal scaling on their environmental axes. This practice is appropriate to the synoptic function of zonal schemes, but it does make inter-region comparisons difficult, since one scheme’s ‘extreme’ may be equivalent another’s ‘moderate’.

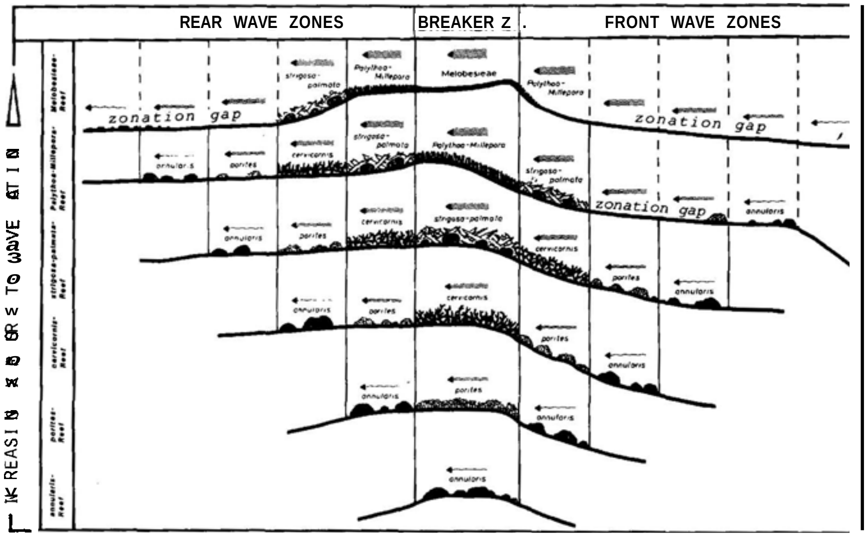


Figure 5 Zonation scheme for Caribbean reefs (reproduced with permission from Giester, 1977). Reefs exposed to maximal wave energy have characteristic coral associations that are not found in sheltered reefs, Shallow water associations on sheltered reefs (e.g. ‘annularis’ and ‘pontes’) are restricted to deeper and/or sheltered habitats on more exposed reefs

Wave related zonation schemes

Of the two or three dimensions which can comfortably be contemplated or represented diagrammatically, wave action invariably takes pride of place. The comparison of zonation schemes therefore becomes a comparison of the other dimensions in the scheme, and the way the scheme is portrayed diagrammatically.

Giester (1977) provided a scheme of ‘climax’ breaker and wave zones for Caribbean reefs consisting of a series of reef profiles arranged vertically (fig. 5). The uppermost profile represented a reef exposed to maximum wave energy, the lowest to a minimum. The scheme shows a successive ‘dropping out’ of high energy alliances with decreasing wave exposure and a shift of deep water alliances to shallower locations on sheltered reefs. A ‘zonation gap’ caused by seasonal sediment abrasion was not present where surface wave action was reduced. Giester’s reef profiles make the zonation trends with exposure and depth readily evident but he stresses that aberrant zonations may result from localized irregularities in bottom topography, substrate change from lagoon to reef facies, seasonal abrasion and unusually shallow reef flat.

Pichon (1978a) provided a ‘worldwide’ scheme based on very broadly defined growth form alliances (see fig. 6). By including a totally stylized reef shape, Pichon’s scheme is more generally representative than Giester’s. This scheme emphasizes that a similar sequence of energy conditions and related growth form predominance occurs on reef flat and reef slope sites. Zonation was evident only in the reefal biocoenose and it was correlated with wave action, not light. An assemblage occupying sub-reefal depths was not conspicuously zoned.

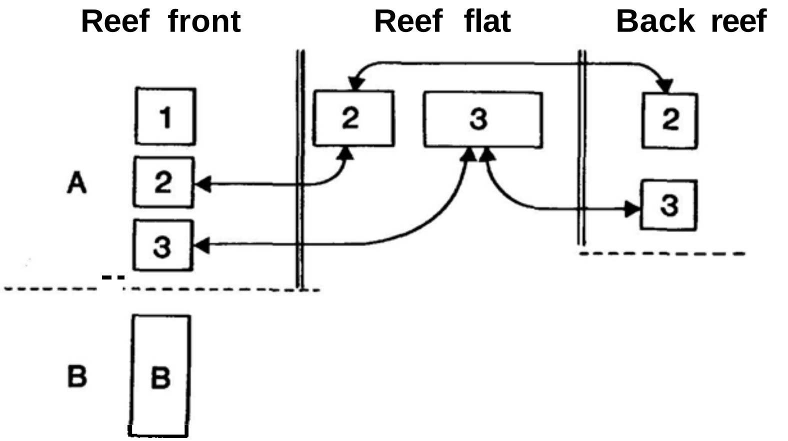


Figure 6 Worldwide coral zonation scheme (redrawn from Pichon 1978). A reefal biocoenose; B: subreefal biocoenose; 1 : dominant growth forms encrusting, with or without short, thick digitations; 2 : branching forms dominant; 3 : massive forms dominant. The reefal biocoenose is conspicuously zoned, with the sequence across the reef flat a mirror image of the sequence down the reef front. The back reef slope sequence lacks association type 1, which is found only in high wave energy area. The sub-reefal biocoenose is able to extend into shallower depths on back reef slopes.

Rosen (1975) also concerned himself mainly with wave-related zonation. Like Pichon, he noted that water movement attenuated both across the reef flat and down the slope from the surf zone (see fig. 7). He also allowed for longshore attenuation of surf intensity (Roberts 1974) and represented ‘water movement’ isopleths on a three dimensional block diagram. The five water movement zones thus delineated were occupied by five ‘associations’ named after the predominant Indo-Pacific taxa. In order of decreasing wave energy they were: the *Porolithon* association, the *Pocillopora* association, the *Acropora* association, the *Faviid* association and the *Porites* association. This scheme is broadly applicable in the Indo-Pacific, but a high energy *Pocillopora* association has not been recognized on the Great Barrier Reef where, in most surf zones in which *Pocillopora* is abundant, *Acropora palifera* (Wells 1954) is significantly more prolific (personal observations; Veron, pers. comm.; Pichon, pers. comm.).

Rosen’s scheme emphasizes that ‘deep’ water movement conditions and associations may occur in shallow depths on a lee shore. Dana (1979) also suggested that deep water environments are so displaced. His scheme (fig. 8) identifies environmental severity, optimately, variability and predictability as primary zoning influences whose actions are reflected in patterns of species coverage, diversity, dominance and successional studies. Although the scheme was derived for a localized study, the ecological concepts embodies are of universal relevance.

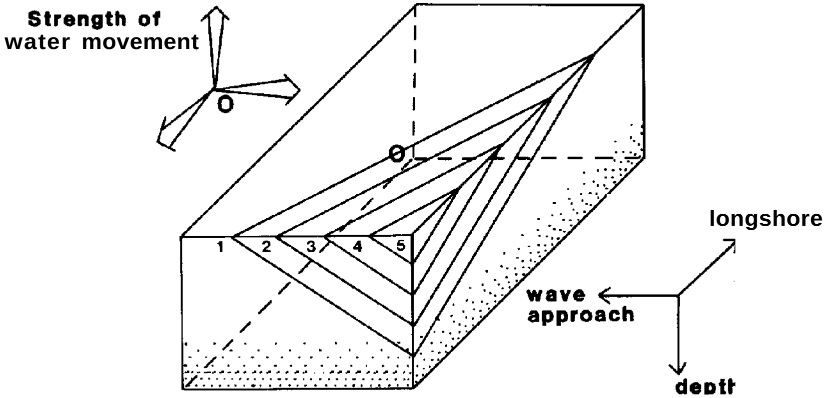


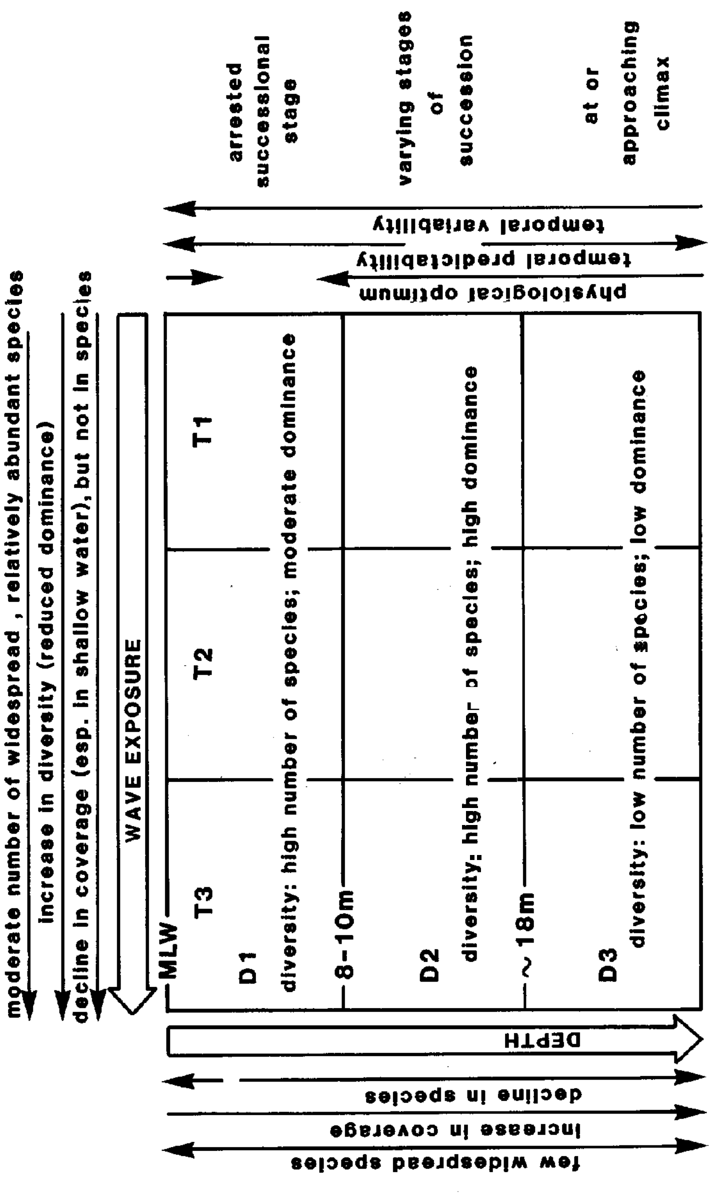
Figure 7 Zonation scheme for Indo-Pacific genera (redrawn from Rosen 1975). The distribution of five shallow water associations is correlated to the attenuation of wave energy in three dimensions; with depth, with distance across a reef flat, and with aspect relative to the direction of wave attack. High energy associations successively 'drop out' as aspect becomes more sheltered. The five associations are characterized by a dominance of the following groups: 1 : *Porites* ; 2 : Faviids; 3 : *Acropora*; 4: *Pocillopora:* 5 : calcareous algae. The *Porites* association occurs in the most sheltered habitats and the calcareous algae in the most exposed.

Adey & Burke (1977) also provide a block diagram zonation scheme (see fig. 9). Unlike Rosen (1975), who uses all three axes to represent wave-attenuating factors, Adey and Burke use only two: the third axis represents turbidity. This scheme shows a marked upward zonal shift associated with turbid water (in which light attenuation and its zoning influence occur in quiet shallow waters). These authors also note similar zonation of the genera *Porolithon, Millepora* and *Acropora* in both Atlantic and Indo-Pacific reefs.

The relationship between wave action and zonation is thus widely observed and emphasized. Many vertical, lateral and transverse zonation sequences correlate with diminution of wave energy from a surf zone which is either moderate or destructively violent. However, consideration should also be given to those reefs which are rarely, if ever, exposed to significant surf.

Zonation in low wave areas

Wave-related zonation schemes have little relevance in areas protected from consistent strong wave action. Rosen's (1975) scheme demonstrates how reef fronts exposed to weak or no waves are weakly zoned in terms of his broadly defined alliances (i.e. one or two alliances compared with five on maximally exposed reef fronts). The zonation which occurs on more sheltered reefs is more at the level of 'association' than alliance (association defined by Scheer 1978; for examples of this more subtle from of zonation see Pillai 1969; Loya & Slobodkin 1971; Loya 1972; van den Hoek et al. 1975,1978; Goodwin *et al.* 1976; Done 1977; Bouchon 1980).



igure 8 Zonation scheme for corals on a Pacific atoll slope (redrawn from Dana 1979). Patterns in coral cover and species distribution, diversity and dominance are presented as a function of depth and exposure. The scheme includes an interpretation of spatial trends in environmental optimality, predictability and variability to account for the observed patterns

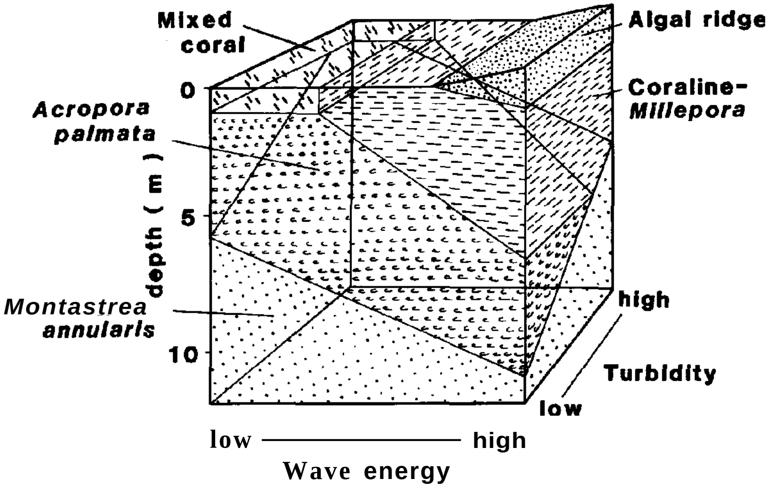


Figure 9 Zonation scheme for dominant Caribbean frame-building corals (redrawn from Adey and Burke 1977). This scheme embodies regional gradients in both wave action and turbidity. High wave energy reefs have the most identifiable zones and high turbidity excludes the *Acropora palmata* zone

Surf on the reefs at Eilat is weak (Mergner 1971) and, although a localized benthic surf zone is described, zonation on most of the reef seems largely a function of longshore current, light levels, substrate and predators. Likewise, Loya & Slobodkin (1971) and Loya (1972) emphasize that a variety of factors is responsible for zonation at Eilat. Bouchon (1980) found difficulty in recognizing zones between the surface and -40 m on a fringing reef in the Gulf of Aqaba which was characterised by low wave action and uniform light attenuation.

In sheltered areas, where biological controls on zonation are obvious, a ‘bioenvironment’ axis might logically replace the wave action axis. For instance, van den Hoek *et al.* (1978) proposed that a bimodal distribution of algal grazing intensity down a reef slope strongly influenced zonation. The role and effects of biological interactions in determining community structure and zonation are considered below.

NUMERICAL METHODS IN ZONATION STUDIES

The rationale for using numerical methods in ecological studies is discussed in Williams (1976). Clifford & Stephenson (1976) and Whittaker (1978 a,b).

Field methods

Until the time of Stoddart’s (1969) review, coral zonation had been studied using two field methods - qualitative survey and quantitative quadrat methods. Stoddart called for optimization of sampling and recording methods for both slopes and reef flats. Several papers in Stoddart & Johannes (1978) refer to recent developments. Several variants of the ‘line intercept’ method introduced by Loya (1972) and Porter (1972) are used in descriptive studies (Pearson 1974, 1981; Wallace & Lovel1 1977; Bull 1977); other workers continue to use quadrats (Spencer-Davies *et al.* 1971; van den Hoek el *al.* 1975, 1978; Goodwin *et al.* 1976). Reviews of these and other sampling methodologies are given by Pichon (1978b,c), Scheer (1978), Kinsey & Snider (1978) and Loya **(1978).** Each method provides a sample of the species present and an estimate of cover and/or abundance of individual species. In general, samples are placed regularly across the study area.

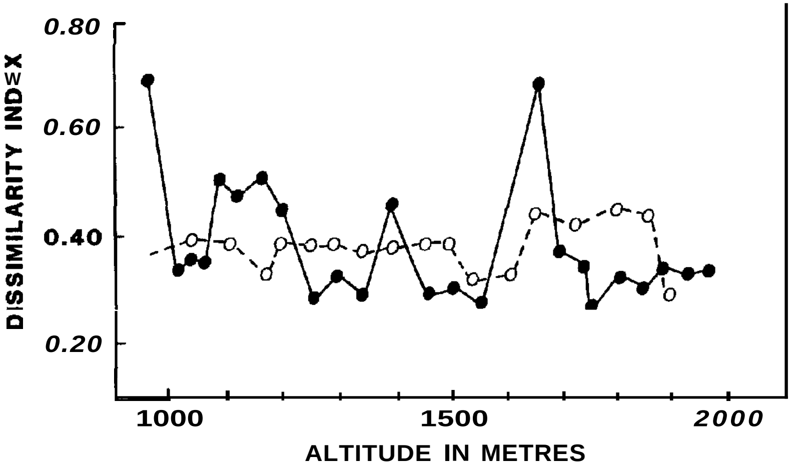


Figure 10 Beals’ gradient analysis. Similarity between adjacent samples is markedly discontinuous in strongly zoned areas and more consistent in weakly zoned areas (redrawn from Beals 1969)

Zone delineation

Ordered samples

A variety of multivariate methods have been used to subdivide sequentially ordered data of this type into groups of samples that may represent zonal communities. All analyses start with a matrix of species (or other attributes such as supraspecific growth form, ecomorph or genus) against sampling units (e.g. individual quadrats or lines). The attributes are entered either qualitatively (presence - absence), semiquantitatively (e.g. importance value or graded cover index) or quantitatively (area cover estimate in quadrats; total line intercept [see Done 19771).

GRADIENT ANALYSIS

In Beals’ (1969) gradient analysis, a similarity index is calculated between spatially consecutive samples and plotted against sample number (see fig. 10). If there are discontinuities present, there will be sharp peaks and troughs on the graph, and their position will suggest where zones are separated. If the study area is not markedly zoned, the peaks and troughs will be small or absent. The technique's clarity and simplicity would seem to warrant its use in reef zonation studies. The main disadvantage is its failure to illustrate affinities between non-adjacent samples or groups of samples.

ORDINATION

Wallace & Dale **(1977)** used a principal co-ordinates analysis in a study of zonation of ***Acropora*** species and morphological types (fig. **11);** lines were drawn between adjacent samples in the ordination. As in Beals' technique, this procedure provides results that indicate whether biotic zones exist and where they may be separated. In addition, it displays between-group affinities. An advantage of ordinations generally is that they may suggest the importance of particular environmental factors causing the zonation (Bradbury & Young 1981). A disadvantage is that sample groups may overlap and that interpretation may be difficult when many points are involved.

Bradbury & Young **(1981)**, improved interpretability by plotting sample position (abscissa) against the scores for each of the first three principal co-ordinates in turn (see fig. **12).** The presentation is more easily interpreted than the Wallace and Dale presentation but, as in any ordination, the ecological significance attributed to the axes is hypothetical.

CLASSIFICATION

The most common multivariate technique used is ecological classification (see figs. 13, **14).** Ecological classification provides a dendrogram (or dendrograph — Jokiel & Maragos **1978)** which suggests a hierarchical relationship between groups of sample units (normal classification) or attributes (inverse classification). Samples have been classified by numerous authors (e.g. Loya 1972; Done 1977; van den Hoek *et al.* 1975, 1979; Jokiel & Maragos **1978).** Major groupings in the classifications were invariably associated with major topographic subdivisions and as such do not provide any unexpected insights. However, minor groupings may suggest similarities and dissimilarities that are not self-evident and may be shown to have ecological significance (e.g. Jokiel & Maragos **1978;** Veron & Done **1979).** Pitfalls for the unwary are indicated by figure **14.**

Non-ordered samples

It is the author's opinion that classification and ordinations are of greatest value when there is no single 'correct' order of sample units in the data matrix. Veron & Done **(1979)** made coral surveys at sixty-six sites, of which half were situated along seven cross reef transects and half were located independently of other stations. Unlike a single cross reef transect, these data did not have an inherent 'correct' order and a classification (fig. 13) produced groups which consisted of sites which were frequently widely dispersed on the reef. Because of the complex morphology of the reef, it was not possible **to** relate the resulting site groups to a single generalized reef profile, but a plot of mean depth versus mean 'aspect' illustrated an ordered distribution of site groups relative to a subjective assessment of water turbulence. This plot of site groups against spatio-environmental axes (fig. **15)** is similar to a 'vegetation chart' used by botanists (e.g. Whittaker **1975,** p. **122).**

Zonation studies, particularly where the samples are not orderable, may in future use a class of 'data display' programs of the 'minimum spanning tree' type (Prim **1957).** This technique is free of the exaggerating tendency of some dendrograms, and is graphically clearer than ordinations. It has been used in a study of mangrove distribution and zonation by Bunt & Williams **(1980).**

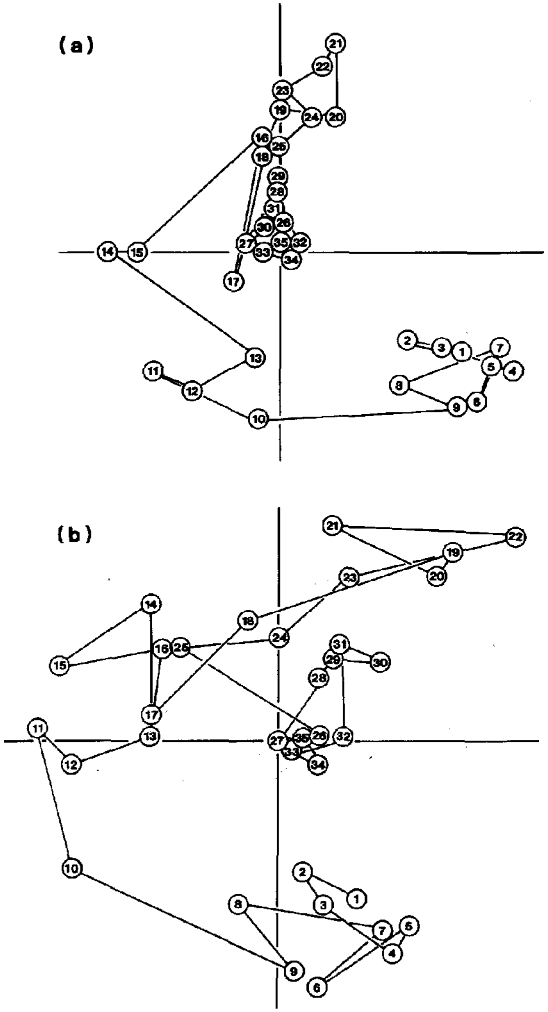


Figure 11 Principal coordinates analysis of line transects down a reef slope (redrawn from Wallace and Dale 1977). Lines in the figure join transects (numbered circles) which are adjacent to each other on the reef. Ordination (a) (based on species composition) illustrates a distinct separation between reef crest (transects 1-9). and reef slope (16 -35) with a loosely coherent 'transition zone' (10-15) between. Ordination (b) (based on colony shape) shows the same reef crest zone, but a much broader transition zone and a smaller deep zone. These differences highlight differences in the way species and growth forms divide up the slope

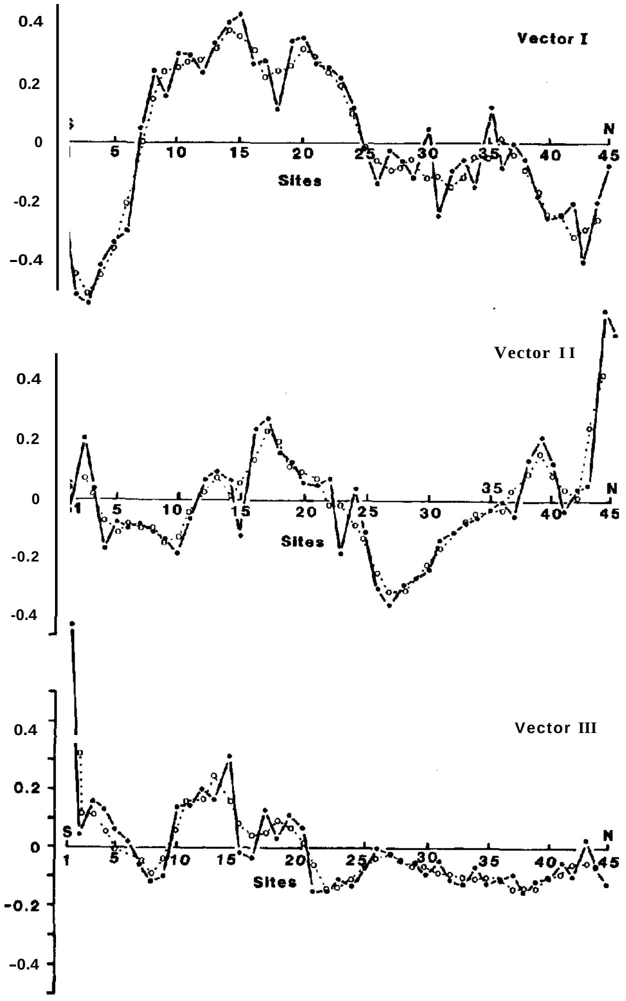


Figure 12 Illustration of structural zonation of a reef flat using principal coordinate vectors I, II and III plotted against transect position (redrawn from Bradbury and Young, 1981a). Vector I differentiated sand from other substrates, vector II rubble from thin ramose corals, and vector III one reef crest from the remainder of the transect. The limits of structural zones are indicated where runs of high positive or negative scores cross the abscissa; the steepness of the crossing reflects the abruptness of the change. The plot of running means (dotted lines) reduces irregularities caused by transects which are dissimilar to neighbours on both sides

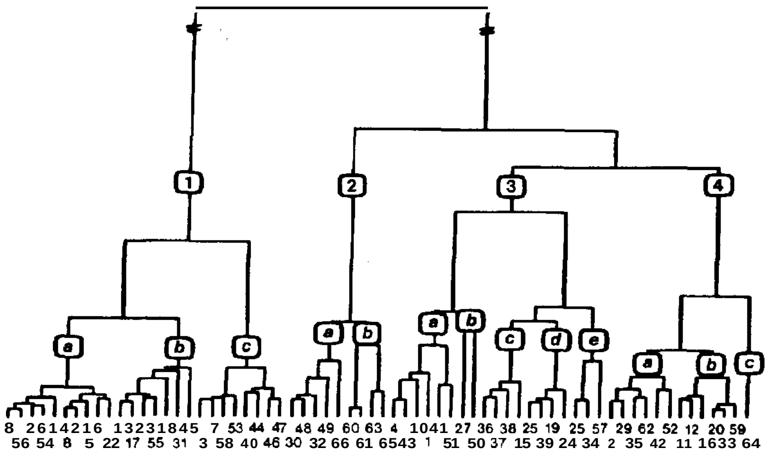


Figure 13 Dendrogram of coral survey data from sixty-six sites widely distributed over Lord Howe Island reef (redrawn from Veron and Done 1979). Groups 1 to 4 reflect the major morphological subdivisions of the reef (flat, lagoon, outer slope, passages); subgroups 'a' to 'e' were composed of faunistically homogeneous sites whose characteristic composition and dominance relationships were tabulated using diagnostic and 'sorting programs

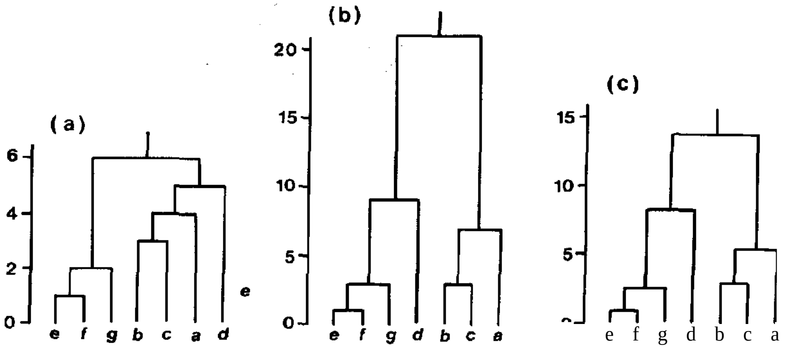


Figure 14 Three classifications of the same hypothetical data matrix using strategies (a) nearest neighbour; (b) furthest neighbour, and (c) group average. Those major patterns and sample groupings which are independent of strategy used may be assumed to have ecological significance. However, the differences (namely, the position of sample and the details of the branching pattern) have no ecological significance, being due solely to differences in computational characteristics of each sorting strategy

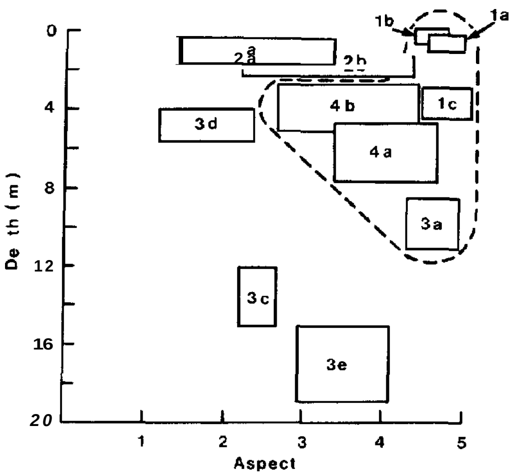


Figure 15 Subjective ordination of site groups (from Fig. 13) against depth and aspect (on a scale of 0 to 5). The lengths of the boxes are equal to the standard deviations of depth and aspect; the centres of the boxes are at mean depth and aspect. The broken line indicates the reef-front series (redrawn from Veron & Done 1979)

Zone composition

A full list of species found in any zone may be reduced to a smaller number which adequately describe the zone and differentiate it from others. These are the 'constant', 'dominant', 'characteristic' and 'differential' species (Scheer 1978). They may readily be defined by various package and special purpose computer programs. Topographic data collected with each sample, such as depth, slope, aspect, substrate composition and total cover may be similarly diagnosed.

Constant and dominant species are easily defined using simple programs which sort the species list for any set of samples in order of descending frequency (number of samples in which attributes was present) and mean cover, respectively. The dominants or constants so defined for a set of zones may be displayed using vector roses, as in figure 16 (after Lamacraft 1979).

The degree to which a species is characteristic of a zone may be quantified as its T-value and its F-ratio (ratios of within zone mean cover and variance to overall mean cover and variance, respectively: Wishart 1975). Species with high T and low F are very characteristic of a zone (though not necessarily dominant). Species with low T and high F have distributions which are indifferent with respect to the zone.

Zone differentiation

Zonal communities of greatly overlapping composition may be discriminated from each other on the basis of the presence or absence of one or more 'differential' species (Scheer 1978). In comparisons of pairs of the sample sets, differential species contribute most to the dissimilarity index. Diagnostic programs 'Grouper' and 'Gowecor' (Lance et *al.* 1968) give each species' contribution to the index, and rank them in descending order. Multiple discriminant analysis (Cooley & Lohnes 1971) has also been used to differentiate zones (Dinesen 1980) using both generic and growth form data.

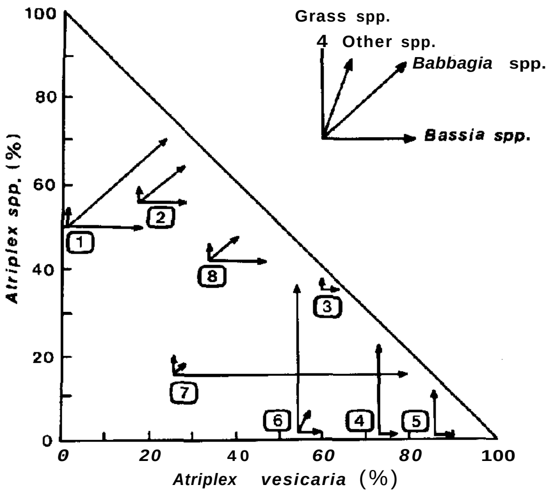


Figure 16 An example of the use of vector roses to display biotic affinities of assemblages (redrawn from Lamacraft 1979). The data are from a study of Australian grasslands

Zone overlap

The extent and nature of overlap between zones can suggest specific hypotheses regarding the role of abiotic factors and spatial competition in determining the zonation pattern (Sheppard, 1980). Methods for sampling and analysis of overlapping distributions, and the biological interpretation of the results, are presented by Pielou (1977). The approach is suitable for habitats exposed to a single, monotonic environmental gradient, and some reef flats and slopes may fit these criteria. However, studies may be restricted to selected areas because species' distributions in many areas respond to 'non-gradient' factors (such as dicontinuous and patchy substrate) or stress gradients acting in opposition or non-monotonically (see Chappell, 1980).

PHYSICAL DETERMINANTS OF CORAL ZONATION

Light and water movement (waves, currents and tides) are the environmental factors recognized as major determinants of the zonal organization of reef benthos. The latter also determines sediment distribution, may be the major proximal cause of benthic distribution patterns. The degree to which a zonal sequence at a particular place may be attributed to these factors depends on both their range and their spatial pattern. Ecologically-orientated introductions to light and water movement in the shallow littoral are provided by Jerlov (1971), Riedl (1971a,b), Schwenke (1971) and Drew (in press). A lucid account of a study of waves and currents on a reef is given by Roberts *et al.* (1975) and a highly technical treatment of waves on a reef is given by Lee & Black (1978).

Coral zonation on reefs is not due to environmental variability per se but to its stratification on the reef's surface (i.e. environmental zonation). Large and continuous tracts of uniform topography are characterized by photic, hydrodynamic and substrate conditions which encompass only a fraction of total reef variability. Small scale topographic features provide fine grain, perhaps irregular environmetal texture (shadows, eddies, etc.) but the larger scale environmetal pattern, being predetermined by geological history and geographic locality, is, by and large, regular and constant through ecological time.

Zoning influences of abiotic factors may be modified to a greater or lesser degree by competitive and/or predatory interactions, depending on the biota (see below). Notwithstanding such biological interactions (or unpredictable exogenous disturbance), the prevailing physical environment does provide the ultimate deterministic framework in which organismic distribution takes place and so some discussion of the physical environment in relation to its zoning effects is presented here. Catastrophic affects of physical events are considered below.

Water motion

Wave action

Ecological zonation schemes sometimes imply that wave action decreases rather uniformly with depth (on the reef slope) and with distance from the reef margin (on the reef flat) (Rosen 1971, 1975; Pichon 1972, 1978a). This implication aligns reef zonation concepts with terrestrial botany, where vegetation zonation is frequently a response to gradients in one or more major environmental factors (Whittaker 1975; Pielou 1977). However, there is evidence to suggest that the gradient concept of water motion may be misleading over-simplification in many real-life situations.

REEF SLOPE

The water mass on a wave-exposed reef or rocky shore may be subdivided into four vertically intergrading water bodies. The subdivisions made on the basis of water particle dynamics (fig. 17) are referred to as lacerating, oscillating, unidirectionally flowing and two-dimensionally flowing water bodies (Riedl 1971b). Boundaries between the water bodies ascend with decreased wave exposure and, in sheltered areas, the lacerating and unidirectionally flowing water bodies disappear. This scheme indicates that there are significant qualitative changes with depth as well as simple vertical diminution of particle velocity. The scheme also shows the relationship between waves and the currents they generate.

Another instance where a simplistic view of wave attenuation with depth is inappropriate has been described by Roberts *et al.* (1975). Their data indicate that the expected decrease of wave force with increasing depth is counterbalanced by an increase in current force. The resulting 'wave plus current' force curve (fig. 18) is bimodal indicating that the total force on the reef benthos at a depth of 21 m is the same as that experienced at about 3 m, close to the reef margin. These areas of high total force corresponded with zones of prolific coral growth; intermediate depths have lower force and less prolific coral growth.

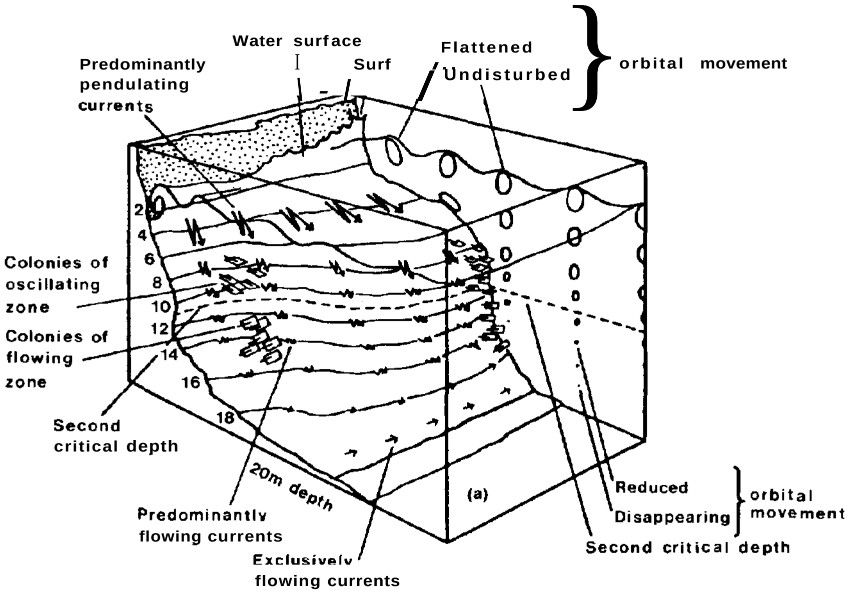


Figure 17 Four intergrading water bodies on a wave-beaten shore. Arrows indicate bottom currents; ellipses indicate orbits of water particles: tags indicate orientation of planar gorgonians (redrawn from Riedl 1971)

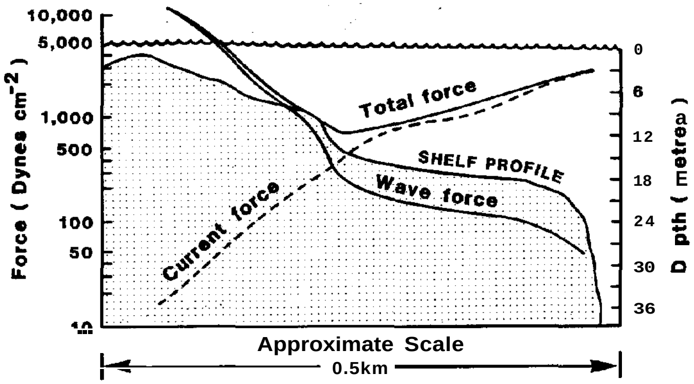


Figure 18 Bimodal distribution of total hydrodynamic force on a reef slope. Although wave and current forces individually attenuate monotonically, their combined affect causes total force at -21 m to equal total force at -3 m (redrawn from Roberts *et al.* 1975)

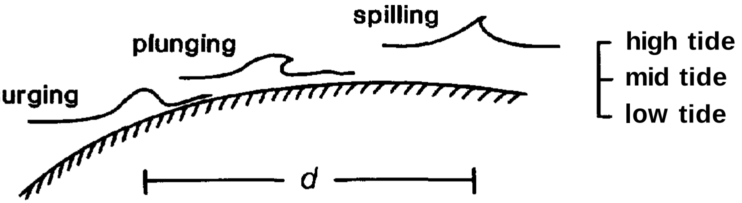


Figure 19 Form and position of wave break for waves of a given height, period and steepness at different tides (based on Wiegel 1964). The distance 'd', occupied by communities adapted to surf conditions, may reach tens to hundreds of metres in macro- to super-tidal areas. In micro-tidal areas, surf has only a localized zoning influence

REEF FLAT

Waves moving onto a reef lose energy in three distinct phases — pre-surf, surf and post-surf. A set of waves crossing the fore-reef shelf at Grand Cayman showed a height reduction of about 20%, attributed to the combined effects of shoaling, refraction, reflection, scattering and extremely high frictional attenuation (Roberts *et al.* 1975). The spectral characteristics of the waves only changed significantly after wave break, at which time 75% of the wave energy was dissipated over a narrow crest region. At Ala Moana (Hawaii), small secondary waves were generated after surf break (Lee & Black **1978).** Large bottom friction and wave break together caused wave height to reduce by about 50% for every 500 ft (150 m) travelled over the reef.

The shape and position of break for a given wave may vary greatly in macro-tidal areas whereas, in atidal areas, it will remain more constant (fig. 19). Breaker shape (either spilling, plunging or surging) depends on a relationship between wave steepness and substrate slope (Wiegel 1964; Huntley & Bowen 1975). The velocity fields of the water in the three breaker types differs significantly and it may be that zonation of coral species and ecomorphs within surf zones is as much a function of these qualitative differences as of a simple attenuation of total wave forces.

The position and intensity of the surf line may indirectly affect benthic zonation through nutrition. It is likely that the surf line effectively isolates reef slope from reef flat waters, just as it isolates inshore and offshore waters adjacent to beaches (US. C.E.R.C. 1977, p. 443). Restriction or channelization, by the surf, of plankton and other nutrients may affect organismic zonation in ways not yet understood (the dependence of downstream 'consumer' zones or upstream 'producer' zones has already been noted; LIMER 1976; Kinsey 1979).

WAVE CLIMATE

The zoning influences of wave action depend ultimately upon long term averages of wave climate (height, period and direction). Distinct weather and leeward slopes are recognizable on reefs with a directional tradewind dominance (Wells 1954, 1957; Stoddart 1971; Roberts 1974). At Grand Cayman Island, an eighty-fold difference in mean annual wave power between weather and leeward shores is reflected in significant differences in reef morphology and zonation (Roberts 1974).

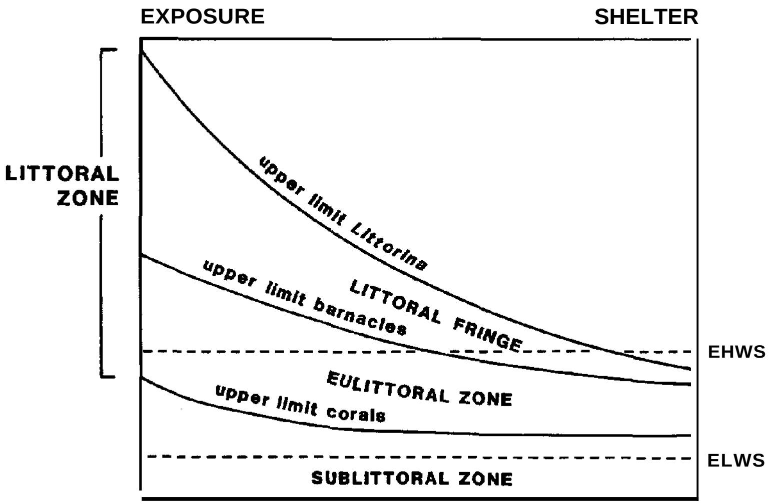


Figure 20 The influence of wave exposure on effective tidal limits and hence, intertidal zonation (redrawn from Taylor, 1978). The vertical limits of intertidal zones on exposed shores are extended beyond the nominal tide limits by wave surge and spray

Data on wave climate are rarely available but may be approximated using hindcasting techniques and numerical wave refraction/friction models (Roberts 1974; Holmes 1975). The approximation may be further stretched to estimate the depth of the wave base (namely, depth of negligible orbital movement) which, for open water waves, is equivalent to half the wave length (Sverdrup *et al.* 1942) or ten times the wave height (Dietrich 1963, Table 3). The complexities of the wave/reef interaction limit this latter approximation to the status of a rough rule of the thumb.

Tides and sea level fluctuations

Reef tops usually have a slight slope or a stepped profile (e.g., Morissey 1980, fig. 3). As a result, the associated reef top communities are subjected to (and limited by) varying frequencies and duration of subaerial exposure and temperature stress associated with both normal tidal fluctuations and longer-term anomalies in mean sea level.

TIDES

Normal tidal fluctuations are responsible for the broadest levels of reef top zonation. A 'tripartite' zonation scheme (Taylor 1978) relates littoral, eulittoral and sublittoral zones with nominal tidal limits, and indicates vertical shifts and extension of zones found in heavily wave-exposed areas (fig. 20).

Coral reefs occur in a wide range of tidal conditions. A regional classification including 'micro-tidal' (0.3-1.0 m), 'meso-tidal' and 'macro-tidal' (>3 m) was used by Stoddart (1971). Reefs in the central Great Barrier Reef (range >6 m; Maxwell 1968) may be termed 'super-tidal'.

Reef flats lie at various depths relative to mean sea level. It is generally held that Caribbean reef tops are deeper than Indo-Pacific reef tops (Stoddart 1969). Periodic tidal emergence and scouring of Indo-Pacific reef flats restricts the coral communities that may persist, or may locally inhibit colonization completely (Stephenson *et al* 1931; Wells 1954, 1957; Ditlev 1978; Morrisey 1980). In many Caribbean reefs, the combination of deeper reef flat and small tidal range restricts the extent of these conditions. A luxuriant community may therefore develop on many reef flats (Stoddart 1969). However, other Caribbean reefs have been shown to lie shallow with respect to mean sea level, and their biotic communities are subjected to periodic emergence and high temperature stress (Glynn 1968, 1973; Scatterday 1977). In this respect they are similar to Indo-Pacific reefs.

SEA LEVEL FLUCTUATIONS

Aperiodic or long-period fluctuations in sea level may drastically change a zonation pattern which had developed during a preceding period of normal tidal activity. Periods of exceptionally low water levels caused extensive mortality of reef flat benthos at Eilat (Fishelson 1973; Loya 1976a), Guam (Yamaguchi 1975) and Puerto Rico (Glynn 1968). Biotic zonation on reef flats which have been so disturbed then becomes a function of time elapsed since disturbance, as well as of the ongoing ambient conditions.

Currents

Habitat selection on the basis of a preferred range of current velocity contributes to observed zonation patterns. Currents influence sessile organisms directly through hydraulic stresses and by supply and removal of dissolved and suspended material. An indirect influence is exerted through the distribution of reefal sediment which in turn limits biotic distributions.

Excessive hydraulic drag appears to exclude or limit corals in certain habitats, such as surf (discussed above) and narrow passes. For example, current velocities of up to $3.8\ m\ s^{-1}$ favoured heavy encrustations of coralline algae almost to the exclusion of corals on a highly illuminated channel wall in the northern Great Barrier Reef (Veron 1978).

At mid-range velocities, currents act more as transport media and less as an environmental stress. It has been suggested that, among suspension feeders, there is an optimum range of ambient velocity in which each species feeds most effectively (Wainwright *et al.* 1975). Predominantly autotrophic species and/or morphologically plastic species may be expected to have somewhat broader preferred velocity ranges and hence, distribution ranges. Some of the principles by which species and ecomorphs may adapt to current environments are discussed in Chamberlain & Graus (1975). Wainwright *et al.* (1975) and Jokiel (1978).

Low current velocities may exclude certain species or colony shapes through stagnation. It is questionable whether open water becomes stagnant under normal ecological conditions (Scbwenke 1974) but laboratory experiments suggest that a branching coral's own growth could cause a stagnant pocket in its interior (Chamberlain & Graus 1975). Death of the colony could result due to starvation of the interior polyps or poisoning by accumulated metabolic wastes.

Sediments

Currents affect zonation indirectly through the sorting and distribution of sediments across the reef structure. Fine sediments accumulate only in habitats with low current velocities. Sediment depth, grain size, suspended load and deposition rate are known determinants of coral distribution and performance (Hubbard & Pockock 1972; Loya 1972, 1976b; Aller & Dodge 1974; Faure 1974).

The transport of sediment itself can affect zonation. The abrasive effect of suspended sand may restrict or inhibit coral growth in high energy areas (Barnes *et al* 1971; Bak 1975; Giester 1977; van den Hoek *et al.* 1978). Deposited sediment that moves *en masse* or is 'worked' by waves does not, in general, provide a long term substrate for macro-benthos.

Light and Turbidity

Most reef corals occur in the euphotic zone, the upper stratum of the water column in which photosynthetically active radiation (PAR) attenuates to 1% of its surface value (Yentsch 1966). This attenuation is a major zoning influence on corals and other benthos. Lower bathymetric limits for autotrophic species are determined by their photosynthetic efficiency at reduced irradiance levels, whereas upper limits for subtidal benthos may depend on species specific adaptation against potentially damaging irradiation by visible or ultra-violet radiation. Reviews of utilization of light by marine plants (including symbiotic zooxanthellae) are provided by McCloskey *et al.* (1978) and Drew (in press).

Lower limit

A complete autotroph is limited to depths in which P/R (the ratio of mean daily photosynthesis to mean daily respiration) exceeds 1.0 (McCloskey *et al.* 1978). The irradiance at which compensation occurs = 1.0) varies between species (Spencer-Davies 1977) and ecomorphs (Jaubert 1977). However, photoadaptation within some species results in a lowering of compensation irradiance in individuals found in habitats with reduced illumination (Wethey & Porter 1976; Porter *et al.* 1980). The total population is therefore characterized by a range of compensation irradiance. Survival below the lower limit of this range requires some degree of heterotrophism (McCloskey *et al.* 1978). Therefore, in principle, the depth at which a species' lowest compensation irradiance exists is a critical determinant of its bathymetric distribution (but see cautionary comments in McCluskey *et al.* 1978).

(Chalker, pers. comm.). This means that photosynthesis in these corals cannot begin to become limiting at a shallower depth than that at which irradiance is about 250 μ Einsteins $m^{-2}\ s^{-1}$ (commonly 10% of its surface value). This depth varies greatly between and within reefs depending on water transparency (see below).

Upper limit

The shallow limit of many species may be determined by photoinhibition in high light intensities, or vulnerability to ultra-violet radiation, which penetrates clear ocean waters almost as well as visible light (Smith & Baker 1979; Jokiel 1980). Many shallow water corals produce compounds which protect their tissues from ultra-violet light (Maragos 1974). Green pigments emit photosynthetically useful wavelengths when exposed to ultra-violet (Kawaguti 1969). Species-specific differences in the degree of ultra-violet light protection or utilization may set different upper Limits to their distribution. Ultra-violet light has been shown to cause death in shallow water transplants of shade-loving bryozoans, sponges and tunicates (Jokiel 1980). This finding gives reason to believe that non-surface corals (*sensu* Wells (1954), including hermatypes and may similarly be upwards-limited by ultra-violet radiation.

Regional and 'within reef' variability

Vertical light attenuation (and hence, depths at which ultra-violet light is damaging, and depth to compensation points) varies from reef to reef and within reefs, depending upon transparency of the water column to radiation. Reef waters off Townsville, Queensland, range in transparency (measured by Secchi disc) from 1-3 m (nearshore) to 20 m (inner line of reefs) to 34 m (outer line of reefs) (Ikeda *et al.* 1980; T.A. Walker, pers. comm.). These data indicate extreme vertical compression of the euphotic zone in nearshore reefs compared to the inner and outer lines of reefs. Coral zonation on nearshore reefs is both condensed into shallow waters, and truncated at the shallow end (Done 1982).

Depth to 90% extinction is a broad ecological index of transparency. The index has its physiological basis in the finding (referred to above) that many corals are not light-limited until approximately 90% attenuation of surface levels. This index (which may readily be extracted from published accounts) varies greatly in some well described reefs: Eilat, outer slope —8 m (Loya 1972); Tulear, lagoon —10 m (Pichon 1978a); Tulear, outer slope — 17 m (Pichon 1978a); Bikini Atoll outer slope — 18 m (Wells 1954); Curacao, outer slope —24 m (van den Hoek *et al.* 1978). Compensation depths, photoinhibition depths, depths at which ultra-violet light is damaging and lightdependent expressions of coral zonation may be correlated with these transparency data. However, differences in light measurement techniques and deficiencies in the physiological data presently preclude synthesis of the published results.

In some reef habitats, reflection from sandy floors and/or walls encrusted with crustose algae may elevate irradiance levels at a given depth (Kinzie 1973). The reduced transparency in some lagoons is due to reefderived suspended material in the water column, and is thus related to flushing rates.

BIOTIC ENVIRONMENT OF CORALS

A coral may be killed by extrinsic biological events over which it has no control or defence. This provides space for colonization by a successor which may not be of the same species. In corals, death may follow coral-coral or coral-algae competition for space, predation upon the colony or boring of the colony. The intensity of biotic interactions many vary between zones; their importance in the determinations of large scale (e.g. zonal) distribution is considered below.

CORAL-CORAL COMPETITION

Different coral species are not equally effective in occupying space on the reef. When two Atlantic species contest the same space, one will usually kill the other by mesenterial aggression or an overtopping growth. The identify of the victor is predictable (Lang 1970. 1973; Porter 1976). In Indo-Pacific corals, the beginnings of a similar aggressive hierarchy have been described by Sheppard (1979) who attributes a deterministic role to interspecific aggression in the composition of biotic zones. Experimental studies of hard/soft coral interactions are currently in progress (Sammarco *et al.* pers. comm.).

CORAL-ALGAL COMPETITION.

Competition for space between coral and algae may result in the death of the coral. For example, displacement of coral spat by algae has been reported by Pearson (1974), Connell (1976) and Sammarco (1980); overgrowth of living adult scleractinia by encrusting coralline algae has been reported by Grigg & Maragos (1974), Littler & Doty (1975) and Dana (1979). It is widely held that coral dominance in many areas is possible only because grazing and cropping organisms (especially sea urchins and fish) keep the standing crop of highly productive fleshy algae at low levels (Ogden 1976; Benayahu & Loya 1977; van den Hoek *et al.* 1978; Sammarco 1980; Hatcher, ch.10 this volume).

CORAL PREDATION AND BORING

The impact of predation on a coral community depends upon coral and predator population levels, and the feeding strategies of the predators, which belong to many animal orders (Endean 1976). At normal population levels, *Acanthaster planci* will frequently kill whole colonies but the feeding pattern is patchy (Porter 1972b; Endean 1973; Glynn 1974a). However, plagues of *Acanthaster* kill corals over large areas, and it appears that this form of perturbation may be equivalent in its ecological-geological time scale effects on coral community structure to other extrinsic disturbances such as floods, cyclones and sediment smothering (Endean 1976; Connell 1978; Pearson, 1981).

Numerous organisms bore into scleractinian corals (Scoffin & Garrett 1974: Warme 1977; Bromley 1978; Risk & MacGeachy 1978). Those which bore into the basal regions of colonies can cause them to topple or accelerate dislodgement by wave action (Tunnicliffe 1979). The effect of borers on community structure may thus be great by comparison with the small amount of carbonate they excavate. Moreover, total borer impact may be zonally distributed (Bromley 1978).

CORAL RESPONSES TO THE ENVIRONMENT

Zoning Influences of Biological Interactions

This section considers the relative importance of biological interactions to coral zonation. To what extent are species which are physiologically and mechanically capable of occupying a habitat, excluded by their inability to hold their place in the face of interspecific competition or localized predation? Are .these interactions simply a rather inconsequential product of distribution patterns determined by overriding physical factors, or are they themselves determinants of the pattern? These concepts have been discussed by Porter (1972a), Connell (1973, 1978). Glynn (1973) and Dana (1976).

Some of the biological mechanisms for the possible exclusion of some species by others have been discussed above. However, the degree to which these mechanisms propagate upscale from an interaction between two individuals to a determinant of overall community structure and zonation remains to be demonstrated conclusively.

An analogous situation exists in the field of island biogeography. Diamond (1975) has proposed a set of 'assembly rules' for fauna on islands. The rules are based upon some distributional data and some mechanistic biological premises. The empirical bases of Diamond's rules have been attacked by Simberloff and colleagues (e.g. Connor & Simberloff 1979). They indicate that demonstration of a biological mechanism for species exclusion does not provide grounds for believing it to be effective at the level of community organization, a statement which holds for coral communities as well as for islands.

The effect of species interactions in limiting species ranges has been examined in quantitative distributional studies and field experiments. The bathymetric distributions of several markedly zoned species at Chagos were found to be strongly truncated

(Sheppard 1980b). With supporting information on the aggressive status of the corals present, these data suggested that competition contributes to determining the nature and extent of coral zones. However, an analysis of coral distribution along a Great Barrier Reef transect suggested that interspecific competition was inconsequential over a similar spatial scale (tens to hundreds of metres; Bradbury & Young, in press).

Grazing by fish and echinoids may significantly affect zonation. For example, the Atlantic echinoid *Diadema antillarum* is seen as functionally analogous to keystone predators in rocky shores (Paine 1969). Its own distribution is strongly zoned on many Caribbean reef slopes (Ogden 1976) with low densities on shallow and deep slopes, and high densities at intermediate depths. Data for algal productivity and consumption rates support the view that the dense mid-slope population of the echinoid indirectly causes the observed high coral cover and diversity by keeping algal standing-crop low (van den Hoek *et al.* 1978). Conversely, absence of the sea urchin from shallow zones (due to a paucity of refuges from wave action) allows high algal standing-crop, which effectively excludes corals. These conclusions are supported by the results of field experiments in which sea urchin density was manipulated (Sammarco *et al.* 1974; Sammarco 1980). The belief that the algal/coral/urchin interaction is a major determinant of community structure is thus well supported in the Caribbean. Echinoid control of algal biomass is suggested on some Indo-Pacific reefs (e.g. Benayahu & Loya 1977) but it is not significant on slopes of several reefs surveyed on the central Great Barrier Reef (Sammarco, pers. comm.).

Age-specific responses

The presence or absence of a given species from a topographic zone may not necessarily be comprehensible in terms of the resource requirements and physiological/mechanical/competitive tolerances of the adult stage alone. Success in a place indicates that the requirements of all life stages (from spat to adult) have been met at the point of settlement. Exceptions are imported mobile coralliths (Glynn 1974b) and adults derived from imported living fragments (Tunnicliffe 1981). Localized barriers to dispersal (such as strongly directional currents or surf barriers) may also cause the absence of a species otherwise capable of surviving and which is, perhaps, abundant nearby.

Little age-specific data is available, although the need is well recognized. Those relevant physiological, behavioural and ecomechanical studies which do exist refer mainly to adult specimens (see sections on water motions, sediment and light in Connell 1973). The deficiency is partly redressed by studies of life history strategies.

Life History Strategies

Life history studies provide species-specific population data which are central to understanding distribution patterns in heterogeneous and zoned environments. Key parameters in the studies include recruitment rate, sediment rejection ability, aggression status, regenerative ability, juvenile and adult survival rates and longevity (Bak & Engel 1979). These authors defined three broadly different life history strategies in terms of these parameters. Similar information was used by Loya (1976c,d), who described an opportunistic life history strategy in one ubiquitous species and drew attention to alternative strategies likely to be found in others. Although life history studies do not necessarily identify the requirements of all life stages, they do identify (and to a degree quantify) key processes and events in the organism/environment interaction.

SYNOPTIC SPATIO-TEMPORAL MODELS

Two recent models together provide a basis for understanding coral community structure and zonation at a synoptic level. These models were devised by Connell (1978) and Chappell (l980).

A decade or so ago, coral cover and diversity in many western Pacific reefs was largely determined by whether or not the community had been infested by *Acanthaster planci* in the past (Pearson 1981). Its appearance depended upon the severity of the infestation, and the stage reached in the secondary succession which that event initiated (Endean 1973, 1976; Pearson 1981).

The successional potential of reef coral communities has been emphasized in a recent synopsis by Connell (l978). Connell reasoned that, because some species are superior to others in occupying space, a succession towards a monospecific stand would result. However, the monospecific end result was not usually attained (i.e. diversity was kept high) because succession was usually interrupted by extrinsic disturbance of varying frequency and intensity. Examples of such disturbances were 'storm waves, freshwater floods, sediments or herds of predators'.

Connell's emphasis on indiscriminate disturbance of extrinsic origin is significant. Work on temperate rocky shores had previously demonstrated a significant role in community organizations for patchy chronic disturbance from within the community (Connell 1961, 1975). It is the opinion of many authors that intrinsic disturbance can similarly maintain a high diversity in coral communities (e.g. sea urchin grazing, Ogden 1976; Sammarco 1980: *Acanthaster* predation, Porter 1972). The question is thus raised as to whether high diversity may be maintained indefinitely without extrinsic disturbance.

Chappell's model has as its basis the premise that a reef is traversed by stress gradients in wave action, subaerial exposure, illumination and sediment (Chappell 1980). Each stress and the sum of the stresses is zonally distributed and provides a predictive basis for the distribution of coral shapes and diversity. However, the successional concepts embodied in Connell (1978) are explicity excluded from the Chappell model.

One may speculate that the next synoptic model will embrace both Connell and Chappell concepts, and thereby rectify their individual deficiencies, namely, zonal differentiation (Connelt) and successional concepts (Chappell). Chappell's stress-indicies may be translatable into zone-specific rates and patterns of space production due to intrinsic perturbation. Connell's extrinsic disturbance may be modelled as variables with zone-specific frequencies and intensities. The composite model would thereby embrace the spatio-tempora1 variables of environmental predictability and severity, which have long been appreciated as zone dependent (Loya 1972; Porter 1972a; Dana 1979).

CONCLUSIONS

Emphasis in reef benthic ecology has changed. Descriptive localized studies of zonation have provided a necessary biological base in the past. Present day time-based process studies, autecological studies and zonal surveys with a broader geographic base are providing an improved basis for understanding reef organization.

Supporting long-term environmental information is essential both for zone/environment correlation, and for process studies. Knowledge of
at scales from square centimetres to one hectare of reef surface is particularly relevant in analysis of community structure and zonation.

Zonation is the most visible of all manifestations of pattern in the distribution and abundance of organisms. It thus provides a focus for many problems in reef ecology, for it results from a grand natural experiment in which the dose rate of virtually all ecological factors (light, wave energy, currents, sediments, space limitations, diversity and predation) are varied in space and time.

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