

## AUTECOLOGY OF SHALLOW-WATER OCTOCORALLIA FROM MEDITERRANEAN ROCKY SUBSTRATA, I. THE BANYULS AREA

by

STEVEN WEINBERG

*Institute of Taxonomic Zoology, University of Amsterdam, The Netherlands*

### ABSTRACT

The autecology of eleven mediterranean octocoral species (3 Stolonifera, 4 Alcyonacea, 4 Gorgonacea) was studied near Banyuls-sur-Mer (southern France). Field observations were carried out by means of SCUBA-diving in forty underwater stations. The ecological amplitude of each species was determined for a number of abiotic factors, viz. water temperature, submarine irradiance, water movement, slope of substratum and sediment. In this way the ecological niche for the different species was defined. The niches of several species partly overlap: the survival "strategy" of these species was defined as "competitiveness". Other species display "specialization", a strategy by which they avoid competitive situations. A third survival mechanism is "opportunism", encountered in species which are extremely tolerant with respect to their environment. Although experimental work is needed to determine how niche selection occurs, larval and juvenile stages are considered to be critical in this respect.

### RÉSUMÉ

Onze espèces d'Octocoralliaires méditerranéens (3 Stolonifères, 4 Alcyonaires, 4 Gorgonaires) ont fait l'objet d'une étude autécologique dans la région de Banyuls-sur-Mer. Dans ce but des observations furent effectuées à l'aide du scaphandre autonome dans quarante stations sous-marines. Les amplitudes écologiques vis-à-vis des facteurs abiotiques suivants furent déterminées: température de l'eau, irradiance sous-marine, mouvement de l'eau, pente du substrat et présence de sédiment. C'est ainsi qu'on a pu définir la niche écologique de chacune des espèces. Les niches de plusieurs espèces se recouvrent partiellement: la stratégie de survie de ces espèces est la "compétitivité". D'autres espèces sont caractérisées par la "spécialisation", une stratégie qui leur permet d'éviter la compétition. Un troisième mode de survie est "l'opportunisme", qui exige des espèces en question d'être extrêmement tolérantes vis-à-vis de leur environnement. Bien qu'un travail expérimental soit nécessaire afin de déterminer comment s'effectue le choix d'une niche, il est probable que les stades larvaires et juvéniles jouent un rôle très important à ce propos.

### I. INTRODUCTION

Submarine communities are very complex systems. In most cases a depth-dependent zonation has been demonstrated (Roos, 1964; Loya, 1972; Schmidt, 1972; Castric-Fey et al., 1973; Bak, 1975; Van den Hoek et al., 1975; Wedler, 1975; Burla et al., 1976; Benayahu & Loya, 1977; Wiedenmayer,

1977). In other cases specific environmental factors seem to dictate community composition and zonation, such as water movement (Wedler, 1975; Geister, 1977; Wiedenmayer, 1977), sedimentation (Chardy, 1970; Weinberg, 1978a) or light (Roos, 1967; Harmelin, 1969; Chardy, 1970; True, 1970; Zander & Heymer, 1970, 1977; Duclaux & Lafargue, 1972; Jaubert & Vasseur, 1973, 1974; Kinzie, 1973; Schuhmacher, 1973; Boutler et al., 1974; Gamulin-Brida, 1974; Grigg, 1974; Wedler, 1975; Weinberg, 1975a, 1978a; Dana, 1976; Zander & Jelinek, 1976).

As most physical parameters are not independent, it is often problematic to state which parameters really determine community composition or zonation. Moreover, quantified measurements are often lacking, leading to rather subjective qualifications of the physical environment. A final difficulty in dealing with a community is the fact that it is virtually impossible to study biotic interrelations in nature.

In an attempt to tackle part of these problems, populations of mediterranean Octocorallia (Coelelenterata, Anthozoa) were studied. Whereas in fact Octocorallian communities as a whole were observed (Weinberg, 1978a), populations of each species are treated separately in the present paper, assuming that the presence of other species does not interfere with them. This was done for two reasons. Firstly even if it is reasonable to suppose that species interaction actually occurs, through spatial competition or biochemical repulsion for instance, there is no means, without experimentation, to determine in that way. Secondly the main purpose of this study is to assess which abiotic environmental parameters determine the presence or absence of a species, and on a more detailed level, which are the ecological amplitudes (tolerances) of each species for those parameters.

## II. MATERIAL AND METHODS

Forty underwater stations were sampled near Banyuls-sur-Mer (France). For a detailed description and comparison of the stations see Weinberg (1978a). Sampling consisted of counting the Octocorallia within a quadrat surrounded by a square PVC frame of 50 × 50 cm for communities of large, sometimes sparsely distributed animals, and a square PVC frame of 20 × 20 cm for "miniaturized" communities of smaller, more crowded animals (surf zone; caves). Number of animals (colonies) was counted and expressed as individuals m<sup>-2</sup>. In the case of intermingled, encrusting colonies (some Stolonifera and Alcyonacea) distinction between individuals was made by pinching one polyp, and counting all the subsequently contracting polyps as belonging to the same colony. Ten counts were made at all stations while staying well within the borders of each community, together forming the sample of that station. Its size, 4000 cm<sup>2</sup> for "miniaturized" communities and 25000 cm<sup>2</sup> for open communities, corresponds with the most conservative estimates on the minimal area in these habitats (Weinberg, 1978b).

The following species were studied (the abbreviations are used in the figures and tables throughout this article) :

### Stolonifera:

- CC = *Cornularia cornucopiae* (Pallas, 1766)
- CO = *Clavularia ochracea* Von Koch, 1878
- RR = *Rolandia rosea* (Philippi, 1842)

### Alcyonacea:

- PC = *Parerythropodium coralloides* (Pallas, 1766)
- AA = *Alcyonium acaule* Marion, 1878
- ME = *Maasella edwardsii* (De Lacaze-Duthiers, 1888)
- PS = *Paralcyonium spinulosum* (Delle Chiaje, 1822)

### Gorgonacea:

- ES = *Eunicella singularis* (Esper, 1794)
- LC = *Lophogorgia ceratophyta* (Linnaeus, 1758)
- PMC = *Paramuricea clavata* (Risso, 1826)
- CR = *Corallium rubrum* (Linnaeus, 1758)

The habitus of colonies of each species is quite distinctive in shape as well as in colour, so that confusion in the field is unlikely to occur. The taxonomic references used were those of Weinberg (1976a, 1977, 1978c).

Together with the faunistic inventory a number of environmental parameters was recorded and/or

calculated for each station. These parameters are: average summer temperature (in °C), submarine daylight (average yearly irradiance in cal cm<sup>-2</sup> year<sup>-1</sup>), average water movement (in four classes), slope (in five classes), absence or presence of sediment, and depth (in m). For a detailed explanation of methods and results, see Weinberg (1976b, 1978a) and Weinberg & Cortel-Breeman (1978). These results are summarized in fig. 4.

Although the forty underwater stations were originally characterized by five slope classes (Weinberg, 1978a: table 3), these were partly united in the present paper to form the following three classes: (1) horizontal or sloping, (2) vertical or overhanging, and (3) cracks and holes. Each station was further classified according to the presence or absence of sediment, whereas the average water movement was classified into one of the following four categories: (1) weak (0-100 m h<sup>-1</sup>), (2) moderate (100-200 m h<sup>-1</sup>), (3) strong (200-350 m h<sup>-1</sup>) and (4) turbulent (>350 m h<sup>-1</sup>).

## III. SPECIES-PARAMETER RELATIONSHIPS

As an example of the type of relationship that may exist between the success (measured as population density) of a species and its abiotic environment, I take the gorgonian *Eunicella singularis*. Since this is the most common octocoral in the area prospected, I possess more data concerning the ecology of this species than of the other ones. Fig. 1 shows population density as a function of average summer temperatures for the forty stations considered. For each temperature interval there are stations with greater or smaller population densities. However, if one considers the stations with maximum population density for a given interval, which are joined by a line in the figure, one obtains a curve roughly representing a probabilistic relationship. Whereas at average summer temperatures higher than 20.1°C the species apparently does not occur (higher average temperatures were not found, but the decline of population density between 19°C and 20°C strongly suggests that at higher temperatures the species does not encounter its optimum conditions), at the lower end of the scale (13.8°C) the species can still occur at fair population densities (about 20 individuals m<sup>-2</sup>).

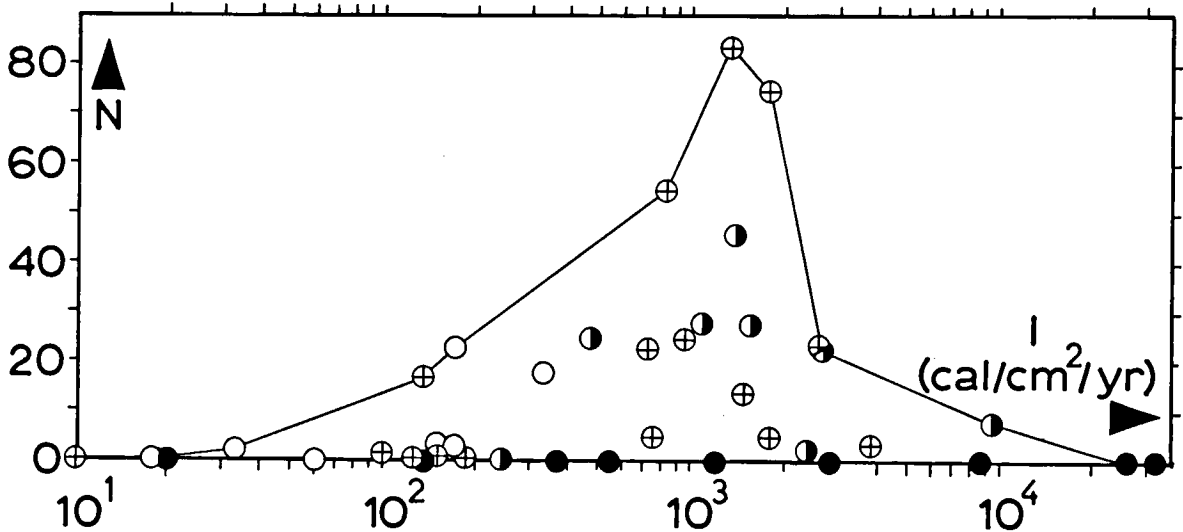
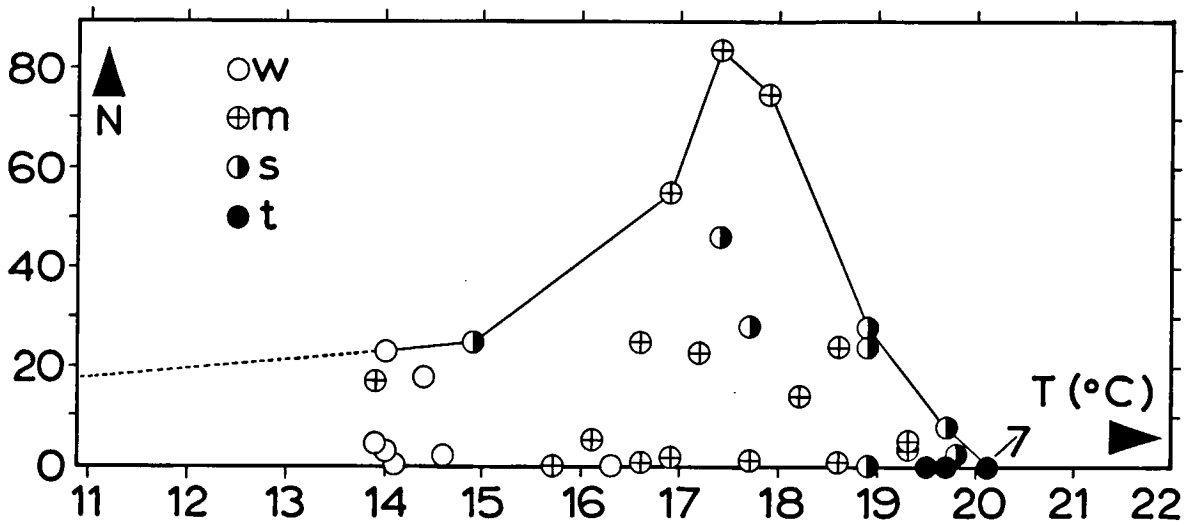


Fig. 1 (top). Number of colonies of *Eunicella singularis* per m<sup>2</sup> (N) as a function of average summer temperature T at forty different stations. Symbols indicate water movement: w = weak, m = moderate, s = strong and t = turbulent. Line joins stations with maximum population densities, the dotted line is a tentative extrapolation for lower temperature intervals.

Fig. 2 (bottom). Number of colonies of *Eunicella singularis* per m<sup>2</sup> (N) as a function of average yearly irradiance (I). For explanation of symbols see fig. 1.

The dotted line is a tentative extrapolation of the curve obtained. These data suggest that although able to live at all local temperatures, *Eunicella singularis* flourishes between 16°C and 19°C. On the other hand, even within this optimum temperature range low population densities occur, and at two stations the species does not occur at all. This fact can be explained by assuming that at

these stations, although temperature conditions are optimal, other conditions are not, thus restricting population density. If this is the case, the line in fig. 1 joins those stations where the parameters other than temperature reach (near) optimum values. Average summer temperature being depth-dependent (Weinberg, 1978a), water movements may also be expected to increase from left to right

in fig. 1. This indeed seems to be the case. The curve obtained might therefore also be a turbulence-dependent one.

Fig. 2, showing population density as a function of yearly submarine irradiance, follows a probabilistic pattern as well. *Eunicella singularis* occurs between 20 and 25000 cal cm<sup>2</sup>year<sup>-1</sup>, with a maximum for values between 300 and 2500 cal cm<sup>2</sup>year<sup>-1</sup>. Irradiance, however, is not solely depth-dependent, as more or less shaded stations are included in the survey (Weinberg, 1978a). Water movement, as indicated by the symbols in the graph, is not correlated with average yearly irradiance. It therefore becomes apparent now that all the stations with turbulent water movements, irrelevant of light conditions, are devoid of *E. singularis*. The species appears to be absent from turbulent waters. On the other hand, weak water movements occurring below certain depths are correlated with weak irradiance. The fact that the population density is rather low at stations with weak water movements probably depends on the low irradiance values at these stations.

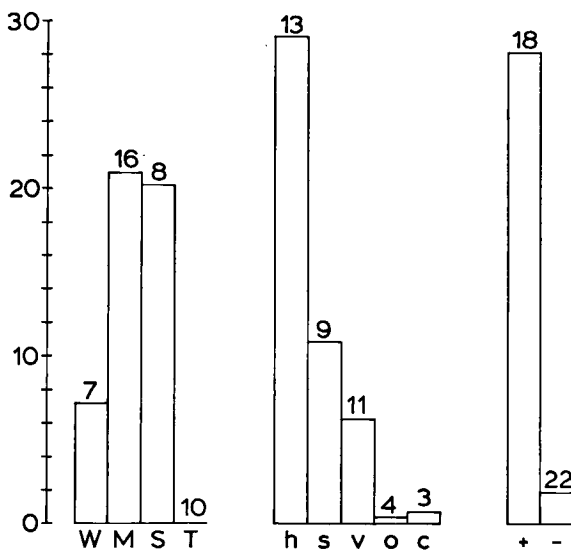


Fig. 3. Histogram showing average population densities of *Eunicella singularis* as a function of different parameters. Numbers indicate number of stations falling into each parameter class. The first histogram shows water movement with the following classes: W = weak, M = moderate, S = strong, T = turbulent. The second histogram shows slope of substratum, with the classes: h = horizontal, s = sloping, v = vertical, o = overhanging and c = cracks and holes. The third histogram shows sediment: + = present, - = absent.

Fig. 3 shows three histograms. The left one depicts the average population density at stations with weak, moderate, strong and turbulent water conditions, respectively. *E. singularis* thrives in the two middle classes, occurs in smaller quantities when average water movement is weak (but as we have seen this may be due to irradiance) and is lacking at stations where turbulent water conditions are encountered. Here also the general shape of the histogram suggests a probabilistic relationship, or a binary one, with the species occurring wherever water conditions are not turbulent.

The central histogram in fig. 3 shows the average population density as a function of slope at the stations concerned. Five slope-classes were used: horizontal (0-30°), sloping (30-60°), vertical (60-90°), overhanging (>90°), cracks and holes. The histogram obtained suggests a rather linear relationship: as substratum becomes more horizontal, population density increases.

An explanation for this relationship is given by the right histogram. At stations retaining sediment on their substratum (predominantly horizontal and sloping ones) average population density (28.1 individuals m<sup>-2</sup>) is more than fifteen times that at stations devoid of sediment (1.84 individuals m<sup>-2</sup>). There seems to be a nearly binary relationship with sediment. In a true binary relationship no *Eunicella* at all would have been found in the class "without sediment". It must be stressed, on the other hand, that sediment is always present in minute quantity. In this way, the existence of three types of relationships is demonstrated: a probabilistic one with temperature and irradiance (and possibly water movement), a gradual (linear?) one with slope, and a binary one with sediment (and probably with water movement as well).

In the following section population density of each species is given as a function of these different parameters. For temperature and irradiance a simultaneous graphical representation is given. Therefore, the forty underwater stations are represented in a graph (fig. 4) where in addition to their place in the plane as defined by average yearly irradiance and average summer temperature, each station has been characterized by its water movement, its slope and the presence or absence of sediment. At a number of stations light and

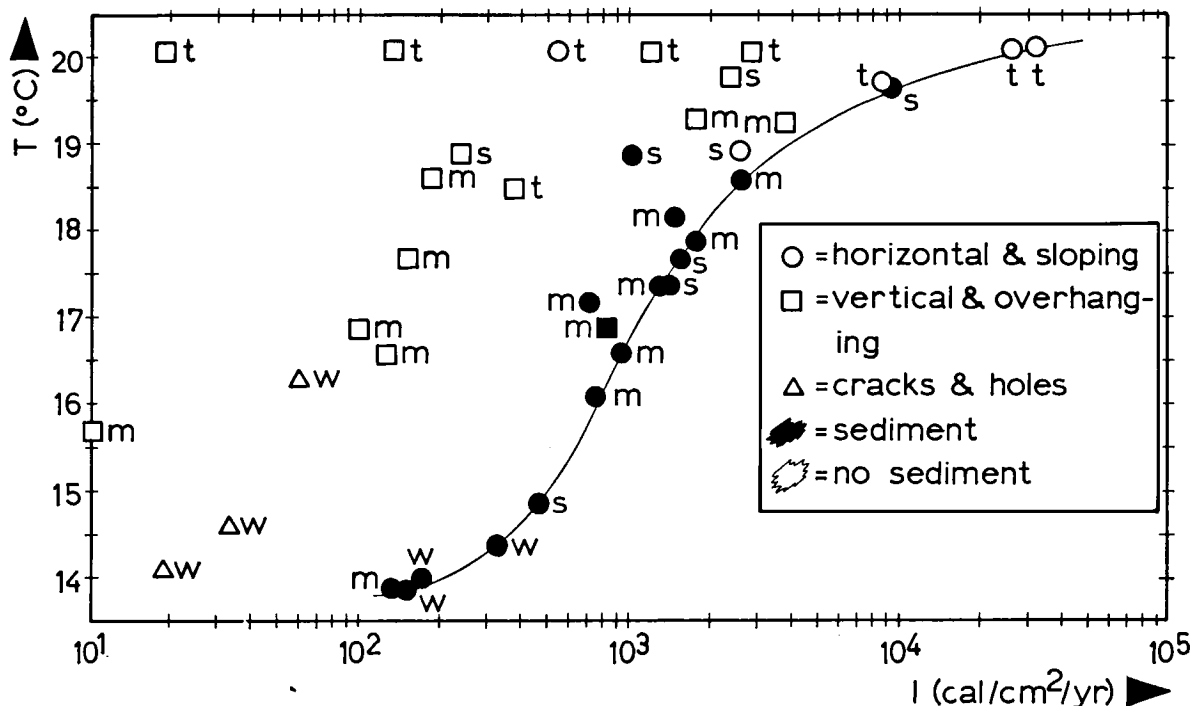


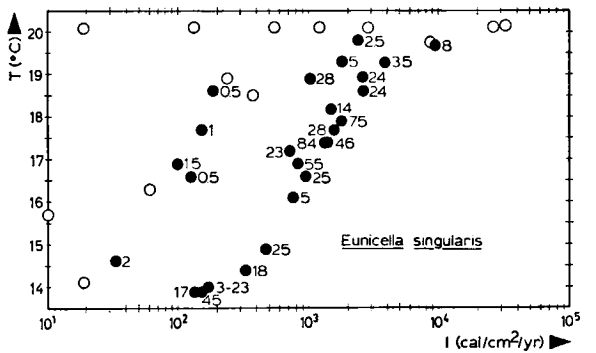
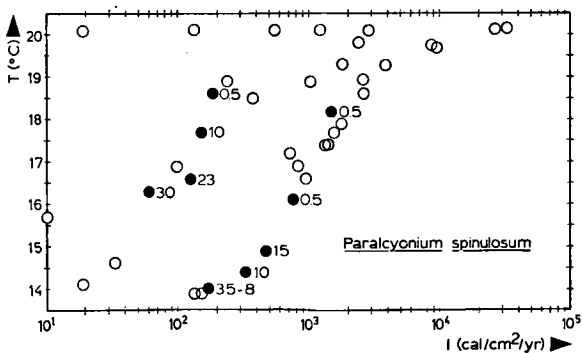
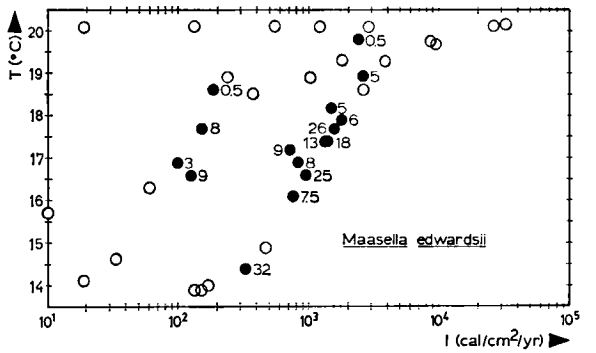
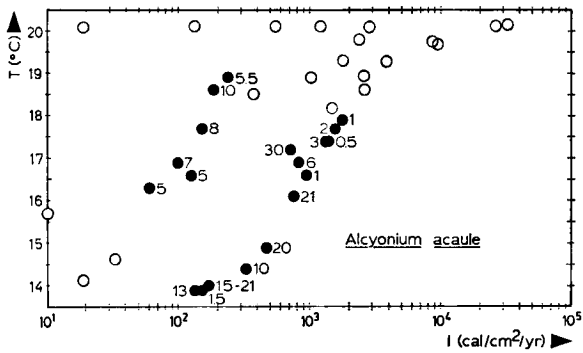
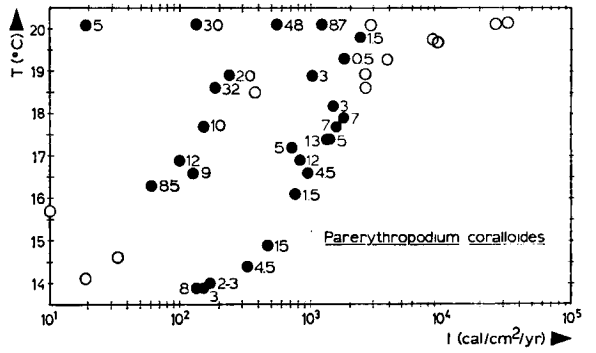
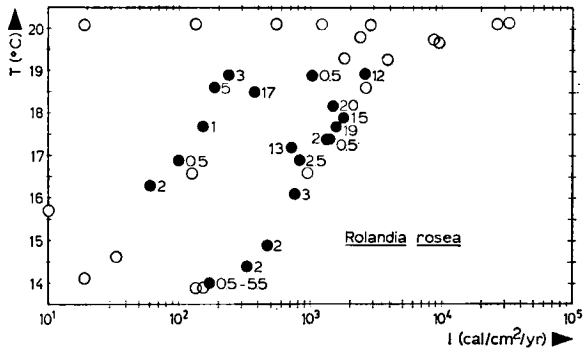
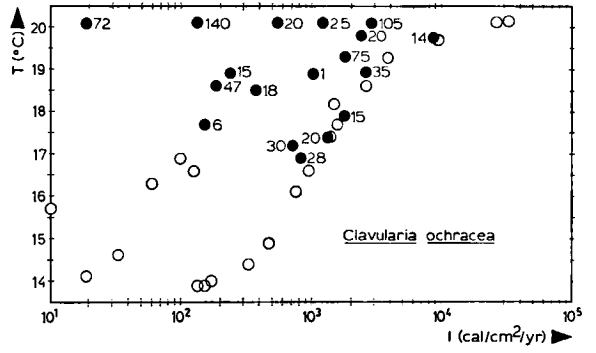
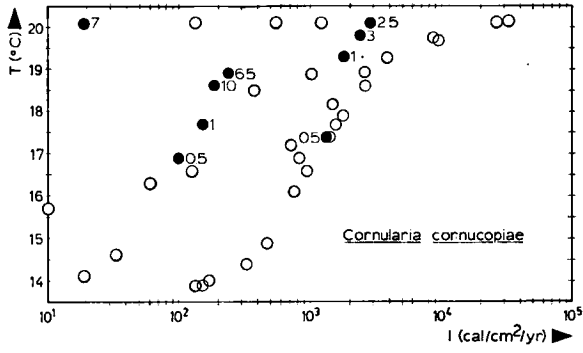
Fig. 4. Representation of the forty stations in the plane defined by yearly irradiance (I) and summer temperature (T). Each symbol represents one station. Slope classes and presence or absence of sediment are indicated by means of symbols. Water movement is indicated by lettering: w = weak, m = moderate, s = strong, t = turbulent. The sigmoid curve joins open horizontal or gently sloping stations, most of them retaining sediment. Other stations receive less light than the possible maximum at each corresponding depth. Most of these stations are not horizontal and lack sediment.

temperature are interdependent, as both vary with depth. This is the case for most horizontal and slightly sloping bottoms. The graphic representation of the values displays a one-sided boundary in the shape of a sigmoid curve which demonstrates the existing relationship between the logarithm of irradiance (which decreases almost linearly with depth) and summer temperature (which is S-shaped because of the thermocline). This relationship is also valid for open water. The other stations have exposition coefficients smaller than 1, and are therefore situated at the left of the curve, corresponding with dark stations as compared to the surrounding open water. In the next section dealing with the ecology of the species, the same graphical representation is used, but the stations are characterized only by the presence (and population density) or absence of each species.

#### IV. ECOLOGY OF THE SPECIES

##### 1. Temperature and irradiance

As can be seen in fig. 5, each species has its own requirements regarding the factors water temperature and submarine daylight. *Cornularia cornucopiae* and *Clavularia ochracea* are obviously surface animals living above the thermocline, but with a large tolerance to irradiance conditions. *Rolandia rosea* and *Parerythropodium coralloides* are very tolerant, and occur under virtually all circumstances, although the former is not found in very shallow stations with an average summer temperature above 19°C. The same can be said for *Alcyonium acaule*, which occurs in stations with medium irradiance values, as does *Maasella edwardsii*. *Paralcyonium spinulosum* occurs in deeper darker places. *Eunicella singularis* is quite tolerant, but thrives on (sub)horizontal stations which are



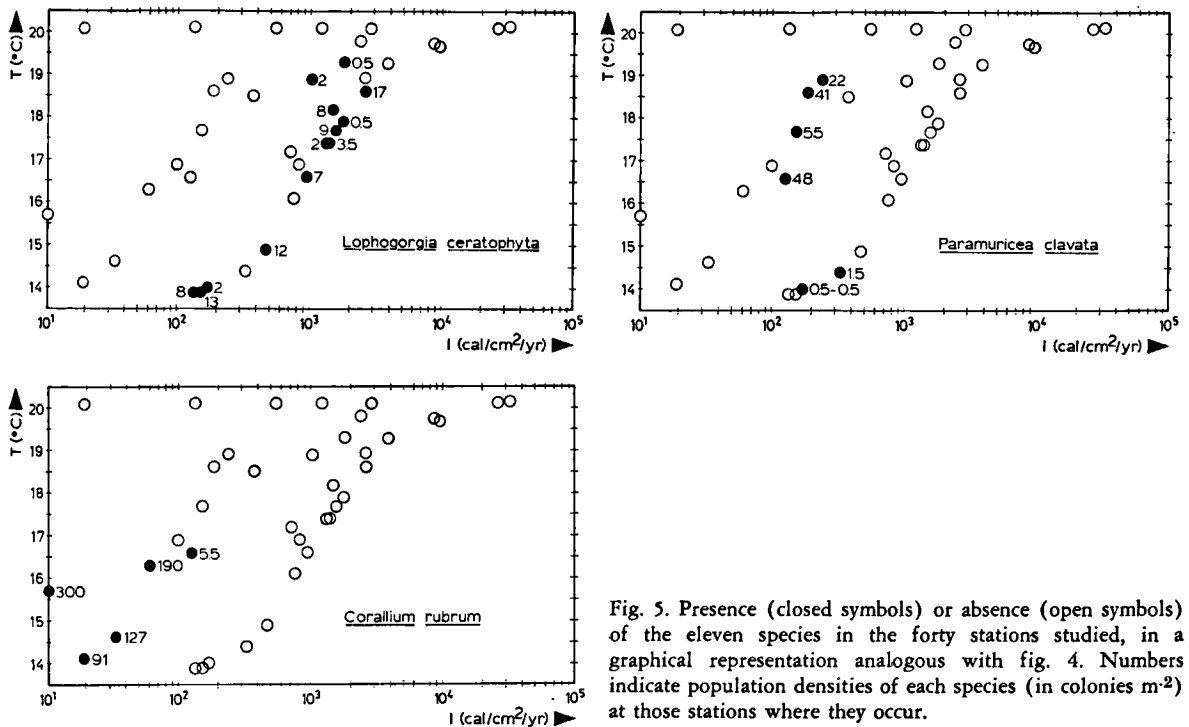


Fig. 5. Presence (closed symbols) or absence (open symbols) of the eleven species in the forty stations studied, in a graphical representation analogous with fig. 4. Numbers indicate population densities of each species (in colonies  $m^{-2}$ ) at those stations where they occur.

represented by points situated on (or near) the sigmoid curve forming the right-hand border of the cloud of points. The same is even more true for *Lophogorgia ceratophyta*. *Paramuricea clavata* tolerates a very narrow band of light conditions only, but is quite tolerant to temperature. *Corallium rubrum* is found exclusively in cooler, darker stations.

It will now be examined what the ecological optima are for each species regarding the factors water temperature and submarine daylight. For this purpose, variance analyses have been carried out, the main principles of which are briefly outlined here. Two types of analyses were used. One was a one-boundary variance analysis, investigating whether the population density of a species on one side of a given boundary value differs significantly from the population density on the other side (e.g.: is the population density of *Clavularia ochracea* at stations with an average summer temperature  $<16^{\circ}C$  significantly different from the one in stations with an average summer temperature  $>16^{\circ}C$ ?). The other was a two-boundaries variance analysis, investigating whether the population densities of a species between two given

boundary values, differs significantly from the ones outside (e.g. is the population density of *Maasella edwardsii* between yearly irradiance values of 330 and 10000  $cal\ cm^{-2}\ year^{-1}$  significantly different from the ones below 330 and over 10000  $cal\ cm^{-2}\ year^{-1}$ ?). The aim of the first analysis is to show whether threshold values exist, below or over which a species occurs most of the time, whereas the second analysis may yield an optimum range for a species, defined by upper and lower threshold values. Analyses were carried out by computer, and all boundary values (or combinations thereof in the second analysis) were scanned automatically over the following (arbitrarily chosen) values.

For average summer temperature: 13, 14, 15, 16, 17, 18, 19, 20 and  $21^{\circ}C$ .

For average yearly irradiance: 0, 10, 330, 1000, 3300, 10000, 33000 and 100000  $cal\ cm^{-2}\ year^{-1}$ .

Each choice of a boundary (or two boundaries) divides the data in two (or three) intervals, which are the experimental groups to be compared. The number of observations<sup>1)</sup> within each interval

1) Each observation is the population density of a given species in a given station.

depends on the boundaries chosen, and is not necessarily the same. Two hypotheses can now be formulated:

- the means of the observations are the same within each interval
- the means of the observations in the various intervals differ from each other.

The first hypothesis ( $H_0$ ) can be tested through the magnitude:

$$F = \frac{\frac{\sum_{k=1}^k (x_k - \bar{x})^2 \cdot n_k / (k-1)}{1}}{\frac{\sum_{i=1}^k \sum_{j=1}^{n_k} (x_{ijk} - x_k)^2 / (n-k)}{1}}$$

where:  $k$  = number of intervals [( $k-1$ ) = number of boundaries]  
 $n$  = number of cases (stations)  
 $n_k$  = number of cases belonging to interval  $k$   
 $x_{ijk}$  = value for station  $i$  and interval  $k$   
 $x_k$  = mean for interval  $k$   
 $\bar{x}$  = total mean for all the intervals

$F$  has ( $n-k$ ) and ( $k-1$ ) degrees of freedom.  $H_0$  can be rejected in the case of the one-boundary test ( $n=40$ ,  $k=2$ ) for  $F$  (38.1):

if  $F \geq 4.06$  (error probability  $P \leq 5\%$ )  
 if  $F \geq 7.36$  (error probability  $P \leq 1\%$ )

and in the case of the two-boundaries test ( $n=40$ ,  $k=3$ ) for  $F$  (37.2):

if  $F \geq 3.25$  (error probability  $P \leq 5\%$ )  
 if  $F \geq 5.24$  (error probability  $P \leq 1\%$ )

These calculations yielded the following results in relation to the average summer temperature (in °C), where  $y$  stands for the temperature interval within which each species is mostly found, and  $P$  the corresponding error probability according to the  $F$ -values calculated.

*Cornularia cornucopiae*:

$18 \leq y$  and  $18 \leq y \leq 19$  ( $P < 5\%$ )

*Clavularia ochracea*:

$20 \leq y$  ( $P < 1\%$ ) ( $F = 14.71$ )

$17 \leq y$  ( $P < 5\%$ )

*Rolandia rosea*:

$17 \leq y \leq 20$  ( $P < 5\%$ ) ( $F = 3.94$ )

highest probability for  $17 \leq y \leq 19$

( $F = 4.59$ )

*Parerythropodium coralloides*:

no conclusion possible with a probability of 95% or better, which means that there is a

probability of 99% to find the species over the entire temperature range.

*Alcyonium acaule*:

$y \leq 19$  ( $P < 1\%$ ) ( $F = 8.01$ )

highest probability for  $y \leq 18$  ( $F = 10.41$ )

*Maasella edwardsii*:

$14 \leq y \leq 18$  and  $y \leq 18$  ( $P < 1\%$ )

$y \leq 19$  ( $P < 5\%$ )

*Paralcyonium spinulosum*:

$16 \leq y \leq 17$  ( $P < 1\%$ )

$y \leq 18$  ( $P < 5\%$ )

*Eunicella singularis*:

$16 \leq y \leq 19$  ( $P < 1\%$ ) ( $F = 6.01$ )

$y \leq 20$  ( $P < 5\%$ )

highest probability for  $17 \leq y \leq 18$   
 ( $F = 11.67$ )

*Lophogorgia ceratophyta*:

$y \leq 14$  ( $P < 1\%$ ) ( $F = 10.08$ )

$y \leq 19$  ( $P < 5\%$ )

*Paramuricea clavata*:

no conclusion possible with a probability of 95% or better, which means that there is a probability of 99% to find the species over the entire temperature interval.

*Corallium rubrum*:

$15 \leq y \leq 16$  ( $P < 1\%$ ) ( $F = 29.27$ )

$y \leq 17$  ( $P < 5\%$ )

These results are represented in fig. 6.

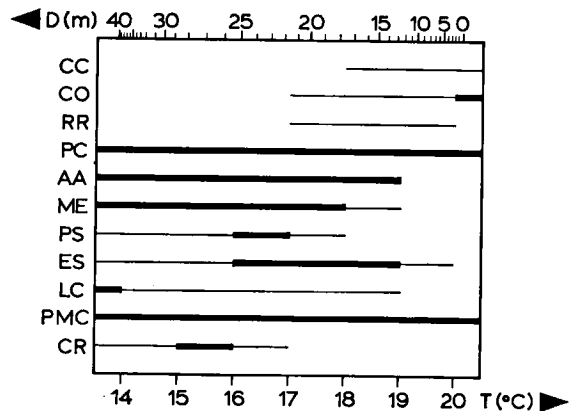


Fig. 6. Probability intervals for the occurrence of each species (for species code see text) as a function of temperature (linear scale) and depth. Thin lines show 95% probability interval, thick lines 99% probability interval as calculated by means of variance analysis.



When regarding yearly irradiance (in cal cm<sup>-2</sup> year<sup>-1</sup>) the following results were obtained, where  $z$  stands for the irradiance interval within which each species is mostly found, and  $P$  is again the corresponding probability.

*Cornularia cornucopiae*:

$$z \leq 330 \quad (P < 5\%)$$

*Clavularia ochracea*:

no conclusion possible with a probability of 95% or better, which means that there is a probability of 99% to find the species over the entire irradiance interval.

*Rolandia rosea*:

$$330 \leq z \leq 3300 \quad (P < 5\%)$$

*Parerythropodium coralloides*:

no conclusion possible with a probability of 95% or better, which means that there is a probability of 99% to find the species over the entire irradiance interval.

*Alcyonium acaule*:

$$z \leq 1000 \text{ and } 10 \leq z \leq 1000 \quad (P < 1\%)$$

*Maasella edwardsii*:

$$330 \leq z \leq 3300 \quad (P < 5\%)$$

*Paralcyonium spinulosum*:

$$z \leq 330 \quad (P < 5\%)$$

*Eunicella singularis*:

$$330 \leq z \leq 3300 \text{ and } 1000 \leq z \leq 3300$$

$$(P < 1\%)$$

$$330 \leq z \quad (P < 5\%)$$

highest probability for  $330 \leq z \leq 3300$

$$(F = 8.03)$$

*Lophogorgia ceratophyta*:

no conclusion possible with a probability of 95% or better, which means that there is a probability of 99% to find the species over the entire irradiance interval.

*Paramuricea clavata*:

$$z \leq 330 \quad (P < 1\%)$$

$$10 \leq z \leq 330 \quad (P < 5\%)$$

*Corallium rubrum*:

$$z \leq 10 \quad (P < 1\%) \quad (F = 55.26!)$$

$$z \leq 330 \quad (P < 5\%)$$

These results are represented in fig. 7.

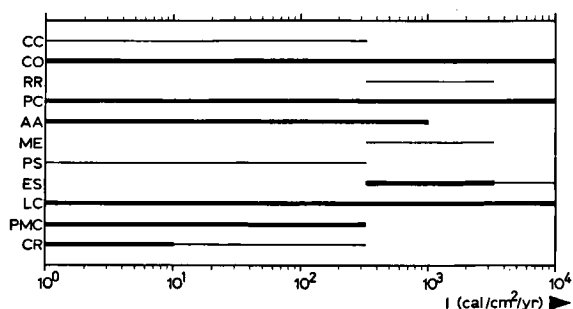


Fig. 7. Probability intervals for the occurrence of each species (for species code see text) as a function of irradiance. Thin lines show 95% probability interval, thick lines 99% probability interval as calculated by means of variance analysis.

## 2. Slope, sediment and water movement

As was shown in section II, the following parameter classes were distinguished. For slope: (1) horizontal or sloping, (2) vertical or overhanging, and (3) cracks and holes. For sediment: (1) presence and (2) absence. For water movement: (1) weak, (2) moderate, (3) strong and (4) turbulent.

For each of the above parameter classes the percentage of stations where a given species is found, and the average number of colonies of each species per m<sup>2</sup> at those stations was calculated. These data combined yielded the average number of colonies per m<sup>2</sup> for each species and for each parameter class. These results appear in table I, from which the optimum intervals of the different species for each parameter can be deduced.

## V. RESULTS

The ecological amplitudes of the different species are given in this section, partly based on the results of the preceding paragraph, partly on what is known about the communities (Weinberg, 1978a), and partly on incidental observations.

### 1. *Cornularia cornucopiae*

This species was found between 0 m depth (Grotte de Béar, Grotte du Troc) and 22 m depth (Cap l'Abeille), on rocky surfaces and on the tunicate *Microcosmus* spp. It is encountered above the thermocline, the minimum summer temperature observed being 17°C and it is found in strongly moving or turbulent waters, mostly in dark places (<330 cal cm<sup>-2</sup>year<sup>-1</sup>), although it is found in

species	slope			sediment		water movement			
	h+s	v+o	c+h	-	+	W	M	S	T
CC	0.03	2.07	0.00	1.48	0.03	0.00	0.81	1.20	1.06
CO	6.18	30.59	0.00	23.93	4.89	0.00	9.64	8.90	41.42
RR	3.72	1.92	1.34	1.93	3.74	0.65	3.02	4.65	1.87
PC	6.06	14.53	28.33	16.13	6.22	13.45	7.29	6.45	18.70
AA	5.72	2.76	1.67	1.97	6.96	5.36	6.68	3.55	0.00
ME	6.62	1.92	0.00	1.25	7.95	4.48	5.87	6.20	0.00
PS	1.08	2.24	10.00	3.02	1.28	6.88	2.14	0.19	0.00
ES	21.65	4.61	0.67	1.94	26.70	3.93	20.96	20.10	0.00
LC	3.85	0.04	0.00	0.03	4.41	1.82	2.68	3.30	0.00
PMC	0.11	11.21	0.00	7.89	0.13	0.28	9.12	2.64	0.00
CR	0.00	19.86	136.00	33.63	0.00	58.48	18.34	0.00	0.00

TABLE I

Average population density of the different species (in colonies  $m^{-2}$ ) at stations belonging to various parameter classes. For slope: h + s = horizontal or sloping, v + o vertical or overhanging, c + h = cracks and holes. For sediment: + = presence, — = absence. For water movement: W = weak, M = moderate, S = strong, T = turbulent. For species code see text.

places with irradiances of up to 10000  $cal\ cm^{-2}\ year^{-1}$ . As a result, it encounters optimum living conditions on the vertical or overhanging walls of near-surface caves, where it is found together with *Clavularia ochracea* and *Parerythropodium coralloides*. It occurs rather sparsely, with population densities never exceeding 10 colonies  $m^{-2}$ .

## 2. *Clavularia ochracea*

This species was also found between 0 m (Grotte de Béar, Grotte du Troc) and 22 m (Cap Rédéris), on the same substrata as the preceding species and once on the decapod crustacean *Pisa nodipes* Leach, 1816 (fig. 8). It likewise lives above the thermocline ( $>17^{\circ}C$ ), mostly occurring in turbulent surface waters ( $>20^{\circ}C$ ). Although being rather indifferent to irradiance conditions (it is found in places with irradiance values of between 30 and 10000  $cal\ cm^{-2}\ year^{-1}$ ), it never occurs in permanently sunlit places but is able to form extensive patches of over 100 colonies  $m^{-2}$  on the vertical and overhanging walls of near-surface caves, where it is encountered together with *Cornularia cornuopiae* and *Parerythropodium coralloides*.

## 3. *Rolandia rosea*

Found from 7.5 m (Jetée Port Vendres) to 38 m depth (Cap l'Abeille), it tolerates a wide range of temperature ( $14-19^{\circ}C$ ) and irradiance (60-2500  $cal\ cm^{-2}\ year^{-1}$ ) conditions, although it is most often found in places not too dark and just below the thermocline, thereby avoiding turbulent surface conditions. It is encountered as inconspicuous warts or stoloniferous growths on rocks and tunicates of the genus *Microcosmus*, but is able to form respectable membranaceous encrustations on dead gorgonian axes (mainly of *Eunicella singularis*), see Weinberg & Weinberg (1979: Plate III C). It may be for the latter reason that this species seems to occur mostly in places with sedimentation (see section V.8), but the species also thrives in turbid and slightly polluted waters. This is demonstrated by the fact that the greatest population densities (17-20 colonies  $m^{-2}$ ) are found just outside the harbour entrance of Port Vendres.

## 4. *Parerythropodium coralloides*

Encountered in depths from 0 m (Grotte de Béar) to 40 m (Cap Béar). It is extremely tolerant to a

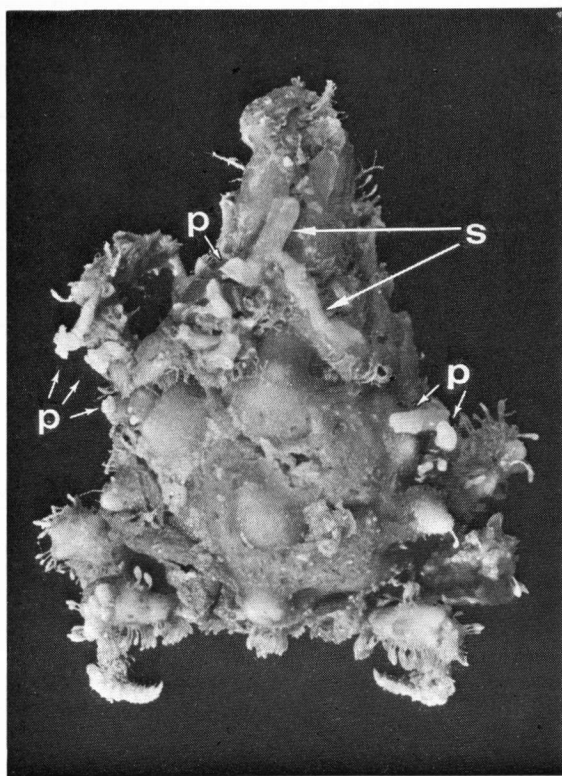


Fig. 8. Small colony of *Clavularia ochracea* on the crab *Pisa nodipes* Leach, 1816. Polyps (p) and stolon (s) are visible. It is not sure whether the stoloniferan actually settled on the decapod crustacean, as the latter is known to camouflage itself with pieces of sponge or small sea-anemones by actively detaching them from their natural substratum and transferring them onto its carapax. This specimen was found at 13 m depth at Cap du Troc, Banyuls-sur-Mer (Photograph: Louis van der Laan).

wide range of temperature and irradiance (30-2300 cal cm<sup>2</sup>year<sup>-1</sup>) conditions, as well as to turbulence and slope. It is found on such different substrata as rock, tunicates (*Microcosmus* spp.), shells (*Pteria hirundo* (Meuschen, 1787)) and gorgonians (*Eunicella singularis*, *Lophogorgia ceratophyta*, *Paramuricea clavata*). Although table I suggests an optimum for cracks and holes, this impression results from the fact that number of colonies was counted instead of percent coverage. The highest population density (85 colonies m<sup>-2</sup>) was encountered in small holes at Cap R  d  ris, but these were small, wartlike colonies. The species finds its optimum conditions in turbulent surface caves, like the Grotte de B  ar, where it is able to form large encrusting colonies sometimes forming

upright lobes reminiscent of *Alcyonium*, and as an encrusting epibiont on gorgonians, especially in deeper waters (cf. Weinberg & Weinberg, 1979: Plate III B, D). Differently coloured specimens occur in the same area (Weinberg, 1975b, 1977). Wine-red colonies are the most common ones and are found at every depth. Pink colonies occur deeper than c. 15 m, while white ones are encountered below c. 25 m only.

##### 5. *Alcyonium acaule*

This species is quite tolerant, except for turbulent surface conditions, and as a result it is found in waters with summer temperatures of below 19°C and yearly irradiance values of below 2000 cal cm<sup>2</sup>year<sup>-1</sup> with a preference for stations with values of below 1000 cal cm<sup>2</sup>year<sup>-1</sup>. It occurs from 10 m depth (Ile Grosse, incidental observation) to 40 m depth (Cap B  ar) on all slope types with a maximum on horizontal and sloping bottoms containing sediment. High population densities (20-30 colonies m<sup>-2</sup>) were encountered at places with a regular, moderate to strong, current (Cap B  ar, Cap R  d  ris).

##### 6. *Maasella edwardsii*

Encountered from 2 m depth (Grotte de B  ar, incidental observation) to 32 m depth (Cap l'Abeille), the species is seldom found in shallow water, and although occurring from 14.4°C to 19.8°C it mostly occurs in cool to medium temperature conditions (14-18°C) and medium irradiance values (100-2500 cal cm<sup>2</sup>year<sup>-1</sup>). Although difficult to discern underwater, the small brown colonies occur in populations with densities up to 32 colonies m<sup>-2</sup>. One incidental observation (see above) excepted, the species is not found in turbulent water conditions. It thrives on horizontal or sloping sediment-covered bottoms, where it is invariably found together with the gorgonian *Eunicella singularis*.

##### 7. *Paralcyonium spinulosum*

This species occurs from 15 m (Cap R  d  ris) downwards, but is mostly known from deeper waters. It lives below the thermocline (<18°C) in rather dark places (60-400 cal cm<sup>2</sup>year<sup>-1</sup>) although incidentally encountered in places with

irradiance values of as much as  $1500 \text{ cal cm}^{-2}\text{year}^{-1}$ . Previously described as exclusively hypolithic (Laubier, 1966), it was found on all slope types, although apparently being more common in cracks and holes with weak or moderate water movement and without sedimentation. The beautiful transparent colonies are not often found in the Banyuls area, but may occur in population densities reaching  $30 \text{ colonies m}^{-2}$  (Cap R  d  ris).

#### 8. *Eunicella singularis*

The most common species in the area studied (these white gorgonians occur at 27 out of 40 stations) it reaches very high population densities (up to  $84 \text{ colonies m}^{-2}$ ) over large areas (several hectares at many places along the coast), thereby often determining the general aspect of the underwater scenery (see Weinberg & Weinberg, 1979: plate 1A). It is virtually absent from places with turbulent surface conditions (although one colony was observed at 2 m depth at the Grotte de B  ar), and reaches maximum population densities in places with medium summer temperature values ( $16\text{-}19^\circ\text{C}$ ). A phenomenon occurring during the summer of 1973 has given another indication of its temperature tolerance. During a long period without wind, the water layer above the thermocline was heated up to temperatures above  $24^\circ\text{C}$ . All the colonies of *Eunicella* died in this zone (observations at Jet  e Port Vendres, Cap B  ar, Ile Grosse and Cap R  d  ris), while colonies of *Lophogorgia ceratophyta* survived these extreme conditions (Weinberg, 1975a). Although encountered at places with irradiance values of  $30\text{-}10000 \text{ cal cm}^{-2}\text{year}^{-1}$ , the species thrives in places with irradiance conditions of  $330\text{-}3300 \text{ cal cm}^{-2}\text{year}^{-1}$ . At two stations where the population extended from deeper water upto a certain limit (5 m at Ile Grosse and 13 m at Cap R  d  ris), the irradiance conditions were quite similar in both ( $2359$  and  $2586 \text{ cal cm}^{-2}\text{year}^{-1}$  respectively). The species occurs mainly on horizontal and slightly sloping sediment-covered bottoms.

#### 9. *Lophogorgia ceratophyta*

Although not as common as the previous species (it occurs at 13 out of 40 stations, with a maximum population density of  $17 \text{ colonies m}^{-2}$ ), these tall

orange gorgonians share *Eunicella's* niche on horizontal and sloping sediment-covered bottoms, in this case situated in depths over 10 m. It thrives on mud-covered deep places, and reaches high population densities in cooler waters. No correlation with submarine irradiance has been established, but fig. 5 shows that it occurs in stations with irradiance values of between  $140$  and  $2600 \text{ cal cm}^{-2}\text{year}^{-1}$ , and apart from warm and turbulent waters, tolerates a wide range of temperatures and water movements.

#### 10. *Paramuricea clavata*

Typical for vertical and overhanging surfaces between 13 m depth (Cap B  ar) and 26 m depth (Cap R  d  ris), where the population reaches densities of up to  $55 \text{ colonies m}^{-2}$ , it is also found in much smaller numbers on horizontal and sloping bottoms in deeper waters (32-38 m at Cap l'Abeille and Cap R  d  ris). As a result, the species appears to be indifferent to temperature conditions, and the stations where it occurs share only one condition: a low level of irradiance ( $<330 \text{ cal cm}^{-2}\text{year}^{-1}$ ). In fig. 5 an even more narrow range of  $120\text{-}330 \text{ cal cm}^{-2}\text{year}^{-1}$  is apparent. In this respect *E. singularis* and *P. clavata* have opposite demands, as was confirmed by measurements at the boundary of two specifically different populations. The population of *Eunicella* received 3.3 times the amount of light than the population of *Paramuricea*, although the measurements were carried out a 50 cm from each other (Weinberg, 1975a). The purple colonies of *Paramuricea* are not found in surface caves probably because of turbulent conditions.

#### 11. *Corallium rubrum*

Absent from horizontal and sloping sediment-covered bottoms, this species is found in deeper water, mostly below the thermocline. It thrives in dark places with irradiance values  $<130 \text{ cal cm}^{-2}\text{year}^{-1}$  and is found in weak or moderate water conditions exclusively. Unfortunately, *Corallium* is an endangered species in the area studied. Inconsiderate divers do great damage to populations of this species, as the colonies are favourite souvenirs. Now, the populations mostly consist of small (on average 7-8 cm high) colonies, with an

estimated age of 20-30 years. Large colonies estimated to be over a century old are not to be found any more. The species may be saved by the establishment of a protected area (Réserve Marine de Banyuls) which is effectuated in January 1979.

## VI. CONCLUSIONS AND DISCUSSION

Field observations at a large number of underwater stations led to the recognition of optimum intervals for a number of abiotic factors for each octocoral species studied.

Correlations with most physical parameters concern average values of the latter. Extremes may play a far more important role, but these values are difficult to assess. However, in places with high average values maxima are more likely to occur than in places with low average values, and vice versa. The correlations therefore clearly indicate in what way a species is sensitive for a given parameter.

Although each species (with the possible exception of *Parerythropodium coralloides*; see below) has its own ecological niche, it will tolerate other species well in the case that their niches overlap. Examples: the co-existence of *Clavularia*, *Cornularia* and *Parerythropodium* in surface caves; or the communities from deeper waters of *Eunicella* and *Lophogorgia* on horizontal bottoms, often associated with *Maasella* and/or *Alcyonium* (see also Weinberg, 1978a). This may be due to the fact that all the species studied are filter feeders, each of them possessing polyps which are equally well equipped for the capture of plankton and particulate organic matter; in this way, they do not really compete with each other.

The observed differences in maximum population density between species are therefore not the result of differences in ecological amplitude, but rather reflect differences in recruitment and vitality. Large gorgonian colonies, with thousands of polyps, emit scores of planula larvae, thus increasing the number of potential settlers, a number impossible to meet for the smaller alcyonacean and stoloniferan colonies. On the other hand, *Lophogorgia* which in spite of its large colonies (with an estimated 10000 polyps for an average colony) does not occur in population densities comparable

to those of other gorgonians in this study, probably has more vulnerable larval and young stages.

Whether the ranges found for each environmental parameter reflect the tolerances of adult colonies, or whether they rather reflect the requirements of larval and juvenile stages cannot be determined without experimentation. However, the young phases being infinitely more vulnerable than the adult colonies (Weinberg & Weinberg, 1979), they probably determine where, and to what extent, a species survives.

Species that tolerate extreme conditions (*Cornularia* and *Clavularia* in surface caves, *Corallium* in very dark places) reach the highest population densities observed, simply because there is little competition for space, either by octocorals or by other organisms. The opposite is displayed by the alcyonacean *Parerythropodium*. This species is not particular about its abiotic environment, which enables it to lead an opportunistic life. Wherever a suitable substratum becomes available (and the species is not very restricted in this respect either), it is able to settle.

Three different survival strategies are thus revealed:

- competitiveness: the species are well equipped for certain environmental conditions. In their niches they are able to compete with the other species. This is the mechanism mostly displayed. Typical species: *Alcyonium acaule*, *Maasella edwardsii*, *Eunicella singularis*, *Paramuricea clavata*.
- specialization: the species are well equipped for extreme environmental conditions where others cannot live, and thus they monopolize or dominate the corresponding niche. Typical example: *Corallium rubrum*.
- opportunism: the species are not particular in their requirements. They are able to settle and survive under most environmental conditions. The fact that they hardly ever become dominant is due to the competitiveness of other species. Typical example: *Parerythropodium coralloides*.

Many species show combinations of these strategies. *Clavularia ochracea* for instance, is a specialist in surface caves, but a competitor in deeper habitats.

The mechanisms involved with the selection of a niche are still not known. The importance of larval and juvenile stages in this respect has still to be shown. Though experiments with octocorals are not easy to carry out, and the sea is not the ideal place for experimental work, I have attempted to clarify some of these aspects. They will be the subject of future publications.

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