

## STRUCTURE AND DYNAMICS OF NORTH-WESTERN MEDITERRANEAN PHYTOBENTHIC COMMUNITIES: A CONCEPTUAL MODEL

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Received: January 1990

### SUMMARY

This paper describes the structural (species richness, species diversity, pattern-diversity, biomass, coverage, specific distribution, homogeneity) and functional (production, P/B ratio) changes observed during the annual cycles of eight phytobenthic Mediterranean communities by using PCA analysis. The first axis obtained discriminated between variables related to pattern-diversity and those related to production and coverage (production-diversification or P-D axis). The second axis was mainly related to biomass and homogeneity (biomass-heterogeneity or b-h axis). Shallow-water communities were positioned in the quadrant of the plane associated with high production while deep-water communities were located in the quadrant characterized by high diversification values. The transit of communities through this plane during their annual cycles suggests their idealization as geometric figures revolving clockwise along the plane defined by the P-D and the b-h axes. These changes allow the distinction of two phases and two stages in the annual cycle of the communities, according to the sequence: diversified community (high heterogeneity) → production phase (high production) → developed community (high biomass) → diversification phase (high pattern-diversity). Peak production occurs in spring for the mediolittoral communities and is delayed towards summer and autumn at increasing depths. This time lag affects the whole annual cycle described above and appears attributable to the adaptation of the different species and communities to the seasonal cycle of the main factors limiting their growth (BALLESTEROS, 1989b).

Although production and diversification are inversely related, P/B ratio is not negatively correlated with diversity because of the different mechanisms generating diversity in natural communities: disturbance and evolution. Short-time diversity increases in periods of intense physical disturbance (diversification phases) due to lack of dominance within the community and the growth of opportunistic species. Thus, short-term diversity and productivity are not inversely correlated. Long-term diversity increases along evolutionary time under environmental stability, explaining the greater diversity of deep-water communities compared to shallow ones, where an inverse correlation between productivity and diversity is observed.

An interannual model of the structural and functional performances of phytobenthic Mediterranean communities can be depicted over the plane defined by the P-D axis and the b-h axis by introducing time as a third axis. In general, the dynamics of persistent communities can be depicted as helicoidal trajectories whose turns represent annual cycles. This representation allows the adequate definition of concepts such as persistence, resistance and resilience of communities, and creates an adequate framework for describing successional processes and the effects of all kind of disturbances. The hypothesized existence of multiple stable points in natural communities closely agrees with the model if different degrees of non-punctual, biotic, disturbances are considered. In our opinion this model could also be extended to other temperate seas.

KEY WORDS: Phytobenthos, structure, dynamics, ecological modelling.

## STRUCTURE AND DYNAMICS OF BENTHIC MARINE COMMUNITIES: A REVIEW

Some of the concepts central to modern ecological theory (e.g., stability and predictability, succession and pattern formation, predation, competition and disturbance in community organization and dynamics, etc.) have been developed largely from the study of benthic ecosystems. This suggests that the structure and dynamics of benthic marine communities must be well understood. We do however, contend, together with SCHIEL & FOSTER (1986) that this is not the case, and base our assertion on the acute imbalance of our present knowledge of benthic ecosystems, which derives predominantly from the study of a few systems (e.g., kelp beds and fouling communities), and focuses mainly on the consequences of environmental forcing.

Most studies of benthic communities focus on intertidal systems (e.g. DAYTON, 1971, 1975; PAINE, 1974; LUBCHENKO & MENGE, 1978; SOUSA, 1979; NIELL, 1979; PAINE & LEVIN, 1981). Consequently, our knowledge of benthic ecosystems is biased towards the peculiarities of these systems. Moreover, whenever subtidal communities are studied, these are often kelp beds (DAYTON *et al.*, 1984; JOHNSON & MANN, 1988) or fouling communities (e.g. SUTHERLAND, 1974; OSMAN, 1977, 1978). Kelp beds are among the most productive ecosystems (MANN, 1972; JACKSON, 1977) and, thereby, support an enhanced energy flow and can undergo radical changes because of their low diversity and the high connectivity between the main components of these systems. On the other hand, fouling communities are essentially unstable and immature, so they are not representative of the more permanent communities that dominate the marine benthos. Thus, there is no guarantee that the results obtained in

these systems will be transferable to other benthic systems, given the great differences that exist among benthic communities both worldwide (ZABALA & BALLESTEROS, 1989) and in particular localities. In fact, the comparison of Atlantic and Pacific kelp beds has demonstrated significant differences in the dynamics of community organization and in the relative importance of the environmental factors that impinge upon them (DAYTON *et al.*, 1984; JOHNSON & MANN, 1988).

The majority of studies in benthic ecology have focused on the factors that control community organization (e.g., physical disturbances, competition, predation) and not on the organization (or structure) itself. As a result, the structural evolution of the communities has been inferred from experimentally induced changes or from changes caused by extreme natural disturbances. The different stages these perturbed communities leave behind have been used to describe the natural pattern of undisturbed communities and has led to the formulation of the multiple stable point hypothesis as the model which best describes the structure and function of highly dynamic systems such as fouling communities (SUTHERLAND & KARLSSON, 1977), communities growing over sandy bottoms (GRAY, 1977) and kelp beds (JOHNSON & MANN, 1988). As a result of the historical development of benthic ecology, most benthic ecosystems are depicted as intrinsically unstable, contrasting with the interannual constancy described for the epibiota of many areas (HISCOCK & MITCHELL, 1980). Moreover, the degree of stability or instability of benthic communities depends on the temporal and spatial scales at which they are examined, the relevant scale of observation depending on the research goals.

There is a paucity of studies of the dynamics of relatively undisturbed benthic communities. Despite extensive use of the

term normal-structured communities to refer to investigated communities, the reality is often that the structural and dynamic changes that the benthic communities of temperate seas experience during the year are generally unknown. Seasonal variations in the Mediterranean (FELDMANN, 1937; BALLESTEROS, 1984, 1987, 1988a, 1988b; VERLAQUE, 1987), as well as in other temperate (NEUSHUL, 1967; NIELL, 1975; HRUBY, 1975; LITTLER, 1980; FERNÁNDEZ *et al.*, 1983; CHOCK & MATHIESON, 1983; MATHIESON & PENNIMAN, 1986; MURRAY & HORN, 1989) and tropical seas (LAWSON, 1957; JOHN *et al.*, 1977; PRICE, 1989) often involve significant changes in community structure. Seasonal changes also involve changes in community structure and organization (HRUBY, 1975; SEAPY & LITTLER, 1982; FERNÁNDEZ *et al.*, 1983; BALLESTEROS, 1984, 1987, 1988a, 1988b), and in functional processes (MANN, 1973; GAGNE *et al.*, 1982; WHEELER & DRUEHL, 1986; BALLESTEROS, 1989b; TUSSENBROEK, 1989; KAIN, 1989). Some of this research focuses on specific attributes of the community (e.g., biomass, diversity, production, P/B ratios) and, while a model has been proposed to explain the seasonal changes in intertidal systems from temperate seas (NIELL, 1975, 1977), an accurate description of the annual cycles for the subtidal vegetation and for a large number of phytobenthic communities is as yet unavailable.

Our goal here is to develop a conceptual model of the dynamics of North-western Mediterranean phytobenthic communities. To achieve this goal we shall use data derived from the study of different communities from the phytal system (mediolittoral, infralittoral and circalittoral levels). The dynamics of these communities have been described within the framework of seasonal changes in structure and production. In addition to this seasonal model, we propose a model to

account for the long-term dynamics of benthic communities. We believe that the model derived for Mediterranean communities can easily be extended to phytobenthic communities, both subtidal and intertidal, in other temperate seas.

### SEASONALITY OF ENVIRONMENTAL FACTORS IN THE NORTH-WESTERN MEDITERRANEAN

Seasonal changes in the structure and function of phytobenthic communities derive from the seasonal nature of the dominant environmental factors. The seasonal variability of environmental factors in the NW Mediterranean Sea is, in general, similar to that observed in most other temperate seas. Potential differences, however, include lower variability, greater underwater irradiance and temperature, and lower nutrient concentrations than those usually observed in oceanic waters elsewhere in the temperate zone (Fig. 1). In addition, seasonal environmental variability differs across a trophic gradient, from the communities in the relatively eutrophic Gulf of Lions to those in oligotrophic insular areas (ZABALA & BALLESTEROS, 1989), although the extreme oligotrophy is found around the Balearic Islands which are traditionally considered as Central Mediterranean. In this paper, because our study is largely devoted to the phytobenthic communities of the North-western Mediterranean (mainly the Gulf of Lions and the Catalan coast), we focus on the annual cycle of environmental factors from this area (see Table I).

### PHYTOBENTHIC COMMUNITIES IN THE NORTH-WESTERN MEDITERRANEAN

The seasonal variability of environmental factors in the Mediterranean

TABLE I. Mean seasonal values of some physical and chemical parameters that affect phyto-benthic communities in coastal waters from a north-western Mediterranean locality (Tossa de Mar, NE Spain, year 1983). The extinction coefficient ( $K_{480}$ ) corresponds to a light with a wavelength of 480 nm. Nitrate and phosphate concentrations are expressed in micromols  $l^{-1}$  and temperature is expressed in degrees centigrade. Data from BALLESTEROS (1984)

Season	$K_{480}$	$NO_4^{3-}$	$PO_4^{3-}$	T	Physical disturbances
Winter	0.120	0.5-2.0	< 0.08	12-14	Violent storms (N winds) Becalmed waters (January)
Spring	0.114	< 1.0	< 0.06	15-20	High hydrodynamism (April) Low sea level (May, June)
Summer	0.090	< 0.1	< 0.03	21-25	High irradiance
Autumn	0.140	< 1.0	< 0.08	15-21	Violent storms (E winds) High hydrodynamism Heavy rains

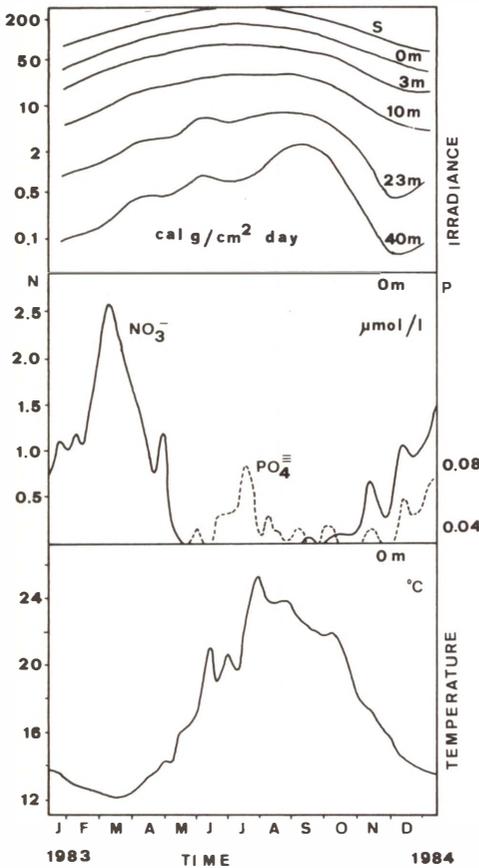


FIGURE 1. Annual cycle of irradiance, nutrient concentration and water temperature from a coastal locality of the North-western Mediterranean (Tossa de Mar, NE Spain). Data from BALLESTEROS (1984).

is similar to that in other temperate seas, but average values tend to be closer to those in tropical and subtropical seas. Kelps and corals have failed to master these phytal systems (ZABALA & BALLESTEROS, 1989), which are dominated by small, erect frondose algae in shallow waters (photophilic communities) and calcareous algae in localities with high densities of sea urchins (AUGIER & BOUDOURESQUE, 1974; VERLAQUE, 1987) and deep waters (sciaphilic communities, coralligenous; cf. ROS *et al.*, 1985). Because of the intensive studies of these communities, using phytosociological and other descriptive methods (FELDMANN, 1937; PÉRÈS & PICARD, 1964; BOUDOURESQUE, 1970, 1985; GIACCONE & BRUNI, 1972; COPPEJANS, 1977; BALLESTEROS, 1984; VERLAQUE, 1987; BOISSET, 1987), current knowledge of their floristic composition is, perhaps, greater than that for any other subtidal communities. One of the salient features of Mediterranean phyto-benthos is the tendency towards miniaturization (COPPEJANS, 1980; BOUDOURESQUE *et al.* 1980; BALLESTEROS, 1984) that allows the study of the communities using very small sample sizes. The high level of knowledge and the extreme miniaturization of phyto-benthic communities renders the Mediterranean a convenient location in which to examine the seasonal variations

of phytobenthic communities.

Zonation patterns, which are well-documented for the Mediterranean, are apparent despite the lack of significant tides (BALLESTEROS & ROMERO, 1988). FELDMANN (1937) established the zonation sequence for rocky bottoms in the Alberes Coast, which was found to adequately describe zonation patterns elsewhere in the Gulf of Lions and the Catalan Coast (ROS *et al.*, 1985). In moderately exposed areas of Tossa de Mar (NE Spain), the gradation of communities from the upper mediolittoral to the lower circalittoral (2 to 60 meters) comprises at least ten well-differentiated seaweed communities (Fig. 2). Their species composition, structure, dynamics, and the forcing environmental factors have been extensively studied by BALLESTEROS (1984, 1988a, 1988b, 1989a, 1990a, 1990b, 1991, in press a, b).

### A METHODOLOGICAL APPROACH TO THE SYNTHETIC DESCRIPTION OF NATURAL COMMUNITIES

Natural communities are generally described through their species composition, implemented with indicative values of their abundance. These values are often derived by using previously standardized scales (BRAUN BLANQUET, 1979) or by quantitative descriptors of abundance, such as the number of individuals, biomass or coverage (MARGALEF, 1974). Biomass (generally expressed as  $g\ dw\ m^{-2}$ ) and coverage (generally expressed as the percentage of surface covered) measurements have been widely used to characterize phytobenthic communities (BOUDOURESQUE, 1971; NIELL, 1974; ROMERO, 1984) because they are excellent indicators of abundance, each emphasizing different properties of benthic organisms (BALLESTEROS, 1986).

In addition, benthic communities are

often described by providing indication of their degree of structure, which is scale-dependent. This characteristic of benthic communities can be described through three main spectral parameters, namely species richness, diversity and homogeneity. Because of their spectral nature, the choice of the area in which to measure these parameters has important implications. Species/area relationships are exponential (GLEASON, 1925; HAWKINS & HARTNOLL, 1980), whereas diversity/area and homogeneity/area curves are asymptotic (NIELL, 1974; NÉDELEC, 1979; BALLESTEROS, 1986). Thus, it is often assumed that the value of each one of these parameters characterizing a particular community is the value achieved when its variation for successive increments in area is minimal. In practice, this minimal variation is assessed using subjective criteria, often consisting in the choice of the

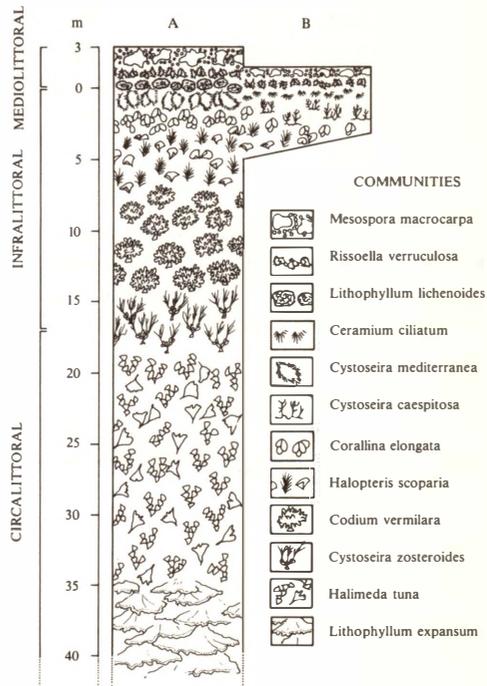


FIGURE 2. Diagrammatic representation of a typical transect in a moderately exposed place (A) and a sheltered place (B) from the Costa Brava (North-western Mediterranean)

abscissa where the curve achieves a particular slope as the relevant area. By using the same criteria to study different communities, the values obtained should be comparable. Obviously, the construction of the parameter/area relationship requires the sampling of much greater areas than the relevant area (GOUNOT, 1969). The area relevant to study the communities in Table II was estimated by sampling from areas nested within larger sampling areas (BALLESTEROS, 1986) and fitting species/area curves to a semilogarithmic function,

$$y = a \ln x + b \quad (1)$$

where  $y$  was the number of species and  $x$  the sampling area in  $\text{cm}^2$ . Species richness ( $R$ ) was estimated as the number of species corresponding to the Calleja point  $5 \times 10^{-2}$  (BALLESTEROS, 1986). Diversity was calculated with the Shannon index (MARGALEF, 1958; PIELOU, 1975), where coverage was used to measure abundance. Diversity/area curves were fitted to a Michaelis-Menten function,

$$y = Ax / B+x \quad (2)$$

where  $y$  was diversity in bits and  $x$  the sampling area in  $\text{cm}^2$ .  $A$ , an asymptotic value of  $y$ , has been considered a good estimate of species diversity or

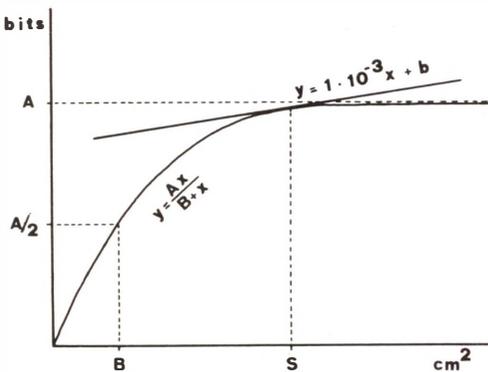


FIGURE 3. Meaning of parameters  $A$ ,  $B$  and  $S$  in a diversity/area curve fitted to a Michaelis-Menten function.

alpha-diversity in the sense of PIELOU (1977) (Fig. 3). The value of the Kulczynski index (BOUDOURESQUE, 1971; KRONBERG, 1987) obtained at half of the largest area sampled, where it always reached the asymptotic value, was used to estimate homogeneity.

Moreover, the shape of these curves reflects important structural features of the communities because it is related to their stability or persistence (MARGALEF, 1969). In fact, the same diversity indexes can be obtained with very different shapes of the diversity/area curve. The extreme shapes of the curves, flat or rectangular spectra and step or diagonal spectra (MARGALEF, 1980, 1985), are characteristic of communities with low and high pattern-diversities, respectively. We have attempted to estimate pattern-diversity (also known as spatial-diversity; PIELOU, 1966) by using two different parameters: (1) the parameter  $B$ , derived from equation 2, which indicates the size of the area at which the diversity index equals half the species diversity of the entire community (Fig. 3), and presents minimum and maximum values for communities with rectangular and diagonal spectra, respectively; and (2) the parameter  $S$ , defined as the area corresponding to the Calleja point  $1 \times 10^{-3}$  in the diversity/area curve fitted to equation 2 (Fig. 3). This parameter corresponds to the area at which diversity is practically stabilized (structural minimal area).

In addition, the shape of the species/area curve can be described by the parameter  $k$ , referred to as specific distribution (BALLESTEROS, 1986), which describe the change in the slope of the species/area curve at different areas. It is calculated as

$$k = e^{-b/a} \quad (3)$$

where  $a$  and  $b$  are derived from the semilogarithmic equation 1; it also corresponds to the value of  $k$  in the potential equation

$$x = k e^{ay} \quad (4)$$

derived from equation 1. Large  $k$  values correspond to communities where large sampling areas are necessary to obtain a representative number of the species in the community (BALLESTEROS, 1986).

From a functional perspective, a community can be described from its primary production, understood as the synthesis of organic matter by the plants (BALLESTEROS, 1989b). Thus, production is measured in units of biomass (g dw) produced per unit of time (days) and surface ( $m^2$ ). Another suitable measure is the ratio of primary production to total biomass (i.e., P/B ratio). The P/B ratio, or productivity, has often been related to the energy flow inside an ecosystem and, as such, is negatively correlated with diversity and with other measures of ecosystem organization (MARGALEF, 1968, 1969; NIELL, 1981; NIELL & VARELA, 1984). Production and P/B ratios are used here to describe the dynamics of phytobenthic communities.

#### SEASONAL CHANGES IN PARADIGMATIC COMMUNITIES: PRODUCTION AND DIVERSIFICATION PHASES

Although some authors have described seasonal variations in the species composition and the biomass of phytobenthic communities (e.g. MANN, 1972; JOSSELYN & WEST, 1985; MCQUAID, 1985; MURRAY & HORN, 1989), the description of significant changes in structural parameters such as the species/area curve (HRUBY, 1975) or diversity (NIELL, 1975; SEAPY & LITTLER, 1982; FERNÁNDEZ *et al.*, 1983) is rare, and the existence of persistent annual rhythms remains uncertain. However, seasonal phenomena are likely to influence dynamic processes from year

to year (PARKE, 1947; MANN, 1972).

We can depart from the description of the changes in some structural (species richness, species diversity, pattern diversity, coverage) and dynamic parameters (production, P/B ratio) in three thoroughly studied phytobenthic communities: the *Rissoella verruculosa* community (mediolittoral zone), the *Cystoseira mediterranea* community (infralittoral zone) and the *Halimeda tuna* community (circalittoral zone) (Fig. 4). Because a detailed description of the observed changes has been provided elsewhere (BALLESTEROS, 1984; 1988b), we focus here on the salient features and relationships within (A) and between (B) communities.

#### (A) WITHIN COMMUNITIES

1. Seasonal changes in community structure and function are evident in all three communities. Similar to the findings of NIELL (1977) for intertidal communities in the temperate Atlantic, the annual change can be separated into a diversification phase, characterized by a low production and P/B ratio, and a production phase, characterized by high production and P/B ratio. Community structure varies with these dynamic changes. Two opposite stages can be recognized as sequences in a continuum: a developed stage and a diversified stage. The developed stage is characterized by communities with high coverage (and biomass) and, often, low pattern-diversity. Conversely, the diversified stage is characterized by low coverage (and biomass) and high pattern-diversity. Species diversity and species richness do not show any distinct trends in the different stages.

2. An inverse relationship between the descriptors of structure (species diversity, pattern diversity, species richness), and coverage and production is apparent for the *Rissoella* and the *Cystoseira* communities, but not for the *Halimeda*, community. In

addition, the postulated negative correlation between P/B ratio and diversity (MARGALEF, 1969, 1980) is not apparent here.

(B) BETWEEN COMMUNITIES

1. The seasonality of the changes in the different parameters decrease with depth,

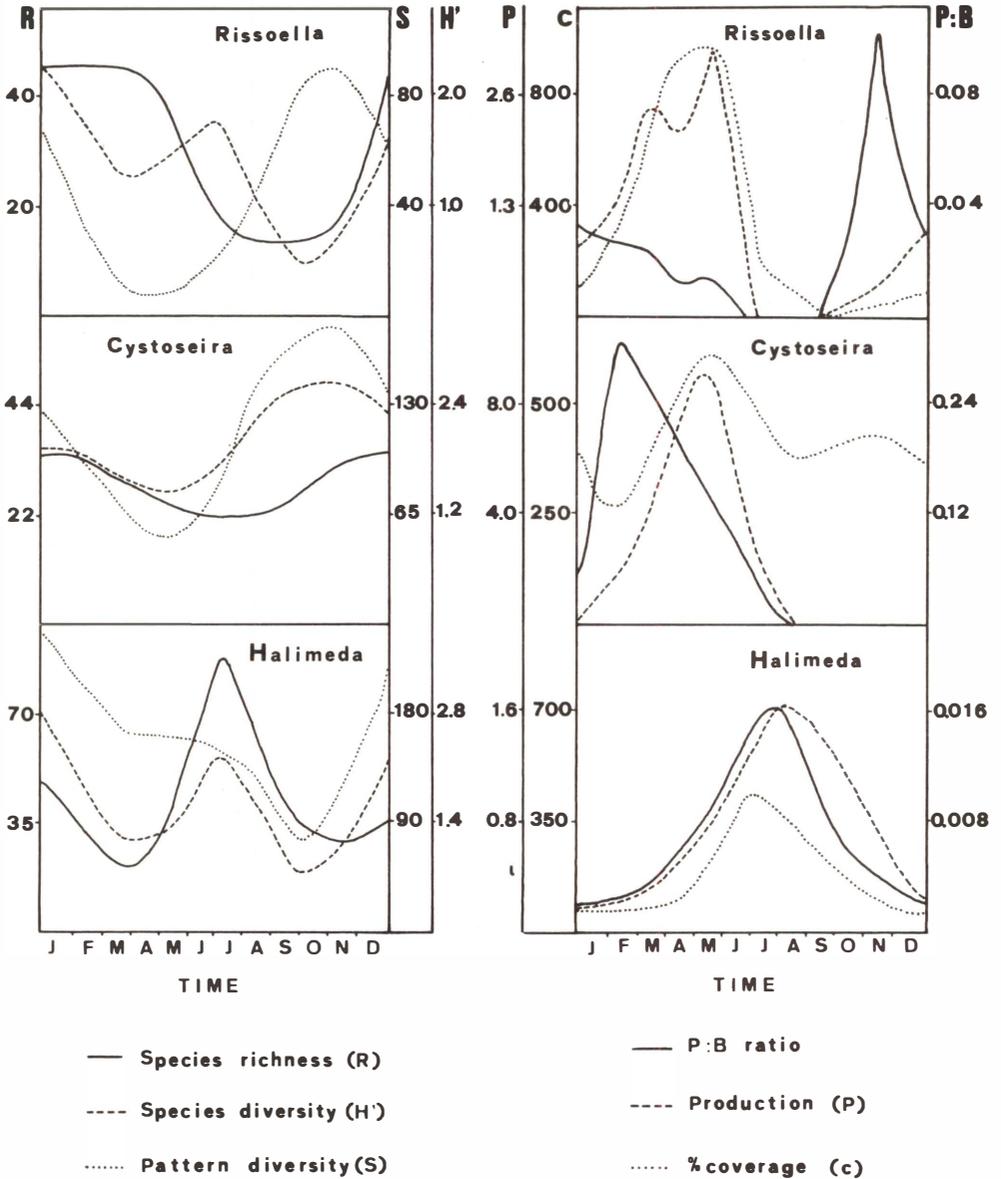


FIGURE 4. Annual variation in species richness, species diversity (in bits per individual), pattern diversity (in  $\text{cm}^2$ ), P/B ratio (in  $\text{days}^{-1}$ ), production (in  $\text{g C m}^{-2} \text{ day}^{-1}$ ) and % coverage in three selected communities from different bathymetric levels in the North-western Mediterranean: *Rissoella verruculosa*, *Cystoseira mediterranea* and *Halimeda tuna*. Data from BALLESTEROS (1984).



TABLE III. Rooted and ordered weight factors matrix.

Pattern diversity-B	0.913	-0.054	0.119
Pattern diversity-S	0.885	-0.283	0.203
Species diversity	0.665	-0.523	0.371
Specific distribution	0.551	0.007	-0.050
Production	-0.682	-0.040	0.033
Coverage	-0.604	-0.098	0.625
Biomass	0.092	0.785	-0.158
Homogeneity	-0.421	0.716	-0.030
Species richness	0.075	-0.187	0.745
P/B ratio	-0.375	-0.559	-0.601

communities. Because of their relationship to different variables, we shall refer hereafter to the axes as production-diversification axis (**P-D** axis) and biomass-heterogeneity axis (**b-h** axis), respectively.

The distribution of the communities studied and their seasonal variations in the plane defined by **P-D** and **b-h** axes is shown in figure 6. The following aspects may be noted:

(1) Communities are ordered along the first axis in relation to their diversification. Temporal variation in their structure appears to be similar for all communities. Ordering along the second axis reflects a biomass increment from low to high values.

(2) Annual cycles of communities are reflected in rotational clockwise paths along

the plane. The position of the communities at the different seasons reflects their structural and functional characteristics. The extremes of each axis can be considered as representative of the two phases and the two stages described before. Further, irregularities in the annual cycle are well reflected in the analysis. For instance, the *Ceramium ciliatum* community, which lacks annual periodicity, has an inverse rotation sense, but this may be peculiar to the year studied. Similarly, temporal discontinuities in structure and dynamics are well reflected in the analysis.

(3) Seasonal variation in the structure and dynamics of each community is proportional to the area comprised within the polygon that describes the seasonal path of the community. Thus, seasonal variations are greatest in *Cystoseira* species communities and are lowest in the *Lithophyllum tortuosum* community.

(4) Periods of peak production - which coincide with a minimum diversification - are attained in spring for the mediolittoral communities, and are progressively displaced to summer and autumn for increasing depths.

Thus, the patterns and trends suggested by the detailed analysis of three selected communities are confirmed when studying a greater number of communities. Thus, we think that these structural and functional patterns can be generalized to other Mediterranean phytobenthic communities.

#### A MODEL OF STRUCTURAL AND FUNCTIONAL DYNAMICS IN PHYTOBENTHIC COMMUNITIES FROM THE MEDITERRANEAN SEA

The model we propose to represent the seasonal variations in the Mediterranean phytobenthic communities is probably applicable to other temperate seas with a distinct growing season. The model considers that the majority of communities belonging to advanced successional stages

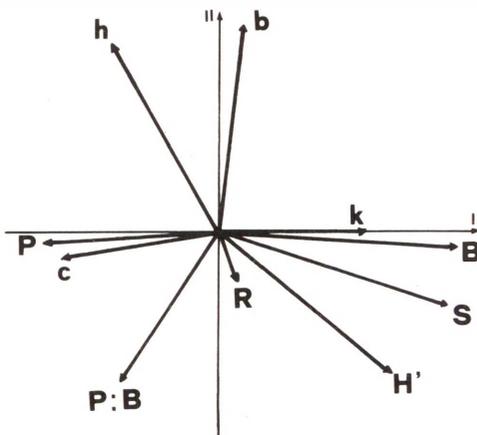


FIGURE 5. Projection of the original variables over the plane defined by the first and the second factorial axes. Symbols as in Table II.

have closed annual cycles that allow for the distinction between a production phase, when the dominant species has an intense growth, and a diversification phase, when a net biomass loss of the dominant species

is detected. Both phases end in two stages: the developed community and the diversified community. The developed community has high biomass and coverage values, a high vertical structuration and a

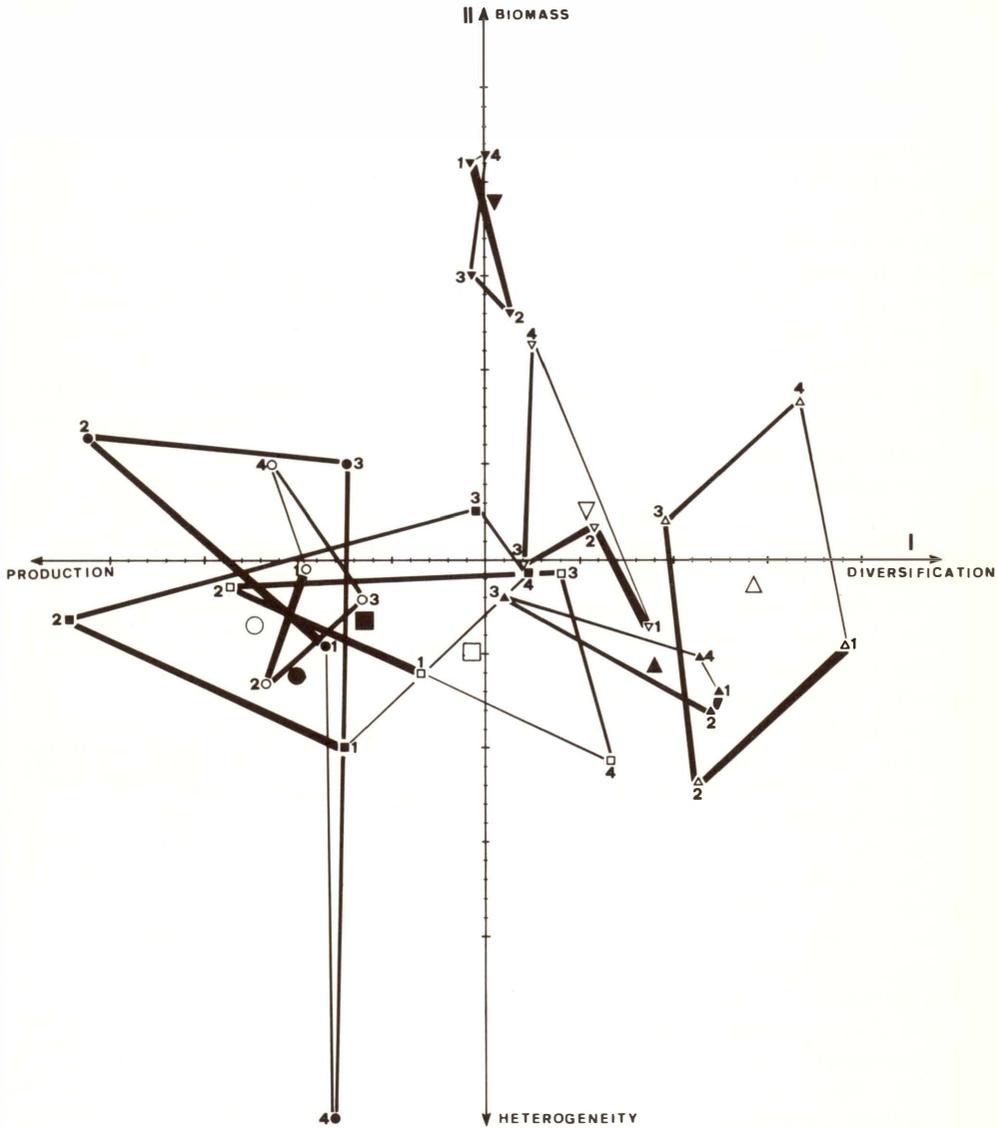


FIGURE 6. Communities representation over the plane defined by the first and the second factorial axes. Each community is represented by its position at each season (1-winter, 2-spring, 3-summer, 4-autumn) and by its average value. Communities are symbolized as follows: *Rissoella verruculosa* (full circles), *Lithophyllum lichenoides* (full reverse triangles), *Ceramium ciliatum* (open circles), *Cystoseira mediterranea* (full squares), *Cystoseira caespitosa* (open squares), *Codium vermilara* (full triangles), *Cystoseira zosteroides* (open triangles), *Halimeda tuna* (open reverse triangles).

high homogeneity, which causes a low diversification or pattern-diversity. The diversified community, in turn, has low values of biomass and coverage, low vertical structuration and significant horizontal heterogeneity, caused by the highly patchy distribution of encrusting and turf algae.

These structural and dynamic variations are evident in the plane defined by a production-diversification axis and a biomass-heterogeneity axis. The possibility of describing fluctuations in such a plane has recently been pointed out by MARGALEF (1989). The annual cycles may be represented by closed figures of diverse shapes which turn in a clockwise direction. The phases and stages described are arranged at the extremes of the two axes in communities with well defined annual cycles. Opportunistic algal communities also fluctuate along this plane, but their paths lack any directionality. This pattern can also be extrapolated to communities elsewhere showing similar production phases in the course of the year. The annual cycle of the communities may be idealized as circumferences whose diameter increases with the degree of seasonality (Fig. 7). In general, the diameter of these circumferences or other geometric figures describing the annual cycle of the communities decreases with increasing complexity. Therefore, it may be considered a good estimate of the energy flow through the community, as suggested by MARGALEF (1989).

The ordering of different communities according to different zonation levels can easily be discerned along the **P-D** axis and the **b-h** axis in relation to their structural and functional properties. The ordering basically follows the **P-D** axis and all the communities are distributed along this axis. Shallow-water communities, dominated by frondose algae, that have little structure and high P/B ratios, are distributed in the portion of the plane defined by high production. On the opposite side of the

axis, deep-water communities, characterized by their high diversification, predominate (Fig. 7).

The delay in peak production towards late summer at increasing depths is a general feature of phytoplanktonic Mediterranean systems (BALLESTEROS, 1989b) because of the typical temporal availability of light and nutrients. Shallow-water communities are often nutrient-limited (BALLESTEROS, 1989b) and, as such, have their period of maximum growth (production phase) in spring, coinciding with higher nitrate concentrations in seawater (Fig. 1). Deep-water communities are light-limited (BALLESTEROS, 1989b), and their annual cycle is accommodated to exploit the high summer irradiances in order to grow (Fig. 1). However, extrapolation of this depth-dependent delay to communities elsewhere still needs confirmation.

It is interesting to note that an inverse relationship between productivity and diversification is not apparent (Table II,

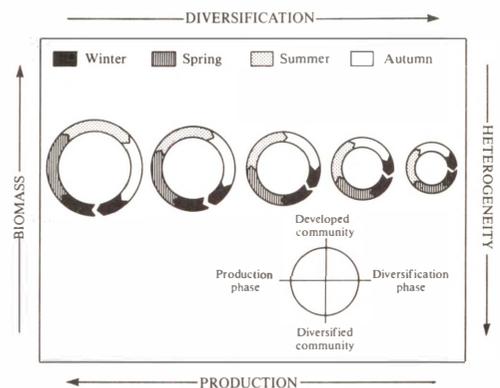


FIGURE 7. Hypothetical representation of the annual cycle of different Mediterranean phytoplanktonic communities from different bathymetric levels in the plane defined by a production-diversification axis (**P-D** axis) and a biomass-heterogeneity axis (**b-h** axis). Production and diversification phases correspond to the extremes of the **P-D** axis and developed community and diversified community stages are situated at the extremes of the **b-h** axis. A time lag in the different phases and stages from spring to summer and from shallow to deep water communities has been represented

Fig. 5). Nevertheless, in our opinion, the term diversification differs when applied to the annual cycle of a certain community or when referred to different communities. Within communities, the concept of diversification is not related to the classical meaning of structure, but to patchiness. High diversities only occur in diversification phases and, therefore, high pattern-diversities result from the spatial heterogeneity in the distribution of species within the community. In a developed community the diversity is usually minimal because of dominance of the main species in the community. On the other hand, the meaning of diversification among-communities corresponds to structure and organization, and is closer to the traditional interpretation (MARGALEF, 1974).

These observations allow us to reconsider the concepts of short-term (non-equilibrium) diversity and long-term (evolutionary) diversity suggested by SLOBODKIN & SANDERS (1969) and formulated by GRASSLE & SANDERS (1973). Short-term diversity reflects local effects and acts on a short time scale. Its variability is induced by small disturbances such as those involved in the annual cycle of temperate seas. The main increase in diversity within a community during an annual cycle results from a sudden increase in diversity at the end of the diversification phase, caused both by the lack of dominance inside the community and by the appearance of some new species. The new species can grow in this stage because of the reduced spatial competition, as predicted by the niche pre-emption model (WHITTAKER, 1975). This increase in diversity is often associated with periods of relatively intense physical disturbance caused by autumnal storms, corresponding to a maximum energy flow through the community. The transition to the production phase and to the developed community involves increased competition and subsequent competitive exclusion of species, yielding - in most Mediterranean

communities - communities dominated by a single species, with the associated reduction in diversity (but not necessarily in structure). Clearly, short-term diversity and productivity need not be inversely correlated, as observed by NIELL (1977) and FERNÁNDEZ *et al.* (1983). Instead, disturbances may be considered as mechanisms leading to increased species richness and diversity (DAYTON & HESSLER, 1972; ABELE, 1976; OSMAN, 1977; CONNELL, 1978). On the other hand, long-term diversity refers to the development of diversity through evolution, and it appears to increase with environmental stability. Long-term diversity agrees with the stability-time hypothesis of SANDERS (1968, 1969). Deep communities are more diverse than shallow communities (Fig. 6), so there is an inverse correlation between productivity and diversity on a between-communities scale.

Seasonal changes generate moderate environmental instabilities or disturbances which allow short-term diversity to operate. At another level, communities and their annual cycles are subject to long-term diversity changes, which result from an evolutionary tendency towards greater species richness and community organization in stable environments (Fig. 8). Indeed, mature communities (coralligenous) are diverse, and immature ones (mediolittoral zone) have low diversity (Fig. 7). Physical and biological disturbances - absorbed or not absorbed by the community - increase the P/B ratio (NIELL, 1981). This effect is apparent in the annual cycle of real communities (Fig. 6). The consequences of this process in our model would be the displacement of the communities - in the case of total destruction of the community - towards areas of the plane defined by low diversification and biomass values. Conversely, succession should transfer the communities to the portion of the plane corresponding to high values of diversification and biomass (Fig. 8).

Up to this point, we have referred community dynamics to the annual cycle, without considering interannual dynamics. Interannual dynamics can be incorporated into the model by considering time as a third axis (Fig. 9). In this implemented model, annual cycles are represented by a 360-degree turn around an ascending helicoidal trajectory that reflects the development of structural and functional community characteristics (Fig. 9). This ascending helix should have some irregularities which represent specific responses to disturbances or to deviations from the average annual behaviour of the environmental factors. Each turn of the helix is different from the others because of the unrepeatability of each and every one of the processes which determine the situation of each community at each moment.

Although the term stability is vague in ecology, it has been defined through three complementary properties (DAYTON *et al.*, 1984): persistence, resistance and resilience. Persistence is here associated to the height of the helix. Even though the community has some capacity to buffer disturbances, which are reflected in modifications of the helix, this capacity is

limited, and it is a function of the community resistance (amplitude stability in the sense of ORIAN, 1975). So, resistance can be figured as a cylinder, (which may be of irregular shape) including the helix (Fig. 9). If disturbance is sufficiently strong, the helix can break and go beyond the limits of the cylinder (Fig. 9). This breakage represents the disappearance of the community and it is always linked to a change in the species assemblage. The new trajectory moves towards lower values of biomass and diversification (Figs. 8 and 9). If disturbance is punctual, the new assemblage may evolve following a successional sequence, perhaps restoring the original community. The time necessary to complete this sequence should be inversely related to its resilience (Fig. 9). The process of succession would be ruled by different phases (HUVÉ, 1974), depending on the intensity of the disturbance. Each phase has its own cycle which may have an annual or lower periodicity, and it moves along the plane defined by the **P-D** and the **b-h** axes. FERNÁNDEZ *et al.* (1981) distinguish different phases, each one with two stages named development moments and transient moments. The energy flow through the community is minimized and the community structure is improved during the development moments, while the transient moments correspond to surges of energy flow (high P/B ratios) through the community. Although this pattern has been described to explain succession in rocky intertidal systems from the temperate Atlantic, it may adequately describe the successional sequence of sublittoral communities and can be easily introduced into our model. Development moments have a very similar performance to the diversification phase, and transient moments have similar properties to the diversification phase. Succession phases reproduce in shorter periods of time and, perhaps more importantly, the annual dynamics of

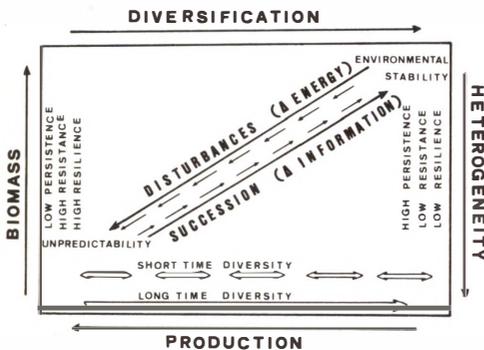


FIGURE 8. Tendencies of change caused by disturbances and succession in the plane defined by the **P-D** axis and the **b-h** axis. The role of short-term diversity and long-time diversity and the main characteristics of community stability at the two extremes of the **P-D** axis are also represented.

normally-constituted phyto-benthic communities.

If the disturbance acts for a long period of time (e.g. an increase of herbivory, some human modifications), the community cannot return to its original state and, thus, it would be stationed at another position on the plane, with its own annual cycle and its own stability properties. This scenario supports the theory that predicts the existence of multiple stable points in natural communities (SUTHERLAND, 1974). At each depth different communities (or stable points) coexist and this

determines the patchy aspect that characterizes the rocky bottoms in temperate seas. The coexistence of different multiple stable points at the same depth and in places subject to similar mean inputs of exosomatic energy, can only be explained if different degrees of biotic or abiotic disturbance are considered. The most usual and well studied situation derives from an excessive grazing pressure by sea-urchins, a situation which has been described in oceanic communities (MANN, 1977) as well as in Mediterranean ones (VERLAQUE, 1987).

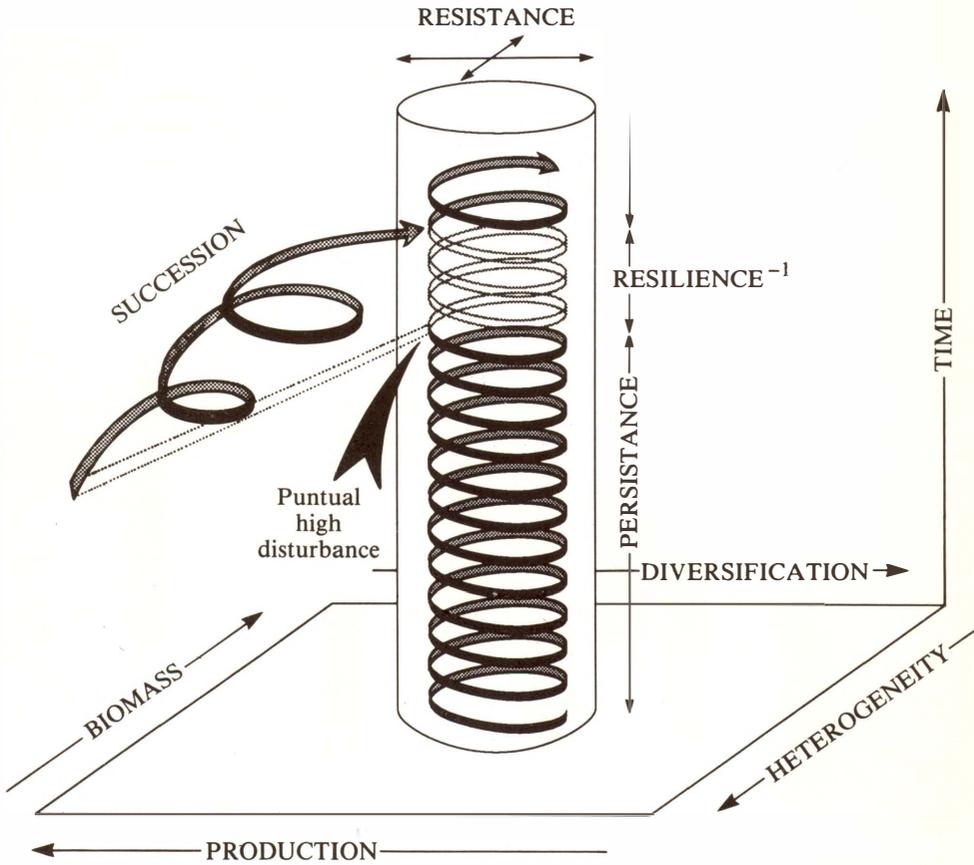


FIGURE 9. Three-dimensional representation of the community dynamics over a long period of time. Each turn of the helix corresponds to an annual cycle. Persistence, resistance and resilience of the community are easily defined in the figure. High disturbances that cannot be absorbed by the community, and the subsequent succession pattern that the new assemblage undergoes after the disturbance, are also schematically represented

In general, the dynamics of the persistent communities from temperate seas can be depicted as helices whose turns represent annual cycles along the plane defined by a **P-D** axis and a **b-h** axis (Fig. 10). The transfer from one community to another is usually rare (i.e., the probability of such a change occurring is very low) because the community structure and dynamics correspond largely to mean values of the physical environment. As an example, a *Cystoseira mediterranea* community will never turn into an *Halimeda tuna* community. However, the existence of some different communities at, for example, the same depth, may be related to catastrophic events or to disturbances attributed to biotic factors. Under these conditions, community interconversion has a certain, time-dependent, non-zero probability of occurring. A good example is provided by the different communities (or multiple stable points) described in

Mediterranean photophilic algae communities according to predation intensity by sea-urchins (VERLAQUE, 1987).

When the model is extrapolated to evolutionary time scales, it is obvious that communities would not persist as rigid cylinders, but would oscillate. The extent of oscillation may be a function of the change in qualitative and quantitative species composition, or in species characteristics. These oscillations may also be interpreted as changes in the interconversion probabilities between different stable points. However, natural selection operates over the individuals belonging to some species, and evolutionary changes in species modify, in turn, the structural and functional performances of communities. Thus, it is difficult to introduce the role of evolution into the model proposed. From a different perspective, two main forces can be assumed to modulate long-term

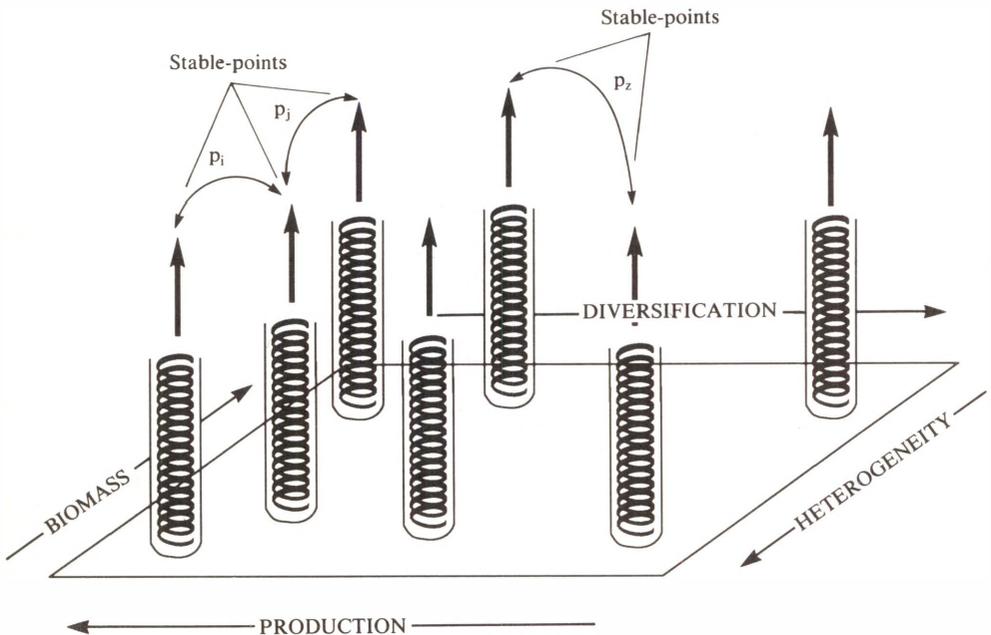


FIGURE 10. Dynamics of some different phytoplankton communities in the space defined by a production-diversification axis, a biomass-heterogeneity axis, and time. Conversion from one community to another is only possible if they are successionaly related or they belong to a bathymetric level with the same energy inputs. Interconversion probabilities may change along evolutionary time.

ecosystem dynamics: environmental stability and disturbances (CONNELL, 1978; WALBRAN *et al.*, 1989). Under stable conditions, communities would tend to increase diversity, accumulate information and use the energy to create persistent structures, minimizing the diameter of the helixes and, sometimes, their resistance. Systems would become more mature, in the classic sense of MARGALEF (1963, 1975). Disturbances would act in the opposite sense. The result is the aspect of the submerged world, scattered into different communities, each one adapted to particular environmental conditions and determined by a series of unavoidable historical factors.

### ACKNOWLEDGEMENTS

Firstly, R. Margalef and J. Romero suggested applying a PCA analysis to data

obtained from different phyto-benthic communities in the course of my Ph. D. thesis. Help in the numerical treatment was provided by J. Romero and O. Delgado.

M. Zabala and A. García were present in a stage in the island of Cabrera, when the conceptual model was established; creative discussions with them served to elaborate the model. J. Romero, C.M. Duarte, J. Camp, J. Flos, M. Zabala, M. J. Uriz and other members of the Centre d'Estudis Avançats, the Department of Ecology of the University of Barcelona and the Institut de Ciències del Mar, helpfully commented on the model and gave me some ideas to be exploited in the future.

C.M. Duarte kindly revised the original text and thoroughly corrected and improved the English version. J. Corbera and my father carefully drew the most difficult figures. The author is grateful to all for their assistance.

### REFERENCES

- ABELE, L.G. 1976. Comparative species richness in fluctuating and constant environments: coral-associated decapod crustaceans. *Science*, 192: 461-463.
- AUGIER, H. & BOUDOURESQUE, C.F. 1974. Dix ans de recherches dans la zone marine du parc national de Port-Cross (France). Deuxième partie. *Ann. Soc. Sci. nat. Archeol. Toulon. Var.*, 26: 119-150.
- BALLESTEROS, E. 1984. *Els vegetals i la zonació litoral: espècies, comunitats i factors que influeixen en la seva distribució*. Ph. D. Thesis. University of Barcelona.
- BALLESTEROS, E. 1986. Métodos de análisis estructural en comunidades naturales, en particular del fitobentos. *Oecol. Aquat.*, 8: 117-131.
- BALLESTEROS, E. 1987. Estructura i dinàmica del poblament algal de les fulles de *Posidonia oceanica* (L.) Delile als herbeis de Tossa de Mar (Girona). *Butll. Inst. Cat. Hist. Nat.*, 54 (Sec. Bot., 6): 13-30.
- BALLESTEROS, E. 1988a. Composición y estructura de la comunidad infralitoral de *Corallina elongata* Ellis & Solander de la Costa Brava (Mediterráneo Occidental). *Inv. Pesq.*, 52(1): 135-151.
- BALLESTEROS, E. 1988b. Estructura y dinàmica de la comunidad de *Cystoseira mediterranea* Sauvageau en el Mediterráneo Noroccidental. *Inv. Pesq.*, 52(3): 313-334.
- BALLESTEROS, E. 1989a. Estructura y dinàmica de la comunidad infralitoral de *Codium vermilara* (Oliv.) Delle Chiaje de la Costa Brava (Mediterráneo Occidental). *Anales de Biología*, 19 (B. Ambiental, 5): 73-90.
- BALLESTEROS, E. 1989b. Production of seaweeds in North-western Mediterranean marine communities: its relation with environmental factors. *Topics in Marine Biology. (Sci. Mar.)*, 53, 2-3: 357-364.
- BALLESTEROS, E. 1989c. El bentos coster: estructura i procés. *Revista de Catalunya*, 30: 48-55.
- BALLESTEROS, E. 1990 a. Structure and dynamics of the community of *Cystoseira caespitosa* Sauvageau (Fucales, Phaeophyceae) in the North-western Mediterranean. *Sci. Mar.*, 54(2): 155-168.
- BALLESTEROS, E. 1990 b. Structure and dynamics of the community of *Cystoseira zosteroides* (Turner) C. Agardh (Fucales, Phaeophyceae) in the North-western Mediterranean. *Sci. Mar.*, 54(3): 217-229.
- BALLESTEROS, E. 1991. Structure and dynamics of the community of *Rissoella verruculosa* (Bertolini) J. Agardh (Gigartinales, Rhodophyceae) in the North-western Mediterranean. *Sci. Mar.*, 55(2): 439-451.
- BALLESTEROS, E. in press a. Growth, production and dynamics of a deep-water population of *Halimeda tuna* (Chlorophyceae, Caulerpaceae) in the North-western Mediterranean. *Bot. Mar.*

- BALLESTEROS, E. in press b. Structure of a deep-water population of *Halimeda tuna* (Chlorophyceae, Caulerpales) in the North-western Mediterranean. *Collect. Bot.*
- BALLESTEROS, E. & ROMERO, J. 1988. Zonation patterns in tideless environments (Northwestern Mediterranean): looking for discontinuities in species distributions. *Inv. Pesq.*, 52(4): 595-616.
- BOISSET, F. 1987. *Estudio del fitobentos esciáfilo infralitoral de sustratos duros en el litoral valenciano (España). Flora y vegetación. Tesis Doctoral. Universidad de Valencia.*
- BOUDOURESQUE, C.F. 1970. *Recherches de bionomie analytique, structurale et expérimentale sur les peuplements benthiques superficiels en Méditerranée Occidentale (fraction algale)*. Thèse. Université d'Aix-Marseille II.
- BOUDOURESQUE, C.F. 1971. Méthodes d'étude qualitative et quantitative du benthos (en particulier du phytobenthos). *Téthys*, 3(1): 79-104.
- BOUDOURESQUE, C.F. 1985. Groupes écologiques d'algues marines et phytocoenoses benthiques en Méditerranée Occidentale: une revue. *Giorn. Bot. ital.*, 118 (suppl.): 7-42.
- BOUDOURESQUE, C.F., MARCOT-COQUEUGNIOT, J., NÉDELEC, H., PERRET-BOUDOURESQUE, M. & BELSHER, T. 1980. Le phytobenthos d'un port méditerranéen, Port-Vendres. *Compt. rend. 105 cong. Nat. Soc. Sav. Caen Sci.*, 3: 261-273.
- BRAUN-BLANQUET, J. 1979. *Fitosociología*. Blume. Madrid.
- CHOCK, J.S. & MATHIESON, A.C. 1983. Variations of New England estuarine seaweed biomass. *Bot. Mar.*, 26: 87-97.
- CONNELL, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*, 199: 1033-1034.
- COPPEJANS, E. 1977. *Bijdrage tot de studie van der wierpopulaties (Chlorophyceae, Phaeophyceae, Rhodophyceae) van het fotofiel infralitoraal in het noordwestelijk mediterranean bekken*. Doktoraat Thesis. Rijksuniversiteit Gent.
- COPPEJANS, E. 1980. Phytosociological studies on mediterranean algal vegetation: rocky surfaces of the photophilic infralittoral zone. In: *The shore environment. Ecosystems*. (J.H. PRICE, D.E.G. IRVINE & W.F. FARNHAM, eds.): 371-393. Academic Press. London.
- DAYTON, P.K. 1971. Competition, disturbance and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecol. Monogr.*, 41: 351-389.
- DAYTON, P.K. 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. *Ecol. Monogr.*, 45: 137-159.
- DAYTON, P.K. & HESSLER, R.R. 1972. The role of disturbance in the maintenance of deep-sea diversity. *Deep Sea. Res.*, 19: 199-208.
- DAYTON, P.K., CURRIE, V., GERRODETTE, T., KELLER, B.D., ROSENTHAL, R. & TRESKA, D.V. 1984. Patch dynamics and stability of some California kelp communities. *Ecol. Monogr.*, 54(3): 253-289.
- FELDMANN, J. 1937. Recherches sur la végétation marine de la Méditerranée: la côte des Albères. *Rev. Algol.*, 10: 1-339.
- FERNÁNDEZ, M.C., NIELL, F.X. & FUENTES, J.M. 1981. Remarks on succession in rocky intertidal systems. *Proceed. Xth Int. Seaweed Symp.*: 283-288. Walter de Gruyter. Berlin.
- FERNÁNDEZ, M.C., NIELL, F.X. & ANADÓN, R. 1983. Comparación de dos comunidades de horizontes intermareales con abundancia de *Bifurcaria bifurcata* Ros. en las costas N y NO de España. *Inv. Pesq.*, 47(3): 435-455.
- GAGNÉ, J.A., MANN, K.H. & CHAPMAN, A.R.O. 1982. Seasonal patterns of growth and storage in *Laminaria longicuris* in relation to differing patterns of availability of nitrogen in the water. *Mar. Biol.*, 69: 91-101.
- GIACCONE, G. & BRUNI, A. 1972. Le cistoseire e la vegetazione sommersa del Mediterraneo. *Att. Inst. Veneto Sci. Lett. Art.*, 81: 59-103.
- GLEASON, H.A. 1925. Species and area. *Ecology*, 6: 66-74.
- GOUNOT, M. 1969. *Méthodes d'étude quantitative de la végétation*. Masson. Paris.
- GRASSLE, J.F. & SANDERS, H.L. 1973. Life histories and the role of disturbance. *Deep Sea Res.*, 20: 643-659.
- GRAY, J.S. 1977. The stability of benthic ecosystems. *Helgol. wiss. Meeres.*, 30: 427-444.
- HAWKINS, S.J. & HARTNOLL, R.G. 1980. A study of the small-scale relationship between species number and area on a rocky shore. *Estuar. Coast. Mar. Sci.*, 10: 201-214.
- HISCOCK, K. & MITCHELL, R. 1980. The description and classification of sublittoral epibenthic ecosystems. In: *The shore environment. Ecosystems*. (J.H. PRICE, D.E.G. IRVINE & W.F. FARNHAM, eds.): 323-370. Academic Press. London.
- HRUBY, T. 1975. Seasonal changes in two algal populations from the coastal waters of Washington state. *J. Ecol.*, 63: 881-889.
- HUVÉ, P. 1974. Considérations sur la genèse de quelques peuplements algues benthiques de Méditerranée Occidentale: les étapes, stades, phases. *Bull. Soc. Phycol. Fr.*, 19: 101-120.
- JACKSON, G.A. 1977. Nutrients and production of giant kelp *Macrocystis pyrifera* of southern California. *Limnol. Oceanogr.*, 22: 979-995.
- JOHN, D.M., LIEBERMAN, D. & LIEBERMAN, M. 1977. A quantitative study of the structure and dynamics of benthic subtidal algal vegetation in Ghana (Tropical West Africa). *J. Ecol.*, 65: 497-521.
- JOHNSON, G.R. & MANN, K.H. 1988. Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. *Ecol. Monogr.*, 58(2): 129-154.
- JOSSELYN, M.N. & WEST, J.A. 1985. The distribution and temporal dynamics of the estuarine macroalgal community of San Francisco Bay. *Microbiol.*, 129: 139-152.
- KAIN, J. 1989. The seasons in the subtidal. *Br. Phycol. J.*, 24: 203-215.
- KRONBERG, I. 1987. Accuracy of species and abundance minimal areas determined by similarity area curves. *Mar. Biol.*, 96: 555-561.
- LAWSON, G.W. 1957. Seasonal variation of intertidal zonation on the coast of Ghana in relation to tidal factors. *J. Ecol.*, 45: 831-860.

- LEGENDRE, L. & LEGENDRE, P. 1979. *Écologie numérique*. Masson. Paris.
- LITTLER, M.M. 1980. Southern California rocky intertidal ecosystems: methods, community structure and variability. In: *The shore environment. Ecosystems*. (J.H. PRICE, D.E.G. IRVING & W.F. FARNHAM eds.): 565-608. Academic Press. London.
- LUBCHENCO, J. & MENGE, B.A. 1978. Community development and persistence in a low rocky intertidal zone. *Ecol. Monogr.*, 59: 67-94.
- MANN, K.H. 1972. Ecological energetics of the seaweed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. *Mar. Biol.*, 14: 199-209.
- MANN, K.H. 1973. Seaweeds: their productivity and strategy for growth. *Science*, 182: 975-981.
- MANN, K.H. 1977. Destruction of kelp beds by sea-urchins: a cyclical phenomenon or irreversible degradation? *Helgol. wiss. Meeres.*, 30: 455-467.
- MARGALEF, R. 1958. Information theory in ecology. *Gen. Syst.*, 3: 36-71.
- MARGALEF, R. 1963. On certain unifying principles in ecology. *Am. Nat.*, 97: 357-374.
- MARGALEF, R. 1968. *Perspectives in ecological theory*. Chicago University Press. Chicago.
- MARGALEF, R. 1969. Diversity and stability: a practical proposal and a model of interdependence. *Brookh. Symp. Biol.*, 22: 25-37.
- MARGALEF, R. 1974. *Ecología*. Omega. Barcelona.
- MARGALEF, R. 1975. Diversity, stability and maturity in natural ecosystems. In: *Unifying concepts in ecology*. (W.H. VAN DOBBEN & R.H. LOWE-MC CONNELL, eds.): 139-150. Junk. The Hague.
- MARGALEF, R. 1980. *La Biosfera, entre la termodinámica y el juego*. Omega. Barcelona.
- MARGALEF, R. 1985. From hydrodynamic processes to structure (information) and from information to process. *Can. Bull. Fish. Aquat. Sci.*, 213: 200-220.
- MARGALEF, R. 1989. Reflexiones sobre la diversidad y significado de su expresión cuantitativa. *Simposio sobre la Diversidad Biológica*. Madrid.
- MATHIESON, A.C. & PENNIMAN, C.A. 1986. Species composition and seasonality of New England seaweeds along an open coastal-estuarine gradient. *Bot. Mar.*, 29: 161-176.
- MC QU Aid, C.D. 1985. Seasonal variation in biomass and zonation of nine intertidal algae in relation to changes in radiation, sea temperature and tidal regime. *Bot. Mar.*, 28: 539-544.
- MURRAY, S.N. & HORN, M.H. 1989. Seasonal dynamics of macrophyte populations from an Eastern North Pacific rocky intertidal habitat. *Bot. Mar.*, 32: 457-473.
- NÉDELEC, H. 1979. *Étude structural et problèmes d'échantillonnage dans une phytocoenose portuaire*. Mém. Univ. P. et M. Curie. Marseille-Luminy.
- NEUSHUL, M. 1967. Studies of subtidal vegetation in Western Washington. *Ecology*, 48: 83-94.
- NIELL, F.X. 1974. Les applications de l'index de Shannon à l'étude de la végétation intertidale. *Soc. Phycol. Fr. Bull.*, 19: 238-254.
- NIELL, F.X. 1975. *Estudios sobre la estructura, dinámica y producción del fitobentos intermareal (facies rocosa) de la ría de Vigo*. Tesis Doctoral. Universidad de Barcelona.
- NIELL, F.X. 1977. Rocky intertidal benthic systems in temperate seas: a synthesis of their functional performances. *Helgol. wiss. Meeres.*, 30: 315-333.
- NIELL, F.X. 1979. Structure and succession in rocky algal communities of a temperate intertidal system. *J. Exp. Mar. Biol. Ecol.*, 36(2): 185-200.
- NIELL, F.X. 1981. Estructuras disipativas en la organización de los sistemas bentónicos. *Oecol. Aquat.*, 5: 239-245.
- NIELL, F.X. & VARELA, M. 1984. Initial colonization stages on rocky coastal substrates. *Mar. Ecol.*, 5(1): 45-56.
- ORIAN, G.H. 1975. Diversity, stability and maturity in natural ecosystems. In: *Unifying concepts in ecology*. (W.H. VAN DOBBEN & R.H. LOWE-MC CONNELL, eds.): 139-150. Junk. The Hague.
- OSMAN, R.W. 1977. The establishment and development of a marine epifaunal community. *Ecol. Monogr.*, 47: 5763.
- OSMAN, R.W. 1978. The influence of seasonality and stability on the species equilibrium. *Ecology*, 59(2): 383-399.
- PAINE, R.T. 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, 15: 93-120.
- PAINE, R.T. & LEVIN, S.A. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. *Ecol. Monogr.*, 51: 145-178.
- PARKE, M. 1947. Studies on British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. *J. Mar. Biol. Ass. U.K.*, 27: 651-709.
- PÉRÈS, J.M. & PICARD, J. 1964. Nouveau manuel de bionomie benthique de la mer Méditerranée. *Rec. Trav. St. Mar. Endoume*, 31(47): 1-137.
- PIELOU, E.C. 1966. Species diversity and pattern diversity in the study of ecological succession. *Theor. Biol.*, 10: 370-383.
- PIELOU, E.C. 1975. *Ecological diversity*. John Wiley. New York.
- PIELOU, E.C. 1977. *Mathematical ecology*. John Wiley. New York.
- PRICE, I.R. 1989. Seaweed phenology in a tropical Australian locality (Townsville, North Queensland). *Bot. Mar.*, 32: 399-406.
- ROMERO, J. 1984. Relaciones entre unidades de volumen y unidades de biomasa en distintas especies de algas bentónicas. Aplicaciones a evaluaciones de biomasa del fitobentos. *Oecol. Aquat.*, 7: 37-42.
- ROS, J., ROMERO, J., BALLESTEROS, E. & GILI, J.M. 1985. Diving in blue water: the benthos. In: *Western Mediterranean* (Margalef, R., ed.): 233-295. Pergamon. Oxford.
- SANDERS, H.L. 1968. Marine benthic diversity: a comparative study. *Am. Nat.*, 102: 243-282.
- SANDERS, H.L. 1969. Benthic marine diversity and the stability-time hypothesis. *Brookh. Symp. Biol.*, 22: 71-80.
- SCHIEL, D.S. & FOSTER, M.S. 1986. The structure of subtidal algal stands in temperate waters. *Oceanogr. Mar. Biol. Ann. Rev.*, 24: 265-307.

- SEAPY, R.R. & LITTLER, M.M. 1982. Population and species diversity fluctuations in a rocky intertidal community relative to severe aerial exposure and sediment burial. *Mar. Biol.*, 71: 87-96.
- SLOBODKIN, L.B. & SANDERS, H.L. 1969. On the contribution of environmental predictability to species diversity. *Brookh. Symp. Biol.*, 22: 82-92.
- SOUSA, W.P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.*, 49(3): 227-254.
- SUTHERLAND, J.P. 1974. Multiple stable points in natural communities. *Am. Nat.*, 108: 859-873.
- SUTHERLAND, J.P. & KARLSSON, R.H. 1977. Development and stability of the fouling community at Beaufort, North Carolina. *Ecol. Monogr.*, 47: 425-446.
- TUSSENBROEK, B.I. 1989. Seasonal growth and competition of fronds of *Macrocystis pyrifera* in the Falkland islands. *Mar. Biol.*, 100: 419-430.
- VERLAQUE, M. 1987. *Contribution à l'étude du phytobenthos d'un écosystème photophile thermophile marin en Méditerranée Occidentale*. Thèse. Université d'Aix-Marseille.
- WALBRAN, P.D., HENDERSON, R.A., TIMOTHY JULL, A.J. & JOHN HEAD, M. 1989. Evidence from sediments of long-term *Acanthaster planci* predation on corals of the Great Barrier Reef. *Science*, 245: 847-850.
- WHEELER, W.N. & DRUEHL, L.D. 1986. Seasonal growth and productivity of *Macrocystis integrifolia* in British Columbia, Canada. *Mar. Biol.*, 90: 181-186.
- WHITTAKER, R.M. 1975. *Communities and ecosystems*. Mc Millan. New York.
- ZABALA, M. & BALLESTEROS, E. 1989. Surface-dependent strategies and energy flux in benthic marine communities, or why corals do not exist in the Mediterranean. *Sci. Mar.*, 53(1): 3-17.