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AUTECOLOGY OF SHALLOW-WATER OCTOCORALLIA FROM MEDITERRANEAN ROCKY SUBSTRATA, II. MARSEILLE, CÔTE D'AZUR AND CORSICA

by

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ABSTRACT

Qualitative sampling of Octocorallia in 226 underwater stations at 23 localities between Marseille and Sardinia yielded information about their tolerances with respect to depth, slope, sediment and relative irradiance. The results are confronted with those previously obtained for the Banyuls area, and some conclusions are drawn regarding the existence of typical habitat-induced Octocorallian communities.

RÉSUMÉ

A partir d'un échantillonnage qualitatif des Octocoralliaires dans 226 stations sous-marines dans 23 localités entre Marseille et la Sardaigne, des données sont obtenues sur la tolérance des espèces vis-à-vis de la profondeur, la pente du substrat, le sédiment et l'irradiance relative. Ces résultats sont comparés avec ceux précédemment obtenus pour la région de Banyuls. On aboutit à certaines conclusions sur l'existence de communautés d'Octocoralliaires typiques pour des habitats bien définis.

I. INTRODUCTION

In two previous papers (Weinberg, 1978a, 1979a) it was shown that the Mediterranean Octocorallia are sensitive to a number of abiotic factors. Light and sediment proved to be the most important environmental parameters, but temperature and water movement seem to play a role as well. Whereas in the first paper (Weinberg, 1978a) Octocorallian communities were studied as a whole, in the second one (Weinberg, 1979a) the species were studied separately and their distributional ranges (ecological amplitudes) were defined by the extreme values for the different environmental parameters at which each species was encountered.

Both studies were carried out near Banyuls-sur-Mer (France), an area characterized by quite turbid and cold waters for Mediterranean standards. It was felt that comparison with areas offering different environmental conditions would shed more light on species/parameter relationships. Having made an exploratory trip to Corsica in 1975, and being offered the opportunity to take part in a diving cruise to the islands of Elba (Italy) and Corsica (France) in June 1979, which are known for the clarity of their waters, I decided to study the distributional ranges of the Octocorallia in this part of the Mediterranean Sea. Additional studies were to be carried out along the Côte d'Azur and near Marseille, with somewhat intermediate hydrological conditions.

Since extensive studies could not be carried out during both cruises, I decided to focus my attention on four environmental data only: depth (an indication for water movement and temperature), slope, sedimentation and relative irradiance.

If the ecological amplitudes found for each species at Banyuls-sur-Mer are universal, the same species could be expected to occur generally deeper or in more shaded places in the areas prospected during the present study.

For this survey a total of 226 stations were sampled in 24 different localities, at only one of which no Octocorallia were encountered (see map, fig. 1).

II. MATERIAL AND METHODS

Sampling was carried out by means of SCUBA diving, and consisted of localizing Octocorallia in as many stations as could be sampled at each locality visited. I call locality a place defined by its geographical coordinates, and station a site

with homogeneous topographical and environmental conditions. At each locality several stations were visited. Special attention was paid to the upper limit of occurrence of a species. The following species were studied (species abbreviations are used in figs. 20 and 21):

Stolonifera:

CC = *Cornularia cornucopiae* (Pallas, 1766)
CCR = *Clavularia crassa* (Milne Edwards, 1848)
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:

EV = *Eunicella verrucosa* (Pallas, 1766)
ES = *Eunicella singularis* (Esper, 1794)
EC = *Eunicella cavolinii* (Von Koch, 1887)
LC = *Lophogorgia ceratophyta* (Linnaeus, 1758)
PMC = *Paramuricea clavata* (Risso, 1826)
CR = *Corallium rubrum* (Linnaeus, 1758)

The habit 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 Carpine & Grasshoff (1975) and Weinberg (1976, 1977, 1978 b & c).

At each station depth was recorded by means of a diver's depth gauge, while slope and presence or absence of a layer of sediment on the substratum were estimated visually. Relative irradiance was measured with an Underwater Hemispherical Irradiance Meter (UHIM) which is described elsewhere (Weinberg, 1979b). Relative irradiance was always measured at high solar elevations (June and July, between 10 a.m. and 3 p.m. local time) and compared with surface values. The percentages thus found, although not giving an adequate estimation of yearly values, can be compared with identical values known for the Banyuls area.

All statistics were performed by means of SPSS programs (Nie et al., 1975-1979).

III. DESCRIPTION OF THE LOCALITIES

The 24 localities visited for this study appear in fig. 1. At one locality, the Island of Capraia, no Octocorallia were found, and this locality will therefore not be described. As expected, the waters were much clearer in the areas visited than in the Banyuls area. Whereas the average irradiance attenuation coefficient $k_{480} = 0.100$ in June and July in the Banyuls area (Weinberg & Cortel-Breeman, 1978), an average value of $k_{480} = 0.042$ (23 measurements) was found in the areas visited for the present study. Hela et al. (1964) give an average depth of disappearance of the Secchi disk $D_{sd} = 20$ meters near Monaco for the summer months, which yields $k_{480} = 0.068$. Furthermore, summer (June-August) surface irradiance is an average 538 cal cm^{-2} day^{-1} in Banyuls (Weinberg, 1978a), whereas it attains 558 cal cm^{-2} day^{-1} in Nice, Côte d'Azur (4% more) and 577 cal cm^{-2} day^{-1} in Ajaccio, Corsica (7% more) (data obtained from the French National Meteorological Bureau). These data on surface irradiance and irradiance attenuation coefficients combined yield the interesting fact that average summer values for submarine irradiance at 20 m depth are 2 × higher at Monaco and 3.5 × higher near Corsica, as compared with the Banyuls area. For 40 m depth these factors are 4 × and 11 ×, respectively.

While the average summer (June-August) surface temperature is 20.1°C at Banyuls (Weinberg, 1978a), it is colder (18.6°C) at Marseille (Thiriot, 1966) and warmer along the Côte d'Azur with 23.3°C (Bougis et al., 1965). At 50 m depth, average summer temperatures are 13.8°C at Banyuls (Weinberg, 1978a) against 15.1°C at the Côte d'Azur (Bougis et al., 1965).

I will now give a detailed description of each locality, the exact position of which is given on a small map in every case. On these maps the 50-meter line is shown by ————, and the 20-meter line by - - - - - - -. In some cases the 10-meter line is shown as —.—.—.— and shoals are indicated by .....

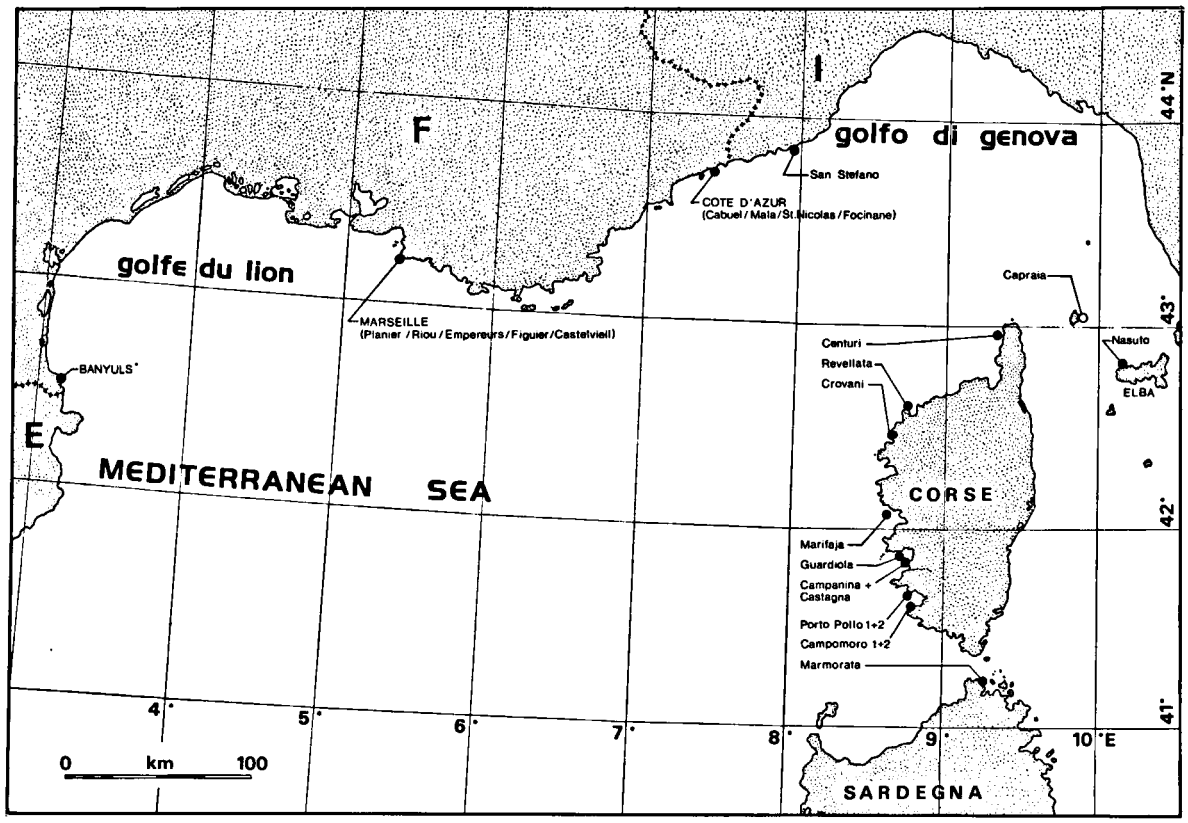

Fig. 1. Map of the northwestern Mediterranean with the localities visited. Black dots indicate that Octocorallia were present, the open circle (Isola di Capraia) indicates that no Octocorallia were found. In Banyuls, 40 underwater stations were previously studied, which are described elsewhere (see text).

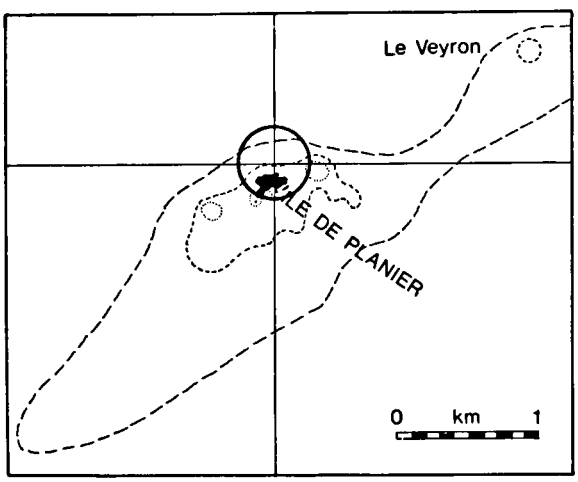

Fig. 2. Ile de Planier, near Marseille. Locality Planier situated at 43°12'02"N 05°13'50"E.

1. Planier (fig. 2)

At 16 km S.S.W. of Marseille lies the small island of Planier, site of many shipwrecks. Near its N.W. point, the bottom is strewn with boulders and slopes down under a 45° angle to about 20 m depth. On their horizontal and sloping sediment-covered surfaces, *Eunicella singularis, Parerythropodium coralloides, Alcyonium acaule* and *Maasella edwardsii* are encountered. On shallow vertical surfaces, *Clavularia ochracea* occurs. Below 20 m, the bottom falls steeply down to 36 m on the sand. The vertical and overhanging surfaces of this large cliff are densely populated by *Paramuricea clavata. Corallium rubrum* is very rare and *Eunicella cavolinii* grows rather near the top of the cliff. At the bottom of the vertical drop-off *Paramuricea clavata* grows on sediment-covered boulders. Farther away, out of the shadow cast permanently by the cliff, *Eunicella singularis* is found on the sediment-covered stones of the gently sloping sandy plain.

2. Riou-Moyade (fig. 3)

Between the Ile Riou and the islet La Moyade extends a shallow calcareous ridge, which descends to about 36 m depth. The steep wall is covered with a rich *Eunicella cavolinii/Paramuricea clavata* community, replaced in its shallower parts by a *Clavularia ochracea/Parerythropodium coralloides* community. *Alcyonium acaule* and *Eunicella singularis* are also encountered. At about 25 m depth, a huge entrance leads to a tunnel cave of about 40 m long. In the middle parts of this cave, which was described in detail by Harmelin

(1969), almost complete darkness is encountered. The walls and ceiling of this cave are densely covered by a *Corallium rubrum* population.

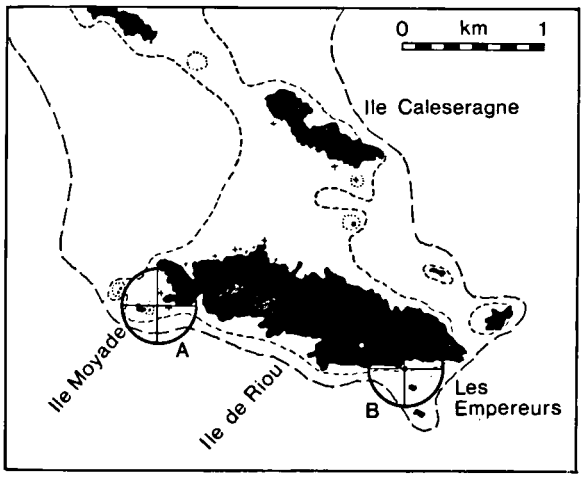

Fig. 3. Riou archipelago, near Marseille. A = locality Riou-Moyade, situated at 43°10'38"N 05°22'20"E. B = locality Empereurs, situated at 43°10'23"N 05°23'38"E.

3. Empereurs (fig. 3)

Near the South coast of the Ile de Riou lie three small islets, called Les Empereurs. The smallest one ("Empereur de Terre") is separated from the main island by a very narrow channel. A strong current is encountered around this rock. The southern cliff of the small island is populated by *Clavularia ochracea* in its shallow parts, and by *Paramuricea clavata* from 10 m downwards. At about 15 m the bottom levels off and a *Eunicella singularis* population is encountered. A tunnel cave of about 15 m long traverses the islet. Its ceiling is densely populated by *Corallium rubrum*, its walls by a *Paramuricea clavata /Eunicella cavolinii/ Parerythropodium coralloides* community. On the northern cliff, which never receives direct sunlight, the latter community extends to only 6 m below the surface.

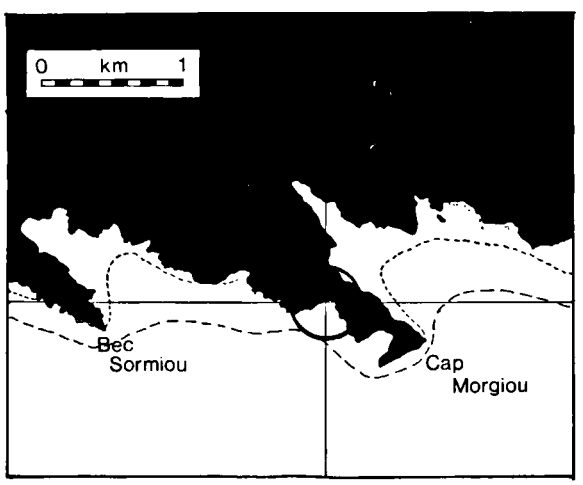

Fig. 4. Cap Morgiou, near Marseille. Locality Figuier, situated at 43°12'19"N 05°26'47"E.

4. Figuier (fig. 4)

To the West of the Cap Morgiou lies a small cove, called Calanque du Figuier. Here, at about 20 m depth in the vertical cliff, a huge underwater cave (40 m deep and 65 m from entrance to exit) is found, which is described in detail by Pouliquen (1972). Even in the darkest places of this cave, *Corallium rubrum* lives on the walls and ceiling. About 50 m to the N.W. of this cave, another one is found, with a wide opening towards the sea. The ceiling of this cave is densely populated by *Corallium rubrum* and *Parerythropodium coralloides*, both species being encountered as shallow as 3 m. Some rare white colonies of *Corallium rubrum* are also to be found here. *Eunicella cavolinii* and *Paramuricea clavata* occur on its walls and bottom, the former species clearly growing towards the light. In front of the cliff, at about 15 m depth, the bottom of the cove levels off, and is covered by boulders on which colonies of *Eunicella singularis* occur.

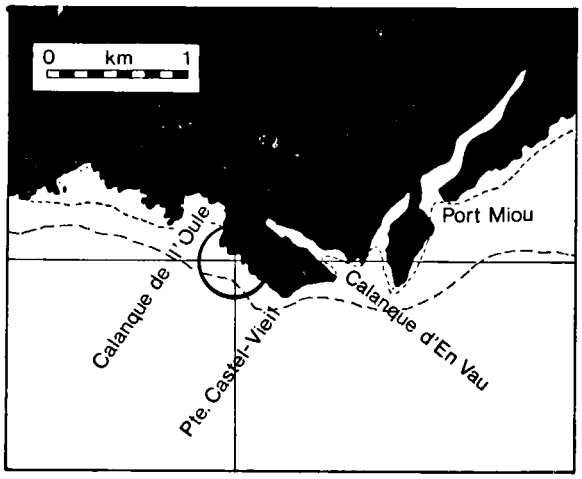

Fig. 5. Les Calanques de Cassis, near Marseille. Locality Castel-Vieil, situated at 43°12'00"N 05°29'50"E.

5. Castel-Vieil (fig. 5)

The calcareous cliffs between the Pointe de Castel-Vieil and the Calanque de l'Oule drop steeply till about 15 m depth. *Clavularia ochracea* grows in the upper zone, *Eunicella singularis* in the lower. From 15 to 35 m depth the bottom slopes down under a 30° angle, with boulders and rocky outcrops separated by sand and meadows of *Posidonia oceanica*. Under the overhanging surfaces of the rocks *Corallium rubrum* is encountered, *Eunicella cavolinii* preferring the vertical sides. On the horizontal surfaces of stones buried in the sand, *Eunicella singularis* occurs. The coastal cliff is pierced by several caves, one of which was visited. It is wedge-shaped, tapering toward its far side situated about 20 m from its 10 m wide entrance. It also narrows from its bottom, which is situated at 15 m depth to its ceiling at 0 m depth. As a result of this topography, along the slightly overhanging sides of this cave a perfect horizontal light gradient is encountered, with the succession (from light to dark) of *Eunicella singularis, Eunicella cavolinii, Clavularia ochracea* and *Parerythropodium coralloides*, and finally *Corallium rubrum*, which occurs in its rare encrusting form as shallow as 4 m.

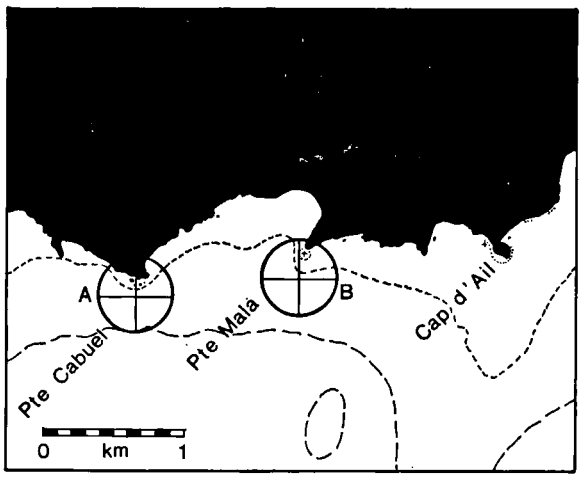

Fig. 6. Côte d'Azur near Cap d'Ail. A = locality Cabuel, situated at 43°43'00"N 07°22'30"E. B = locality Mala, situated at 43°43'04"N 07°23'21"E.

6. Cabuel (fig. 6)

In front of the Pointe de Cabuel (between Èze-sur-Mer and Cap d'Ail) the underwater landscape consists of a shallow (5-15 m depth) plateau covered with the seagrass *Posidonia oceanica.* At its borders, the rock falls steeply down to the sediment-covered bottom at 30 m. In many places, the steep calcareous cliffs are undercut and dark tunnels and overhangings are encountered. In these places *Corallium rubrum* was never found, but *Eunicella cavolinii* occurs in small amounts. The vertical walls are densely covered by an *Eunicella cavolinii/Paramuricea clavata* community, while *Parerythropodium coralloides* is not rare.

7. Mala (fig. 6)

Near the Pointe de Mala the rock slopes down gently till about 15 m depth and is covered by a meadow of *Posidonia oceanica.* Then, steep rocky surfaces and dark crevices, which are covered with dense populations of *Eunicella cavolinii,* tumble down from 13 to 34 m depth. Below 28 m, colonies of *Eunicella singularis* are encountered on horizontal surfaces, on one occasion the base of the colonies and its rocky substratum being buried in the muddy sand. *Parerythropodium coralloides* was encountered in one station only, and surprisingly in none of the dark caves and overhanging surfaces *Corallium rubrum* was found.

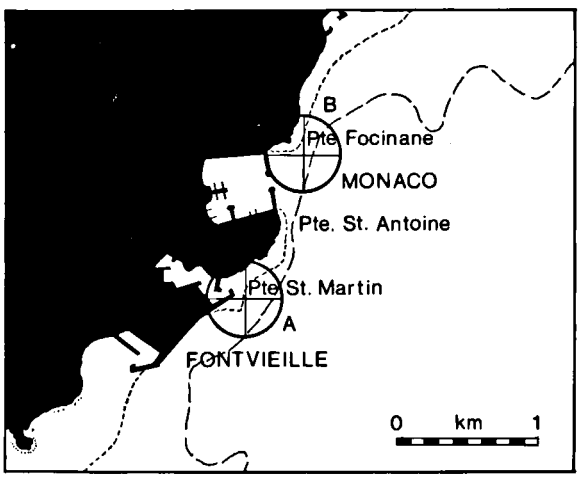

Fig. 7. Principality of Monaco. A = locality Saint Nicolas, situated at 43°43'43"N 07°25'36"E. B = locality Focinane, situated at 43°44'12"N 07°25'55"E.

8. Saint Nicolas (fig. 7)

Between the Pointe Saint Martin and the southern pier of the new harbour of Fontvieille (Monaco) lies a complex formerly known by local fishermen as the "Rocher Saint Nicolas". Several nearly vertical calcareous pillars and domes rise from over 30 m to less than 15 m depth. The rock is densely covered by algae (mainly *Dictyota dichotoma).* On the vertical and overhanging surfaces *Eunicella cavolinii* and *Parerythropodium coralloides* are common, the latter frequently overgrowing the former. On some occasions they are found on the horizontal surfaces amidst the algae. Dark holes and crevices were explored, in some of which *Eunicella cavolinii* lives, but not a single colony of *Corallium rubrum* was encountered in this particular habitat.

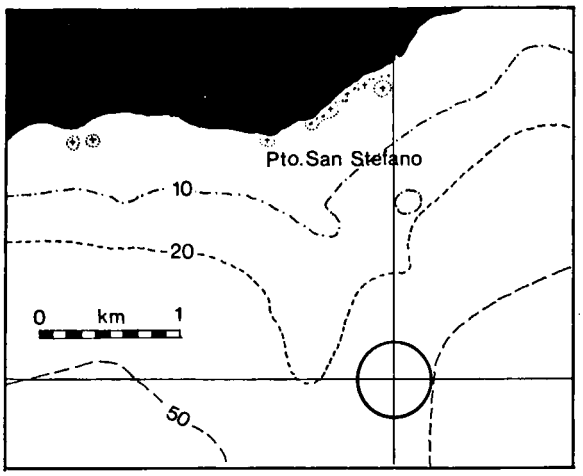

Fig. 8. Ligurian coast near San Stefano. Locality San Stefano situated at 43°48'55"N 07°54'55"E.

9. Focinane (fig. 7)

In front of the Pointe Focinane (commonly called "Tir aux Pigeons" in Monaco) the bottom slopes down under a 45° angle till about 20 m depth. Much of the bottom is covered with blocks of calcareous stone which were used for construction works ashore. On the lower part of this slope *Eunicella singularis* and *Eunicella cavolinii* are encountered amidst dense algal populations, the latter species never occurring on horizontal surfaces. At about 20 m depth a South facing vertical wall falls down to the muddy sand nearly 20 m below. This wall and its many crevices are densely covered by *Eunicella cavolinii, Corallium rubrum* and small colonies of *Parerythropodium coralloides.* Curiously enough, *Paramuricea clavata* does not live here. *Corallium rubrum* occurs even outside the crevices in places receiving as much as 10% irradiance as compared to surface values. In the sediment at the foot of the wall, some shells and rocks were found bearing colonies of *Eunicella verrucosa.*

10. San Stefano (fig. 8)

In front of the small Ligurian town of San Stefano (near San Lorenzo) a vast and shallow plateau extends far into the sea. The eastern border of this plateau was visited at about 32 m depth, where it is covered with *Posidonia oceanica* on the rhizomes of which *Clavularia crassa* was found. At the rim of the plateau, the rock forms several knolls and ridges which fall down to 35 m at the sand. Here, large colonies of *Paramuricea clavata* and *Eunicella cavolinii* occur, sometimes partly overgrown by *Parerythropodium coralloides.*

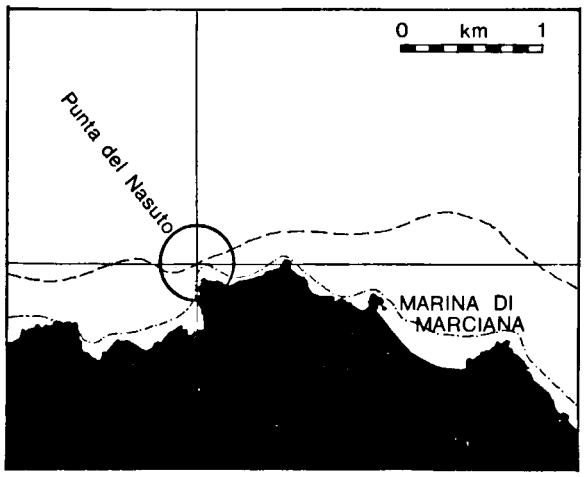

Fig. 9. Northwest coast of Elba. Locality Nasuto, situated at 42°48'42"N 10°10'48"E.

11. Nasuto (fig. 9)

At the Punta del Nasuto (N.W. coast of Elba) the rock falls steeply down from the surface to 42 m at the sand. Some horizontal ridges interrupt the nearly vertical cliff. On these, algal cover is massive and no Octocorallia occur. *Eunicella cavolinii* and *Eunicella singularis* were encountered in small amounts from 20 m downwards, the latter even growing on stones completely covered by sediment.

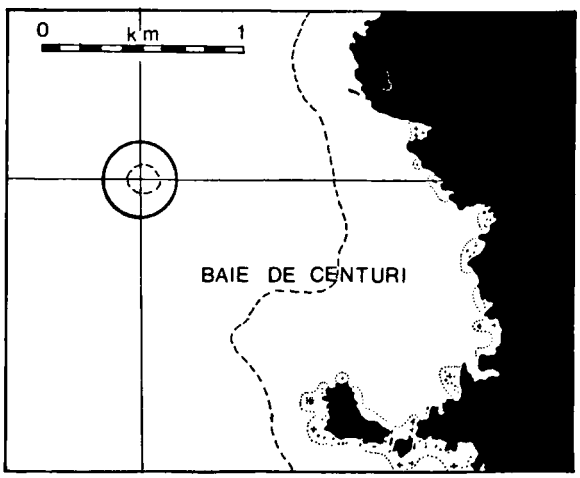

Fig. 10. West coast of Cap Corse (Corsica). Locality Centuri, situated at 42°58'25"N 09°19'50"E.

12. Centuri (fig. 10)

The "Haut-fond de Centuri" is a pyramidal dome (depth: 17 m), situated at more than 1 km from the coast. All around, the rock is densely covered with algae and falls gradually down to depths of about 30 m. Octocorallia are scarce and mostly found under overhanging rocks and in crevices. *Eunicella cavolinii* and *Parerythropodium coralloides* occur here, and some very small unbranched colonies of *Alcyonium acaule.*

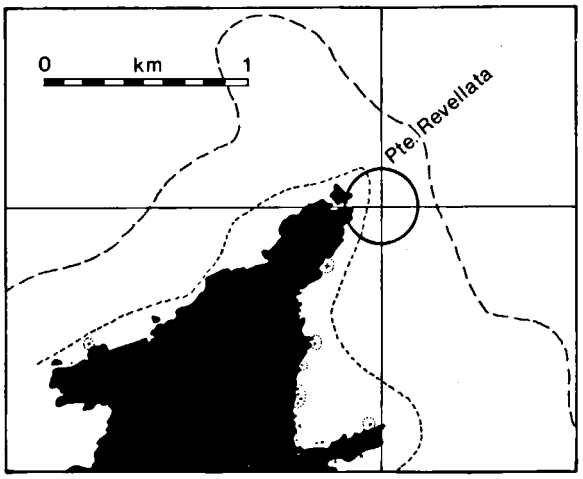

Fig. 11. Pointe Revellata, near Calvi, Corsica. Locality Revellata, situated at 42°35'00"N 08°43'49"E.

13. Revellata (fig. 11)

Near the Pointe Revellata, the rock is densely populated by algae. The sides of vertical gullies, however, are populated by *Eunicella cavolinii* and *Parerythropodium coralloides.* On some occasions *Paramuricea clavata* and *Eunicella singularis* are found.

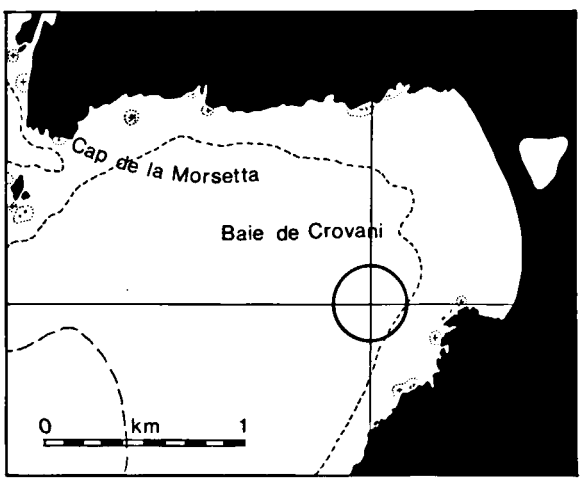

Fig. 12. Baie de Crovani, N.W. Corsica. Locality Crovani, situated at 42°28'02"N 08°40'23"E.

14. Crovani (fig. 12)

The bottom of the sheltered bay of Crovani is covered with a meadow of *Posidonia oceanica,* interrupted by large

boulders, on the overhanging and vertical sides of which some small populations of *Eunicella cavolinii* occur from 17 m downwards.

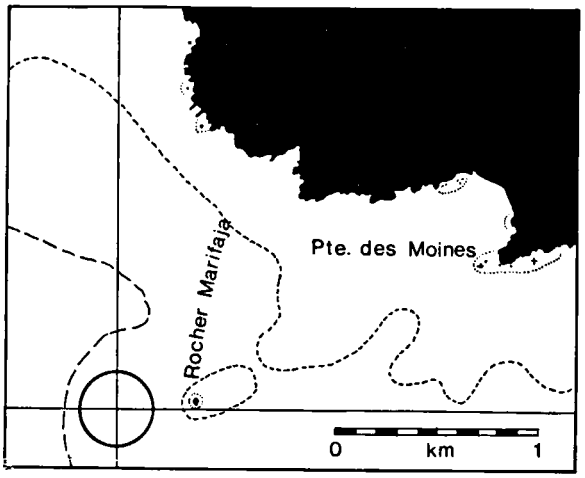

Fig. 13. Rocher Marifaja, near Cargèse, Corsica. Locality Marifaja, situated at 42°06'38"N 08°36'45"E.

15. Marifaja (fig. 13)

Situated between the Pointe de Cargèse and the Pointe Puntiglione, the Rocher Marifaja is an emerging rock which falls steeply down to the surrounding sand on the seaside. The sand slopes down and is interrupted here and there by small rocky outcrops which were explored in depths between 35 and 38 m. *Eunicella cavolinii* occurs typically on vertical and overhanging surfaces, on which *Eunicella singularis* is sometimes found. The latter species is mostly found on horizontal surfaces however, its substratum sometimes being covered with sand.

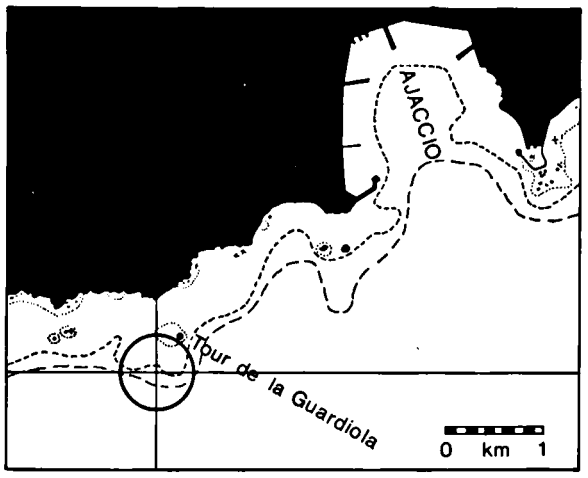

Fig. 14. Ajaccio, Corsica. Locality Guardiola, situated at 41°53'57"N 08°43'09"E.

16. Guardiola (fig. 14)

Situated to the West of the city of Ajaccio, the Guardiola Tower is a navigation beacon. To its South, the rock falls steeply down to about 30 m depth. From 24 m downwards *Eunicella cavolinii* and *Paramuricea clavata* occur on its vertical and overhanging surfaces.

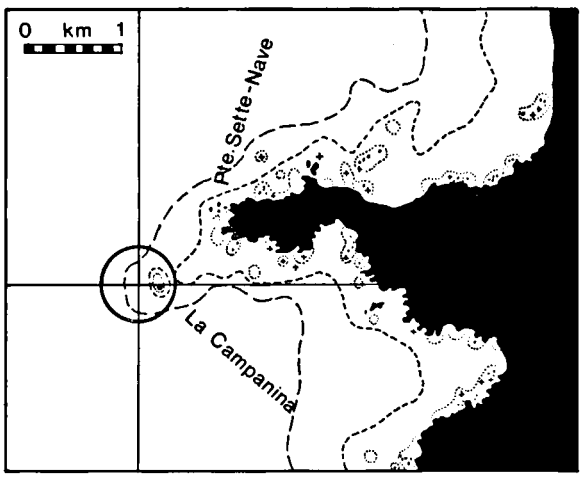

Fig. 15. Southern Golfe d'Ajaccio. Locality Campanina, situated at 41°50'16"N 08°44'30"E.

17. Campanina (fig. 15)

La Campanina is a shoal to the South of Ajaccio, on which a tower was built. On its seaside, the rock descends like a giant staircase to about 40 m depth. All the horizontal surfaces are densely covered with algae, and are devoid of Octocorallia, whereas on the shaded vertical and overhanging surfaces dense populations of *Eunicella cavolinii, Paramuricea clavata* and *Parerythropodium coralloides* occur. *Corallium rubrum* was not found, although many very dark holes were explored. Between 15 and 19 m depth *Clavularia ochracea* was encountered, and, on one occasion, a dense population of *Rolandia rosea*, the only one I was able to locate in this part of the Mediterranean.

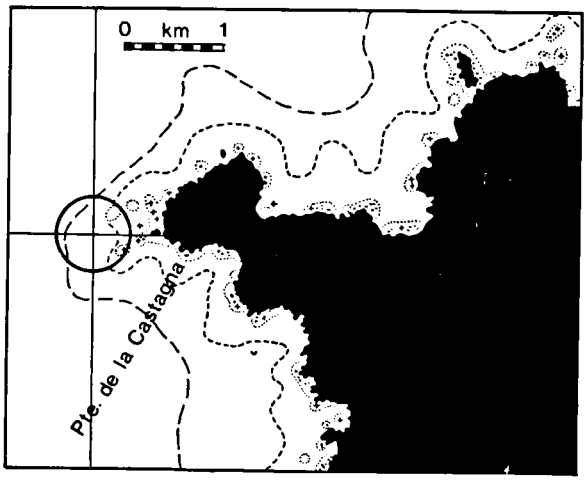

Fig. 16. Pointe de la Castagna, southern Golfe d'Ajaccio, Corsica. Locality Castagna, situated at 41°47'45"N 08°42'15"E.

18. Castagna (fig. 16)

In a magnificent scenery of towering rocks and steep gullies,

the vertical and overhanging surfaces off the Pointe de la Castagna are covered by dense populations of *Eunicella cavolinii* from 23 m downwards. An occasional colony of *Paramuricea clavata* is also found.

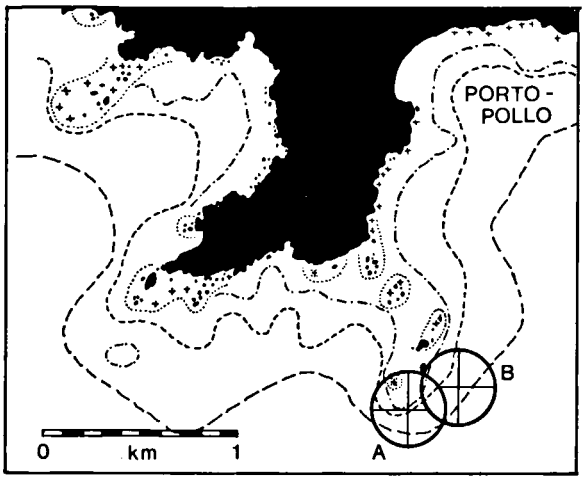

Fig. 17. Northern Golfe de Valinco, near Propriano, Corsica. A = locality Porto Pollo 1, situated at 41°41'35"N 08°47'40"E. B = locality Porto Pollo 2, situated at 41°41'38"N 08°47'54"E.

19. Porto Pollo 1 (fig. 17)

The Pointe de Porto Pollo offers a majestic underwater landscape of granitic pillars rising from almost 50 m depth to the surface. The vertical rocks with their numerous clefts are densely covered by a community consisting mainly of *Eunicella cavolinii* and *Paramuricea clavata*. In the darker holes *Corallium rubrum* occurs, while on horizontal and sloping bottoms a few colonies of *Eunicella singularis* are encountered.

20. Porto Pollo 2 (fig. 17)

This site has the same characteristics as the previous one, which is only 300 m away. *Eunicella singularis* was encountered more often, however, and in one station some encrusting colonies of *Parerythropodium coralloides* were found.

21. Campo Moro 1 (fig. 18)

This locality, halfway between the Pointe de Campo Moro and the Pointe dello Scalono, consists of enormous granitic boulders descending from only a few meters depth to over 30 m. Octocorallia occur from 15 m downwards, only in places (vertical or overhanging rock) where algal cover is thin or nonexistant. The vertical surfaces are characterized by communities of *Eunicella cavolinii, Paramuricea clavata, Parerythropodium coralloides* and *Alcyonium acaule*. Whereas most colonies of the latter species were small, on two occasions large, branched colonies were found. Under the overhanging rocks *Eunicella cavolinii* and *Corallium rubrum* occur together.

22. Campo Moro 2 (fig. 18)

Situated near the Pointe de Campo Moro. From the sandy bottom at 40 m depth, a steep rock rises to the surface.

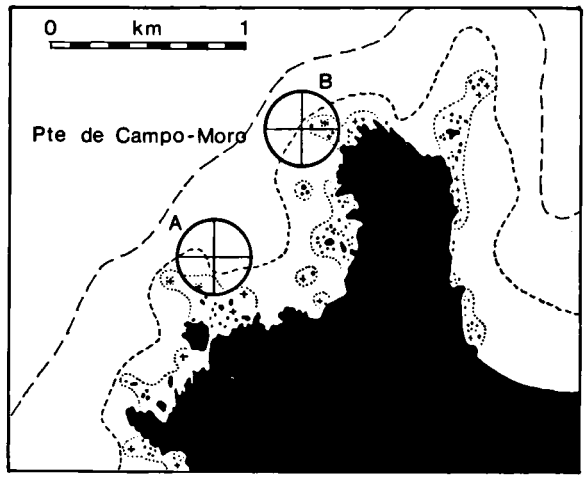

Fig. 18. Southern Golfe de Valinco, near Propriano, Corsica. A = locality Campo Moro 1, situated at 41°38'06"N 08°47'50"E. B = locality Campo Moro 2, situated at 41°38'26"N 08°48'11"E.

Most of its vertical surfaces are covered by dense communities of *Eunicella cavolinii* and *Paramuricea clavata*, the latter species being largely dominant in some places. *Parerythropodium coralloides* and *Alcyonium acaule* are also often encountered. Striking is the absence of *Corallium rubrum*, even in the darkest places. In the turbulent water near the surface, between 7 and 12 m depth, communities of *Clavularia ochracea* and *Parerythropodium coralloides* occur on vertical surfaces.

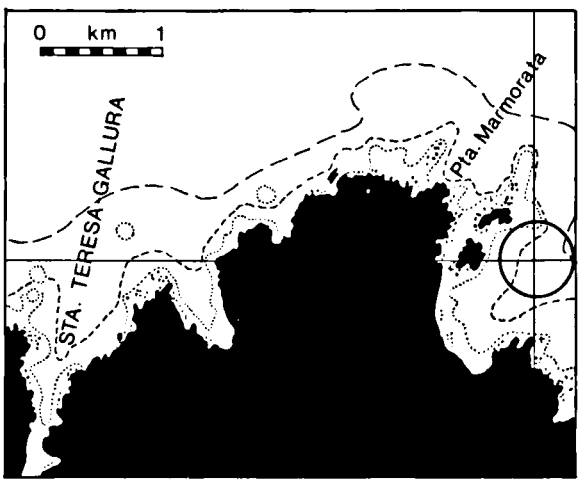

Fig. 19. Straits of Bonifacio, northern Sardinia. Locality Marmorata, situated at 41°15'06"N 09°12'45"E.

23. Marmorata (fig. 19)

A sheltered bay in the crystalline waters of the Straits of Bonifacio. The rock is cut by large crevices, on the steep walls of which *Eunicella cavolinii* occurs from 24 m downwards. On horizontal and sloping surfaces *Eunicella singularis* and *Parerythropodium coralloides* are quite abundant.

IV. RESULTS

1. *Cornularia cornucopiae*

The species was encountered only twice, at the same locality (Castel-Vieil), between 10 and 11 m depth, in both cases on vertical walls without sediment. Relative irradiance ranged from 4.9 to 12.3%. It was also found in the Golfe de Fos (West of Marseille) in 10-12 m depth (Eugène, pers. comm.) and at the Pointe de la Croisette (Cannes) in 1-2 m depth (personal observation), in both cases on the rhizomes of *Posidonia oceanica*. This, together with previous observations from the Banyuls area (Weinberg, 1978a, 1979a), confirms that the species lives above the thermocline in rather shaded habitats.

2. *Clavularia crassa*

This species, which lives exclusively on the rhizomes of *Posidonia oceanica*, was found only once during the present survey, in 33 m depth at San Stefano, where relative irradiance amounted to 3.5%. This is the deepest record of the species so far. Other recent records from the prospected region include Marseille (Golfe de Fos, Ile Tiboulen du Frioul, Rade d'Endoume, Plateau des Chèvres) and Ile de Port-Cros, from 10 to 28 m depth (Eugène, pers. comm.) and Pointe de la Croisette (Cannes), from 0.5 to 8 m depth (d'Hondt & Tixier-Durivault, 1975; personal observation).

3. *Clavularia ochracea*

This species was encountered in 23 stations (10% of the total visited) in 7 localities. Present in all the Marseillais localities, the species was not found on the Côte d'Azur and very scarce in Corsica. It is a species from shallow water found between 2 and 25 m depth, with a mean of about 10 m. Although in extreme cases it lives on sloping or overhanging surfaces, the species predominantly grows on vertical ones without sediment (sediment present in 4% of the cases only). Although the species seems to be quite tolerant to irradiance conditions (extremes: 0.46-44.3%), the mean (21.4%) and quite narrow 95% confidence interval (16.1-27.7%) indicate a preference for rather sunlit places. In Banyuls it was found in similar depths, but more often in darker habitats (Weinberg, 1978a, 1979a).

4. *Rolandia rosea*

This encrusting stoloniferan was found only once, at La Campanina, where it lives under an overhanging rock at 15 m depth, where relative irradiance amounts to 5% of the surface intensity. Near Marseille, it occurs on the rhizomes of *Posidonia oceanica*, between 12 and 28 m depth, at Ile Tiboulen du Frioul (Eugène, pers. comm.). Near Banyuls the species is quite common on rock and as an epibiont on gorgonians, and is found in similar environmental conditions (Weinberg, 1978a, 1979a).

5. *Parerythropodium coralloides*

Extremely common in the entire area. It was found in 63 stations (28% of the total visited), mostly as small encrusting colonies on the rock, but also quite often as epibiont on gorgonians. It was found between 3 and 35 m depth (mean: 19.7 m). It occurs on all slope types, but prefers stations without sediment (80% of the cases). Relative irradiance values go from 0.03 to 34.6% (mean: 7.6%), indicating a large degree of tolerance with respect to this parameter. Near Banyuls the species seems to occur under somewhat darker conditions (Weinberg, 1978a, 1979a).

6. *Alcyonium acaule*

This species was found in only 12 stations, quite often as extremely small unbranched colonies. Quite tolerant with respect to slope and sediment, it was found between 12 and 33 m depth, in relative irradiance conditions ranging from 0.72 to 31.3%. The upper depth limit corresponds to the one found in Banyuls (Weinberg, 1979a), where the species is very common.

7. *Maasella edwardsii*

This Alcyonacean was encountered in two stations during the present survey both at Ile du Planier (Marseille), in depths around 20 m and relative irradiance values of 11.5 and 28%. It was also found by Eugène (pers. comm.) on the rhizomes of *Posidonia oceanica*, near Marseille (Golfe de

Fos, Ile Tiboulen du Frioul, Plateau des Chèvres) and at Ile de Port Cros, between 13 and 33 m depth, indicating a preference for rather shaded places where much sediment is present. In Banyuls this species is found under similar conditions (Weinberg, 1978a, 1979a).

8. *Paralcyonium spinulosum*

I did not see this species during the present survey, but it is known from the prospected area, mostly in deeper waters (150-250 m) in the Canyon de Cassidaigne near Marseille (Laborel et al., 1961), and it was once found in about 30 m near the same locality (Zibrowius, pers. comm.). This seems to indicate that the species does not tolerate high irradiance values, which is confirmed by its niche near Banyuls (Weinberg, 1978a, 1979a).

9. *Eunicella verrucosa*

This gorgonian was found between 35 and 37 m, near Monaco, where it lives on dead shells and stones buried in the mud. The relative irradiance values recorded were 10 and 11.4%. According to Carpine & Grasshoff (1975), this corresponds to the upper limit of the species' depth range. In Banyuls, I once found colonies of *Eunicella verrucosa* living on dead shells which had been dredged from muddy bottoms at about 90 m depth.

10. *Eunicella singularis*

This species, which occurred in 36 stations, lives predominantly on horizontal or sloping sediment-covered bottoms, between 7 and 42 m depth (mean: 24 m), in relative irradiance conditions going from 3 to 44% (mean: 18.6%). In Banyuls, where the species is extremely common, it lives under similar conditions, except for relative irradiance, which on the average is about three times lower.

11. *Eunicella cavolinii*

The most common species in the area prospected (it occurred in 135 stations, or 60% of the total visited), this yellow gorgonian lives mostly on vertical walls without sediment, very often together with *Paramuricea clavata*, but it can also be found on all other slope types, and in nearly 20% of the cases sediment was present. Depths range from 5 to 42 m (mean: 24 m) and relative irradiance values from 0.1 to 44% (mean: 6.8%). Curiously enough, this species was never found in the Banyuls area.

12. *Lophogorgia ceratophyta*

Although I did not see the species during the present survey, it lives in the entrance of Marseille harbour, in turbid water with a strong current, on a sediment-covered bottom, in depths of about 20 m (Harmelin & Zibrowius, pers. comm.). This corresponds exactly to its niche in Banyuls (Weinberg, 1978a, 1979a).

13. *Paramuricea clavata*

A typical species of vertical surfaces, although it is also found on other slope types, it prefers sediment-free bottoms. It was found in 54 stations, in depths ranging from 5 to 38 m (mean: 22 m) and at irradiance values between 0.12 and 27.6% (mean: 7.6%), indicating a much larger tolerance than my previous studies in Banyuls suggested (Weinberg, 1978a, 1979a).

14. *Corallium rubrum*

A species characteristic of sediment-free dark places, it is found in cracks and holes, under overhanging surfaces and in caves. When these conditions are met, the species can be found as shallow as 3 m (Marseille area) but mostly deeper (mean: 21 m). Irradiance values range from absolute darkness (ceiling of the Grotte du Figuier) to a very tolerant 10.4% on a South facing vertical wall (Pointe Focinane, Monaco), and the mean, although quite low (1.8%) is five times higher than the one found in the Banyuls area. The occurrence in the "open" cave in the Calanque de Figuier indicates that this species even tolerates an important hydrodynamism.

V. CONCLUSIONS AND DISCUSSION

During this study, species were treated separately, irrespective of the community in which they occur. Hence, importance was only attached to presence

of a species, and no conclusions drawn from its absence under certain conditions. Therefore, the results can only be interpreted in one way: if a species was found under certain conditions, that means that the species is able to tolerate those conditions as a larva and as an adult. The data consist of a presence/absence-station matrix which was treated statistically. Much less information is to be gained from such a matrix than from one containing information about population densities, as was the case in my previous studies in Banyuls (Weinberg, 1978a, 1979a). For sake of comparison, however, the data available for Banyuls were reduced to a presence/absence-station matrix also, and they were treated in the same way as those of the present survey. When one compares the data of both areas (figs. 20, 21), with emphasis on means and 95% confidence intervals [1]), it appears that contrarily to what was supposed, the species occur in roughly the same depths in both areas, but relative irradiance values are about three times lower in the Banyuls area.

The question arises whether the species react in a different way to irradiance in different areas, and one may even ponder whether light plays an important role at all.

If one looks at the occurrence of the different species in each area separately, however, the same pattern emerges. For example: *Eunicella singularis* and *Clavularia ochracea* live under comparable relative irradiance conditions, but in different depths (and in different slope and sediment conditions). *Eunicella singularis, Paramuricea clavata* and *Corallium rubrum* on the other hand, although living in roughly the same depth range, are almost mutually exclusive, mainly because of the preferred relative irradiance ranges.

The observation of the succession of different species populations in the horizontal light gradient of the cave at Pointe de Castel-Vieil also underlines the importance of submarine irradiance as an ecological factor.

The differences between the two areas which emerge from this statistical comparison are therefore believed to be artificial, and mainly to reflect differences in methodological approach. Whereas in Banyuls the different stations were chosen as representatives of different ecological conditions, irrespective of the Octocorallia present (which were even absent in 2 out of 40 stations), in the present survey the choice of the stations was strongly biased towards the upper limit of occurrence of octocorallian species. Hence sampling was rather subjective in the latter study, and yielded a high proportion of shallow records for each species. The relative irradiance ranges as found for the Banyuls area are therefore believed to be the most representative for the different species, but the extreme values encountered during the present survey broaden the ecological amplitudes found for most species, especially as far as upper limits of occurrence (depth and irradiance) are concerned. As for the lower depth limit of the different species, I believe to have reached it (approximately) for only a few of them: *Cornularia cornucopiae* (22 m), *Clavularia crassa* (33 m), *Clavularia ochracea* (25 m), and *Maasella edwardsii* (32 m).

Several species have been found in deeper habitats than I was able to study. Maximum known depths are given here for most other species: *Parerythropodium coralloides* and *Alcyonium aucale* in 125-135 m (Molinier, 1960), *Paralcyonium spinulosum* in 250 m (Laborel et al., 1961), *Eunicella verrucosa* in 200 m (Carpine & Grasshoff, 1975) [2]), *Eunicella singularis* in 40-56 m (Laborel et al., 1961), *Eunicella cavolinii* in 125-135 m (Molinier, 1960), *Lophogorgia ceratophyta* in 250 m (Carpine & Grasshoff, 1975), *Paramuricea clavata* in 110 m (Carpine & Grasshoff, 1975), and *Corallium rubrum* in 280 m (Reyss, 1971).

More studies involving quantitative sampling,

[1]) In SPSS (Nie et al., 1975-1979), the 95% confidence interval (.95 C. I.) is calculated as follows:

$$.95 \text{ C. I.} = \bar{x} \pm T\ (\sigma / \sqrt{N})$$

in which

$\bar{x}$ = sample mean
N = number of cases
σ = sample standard deviation
T = 0.025 t-value for N-1 degrees of freedom

[2]) Reyss (1971) mentions white and pink colonies of *Eunicella "stricta"* (= *singularis*) between 220 and 250 m in a submarine canyon off Banyuls-sur-Mer. I strongly believe he saw specimens of *Eunicella verrucosa*, which should then constitute the deepest record of the species so far.

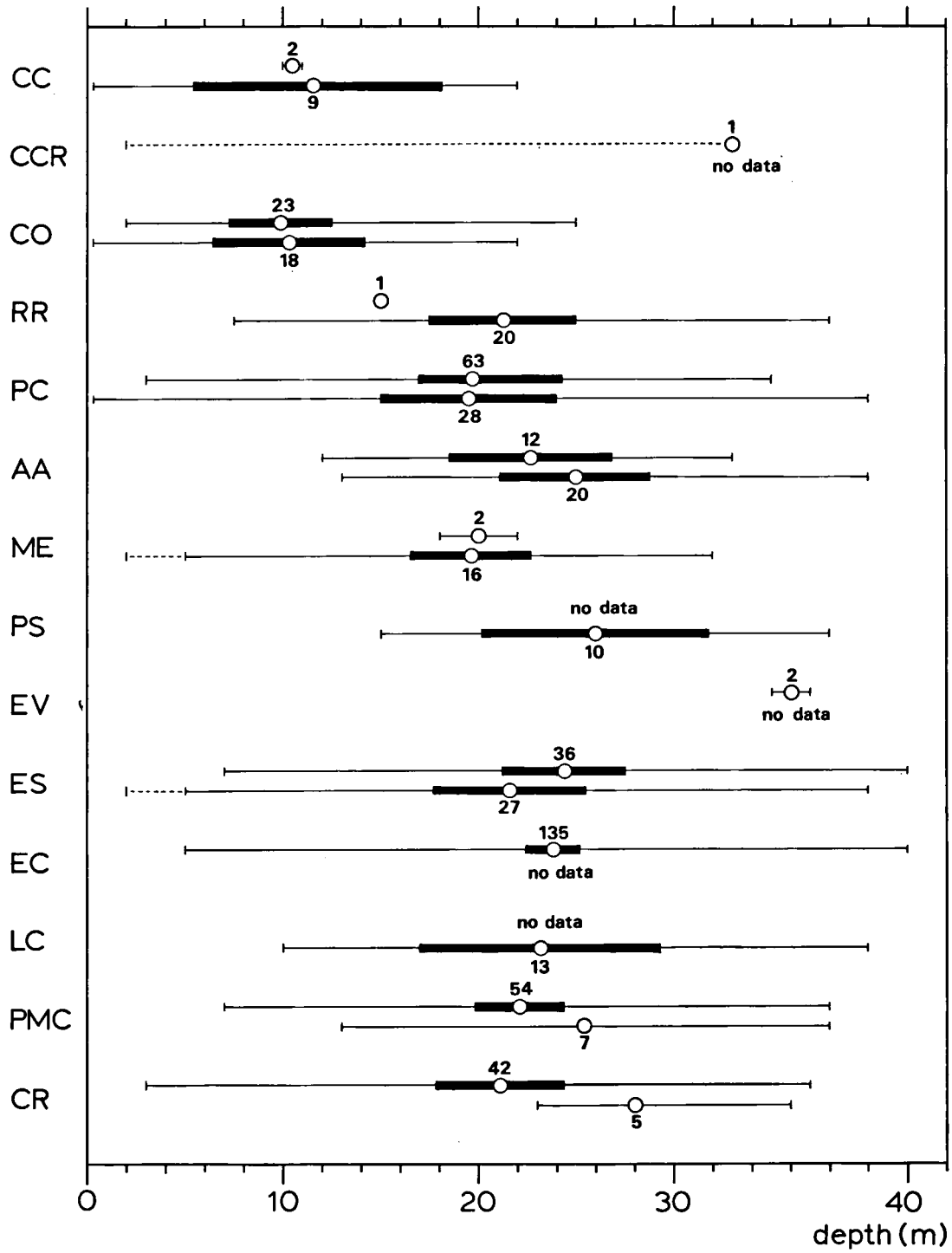

Fig. 20. Depth ranges of 14 Mediterranean octocorallian species as found by the author. For each species two graphs are given, the top one for the areas studied in the present article, the bottom one for the Banyuls area. The mention "no data" indicates that a species was not found in the area concerned. The circle indicates the mean depth (number = number of stations), the heavy bar corresponds to the 95% confidence interval (only given for 9 or more observations) and the thin line indicates extreme values. Broken lines indicate occasional values found by the author, which were, however, not treated statistically. For explanation of species code, see section II, "Material and Methods".

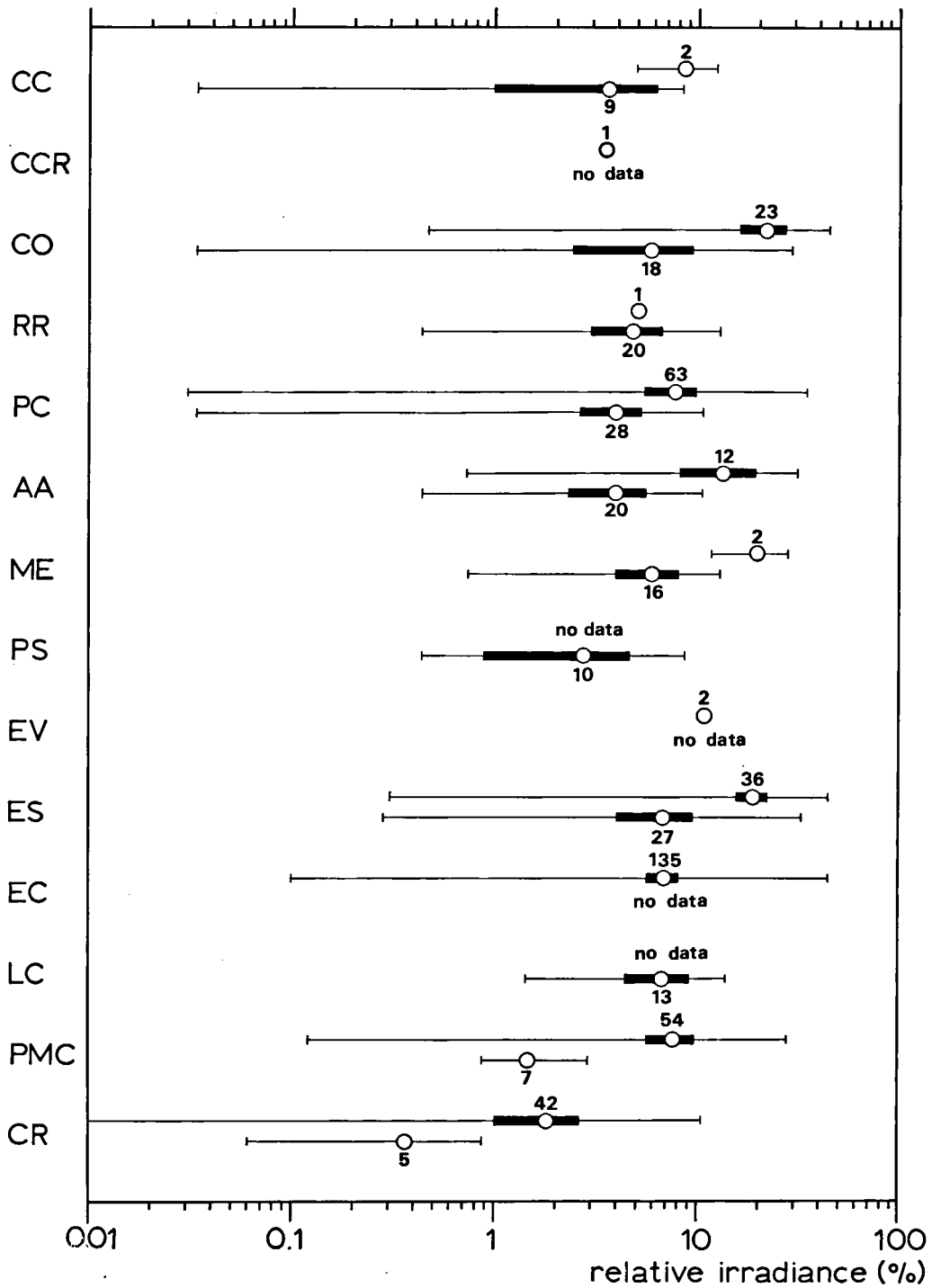

Fig. 21. Relative irradiance ranges for 14 Mediterranean Octocorallian species as found by the author. For further explanation see caption of fig. 20.

especially deeper ones, are needed in order to define the tolerances and optimum living conditions of the species over their entire depth range.

As for the shallow habitats presently studied, they confirm the existence of the five communities I defined in an earlier paper (Weinberg, 1978a), while the species *Eunicella cavolinii* (which does not occur in the Banyuls area) should definitely be included in community E, characteristic of vertical or overhanging, shaded, sediment-free habitats.

This study gives no clue to the regional variations that occur (abundance of *Lophogorgia ceratophyta* and absence of *Eunicella cavolinii* in the Banyuls area, paucity of species in Corsica, especially in its northern half). An extensive zoogeographical study of the entire Mediterranean, in particular its badly known eastern basin and North-African coasts should cast some light on these phenomena.

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