Cnidarian Zonation at Ilha do Sal (Arquipélago de Cabo Verde)

Cnidarier-Zonierung an der Insel Sal (Kapverdische Inseln)

by

Carla MORRI * & Carlo N. BIANCHI**

MORRI, C. & BIANCHI, C.N., 1995. Cnidarian Zonation at Ilha do Sal (Arquipélago de Cabo Verde). — Beitr. Paläont., **20**:41–49, 6 Figures, 4 Tables, Wien.

Abstract

A total of 19 conspicuous species was inventoried by SCUBA diving along 10 depth-transects, 0 to 33 m depth. Multivariate analysis allowed the recognition of 5 cnidarian zones, namely: lower midlittoral zone, *Millepora* zone, mixed coral zone, overhang zone, gorgonian-antipatharian zone. Species substitution with depth is mainly related to gradients in light intensity and water movement; the possible role of competition and predation is also discussed. Although no true coral reefs exist at Sal, the observed zonation patterns are consistent with those typical of coral reef areas.

Zusammenfassung

Entlang von 10 Tiefentransekten (0–33 m Wassertiefe) konnten 19 "auffällige" Arten bei Scuba-Tauchabstiegen festgestellt werden. Mittels einer multivariaten Analyse ließen sich 5 Cnidarier-Zonen ausscheiden: untere Mittlitoral Zone, *Millepora* Zone, gemischte Korallen Zone, Überhang Zone, Gorgonien-Antipatharien Zone. Artsubstitutionen mit der Tiefe können mit Gradienten der Lichtintensität und Wasserbewegung korreliert werden; die mögliche Rolle von Wettbewerb und Beutefang wird auch diskutiert. Obwohl auf der Insel Sal keine Korallenriffe existieren, zeigt die beobachtete Zonierung starke Ähnlichkeiten zu jenen wie sie für Korallenriffe typisch sind.

1. Introduction

Cnidarians are important constituents of shallow-water epibenthic communities (MORRI et al., 1991) especially in tropical seas, where they comprise the main framebuilders of coral reefs (FAGERSTROM, 1987).

Cnidarian species are zoned in the different parts of a

coral reef according to their ecological requirements with respect to a number of abiotic and biotic factors (see DONE, 1983, for a review). However, little is known on the cnidarian zonation in tropical areas deprived of coral reefs.

The Eastern Tropical Atlantic is one of such areas (EKMAN, 1953). Although no true coral reefs exist along the West African coast or in the neighbouring archipelagos, nevertheless there are a number of sites with rich coral communities (WELLS, 1988) and several species of hermatypic corals are known from the region (LABOREL, 1974; BOEKSCHOTEN & BOREL-BEST, 1988).

Corals and other reef cnidarians turned out to be abundant on shallow (0 to 33 m deep) rocky bottoms at Ilha do Sal (Arquipélago de Cabo Verde), during a SCUBA diving expedition organised in the winter of 1990–1991, by the Zoological Institute of Genova University.

The aim of this paper is to describe the cnidarian zonation we observed at Sal, and to relate it to depth, substrate inclination, and wave exposure.

2. Materials and Methods

Cnidarian zonation was examined according to the method frequently adopted in the Mediterranean Sea for SCUBA benthic surveys (BIANCHI et al., 1991; GILI & ROS, 1985).

Two divers working together swam along idealised depthtransects perpendicular to the shore (note that "transect" here is not intended in the sense of LOYA, 1978). One of these depth-transects was effectuated at each of ten stations (Fig. 1). Due to persistent bad weather conditions, only west and, to a lesser extent, south coasts of Sal were explored.

In each depth-transect (numbered 1 to 10), the two divers recognised homogeneous areas (named a, b, c ...: Fig. 2) through a physiognomic approach (BEARD, 1978): i.e., areas were considered homogeneous for substratum type and the "aspect" of their biotic cover (a similar approach was used by GOMEZ & ALCALA, 1984, to divide the reef in sampling "strata"). These areas had varying sizes,

Istituto di Zoologia, Università di Genova, via Balbi 5, I-16126 Genova (Italia)

^{**} Centro Ricerche Ambiente Marino, ENEA S.Teresa CP 316, I-19100 La Spezia (Italia)

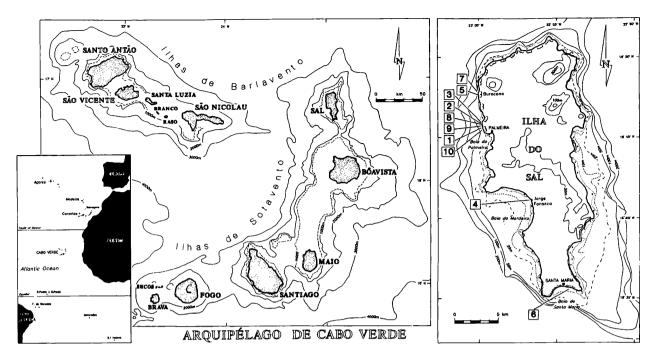


Figure 1: Geographical setting of the study area. Numbers in boxes are stations.

usually about 20 m² or more, and were treated as "relevés", according to phytosociological usage (BOUDOURES-QUE, 1971; COPPEJANS, 1980). In total, 29 "relevés" were sampled between 33 m depth and the water surface (transect 5 gave no cnidarians).

In each relevé, cnidarians were inventoried and, when necessary for identification purposes, collected. All species large enough to be easily seen underwater were taken into account. The smallest species of hydroids and cryptic anthozoans such as stoloniferans, if not abundant, might have escaped recording. No quantitative analysis was attempted. Species importance was evaluated through visual estimates of their substratum cover (DETHIER et al., 1993), subsequently converted into a semi-quantitative three-point scale (HISCOCK, 1987); absence was given a zero score.

Depth of each relevé was measured by diving computer, and substrate inclination with a hand-made clinometer (GAMBLE, 1984). Wave exposure was evaluated through the fetch-energy index proposed by HUMMON (1989): in order to account for the exponential decrease of water movement with increasing depth, the computed fetchenergy index was divided by the logarithm of depth.

The species x relevés matrix was submitted to multivariate analysis (WILDI & ORLOCI, 1980). Cluster analysis was performed on relevés, using VAN DER MAAREL's coefficient as a similarity index, and clustering by complete linkage. Species and relevés were also ordered by correspondence analysis: the significance of the axes was evaluated using the tables of LEBART (1975). Significant axes were compared to depth, substrate inclination, and exposure index by standard linear correlation analysis.

3. Results

A total of 19 species was inventoried (Tab. 1). Due to the poor faunal knowledge of the zone, taxonomy was, to some extent, uncertain in a few cases. More detailed faunal and taxonomic notes will be given in a further paper.

Depth distribution of these species showed three major groups (Fig. 3): 1) surface species (*Actinia equina* and *Porites porites*), never found below 0.5 m depth; 2) shallow-water species (the remaining scleractinians, the hydrozoans, and *Palythoa caribaeorum*) preferring depths around 10 m but ranging from near the surface down to 20 m; 3) deep-water species (all the gorgonians and antipatharians), found between 20 and 33 m.

Relevés clustered in five major groups (Fig. 4). Group A was formed by relevé 9a alone, in which only *Actinia equina* was found.

Group B comprised 7 shallow-water relevés in exposed sites. All of them shared the presence of *Millepora* sp. (an encrusting and robust growth-form, yellow-greenish in colour, maybe an ecomorph of *M. alcicornis*), but *Halocordyle disticha* was equally abundant in some cases.

Group C contained 9 relevés, all in well-lit sites. They were largely dominated by zooxanthellate species, among which were all hermatypic corals. The most frequent species was *Porites astreoides*. *Siderastrea radians* was important in relevés in the vicinity of sand, whereas *Palythoa caribaeorum* was often dominant, forming carpets over rocks and large boulders, at around 5–10 m depth. *Porites porites* and *Balanophyllia "italica"* (sensu CHEVALIER, 1966; not *B. europaea*: ZIBROWIUS, in litteris) were found only once (relevés 4a and 7b, respectively).

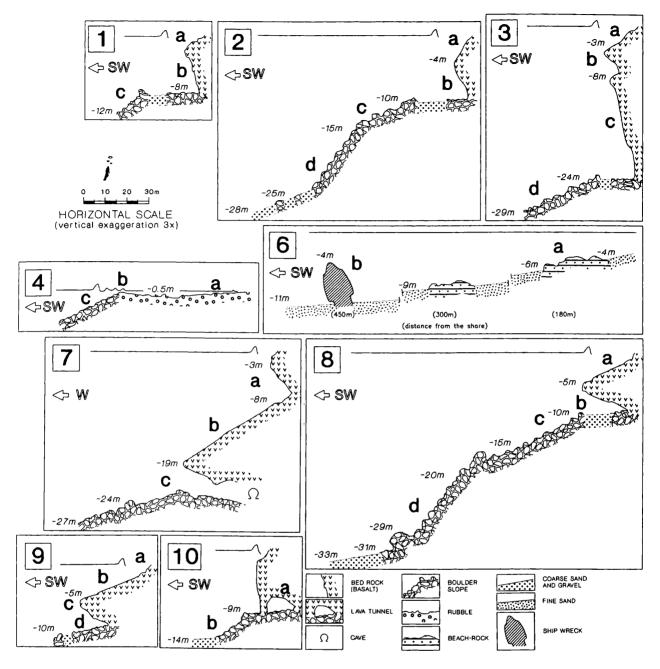


Figure 2: Schematic profiles of depth-transects: note that vertical scale is exaggerated. Numbers in boxes are transect stations, bold lowercase letters are relevés. Transect 5 gave no conspicuous cnidarians and is not shown here.

Group D was formed by 9 relevés located under overhangs at the base of basaltic cliffs or in caves and lava tunnels. *Tubastraea aurea* was extremely abundant in all sites, covering large portions of rock, and sometimes accompanied by *Thyroscyphus marginatus*.

Finally, group E contained the remaining 3 relevés, the deepest ones. Cnidarians were represented by gorgonians (*Eunicella granulata, E. papillifera, Leptogorgia capverdensis, L. gaini*) and antipatharians (*Antipathes barbadensis, A. tanacetum, Stichopathes lutkeni*). On the whole, the most abundant species was *Leptogorgia capverdensis*.

Correspondence analysis on semi-quantitative data (Tab. 2) produced three significant axes: taken together, they explained 67.5 % of the total variance, i.e., 27.1 %, 23.8 %,

and 16.6 %, respectively (Fig. 5).

The first axis mainly discriminated between shallowwater relevés, dominated by zooxanthellate species, and deep ones, with only azooxanthellate species. The second axis separated overhangs and cave or tunnel vaults, with *T. aurea* and *T. marginatus*, from all the remaining relevés. The third axis mainly distinguished exposed relevés, with *Millepora* sp. and *H. disticha*, from the others, especially those at comparable depths but more sheltered and inhabited by hermatypic corals.

Linear correlation analysis confirmed such a picture, the first axis being chiefly related to depth, the second to substrate inclination, and the third to the exposure index we adopted (Tab. 3).

Hydrozoa

Anthomedusae

- Hdi Halocordyle disticha (GOLDFUSS)
- Mal Millepora alcicornis L.
- Msp Millepora sp.
 - Leptomedusae
- Tma Thyroscyphus marginatus (ALLMAN)

Octocorallia

Gorgonacea

- *Epa Eunicella papillifera* (MILNE-EDWARDS & HAIME)
- *Egr Eunicella granulata* GRASSHOFF
- *Lca Leptogorgia capverdensis* (GRASSHOFF)
- *Lga Leptogorgia gaini* (STIASNY)

Hexacorallia

Antipatharia

- *Slu Stichopathes lutkeni* BROOK
- Aba Antipathes barbadensis (BROOK)
- Ata Antipathes tanacetum POURTALÈS Zoantharia
- Pca Palythoa caribaeorum DUCHASSAING & MICHELOTTI

Actiniaria

- Aeq Actinia equina (L.) Scleractinia
- Sra Siderastrea radians (PALLAS)
- Pas Porites astreoides LAMARCK
- Ppo Porites porites (PALLAS)
- *Ffr Favia fragum* (ESPER)
- Bit Balanophyllia italica, sensu CHEVALIER
- Tau Tubastraea aurea (QUOY & GAIMARD)

 Table 1: Systematic list of the species (coded as they appear in Fig. 5)

4. Discussion and Conclusions

The five groups of relevés identified through cluster analysis correspond well to as many different cnidarian zones (Tab. 4).

One zone (group A) might be the lower midlittoral, with *Actinia equina* as the main species, as typical on temperate Atlantic and Mediterranean coasts (PATRITI, 1970; SCHMIDT, 1972). However, this presumed zone was surely undersampled (one relevé only) and will not be discussed further here.

The following four, fully subtidal, zones are strongly consistent with those that can be encountered on a typical coral reef, especially in the Western Atlantic region (GOREAU & GOREAU, 1973; GEISTER, 1983).

On exposed infralittoral rocks, in shallow waters (group B), a *Millepora* zone could be defined: both the dominant species, *Millepora* sp. and *Halocordyle disticha*, can be considered photophilic and rheophilous (MERGNER, 1977; LEWIS, 1989).

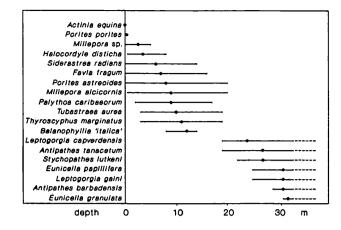


Figure 3: Overall depth distribution of the species. Diamonds are the all-station means for each species.

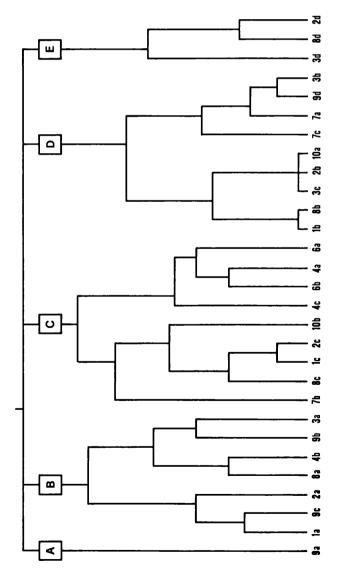


Figure 4: Cluster analysis of relevés. VAN DER MAAREL's coefficient, complete linkage. Similarity range in the dendrogramm: 0 to 1.

Depth-transects		1			2	;				3			4		6			7			8	;		-	9)		1	.0
Relevés	a	b	с	a	b	с	d	a	b	с	d	a	b	c	a	b	a	b	с	a	b	c	d	a	b	с	d	a	b
Species																													
H. disticha	2	2	1	2				2													2					1	1		
M. alcicornis			2			2						2			2	2		1				2							2
<i>Millepora</i> sp.	3			1				3					3	1	1			1		3				1	2	2			
T. marginatus									2								2		3								2		
E. papillifera																							1						
E. granulata											2												2						
L. capverdensis	ļ						3				3								1				3						
L. gaini							2																1						
S. lutkeni							2																2						
A. barbadensis							2																2						
A. tanacetum							2				2								2				2						
P. caribaeorum			3			3		2										1		1		3		1	2				3
A. equina																								2					
S. radians												3		3	2	3													3
P. astreoides			2			2						2	1	2	2	1		3				2			1				2
P. porites												2																	
F. fragum			2			2						1	1	2		2													
B. "italica"																		2											
T. aurea		3	1		3				3	3							2		3		3						3	3	

Table 2: Semi-quantitative estimates of cnidarian species importance (. = absent; 1 = < 1 % cover; 2 = 1-5 % cover; 3 = 5-20 % cover)

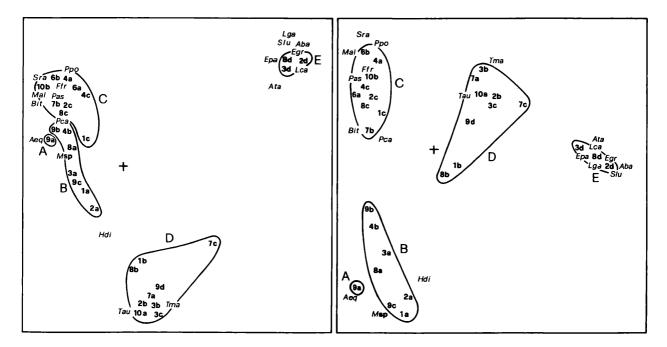


Figure 5: Correspondence analysis: combined plot of relevés and species (coded according to Tab. 1) on 1^{st} and 2^{nd} axis (left) and on 1^{st} and 3^{rd} axis (right). Relevé groups from cluster analysis are superimposed. Horizontal axis is 1^{st} axis in both graphs. Explained variance: 1^{st} axis = 27.1%; 2^{nd} axis = 23.8%; 3^{rd} axis = 16.6%.

Sheltered infralittoral rocks, down to about 15–20 m depth (group C), harboured a mixed coral assemblage, dominated by hermatypic species; the ecological distribution of these species is reminiscent of that described in Bermuda (LOGAN, 1988) and in the Caribbean-West Indian region (BUNT et al., 1981; LABOREL, 1982; KENNY,

1988; etc.). For example, *Porites astreoides*, *P. porites*, and *Siderastrea radians* are known to exhibit maximum growth rates within 15 m depth in Jamaica (HUSTON, 1985).

An ahermatypic coral (*Tubastraea aurea*) was the dominant species in the overhang zone (group D). Below

Values of "r"										
	Depth	Substr. Incl.	Expos. Index							
1 st axis	0.729 ***	0.379 *	–0.253 ns							
2 nd axis	0.175 ns	-0.868 ***	-0.036 ns							
3 rd axis	0.371 *	0.071 ns	0.510 **							
(***: p < 0.001; **: p < 0.01; *: p < 0.05; <i>ns</i> : not significant)										

 Table 3: Correlation coefficients (r) between axes from correspondence analysis and depth, substrate inclination, and exposure index.

20 m, a circalittoral gorgonian-antipatharian zone (group E) could be described. Both assemblages have their analogous counterparts in the west Atlantic reefs (e.g., GOLDBERG, 1973; SCATTERDAY, 1974).

Our *Millepora* and mixed corals assemblages can be ascribed to a typical "reefal biocoenosis", whereas overhang and gorgonian-antipatharian assemblages to a "subreefal biocoenosis", according to PICHON's (1978) terminology. It must be noted that most members of the aforementioned reefal biocoenosis, being zooxanthellate species, are autotrophic or at least polytrophic (SCHLICH-TER, 1982), whereas members of the subreefal biocoenosis are strictly heterotrophic.

This implies that a major factor in differentiating the four subtidal cnidarian zones at Sal is light availability. The decrease of light is said to be the main factor affecting coral growth and community structure (HUSTON, 1985). Correspondence analysis, together with linear correlation, indicated that depth was likely to be the principal factor in influencing cnidarian zonation, being correlated especially to axis I. Substrate inclination was likely to be the second factor, in order of importance. Both depth and substrate inclination clearly affect the amount of light reaching the bottom on which colonies settle, and therefore the two parameters may in reality be the expression of the same ecological factor: light. This hypothesis may also be corroborated by the general parabolic shape of the pointcloud on the plane formed by the first two axes from correspondence analysis, since such a configuration is usually evident when a single polarising factor exists (GAUCH, 1984): light, once again, in our case.

The further important factor related to the coral zonation observed at Sal turned out to be wave-exposure, and hence water movement (GEISTER, 1977). RIEDL(1971) considered water movement as one of the major factors in selecting rocky subtidal benthos, and distinguished four depth-related water bodies: in these terms, our *Millepora* zone would mainly lie in the "lacerating" water body, the mixed coral zone in the "oscillating" water body, and the gorgonian-antipatharian zone in the "unidimensionally flowing" water body.

Thus, species substitution with depth was mainly determined by gradients in light intensity and water movement (Fig. 6), as in coral reefs of the Caribbean region (VAN DEN HOEK et al., 1978; GRAUS & MACINTYRE, 1989).

Lower midlittoral zone

Depth: 0 m Substrate inclination: 30° Exposure index: 45 % Important species: A. equina

Millepora zone

Depth: 0–8 m; average: 2.5 m Substrate inclination: 0–90°; average: 55° Exposure index: 15–32 %; average: 21 % Important species: *Millepora* sp., *H. disticha*

Mixed coral zone

Depth: 0–20 m; average: 8 m Substrate inclination: 0–60°; average: 22° Exposure index: 9–21 %; average: 13 % Important species: *P. astreoides, M. alcicornis, S. radians, P. caribaeorum*

Overhang zone

Depth: 3–19 m; average: 10 m Substrate inclination: 100–150°; average: 124° Exposure index: 12–28 %; average: 16 % Important species: *T. aurea, T. marginatus*

Gorgonian-antipatharian zone

Depth: 19–33 m; average: 25 m Substrate inclination: 30–45°; average: 35° Exposure index: 10–11 %; average: 11 % Important species: L. capverdensis, A. tanacetum, S. lutkeni, E. granulata

Table 4: Cnidarian zones at Ilha do Sal: definition, and summary of main physical and biological features.

Biotic factors were not taken into account in this study. However, some speculations on their importance can be made discussing observational data.

The observed extreme abundance (up to 26 individuals per m²) of the fire-worm *Hermodice carunculata* PALLAS, which is known to feed on a wide variety of reef cnidarians (VREELAND & LASKER, 1989), might indicate a high degree of predation. Similarly abundant was the sea-urchin *Diadema antillarum* (PHILIPPI) and several coral-eating fishes, especially *Sparisoma cretense* (L.) and other Scaridae (but also Tetraodontidae, Monacanthidae, and Chaetodontidae). Thus, predation might act as a regulating factor at intermediate depth: for example, it might be responsible for the occurrence of huge colonies (2–3 m² in surface area, together covering up to 50 % of the substratum in some sites) of *Palythoa caribaeorum*, an impalatable species producing highly toxic biochemicals (MOORE & SCHEUER, 1971).

Competition between macroalgae and zooxanthellate cnidarians could play a role at shallow depths, where algal communities were flourishing (OTERO-SCHMITT, 1993). Similarly, the replacement of zooxanthellate species by azooxanthellate species at 15–20 m depth could be sharpened by competitive effects. However, total cover of the substratum was usually less than 100 %, and life

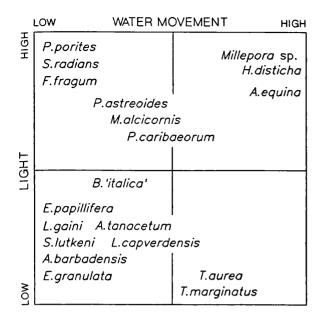


Figure 6: Conceptual scheme of the ecological zonation of cnidarian species at Ilha do Sal.

strategies of the dominant coral species (PICHON, 1981; LOGAN, 1988; TOMASCIK, 1991) suggest competition should not be of much importance.

Judging from the above evidences, biotic factors are supposed to play a role in shaping cnidarian assemblages within zones, but are probably secondary to physical ones in defining such zones. BARRY & DAYTON (1991) underline that biotic interactions must always be considered in the context of physical - and especially hydrodynamic - factors. Storms may be responsible for the low substratum cover values we observed at shallow to intermediate depths: the only exception was the small bay Jorge Fonseca (transect 4), where Porites porites characterized a rich and diverse coral community in waters sheltered from oceanic waves. In deeper water, the wave-generated longshore currents can constantly supply renewed food to long-lived, filter-feeder species. It can therefore be hypothesised that frequency and intensity of physical disturbance (at shallow depths) and environmental stability (at deeper sites) are probably the major determinants of the observed patterns in cnidarian assemblages.

Acknowledgements

The Cabo Verde expedition was organised within the research project "Gli Cnidari del benthos marino: ecologia e biogeografia" (60 % MURST). Staff of "Dive Cape Verde" at Ilha do Sal helped with logistic and diving assistance. A. Peirano (La Spezia) criticised the manuscript, and M. Peebles (London) revised the English text. Special thanks are due to P.F.S. Cornelius (London), M. Grasshoff (Frankfurt), G. Warner (Reading), and H. Zibrowius (Marseille) for help with taxonomic problems and for advice.

5. References

- BARRY, J.P. & DAYTON, P.K., 1991. Physical heterogeneity and the organization of marine communities. – [in:] KOLASA, J. & PICKETT, S.T.A. (eds.). Ecological heterogeneity. — :270–320, New York (Springer-Verlag).
- BEARD, J.S., 1978. The physiognomic approach. [in:] Whittaker, R.H. (ed.). Classification of plant communities. — :33–64, The Hague (W. Junk Publ.).
- BIANCHI, C.N., COCITO, S., MORRI, C. & SGORBINI, S., 1991. Rilevamento bionomico subacqueo. – [in:] ABBIATI, M. (ed.). Lezioni del corso formativo per ricercatore scientifico subacqueo. — 67–83, Pisa (International School for Scientific Diving).
- BOEKSCHOTEN, G.J. & BOREL-BEST, M., 1988. Fossil and recent shallow water corals from the Atlantic Islands off Western Africa. — Zool. Meded. Leiden, 62(8):99–112, Leiden.
- BOUDOURESQUE, C.F., 1971. Méthodes d'étude qualitative et quantitative du benthos (en particulier du phytobenthos). —Tethys, **3**(1):79–104, Marseille.
- BUNT, J.S., WILLIAMS, W.T. & CHALKER, B.E., 1981.
 Coral associations at depths of 45 to 125 feet in the Bahamian region. [in:] GOMEZ, E.D., BIRKELAND, C.E., BUDDEMEIER, R.W., JOHANNES, J.A., MARSH, R.E. & TSUDA, T. (eds.). The reef and man. Proceedings of the 4th international coral reef symposium. Marine Sciences Center, University of the Philippines, Manila, 1:707–714, Manila.
- CHEVALIER, J.P., 1966. Contribution à l'étude des Madréporaires des côtes occidentales de l'Afrique tropicale (2^e partie). — Bull. Ist. fran. Afr. Noire, 28, sér. A (4):1356–1405, Abidjan.
- COPPEJANS, E., 1980. Phytosociological studies on Mediterranean algal vegetation: rocky surfaces of the photophilic infralittoral zone. – [in:] PRICE, J.H., IRVINE, D.E.G. & FARNHAM, W.F. (eds.). The shore environment. Vol. 2: Ecosystems. — The Systematic Association Special Volume, 17(a):371–393, London (Academic Press).
- DETHIER, M.D., GRAHAM, E.S., COHEN, S. & TEAR, L.M., 1993. Visual versus random-point percent cover estimations: "objective" is not always better. — Mar. Ecol. Prog. Ser., 96:93–100, Halstenbek.
- DONE, T.J., 1983. Coral zonation: its nature and significance. [in:] BARNES, D.J. (ed.). Perspectives on coral reefs. Australian Institute of Marine Sciences, :107–147, Manuka, Australia (B. Clouston Publ.).
- EKMAN, S., 1953. Zoogeography of the sea. 417 pp., London (Sidgwick & Jackson).
- FAGERSTROM, J.A., 1987. The evolution of reef communities. — 600 pp., New York (J.Wiley & Sons).
- GAMBLE, J.C., 1984. Diving. [in:] HOLME, N.A. & MCINTYRE, A.D. (eds.). Methods for the study of marine benthos. – IBP Handbook, 16:99–139, Oxford (Blackwell Sci., 2nd edition).
- GAUCH, H.G., 1984. Multivariate analysis in community ecology. —298 pp., Cambridge (Cambridge Univ. Press).

- GEISTER, J., 1977. The influence of wave exposure on the ecological zonation of Caribbean coral reefs. [in:]
 TAYLOR, D.L. (ed.). Proceedings: 3rd international coral reef symposium. Rosenstiel School of Marine and Atmospheric Science, 1:23–29, Miami.
- GEISTER, J., 1983. Holocene west Indian coral reefs: geomorphology, ecology and facies. — Facies, 9:173– 284, Erlangen.
- GILI, J.P. & ROS, J., 1985. Study and cartography of the benthic communities of Medes Islands (NE Spain). — P.S.Z.N. I: Mar. Ecol., 6(3):219–238, Berlin.
- GOLDBERG, W.M., 1973. The ecology of the coraloctocoral communities off the southeast Florida coast: geomorphology, species composition and zonation. — Bull. mar. Sci, 23(3):465–488, Miami.
- GOMEZ, E.D. & ALCALA, A.C., 1984. Survey of Philippine coral reefs using transect and quadrat techniques. –
 [in:] Comparing coral reef survey methods. Unesco, Paris, Reports in marine science, 21:57–69, Paris.
- GOREAU, Th.F. & GOREAU, N.I., 1973. The ecology of Jamaican coral reefs. II. Geomorphology, zonation and sedimentary phases. — Bull. mar. Sci., 23(2):399–464, Miami.
- GRAUS, R.R. & MACINTYRE, I.G., 1989. The zonation patterns of Caribbean coral reefs as controlled by wave and light energy input, bathymetric setting and reef morphology: computer simulation experiments.—Coral Reefs, 8:9–18, Berlin.
- HISCOCK, K., 1987. Subtidal rock and shallow sediments using diving. – [in:] BAKER, J.M. & WOLFF, W.J. (eds.). Biological surveys of estuaries and coasts. – :198–237, Cambridge (Cambridge University Press).
- HUMMON, W.D., 1989. The fetch-energy index: an *a priori* estimator of coastal exposure, applied to littoral marine Gastrotricha of the British Isles. [in:] RY-LAND, J.S. & TYLER, P.A. (eds.). Reproduction, genetics and distribution of marine organisms. —:387–393, Fredensborg (Olsen & Olsen).
- HUSTON, M., 1985. Variation in coral growth rates with depth at Discovery Bay, Jamaica. Coral Reefs, 4:19–25, Berlin.
- KENNY, J.S., 1988. Hermatypic scleractinian corals of Trinidad.—Publ. Found. sci. Res. Surinam and Netherlands Antilles, 123:83–100, Amsterdam.
- LABOREL, J., 1974. West African reef corals: an hypothesis on their origin. – [in:] CAMERON, A.M., CAMP-BELL, B.M., CRIBB, A.B., ENDEAN, R., JELL, J.S., JONES, O.A., MATHER, P. & TALBOT, F.H. (eds.). Proceedings of the 2nd international coral reef symposium. — Great Barrier Reef Committee Brisbane, 1:425-443, Brisbane.
- LABOREL, J., 1982. Formations coralliens des Antilles françaises. Oceanis, **8**(4):339–353, Paris.
- LEBART, L., 1975. Validité des résultats en analyse des données. — Centre de Recherches et de Documentation sur la Consommation, Paris, L.L/cd No. 4465:1–157, Paris.
- LEWIS, J.B., 1989. The ecology of *Millepora*: a review. Coral Reefs, **8**:99–107, Berlin.

- LOGAN, A., 1988. Holocene reefs of Bermuda. Sedimenta, 11:1–63, Miami.
- LOYA, Y., 1978. Plotless and transect methods. [in:] STODDART, D.R. & JOHANNES, R.E. (eds.). Coral reefs: research methods. — Unesco, Paris, Monographs on oceanographic methodology, 5:197–217, Paris.
- MERGNER, H., 1977. Hydroids as indicator species for ecological parameters in Caribbean and Red Sea coral reefs. – [in:] TAYLOR, D.L. (ed.). Proceedings: 3rd international coral reef symposium.—Rosenstiel School of Marine and Atmospheric Science, Miami, 1:119– 125, Miami.
- MOORE, R.E. & SCHEUER, R.J., 1971. Palytoxin: a new marine toxin from a coelerenterate. Science, **172**:495–498, New York.
- MORRI, C., BAVESTRELLO, G. & BIANCHI, C.N., 1991. Faunal and ecological notes on some benthic cnidarian species from the Tuscan Archipelago and eastern Ligurian Sea (western Mediterranean). — Boll. Mus. Ist. biol. Univ. Genova, 54-55(1988–1989):27– 47, Genova.
- OTERO-SCHMITT, J., 1993. The communities of *Galaxaura* (Chaetangiaceae, Rhodophyta) at the Cape Verde Islands. – [in:] BISCOITO, M.J. & ABREU, A.D. (eds.). First Symposium "Fauna and Flora of the Atlantic Islands". Abstracts. — Museu Municipal do Funchal, and Delegação Regional da Madeira da Associação Portuguesa de Biologos:46, Funchal.
- PATRITI, G., 1970. Catalogue des Cnidaires et Cténaires des côtes atlantiques marocaines. — Trav. Inst. scient. chérifien, Sér. zool., 35:1–149, Rabat.
- PICHON, M., 1978. Recherches sur les peuplements à dominance d'anthozoaires dans les récifs coralliens de Tuléar (Madagascar). — Atoll Res. Bull., 222:1–447, Washington.
- PICHON, M., 1981. Dynamic aspects of coral reef benthic structures and zonation. – [in:] GOMEZ, E.D., BIRKE-LAND, C.E., BUDDEMEIER, R.W., JOHANNES, R.E., MARSH, J.A. & TSUDA, T. (eds.). The reef and man. Proceedings of the 4th international coral reef symposium. — Marine Sciences Center, University of the Philippines, Manila, 1:581–594, Manila.
- RIEDL, R., 1971. Water movement. Animals. [in:] KIN-NE, O. (ed.). Marine Ecology. Vol. 1. Environmental factors. Part 2. — :1123–1149, New York (J.Wiley & Sons).
- SCATTERDAY, J.W., 1974. Reefs and associated coral assemblages off Bonaires, Netherlands Antilles, and their bearing on Pleistocene and recent reef models. [in:] CAMERON, A.M., CAMPBELL, B.M., CRIBB, A.B., ENDEAN, R., JELL, J.S., JONES, O.A., MATHER, P. & TALBOT, F.H. (eds.). Proceedings of the 2nd international corals reef symposium. Great Barrier Reef Committee, Brisbane, 1:85–106, Brisbane.
- SCHLICHTER, D., 1982. Nutritional strategies of cnidarians: the absorption, translocation and utilization of dissolved nutrients by *Heteroxenia fuscescens*. — Amer. Zool., 22:659–669, Chicago.
- SCHMIDT, H., 1972. Prodomus zu einer Monographie der

mediterranen Aktinien. — Zoologica, **42**(2/121):1–146, Wien.

- TOMASCIK, T., 1991. Settlement patterns of Caribbean scleractinian corals on artificial substrata along a eutrophication gradient, Barbados, West Indies. — Mar. Ecol. Progr. Ser., 77:261–269, Halstenbek.
- VAN DEN HOEK, C., BREEMAN, A.M., BAK, R.P.M. & VAN BUURT, G., 1978. The distribution of algae, corals and gorgonians in relation to depth, light attenuation, water movement and grazing pressure in the fringing coral reef of Curaçao, Netherlands Antilles.
 Aquatic Botany, 5:1–46, Amsterdam.
- VREELAND, H.V. & LASKER, H.R., 1989. Selective feeding of the polychaete *Hermodice carunculata* Pallas on Caribbean gorgonians. — J. exp. mar. Biol. Ecol., 129:265–277, Amsterdam.
- WELLS, S.M., 1988. Coral reefs of the world. 1: Atlantic and Eastern Pacific. — U.N.E.P., Nairobi, and I.U.C.N., Gland and Cambridge: 1–373, Cambridge.
- WILDI, O. & ORLOCI, L., 1980. Management and multivariate analysis of vegetation data. — Swiss Federal Institute of Forestry Research, Rep. 215:1–68, Birmensdorf.