Surface-dependent strategies and energy flux in benthic marine communities or, why corals do not exist in the Mediterranean*

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SUMMARY: Most structure-building organisms in rocky benthic communities are surface-dependent because their energy inputs depend mainly on the surface they expose to water. Two photosynthetic strategies, divided into calcareous and non calcareous algae, strict suspension-feeders and photosynthetic suspension feeders (e.g. hermatypic corals) are the four main strategies evolutively acquired by benthic organisms. Competition between those strategies occur in relation to productivity of the different species, in such a way that, for given environmental conditions, species with a higher growth (P/B ratio) would dominate. At a worldwide scale, littoral marine benthos can be considered to fit into the four fields defined by two main axes: the first, relates to productivity and relies eutrophic and oligotrophic waters and the second is defined by the degree of environmental variability or seasonality (from high to low). Coral reefs (marine ecosystems dominated by photosynthetic suspension feeders) develop in the space of oligotrophic areas with low variability, while kelp beds (marine ecosystems dominated by large, non calcareous algae) are to be found only in eutrophic places with a high variability. The space of eutrophic waters with a low variability do not has specially adapted, high structured, benthic marine ecosystems, and in these conditions opportunistic algae and animals predominate. Finally, photophilic mediterranean benthos — devoid of kelps and without hermatypic corals — typifies the field of oligotrophic areas with high variability; in its more genuine aspect, Mediterranean benthos is represented by small algae with a high percentage of calcareous thallii. In all cases strict suspension-feeders compete successfully with photosynthetic organisms only in situations of low irradiances or very high inputs of POM. In its turn, Mediterranean rocky benthos, in spite of its relative uniformity, is geographically organized along the same axes. The Gulf of Lions and the insular bottoms (Balearic Islands, for example) would correspond to the extremes of eutrophic-high variability areas and oligotrophic-low variability areas, respectively. Irradiance, nutrient and POM concentration, and hydrodynamism are the three variables which mainly affect the distribution of the different surface-dependent strategies, and thus, these parameters are of paramount interest for understanding the trophic structure of Mediterranean benthic communities. In environments non limited by light, nutrient availability, defined as the product between nutrient —POM concentration and hydrodynamism, states the dominance of calcareous versus non calcareous algae. Calcareous algae dominate in oligotrophic waters while non-calcareous algae dominate in moderately eutrophic waters. In light-limited environments, passive suspension feeders (octocorallaria, gorgonians) become dominant species if POM availability is enhanced by a high hydrodynamism (strong currents); in waters with a low charge of POM organisms of other groups, mainly active suspension feeders, predominate (sponges, bryozoans, scleractiniarians). In any case, there always exists a very variable bathymetric zone, depending on light attenuation and nutrient-POM availability, where encrusting calcareous algae strongly compete with suspension feeders (coralligenous).

Key words: Mediterranean benthos, coral reefs, energy flux, spatial competition, trophic strategies, P/B ratios.

RESUMEN: ESTRATEGIAS DEPENDIENTES DE LA SUPERFICIE Y FLUJO DE ENERGÍA EN COMUNIDADES BENTÓNICAS MARINAS O, PORQUÉ NO HAY CORALES EN EL MEDITERRÁNEO. — La mayoría de organismos creadores de estructura en las comunidades bentónicas son superficie-dependientes puesto que la entrada de energía depende, en gran parte, de la superficie expuesta al medio. Fotosintetizadores carbonatados y no carbonatados, suspensívoros estrictos y fotosuspensívoros (principalmente corales hermatípicos) son las cuatro estrategias básicas adquiridas por los organismos bentónicos. La competencia entre estas estrategias se establece en función de la productividad de las distintas especies de tal forma que, para unas condiciones ambientales dadas, las especies con un mayor crecimiento (P/B) serán las dominantes. El bentos marino se asienta a nivel mundial sobre dos ejes principales: eutrofia-oligotrofia y alta variabilidad-baja variabilidad. Los arrecifes de coral, dominados por fotosuspensívoros, se desarrollan en el espacio de oligotrofia-baja variabilidad mientras que las praderas de grandes algas (fotosintetizadores erectos no carbonatados) se sitúan en el sector de eutrofia-alta variabilidad. El sector eutrofia-baja variabilidad no posee sistemas especialmente adaptados y, en estas situaciones, predominan especies de algas y animales claramente oportunistas. Finalmente, el bentos fotófi-

lo mediterráneo, desprovisto de laminariales y corales hermatípicos, caracteriza el espacio de oligotrofia-alta variabilidad. En su aspecto más genuino estaría representado por praderas de algas con un elevado porcentaje de especies carbonatadas. En todos los casos, los organismos suspensívoros estrictos únicamente desplazan a los fotosintetizadores en condiciones de baja irradiancia o aportes muy considerables de MOP. A su vez, el bentos rocoso mediterráneo; pese a su relativa uniformidad, se organiza también a nivel geográfico según los mismos ejes. El golfo de León y los territorios insulares (Baleares, por ejemplo) corresponderían a los extremos de eutrofia-alta variabilidad y oligotrofia-baja variabilidad respectivamente. Tres son las variables que tienen mayor incidencia sobre la distribución de las distintas estrategias superficie-dependientes y, por ende, afectan de manera primordial la estructura trófica de las comunidades: la iluminación, la concentración de nutrientes y materia orgánica particulada y el hidrodinamismo. En el Mediterráneo, cuando la luz no es limitante, predomina la estrategia fotosintética. La disponibilidad de nutrientes, entendida como el producto entre concentración de nutrientes-MOP y el hidrodinamismo es, en esta situación, la determinante de la dominancia de los fotosintetizadores carbonatados o no carbonatados. Los primeros dominan en situaciones oligotróficas mientras que los segundos lo hacen en condiciones de eutrofia moderada. En situaciones de baja irradiancia, si la disponibilidad de MOP está acentuada por un elevado hidrodinamismo, los octocoralarios se ven muy favorecidos; en aguas muy pobres en MOP son substituidos por organismos de otros grupos (esponjas, briozoos, escleractiniarios). En todo caso siempre existe una zona de tránsito en que las algas incrustantes carbonatadas compiten fuertemente con los organismos suspensívoros.

Palabras clave: Bentos mediterráneo, arrecifes de coral, flujo de energía, competencia espacial, estrategias tróficas, cocientes P/B.

INTRODUCTION

The recent introduction of the hermatypic coral *Oculina patagonica* in the Western Mediterranean (ZIBROWIUS, 1974) and its ability to reproduce and spread itself along the Iberian coasts (ZIBROWIUS & RAMOS, 1983), serves as an excuse to bring to question why coral reefs do not exist in the Mediterranean.

As a first approach we can compare the physico-chemical conditions and the biological conditions under which coral reefs and Mediterranean rocky benthos develop.

Hermatypic corals are amply tolerant to the tidal regime, exposure to surf-waves and a certain range of salinity. However, they have very specific requirements as regards light (a day-night cycle of the same period and length throughout the year), temperature (23-28 °C) and nutrient concentration (below 0.5 micromols of nitrate per 1). The Mediterranean approaches these conditions in summer but displays great variations over a full annual cycle (fig. 1).

Traditionally temperature has been considered as responsible for the distribution of reefs (MANN, 1982; BARNES & HUGHES, 1982). There is a narrow superposition between the geographical limits of the corals and the surface isotherm of 20 °C (fig. 2). In this study we maintain the notion that the stability of energy sources (solar light and exosomatic energy, mainly the hydrodynamism and the availability of nutrients and particulate organic matter (POM)) are as much, if not more important.

One essential characteristic of the reefs is the precipitation of carbonates on the coral skeletons. The system of equilibrium which intervenes, converts this into a complex process but the experiments carried out demonstrate that the precipitation is much more active if it is associated with a photosynthetic process (GOREAU & GOREAU, 1959; MUSCATINE, 1973), high temperatures (CLAUSEN, 1971) or with evaporation processes which increase the concentration of calcium and the alkalinity of the water (MUSCATINE, 1971). With a Q10 of 6.7-12.7 (CLAUSEN, *op. cit.*) this reaction is highly dependent upon temperature, and temperatures lower than 18 °C are critical to the corals. The observed active precipitation in certain calcareous algae found in the Mediterranean, makes it worth considering that a higher, specific and absolute alkalinity (MILLERO *et al.*, 1979; POROT & POISSON, 1983; Delgado, com. pers.) might compensate for the effect of the low temperature. However, hermatypic corals do not grow in the Mediterranean.

SUSPENSION-FEEDER ORGANISMS: A SURFACE-DEPENDENT STRATEGY

The marine benthic system has some very special characteristics within the different natural systems. The physical characteristics of water — density and transport — permit beings and particles to remain in suspension, so it is possible the existence of a trophic strategy that do not exist in the terrestrial systems: the suspension-feeders. Spectacular adaptations in all the large zoological groups found in the marine benthos, allowing them to converge on a morphological model which is suitable to this strategy, are an indirect proof of their importance (JORGENSEN, 1966).
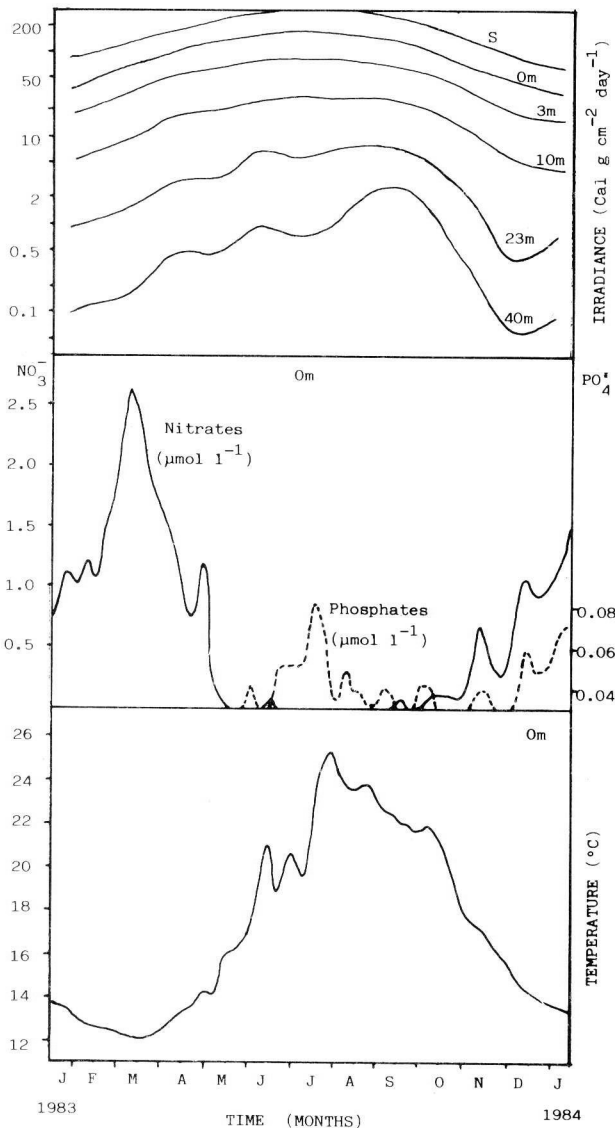
FIG. 1. — Annual cycle of irradiance, nutrient concentration and water temperature from a coastal locality of the Northwestern Mediterranean (data from BALLESTEROS, 1984).

Suspension-feeder organisms act as consumers of a material which has been produced, at least partially, in the planktonic system. In this way, an energy which does not come from that provided by benthic photosynthetic organisms, can be incorporated into the system. Viewing the benthos on a local perspective, the suspension-feeders are situated at a level which is parallel to and independent of that of the primary benthic producers (SIEBERT & NAIMAN, 1980). This independence causes the trophic structure of the benthic communities to be open to different combinations, often very separate from the ideal pyramid of the food-chain theory (MARGALEF, 1974). However, it must be pointed out that this pe-

culiarity is simply a result of considering the benthos as a system from the structural point of view, which does not correspond to viewing it from a functional perspective (MARGALEF, 1981).

Some benthic suspension-feeders (sponges, cnidarians, bryozoans) have a trophic capacity dependent upon surface capture (JACKSON, 1977). For this reason they are surface-dependent like photosynthetic organisms and, like them, they tend to maximize their surface/volume ratio (JACKSON, 1979).

The coastal rocky bottoms are saturated spaces (DAYTON, 1971) and all the surface-dependent trophic strategies enter into competition for the substratum. The mechanism of competition consists of the covering of some species by others which thus leads to a consequent gain of active surface (JACKSON & BUSS, 1975; BUSS, 1979).

COMPETITION, PRODUCTIVITY AND PROTECTION MECHANISMS

Competing for space, those organisms which have a greater net growth and/or a greater durability have an advantage. The productive capacity (P) of each organism is conditioned by its efficiency but, above all, it depends upon the quantity and quality of the energy which it uses. In this way, photosynthetic organisms need light and inorganic nutrients whilst suspension-feeders need particulate organic matter (POM).

When energy is abundant and/or its entry suffers strong fluctuations, the organism which grows quicker, that is, has a higher production/biomass ratio (P/B), is in advantage with organisms which grow slowly (fig. 3). However, if energy inputs are limited and they have only small fluctuations, productivity values are so low that the interactions between organisms (predation, competition mechanisms) act as modulators and can give an advantatge to strategies which, having a lower productivity rate, are better defended. There are numerous references on the use of chemical defense mechanisms within benthic organisms, particularly in algae (MC CLINTOCK et al., 1982; PAUL et al., 1982), sponges (GREEN, 1977; BAKUS & THUN, 1979), cnidarians (COLL et al., 1982), bryozoans (AL-OGILY & KNIGHT JONES, 1977; DYRINDA, 1984) and ascidians (STOECKER, 1980a, 1980b). The possession of a skeleton could also be interpreted as a protection mechanism. The possession of spicules in the sponges (SARA & VACELET, 1973) or of carbonates in the bryozoans
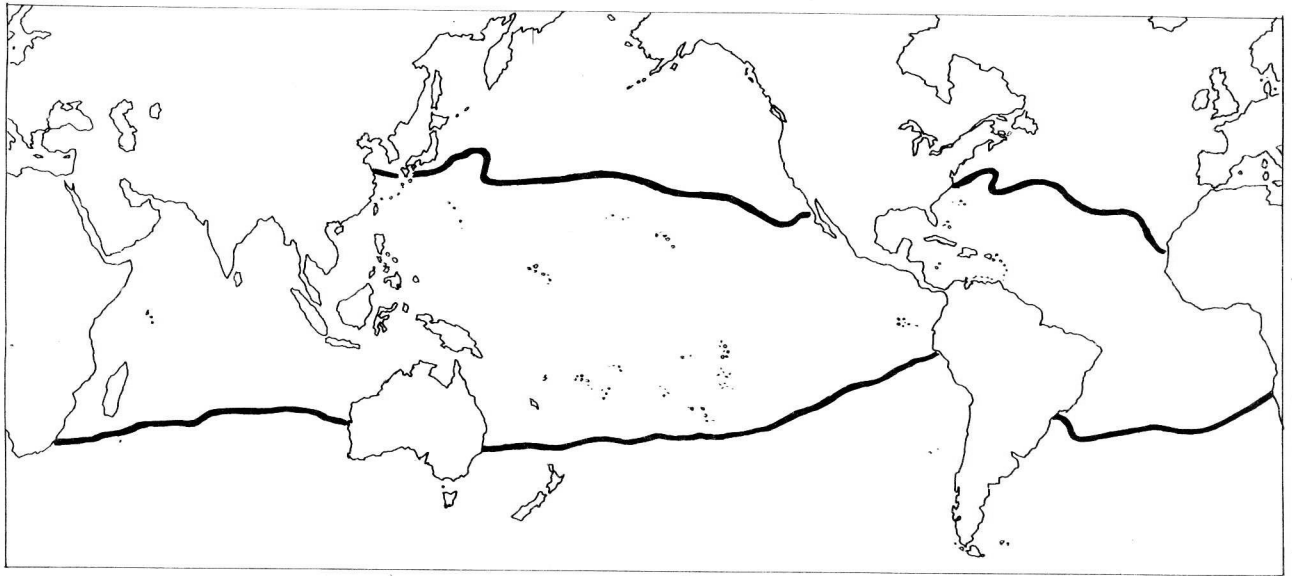
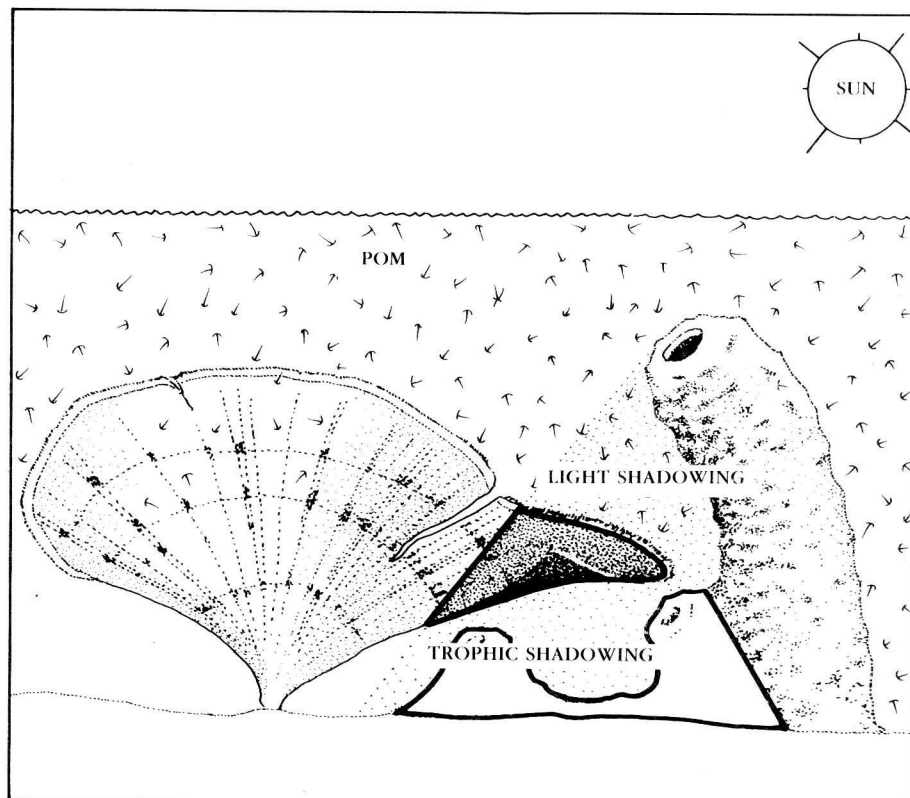FIG. 2. — Correspondence between reef-corals distribution and the 20 C winter isotherm (data from MANN 1982).

FIG. 3. — Hypothetical mechanism of space-competence and coverage between two surface-dependent strategies: a photosynthetic organism and a suspension-feeder. In both situations an umbrela-effect is produced: the photosynthetic organism deprives the suspension feeder of organic matter while the suspension-feeder deprives the photosynthetic organism of light. The species which could maintain a higher growth rate (P/B) in these conditions would cover its competitor.

(ZABALA, 1986) and in certain algae (LITTLER, 1976; LITTLER & DOTY, 1975) act, in part, in this way. The greater resistance to predation by crustose (calcareous and non calcareous) algae is also well documented (LITTLER & LITTLER, 1980; LUBCHENCO & CUBIT, 1980; DETHIER, 1981; LITTLER et al., 1983).

Heeding to this reasons, four surface-dependent trophic strategies can be distinguished in a first approximation:

1. Non-calcareous photosynthetic organisms, generally erect.

2. Calcareous photosynthetic organisms, generally crustose.

3. Strict suspension-feeders.

4. Photosynthetic suspension-feeders: suspension-feeders and assembled photosynthetic organisms.

It is enlightening to compare the biomass, production, productivity and turn-over time values for these four groups which can be obtained from own data and from the bibliography (table 1). These groups dominate in different marine benthic communities with a decreasing degree of fluctuation in energy inputs (warm and warm-cold seas, Mediterranean and tropical seas, respectively). A progressive decrease in productivity and a correlative increase in the turnover time rate can be observed, as the environmental conditions become more stable, so, the seasonality, understood as a variance in the temporal distribution of the environmental variables, diminishes.

PHOTOPHILIC BENTHOS: KELPS VERSUS HERMATYPIC CORALS

Two large types of systems can be clearly differentiated when looking at the peculiarities of photophilic marine benthos on a world wide scale: the coral reefs, situated at the tropics, and the kelp meadows in higher latitudes.

Non calcareous, erect algae always quantitatively displace the other three strategies in systems where light is not a limiting factor for the growth of algae and also when the availability of nutrients is abundant and fluctuating. These are the predominant traits of the warm and warm-cold seas, characterized by strong seasonal variations which result in fluctuations in the entry of nutrients and light. Kelps are especially adapted to conditions where a marked seasonality prevails as regards the availability of nutrients and light. Their capacity to store nutrients and make use of them when the surrounding water is deprived of these elements has been amply proven (CHAPMAN & GRAIGIE, 1977; WALLENTINUS, 1981; GAGNÉ & MANN, 1981; CONOLLY & DREW, 1985). Similarly, they also have the capacity to store reserve subtances which are mobilized when it is possible to maintain an increased growth rate due to the availability of nitrogen and phosphorus in the Water (MANN, 1973; GAGNÉ et al., 1982; BUGGELN, 1983; DUNTON, 1985). This ability to translocate nutrients and storage compounds, along with the capacity to attain very high growth rates when conditions are favourable, are possibly the reasons for the success of

TABLE 1. — Net production (in g C m^{-2} year^{-1}), biomass (in g C m-2), productivity (P/B) and turnover (P/B-1) (in years) for different communities from seas with a decreasing step of oscillation in energy inputs (North-Atlantic, Mediterranean, tropical seas). Data from the authors and from MANN (1973, 1982), NORTH (1971), KAIN (1979), FIELD et al. (1980), KREMER (1981), NIELL (1979), FERNANDEZ et al. (1983), GUTERSTAM (1981), COUSENS (1984), BALLESTEROS (1984), GILI & GARCÍA (1985) and MUSCATINE (1973).

| | Non calcareous algae | | | | | Calcareous algae | | Suspension-feeders | | Hermatypicocorals | |
| | Atlantic Pacific | | Mediterranean | | | | | | | Pacific | |
	Kelps	Inter-tidal	Medio-littoral	Upper infralittoral	Lower-infralittoral	Circalittoral (coralligenous)	Circalittoral (Mäerl)	Young gorgonians	Old gorgonians	Montipora	Acropora
P gC/m^2 year	400-2000	365-840	70-400	365-900	105	36-65	3.6-10	44	12	193	630-800
B gC/m^2	300-1800	280-560	125-350	380-1000	150	90	36-110	144	160	1330	1400-2130
P/B	1.0-4.0	1.0-3.0	1.1-4.0	0.9	0.7	0.4-0.7	0.1	0.3	0.07	0.3	0.37-0.45
P/B^{-1} (years)	0.3-1.0	0.4-0.9	0.9-0.25	1.1	1.4	1.4-2.5	10	3.3	13.3	3.3	2.2-2.7

these large phaeophyceans in warm seas. The exhaustive predation of kelps by herbivores converts the kelp beds into populations of small ephemerophycean algae (PAINE & VADAS, 1969; DUGGINS, 1980) or into communities dominated by crustose corallines (WHARTON & MANN, 1981; NOVACZEK & MC LACHLAN, 1986). In the absence of kelp beds in warm seas, the communities are dominated by fucacean algae (intertidal zone) or by species of other groups (e. g. *Desmarestia, Phyllophora, Polysiphonia, Gelidium, Corallina, Gymnogongrus, Chondrus*) in the sublittoral zone. In any case, the crustose calcareous algae do not have an excessive relative importance, even though they usually completely cover the substratum (EDELSTEIN *et al.*, 1969). Suspension-feeders, although abundant in kelp meadows (constituting between 47 and 75 % of the fauna associated with the rizoids) (JONES, 1971), possess a biomass of quantitative little importance (NORTH, 1971).

The conditions are very stable in the tropics and the systems are very oligotrophic. In these circumstances as much the photosynthetic organisms as the strict suspension-feeders encounter limitations to their development. It is only in this situation that the linking-up of both strategies has been able to have evolutionary success (MUSCATINE & PORTER, 1977). The corals with zooxanthellae are ecologically equivalent to the kelps, as they basically function as primary producers (PORTER, 1976, 1980; DAVIES, 1977; MUSCATINE, 1980). The calcareous skeleton of the hermatypic corals and the presence of nematocystes are of capital importance when evaluating its evolutionary success, given that they seem to be the main causes of the existence of so few animals which feed from them (STODDARD, 1969; WARNER, 1984). The local enrichment produced by the coral metabolism allows the coexistence of the other three strategies, but always with a subordinate structural importance (D'ELIA & WEBB, 1977; LEWIS, 1977). Strict suspension-feeders are limited by the low productivity of the surrounding ocean, and its abundance is proportional to this production (HIGHSMITH, 1980); they can only be dominant in the deep areas of the reef where the zooxanthellae cannot carry out a net positive production. Non calcareous, erect algae are scarce due to intense grazing by herbivores (BAKUS, 1966; LEWIS & WRAINWRIGHT, 1985; FOSTER, 1987; LITTLER *et al.*, 1987) and the same happens with crustose species at a lower intensity (ADEY & VASSAR, 1975; HOEK *et al.*, 1975). In fact, it has been demonstrated that the elimination of herbivores favours the development of algae over the corals, be

it for natural reasons (HOEK, 1969) or experimentally provoked (VINE, 1974; CARPENTER, 1986). On the other hand, any alteration which increases the productive potential of the algae in detriment to the corals (eutrophy) causes the regression of the entire reef (WARNER, 1984; LITTLER & LITTLER, 1985). The maintenance and development of coral reefs is only possible in permanently oligotrophic conditions where the multiple interactions, which are established within the different organisms, favour the photosynthetic suspension-feeders strategy defended as they are from external agressions by a calcareous skeleton and some chemical defense mechanisms, both of these being factors which increase its durability and structural capacity. These hypothesis could be tested in tropical areas with upwelling waters or, even more so, where enrichment is produced by fluvial run-off. In both cases the presence of corals with symbiont zooxanthellae is limited and they never manage to form reefs (e. g. West African coasts).

THE MEDITERRANEAN AS A SEA OF TRANSITION

In the Mediterranean one can observe an intermediate situation but with more proximity to that of temperate seas. In spite of the low nutrient concentrations and of the relatively high irradiances, the seasonal variation of both parameters is the most notable difference to that of tropical seas. We have already mentioned the practical absence of hermatypic corals in the Mediterranean. Kelps are represented by only a few species, of which only the endemic *Laminaria rodriguezii* manage to form real meadows in the circalittoral zone (ROS *et al.*, 1985), where relatively high nutrient concentrations are maintained all the year round (BALLESTEROS, 1984). The result of this is the dominance of algae in photophilic environments, be it species of tropical affinities *(Padina, Acetabularia, Halimeda, Dasycladus, Caulerpa)*, endemic *(Cystoseira)* or subcosmopolitan *(Dictyota, Halopteris, Codium)*. Crustose algae usually totally cover the substratum and become dominant in situations of excessive grazing by sea-urchins (KEMPF, 1962; AUGIER & BOUDOURESQUE, 1970; VERLAQUE, 1987). Suspension-feeders are generally quantitatively of little importance in spite of the fact that in situations of a high hydrodynamism or of a notable load of suspended POM, *Mytilus* may develop substantially (BELLAN SANTINI, 1969) (fig. 4, table 2).

TABLE 2. — Biomass values (g dwt m^{-2}) in the three surface-dependent strategies present in Mediterranean rocky benthic communities ordered from shallow to deep waters. Data obtained from different authors.

Community	Erect algae	Crustose Algae	Suspension-feeders	Other groups	Depth intervals
Cystoseira mediterranea	1.310	388	5.040	23	0-1 m
Halopteris scoparia	645	1.439	57	12	3-8 m
Codium vermilara	331	1.478	138	48	10-15 m
Cystoseira zosteroides	290	1.134	98	3	18-20 m
Halimeda tuna	322	1.326	167	7	23-30 m
Lithophyllum expansum	119	1.477	328	2	35-50 m
Eunicella singularis	5	150	422	—	
Paramuricea clavata	—	—	2.208	—	
Parazoanthus axinellae	—	—	6.223	—	
Corallium rubrum	—	—	3.328	—	

It is possible that the different situations which we have mentioned, representative of the main photophilic marine benthic systems, may fit along a eutrophy-oligotrophy axis and an axis marked by seasonality (fig. 5). This seasonality may be represented by the annual variance in the nutrient concentration or, better, by its variance/mean ratio. In this way, hermatypic corals would remain restrained in situations of permanent oligotrophy, whilst kelp beds would characterize the eutrophic situations with a marked seasonality. The communities of Mediterranean or subtropical algae would belong to oligotrophic conditions with important fluctuations. Finally, permanent eutrophication, which is extremely rare in marine environments (e. g. estuarine conditions) would be dominated by opportunistic algae communities. In this last case there is no restricted geographical distribution and, at present, their presence is closely related to density of human occupation of the coastal area.

DISTRIBUTION OF SURFACE-DEPENDENT STRATEGIES IN THE MEDITERRANEAN: SOME DATA

In the analysis of the different communities carried out up to now, only the situations in which light was not a limiting factor in the growth of algae have been considered. In these situations photosynthetic strategies dominate in every case. However it is relevant to ask oneself what happens in
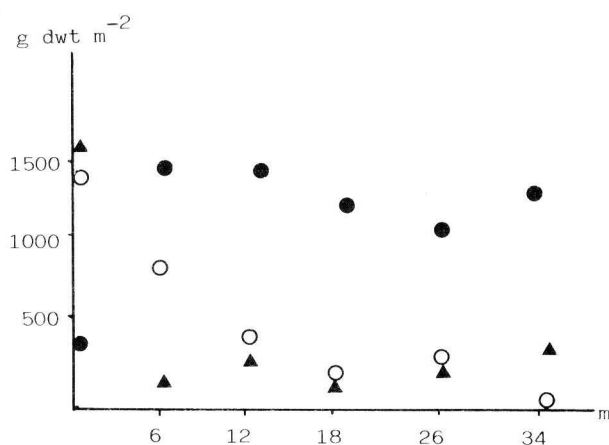
FIG. 4. — Biomass variation in the three kinds of strategies (erect algae, crustose calcareous algae, suspension feeders) along an ideal transect made in a locality from the Northwestern Mediterranean coast (data from BALLESTEROS, 1984).
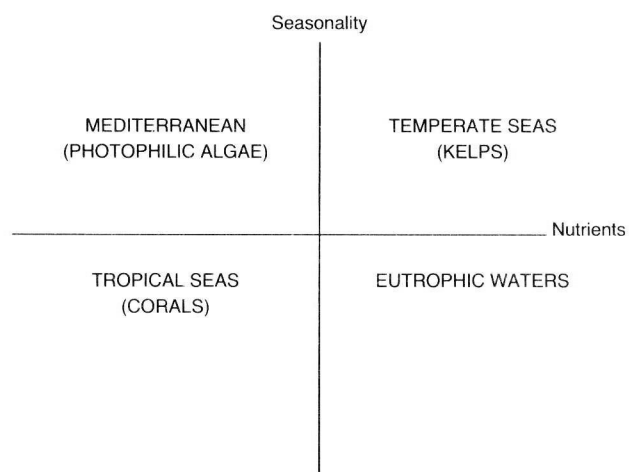
FIG. 5. — Ordenation of the main kinds of photophilic benthic formations in relation to nutrient availability and seasonality.

depth, going along the bathymetric axis and obviously reducing irradiance. This aspect is analysed from different observations made by the authors on the distribution of the different strategies as a function of the depth in the Mediterranean benthos.

In spite of its relative uniformity, Mediterranean benthos may organize itself on a geographical level along an eutrophic-high variability axis versus an oligotrophic-low variability axis, bearing in mind that the difference between both poles is much more subtle than previously exposed for the world benthos. Characteristic habitats of the two extremes of these hypothetical axes would be the Medas islands (Gulf of Lions) and Cabrera island (Balearic Islands).

In the Balearic Islands the transparency of the water allows the penetration of erect algae for up to a depth of 80 or more meters *(Vidalia, Phyllophora, Udotea)*. Oligotrophy implies a scarcity of land run-off with the subsequent lowering of primary production which favours crustose and calcareous algae over soft and erect algae due to their greater resistance to predation. Suspension-feeders are also greatly limited due to the scarce quantity of suspended POM. In Cabrera, for example, gorgonians hardly exist, and only a few sponges *(Ircinia, Spongia)* and bryozoans *(Myriapora)* are abundant in conditions where strong currents are found. As an example, two transects are presented, carried out on the island of Cabrera (figs. 6.1 and 6.2). In both cases an absolute dominance of algae can be observed across the whole transect. If the orientation is to the South (Estels, fig. 6.1) the growth of calcareous crustose algae does not begin to form an incipient coralligenous for up to 45 meters. Suspension-feeders remain limited — with the exception of a few sponges with symbiotic Cyanophyceae— in the lower part of the transect *(Myriapora truncata, Aplidium tabarquensis, Halocynthia papillosa,* some sponges) or in some especially dark cavities *(Leptopsammia pruvotii, Axinella damicornis, Parazoanthus axinellae)*. In a Northerly direction (Cap Llebeig, fig. 6.2) the precoralligenous of *Udotea petiolata* begins at 35 meters and for up to 45 meters one can find a well constituted coralligenous with the corallines *Mesophyllum lichenoides* and *Lithophyllum expansum* being the main bioconstructors. Suspension-feeders already have a certain importance, these mainly being the bryozoans *(Myriapora truncata, Schizotheca serratimargo, Hornera frondiculata),* certain sponges *(Dysidea avara, Anchinoe tenacior)* and some cnidarians *(Alcyonium acaule, Eudendrium racemosum)*.

In the Medas islands, the proximity of fluvial run-off and strong currents coming from North to South increases the quantity of nutrients and POM along with the consequential diminution in the transparency of the water. Erect algae only penetrate for up to 15-25 meters (GILI & ROS, 1985), depending on the inclination and orientation. As from this depth calcareous crustose algae, associated to a large biomass of suspension-feeders, constitute communities attributables to coralligenous, and in areas with strong currents and scarce illumination there exists communities dominated exclusively by suspension-feeders. Typical transects of this situation are shown in figures 6.3 and 6.4, transects already described and commented in GILI & ROS (1982, 1985). A detailed study of the dominance of the different strategies quantified through coverage (vertical projection) taken from each photographical transect, enables us to obtain a fairly good idea of the bathymetric distribution of the three strategies considered (fig. 7). In the first transect (Cuetera, west-oriented) the erect algae and *Posidonia* dominate in the areas of little depth and in horizontal bottoms for up to 20 meters. The relative dominance of suspension-feeders in the first meter of depth is due to the abundance of filter-feeders (mainly *Mytilus*). Crustose algae have a relatively important coverage as from a depth of 13 meters, in particular in the case of a high inclination of the substratum. Suspension-feeders are of little importance across the whole transect, apart from between depths of 13 and 15 meters, coinciding with a scarcely illuminated wall. In the second transect (Pota del Llop, northerly oriented) the changes in the dominance of the different strategies are much stronger. Three zones can be clearly defined: a first superficial zone (0-10 meters) dominated by erect algae, a second zone (10-15 meters) with a codominance of the three strategies and a third zone (15-42 meters) totally dominated by suspension-feeders *(Paramuricea clavata* principally).

THE MEDITERRANEAN BENTHOS: A MODEL

Heeding to the hypothesis previously mentioned on the dominance of each one of the surface-dependent strategies depending on the energy flow and supported by the observed distribution of the different strategies in the bathymetric transects considered, it is possible to present a structural model of Mediterranean rocky benthos. The model takes into account three axes of variation: light, nutrients-POM
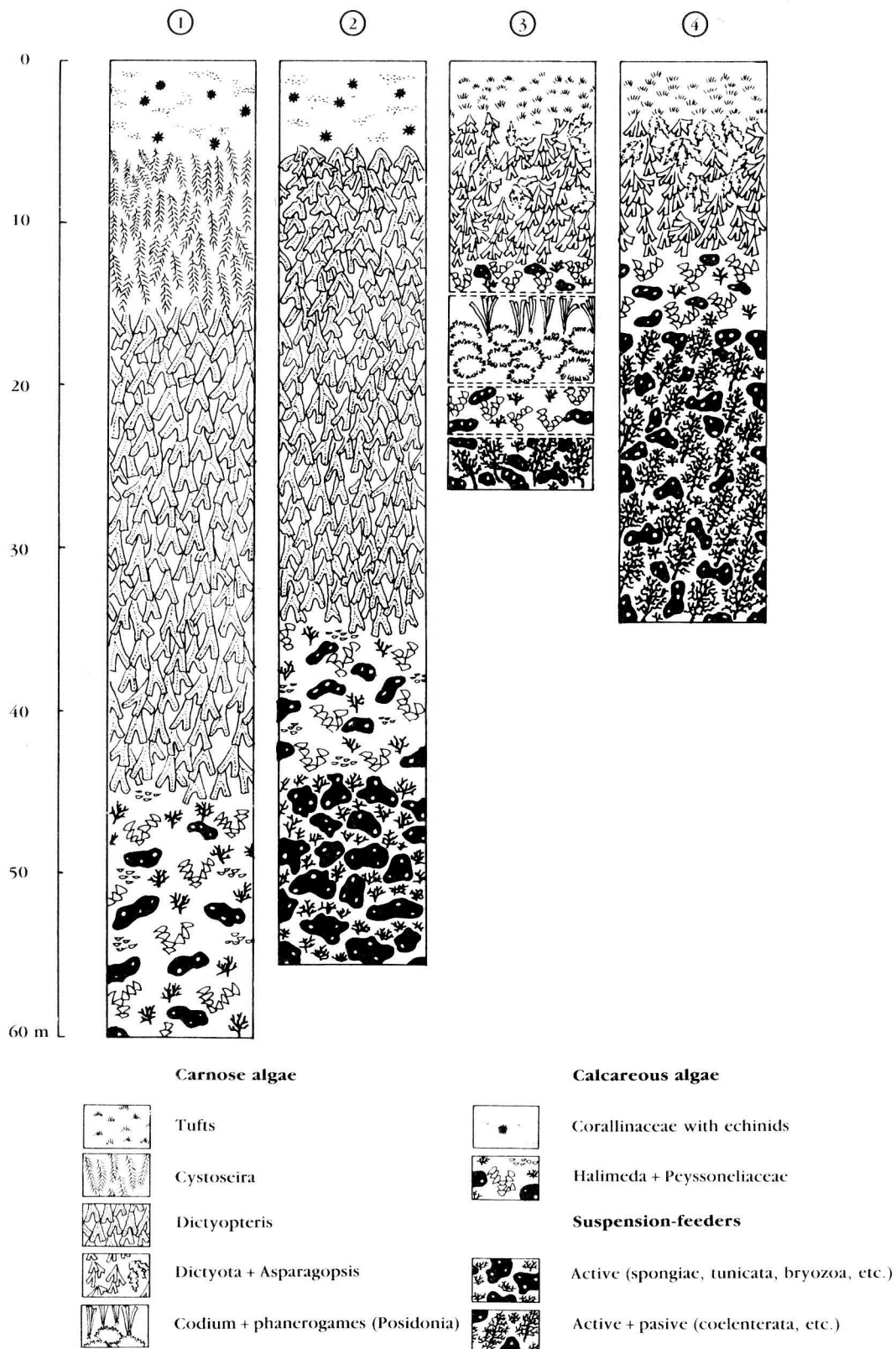
FIG. 6. — Diagrammatic representation of four transects representative of four different situations in Western Mediterranean benthic communities: Estels (Orientation South, Cabrera Island) (1), Cap Llebeig (Orientation North, Cabrera Island) (2), Sa Cuetera (Orientation South, Medas Islands) (3) and Pota del Llop (Orientation North, Medas Islands) (4).

% COVERAGE

TRANSECT FIGURE 6.3

% COVERAGE

TRANSECT FIGURE 6.4

☐ Erect and carnose algae

▦ Suspension feeders

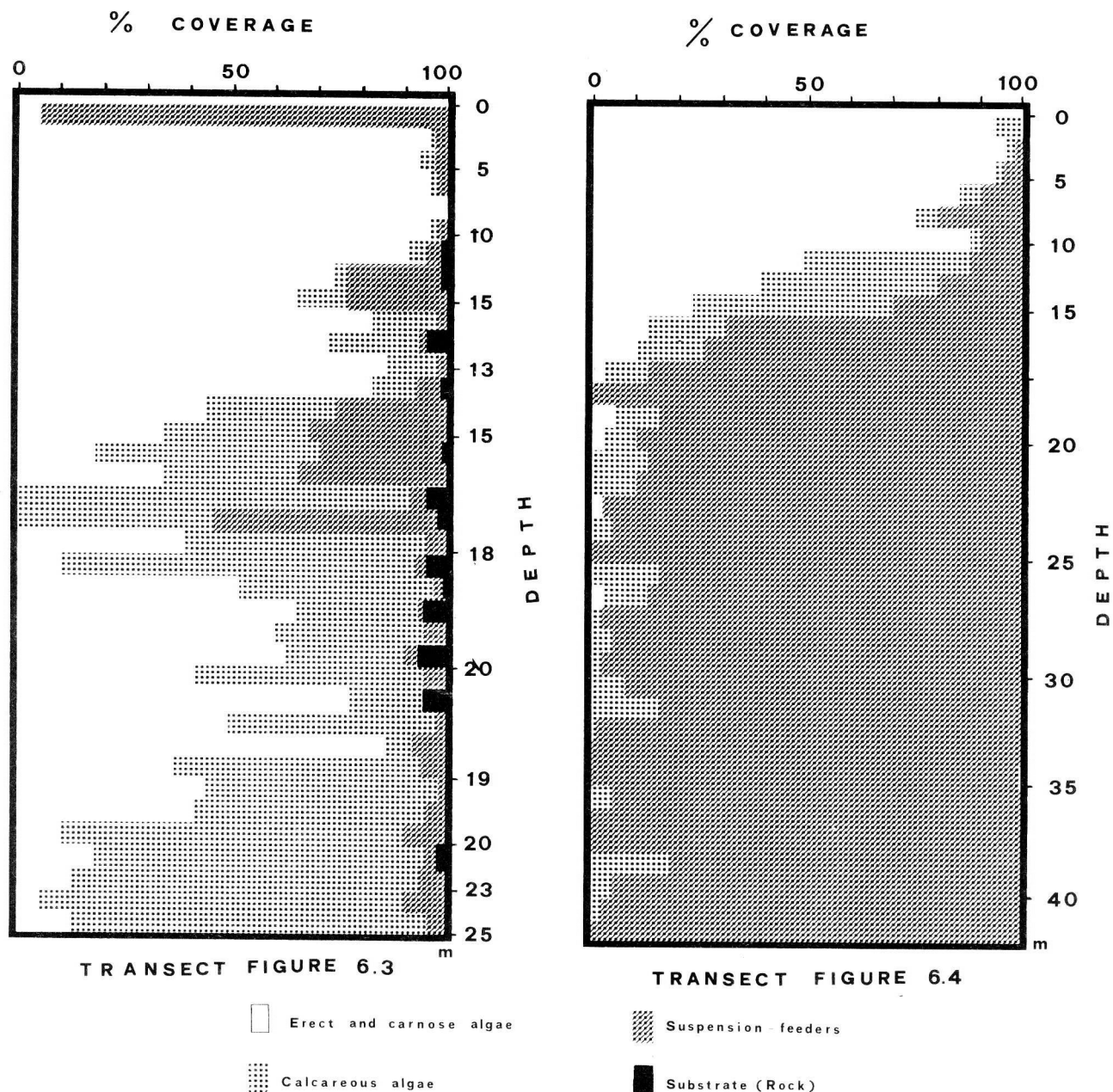▦ Calcareous algae

■ Substrate (Rock)

FIG. 7. — Changes in dominance (coverage) of the three kinds of strategies evaluated from two photographic transects made in transects represented in figures 6.3 and 6.4.

and hydrodynamism (figs. 8, 9). This model is formally identical to the one developed for the plankton by MARGALEF (1978). Moreover, in benthic systems the picture is clearer, because of the higher spatio-temporal persistence of sessil organisms. Light is a factor which acts assimetrically: firstly it promotes algal growth but it does not have a direct effect upon the suspension-feeder organisms. The algae dominate over the suspension-feeders if there is sufficent light which allows them to maintain some elevated

P/B ratios. The suspension-feeders have to "wait" until the algal productivity diminishes, so that their strategy becomes competitive. The concentration of nutrients and POM indicate the trophic richness of the system given that they are essential for the growth of algae and suspension-feeders respectively. Both factors, in spite of the fact that they are different, are narrowly correlated and, in natural situations, high nutrient concentrations correspond also with high concentrations of suspended POM. Hydrodynamism or
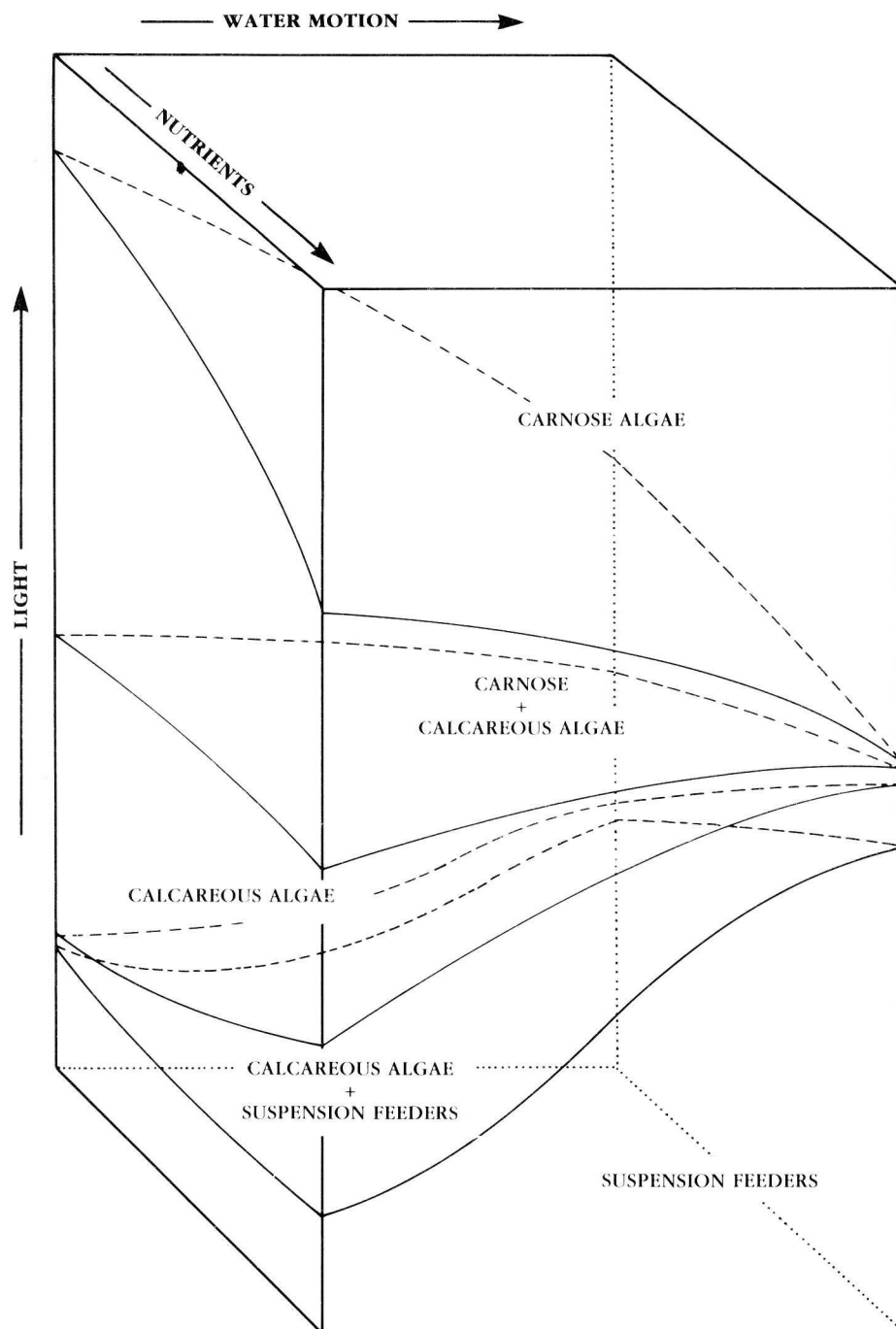
FIG. 8. — Ordenation model of dominance of the three main surface-dependent strategies present in Mediterranean benthic communities from rocky places in relation to light, hydrodynamism and nutrient and POM concentration in seawater.

turbulence, for their part, is a mechanism of transport which renovates the water surrounding the organisms, putting at their disposition the nutrients and the POM. The product between the concentration of nutrients and POM with the hydrodynamism indicates the trophic availability of the system given that it reflects the flow of nutrients and POM available to the organisms.

In situations in which light is not a limiting factor the photosynthetic strategy will predominate. The erect photosynthetic organisms, due to their greater productivity, will mainly dominate in situations of high hydrodynamism, in spite of the fact that the nutrient concentration is low. The calcareous crustose algae will only have a significant relative importance in those conditions of a low nutrient availability (due
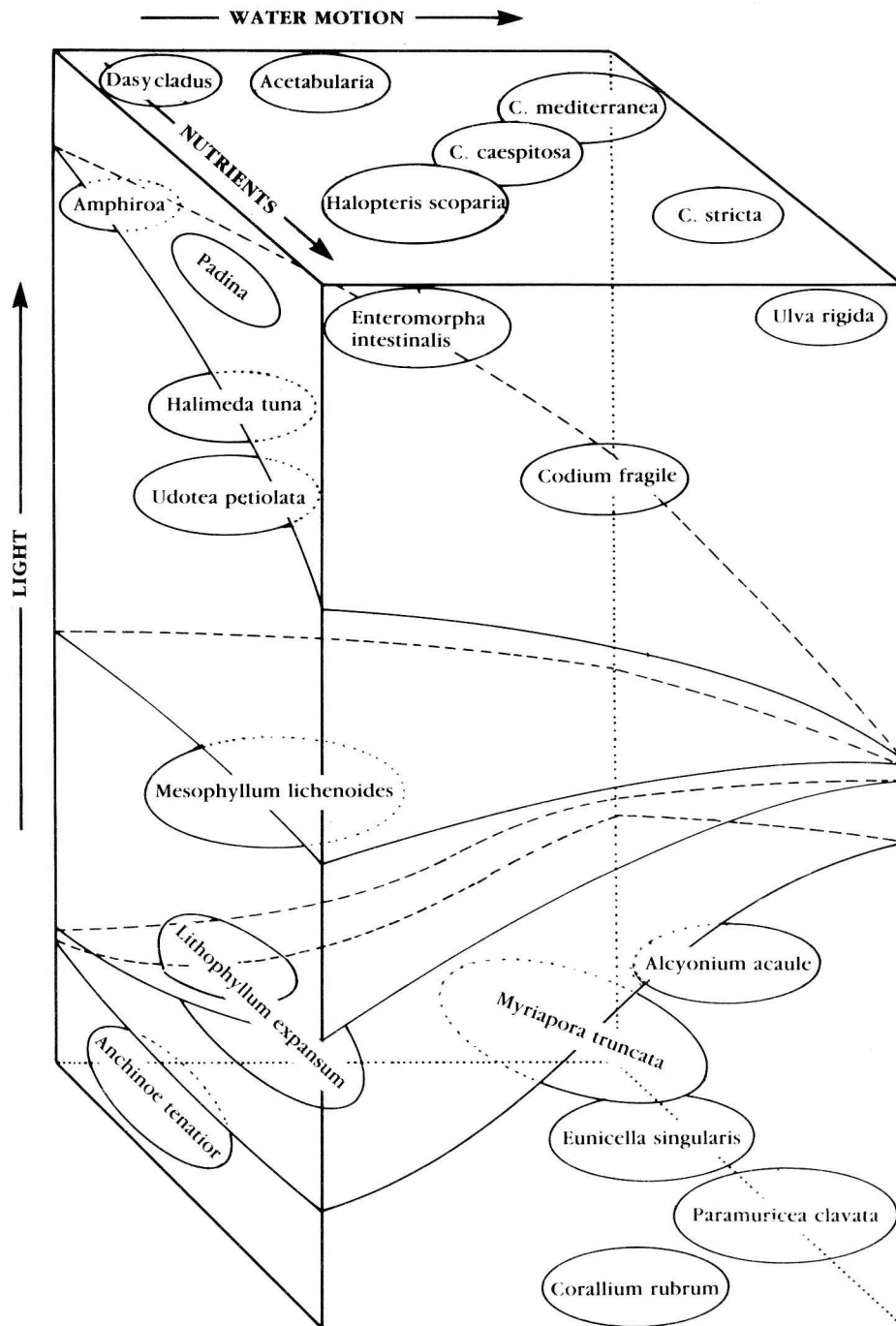
FIG. 9. — Ordenation model of distribution of some representative species in Mediterranean benthic communities from rocky places in relation to light, hydrodynamism and nutrient and POM concentration in seawater.

to a scarce hydrodynamism and a low nutrient concentration); in these circumstances the high resistance to grazing constitutes a determinate selection factor over the erect species. The communities of photophilic algae from Cabrera are a clear exponent of this situation. If light is abundant, the concentration of nutrients is relatively high and the hydrodynamism is scarce, the conditions are close to those which are found in harbour environments with a dominance of ulvales and filamentous algae (BALLESTEROS et al., 1984). When these three factors have high values (a lot of light and nutrients, a high hydrodynamism) the dominance of algae may diminish, as certain filter-feeding organisms are extraordinarily favoured if there is a high quantity of POM (e. g. *Mytilus galloprovinciale*, *Ostraea edulis*,

Anemonia sulcata, Balanus perforatus). It must be emphasized that conditions of a high nutrient concentration were, until today, untypical of the Mediterranean and there are no species of Mediterranean algae adapted to these circumstances; opportunistic species occupy their place, generally cosmopolitan (*Ulva, Corallina*, ectocarpacean and ceramiacean algae) or these biotops are well appropiated for the introduction of exotic species (e. g. *Codium fragile, Sargassum muticum, Undaria pinnatifida*) (FELDMANN, 1956; BELSHER *et al.*, 1985; BOUDOURESQUE *et al.*, 1985).

In situations of low irradiance, the availability of nutrients and POM acquires capital importance. In cases where both a high hydrodynamism and a high concentration of POM exists (e. g. Medas islands), suspension-feeders are very favoured, mainly octocorallarians, which constitute the dominant group. If the hydrodynamism remains high but the POM concentration diminishes we have a situation similar to that found in Cabrera (Punta Llebeig); always and when the level of irradiance is sufficiently reduced, the suspension-feeders may become dominant over the crustose algae; the dominant groups are thus the bryozoans, the sponges and the scleractiniarians. If the hydrodynamism also diminishes, the suspension-feeders need less irradiance in order to dominate over the crustose photosynthetic organisms. Finally, the combination of low irradiance, scarce hydrodynamism and a high quantity of nutrients and POM is unusual in Mediterranean waters; such a situation generates conditions of high sedimentation which is unfavourable for the majority of crustose algae but favours certain suspension-feeders (certain actiniarians, gorgonians and molluscs).

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