2 | Phytosociological Studies on Mediterranean Algal Vegetation: Rocky Surfaces of the Photophilic Infralittoral Zone

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Abstract: No thorough bionomic study of the photophilic infralittoral algal vegetation of western Mediterranean rocky surfaces exists, despite the fact that this vegetation-type covers large areas along the coasts.

A description of the biotope to be studied is first presented; thereafter, different features and problems arising with the Mediterranean algal vegetation are discussed. Particularly in this biotope, the overall size and height of the constituents are small, so that we had to develop sampling procedures and methods of detailed laboratory study. Quadrats of 20 × 20 cm were the samples;* rock surface of the whole sample area was removed with hammer and chisel so that the smaller algae and crustose forms in the underlying flora were not missed. Following a minimum area study, the homogeneity of the vegetation from which the samples were taken was checked.

Species diversity appears to be very high in this biotope and a list of rarer taxa has been compiled. As yet, phytosociological interpretation has not been attempted since we lack data from some seasons. A survey of previously

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*The French term "relevé" has generally been translated here as "sample" (Editors). A more precise and detailed equivalent is required elsewhere; see footnote to p. 51.

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recognized bionomic categories is presented for the photophilic infralittoral algal vegetation.

Résumé: Les végétations algales de l'infralittoral photophile sur substrat rocheux du bassin méditerranéen occidental n'ont pas encore été le sujet d'études phytosociologiques approfondies malgré le fait qu'elles couvrent d'énormes surfaces le long des côtes.

Après un essai de délimitation du biotope à étudier, divers problèmes, propres aux végétations algales méditerranéennes sont discutés. A cause de la miniaturisation de ces populations, surtout dans le biotope étudié, nous devions effectuer une procédure d'échantillonage et l'étude détaillée des relevés au laboratoire. Ces relevés de 20 × 20 cm fûrent effectués en cassant le substrat à l'aide de marteau et burin; ainsi les petites algues et les algues encroûtantes de la sous-strate sont également récoltées. Après une étude d'aire minima, l'homogénéité de la végétation étudiée a été vérifiée.

La richesse floristique semble être trés élevée dans ce biotope, et un grand nombre, d'espèces extrêmement rares a été identifié. Une interprétation phytosociologique de nos données n'a pas encore été effectuée à cause du manque de données de certaines saisons. Un aperçu des classifications bionomiques antérieures des végétations algales de l'infralittoral photophile est donné.

INTRODUCTION

Whereas ecological data on terrestrial plants have been sought since the beginning of the last century, and terrestrial vegetation has been studied by rigorous phytosociological methods for over 50 years, this is not at all the case for marine vegetation. Some of the phycologists who worked along the coasts of the Atlantic Ocean during the last century added only, as ecological data to their herbarium specimens, the tidal level at which they had been collected.

The Mediterranean Sea has small tides, roughly 30 cm in amplitude; this is mainly due to the effects of wind and pressure-systems. Sampling below the water surface remained extremely fragmentary until recently, especially on rocky surfaces where dredging is excluded. It was not until the studies of Funk (1927) at Naples and of J. Feldmann (1937) at Banyuls that important ecological information on Mediterranean infralittoral seaweeds was recorded. Even then, it was difficult to describe the exact biotope (horizontal rock, vertical rock, overhanging rocky surfaces, precise depth) of the algae collected, since they were dredged.

Molinier (1960) carried out pioneering phytosociological studies of the algal communities near the water surface at Cap Corse; for this purpose, he used a simple Braun–Blanquet method.

The development and popularization of SCUBA diving made possible *in situ* studies of the marine infralittoral biotope. This diving technique is not without its problems, as it still remains difficult to carry out a relevé* near the surface because of water movement. At greater depths, only one or two relevés per dive are possible as availability of air and physical activities are limited.

Boudouresque, himself a diver, was the first to carry out (in the 1960s) quantitative ecological recording in the infralittoral by developing a bionomic technique adapted for immersed marine benthic vegetation.

The method was derived from the Braun–Blanquet school (Boudouresque, 1971a) and was used for the study of sciaphilic (shade-requiring) vegetation. He defined distinct sociological categories (Boudouresque, 1970, 1971b, 1972, 1974a, b).

We used this same method to study the so-called "photophilic (light-requiring) infralittoral algal vegetation" of the western Mediterranean basin. This had never previously been thoroughly studied, although widespread along the shores.

PHYSICAL CHARACTERISTICS OF THE PHOTOPHILIC INFRALITTORAL BIOTOPE

The existing literature does not give a well-defined description of the photophilic infralittoral biotope. According to Pérès and Picard (1956, 1958, 1964) and Pérès (1967), the infralittoral zone starts at low-water level and extends down to the deepest levels of marine phanerogams. The lower limit depends on the turbidity of the water and lies at an average depth of 35 m. The infralittoral zone is bionomically characterized by the luxuriance of the flora, both of seaweeds and marine phanerogams. Pérès and Picard did not separate the photophilic and sciaphilic biotopes within the infralittoral zone, as faunistically they did not find any differences.

Feldmann (1937, 1962) assumed that the boundary between photophilic and sciaphilic algae is at a depth of 5–10 m where, as he

*"A relevé refers to a site analyzed with detailed records of total species present, their relative importance, and other analytic characters of the flora and habit" (A. R. O. Chapman, 1979).

Table I. Monthly values of the sun energy in cal/cm^2/day at different depths, in the region of Banyuls-sur-Mer (Weinberg, personal communication)

Month	E_{tot}	E_{480}	E_{0^-}	E_{10^-}	E_{20^-}	E_{30^-}	E_{40^-}
January	163.52	17.99	14.24	1.047	0.123	0.014	0.002
February	223.17	24.55	20.80	1.545	0.184	0.022	0.003
March	337.38	37.11	32.74	2.741	0.367	0.049	0.007
April	415.58	45.72	40.95	4.770	0.889	0.166	0.031
May	521.26	57.34	51.91	9.388	2.717	0.786	0.228
June	564.96	62.15	56.27	13.876	5.475	2.160	0.852
July	560.11	61.61	55.84	16.158	7.481	3.464	1.604
August	488.86	53.78	48.73	14.532	6.933	3.308	1.578
September	367.13	40.38	36.01	9.429	3.950	1.655	0.693
October	254.00	27.74	24.18	4.691	1.456	0.542	0.140
November	169.46	18.64	15.26	2.045	0.438	0.094	0.020
December	133.99	14.74	11.48	1.073	0.161	0.024	0.004

E_{tot} = total light energy, just above the surface of the sea.
E_{480} = light energy of wavelength of 480 nm.
E_{0^-} = light energy just below the surface of the sea.
$E_{10^-,etc.}$ = light energy at a depth of 10 m, etc.

says, "light-liking algae are replaced by shade-liking ones". This only shifts the problem as there existed no list of shade-liking algae.

Therefore, we investigated the possibility of defining the photophilic infralittoral biotope by physical factors. Results were as follows:

(a) The light quantity does not show a clear-cut threshold value (Table I). At Banyuls, the 10% value for the light penetration lies at less than 10 m depth in winter and at more than 20 m in summer (Weinberg, 1975). This is due to the higher turbidity of the water in winter (Fig. 1); as a consequence, the winter season represents more pronounced difference in greater depths than it does closer to the surface.

(b) A thermocline is only present in summer, as turbulence of the water is too great during the winter (Fig. 2). Thermocline depth fluctuates daily; at Banyuls, it is between 15 and 30 m (Weinberg, 1975).

(c) On the basis of turbulence, Riedl (1964) divided the infralittoral zone into three sub-zones (Fig. 3): an upper one, 0–2 m in depth, with multi-directional movements of the water; a second one, from 2 m to 10–12 m depth, with bi-

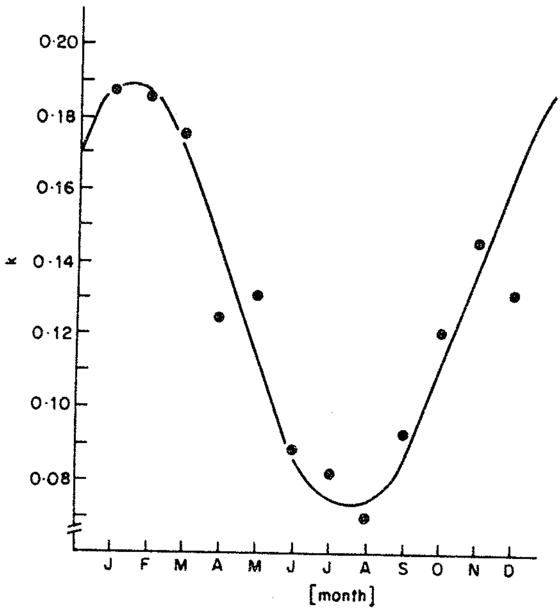

Fig. 1. Annual variations of the extinction coefficient *k* in the region of Banyuls-sur-Mer (after Weinberg, 1975).

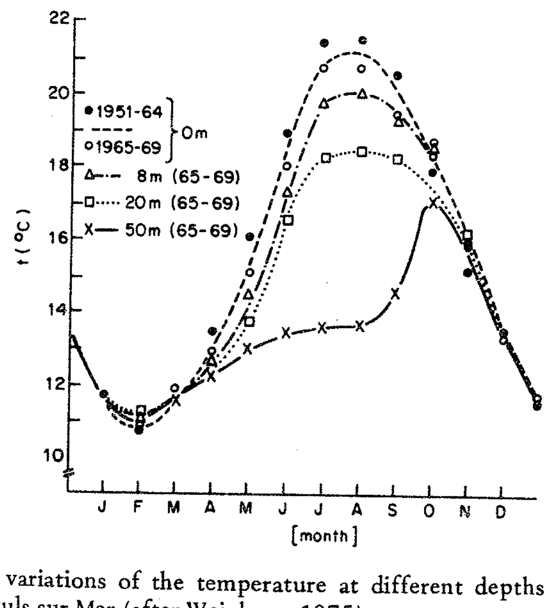

Fig. 2. Annual variations of the temperature at different depths, in the region of Banyuls-sur-Mer (after Weinberg, 1975).

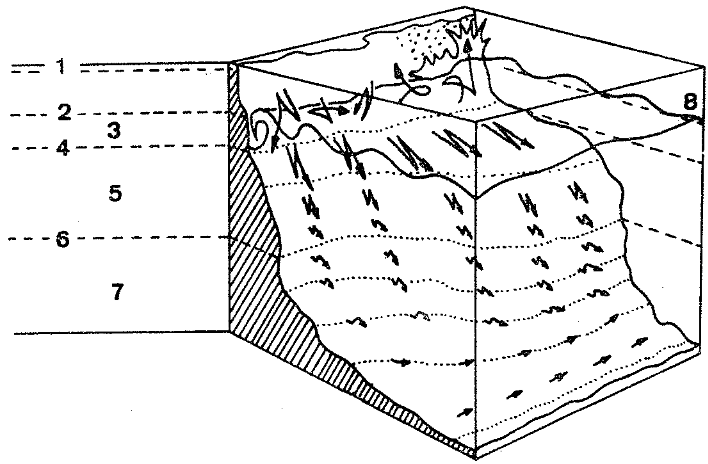

Fig. 3. Hydrodynamic zones (after Riedl, 1964). 1, Upper limit of the spray of the waves. 2, Water level with calm sea. 3, Zone of multi-directional water movements. 4, First critical level. 5, Zone of bi-directional water movements. 6, Second critical level. 7, Zone of uni-directional water movements. 8, Water surface.

directional movements; the lowest one, with a uni-directional movement of the water (the general coastal current).

It is still not known if the lower boundary coincides with a biological boundary. The physical factors (light, temperature, water movement) do not give a clear-cut boundary between the photophilic and sciaphilic infralittoral zones, but some features indicate that this must be around 15 m depth. Quadrat samples were taken down to 20 m, and even some at 30 m, always on horizontal substrata without any shade.

FEATURES AND PROBLEMS PERTINENT TO THE MEDITERRANEAN ALGAL VEGETATION

Because of the small size of Mediterranean algae generally, particularly in the biotope studied here (the largest algae in our relevés were only 10 cm high), and of the difficulty in distinguishing differentiating characters under water, it was impossible definitely to identify algal species *in situ*. In the relevé REC 5, containing (after laboratory study) 109 spp., only *Padina pavonica* (L.) Lamour. could be identified *in situ*. Therefore, it was necessary to utilize a sampling procedure and to undertake detailed study of the samples in the laboratory. The rocky substratum was removed by hammer and chisel, so that the smaller and crustose algae of the underlying flora were sampled as well. All the fragments of the relevé have to be studied microscopically, which results in a long sorting time, even when Cyanophyceae and Bacillariophyceae are excluded.

The fact that species cannot be identified *in situ* has important consequences; according to the Braun-Blanquet method, a relevé has to be taken in homogeneous vegetation. Therefore, we had to determine whether "homogeneous" vegetation, as seen with the naked eye, really is homogeneous (see section on Homogeneity, p. 382).

Another consequence of the miniaturization of the algal vegetation is the fact that the minimum area is very small. An important part of our research was to determine the minimum area for the biotope studied.

THE QUALITATIVE MINIMUM AREA

Whereas it seems easy to give an approximate definition of the "qualitative minimum area" (the smallest surface where almost all the species of the community studied are present), it is much more difficult to give a rigorous definition (avoiding the qualification "almost all the species"). This problem has been studied by a large number of terrestrial phytosociologists. Tüxen (1970) gives 170 references on that subject; Gleason (1922, 1925), Moravec (1973) and van der Maarel (1970) present extra ones. Marine phytosociologists, on the contrary, have only recently considered this concept. Boudouresque (1974b) made a minimum area study of the sciaphilic algal vegetation of the Mediterranean Sea, and we have determined it for the photophilic infralittoral biotope (Dhondt, 1976; Dhondt and Coppejans, 1977). Some other minimum area studies for algal vegetation have been carried out more recently (Cinelli *et al.*, 1977a, b).

Different authors have proposed a range of methods for calculating the minimum area; they mainly need the species numbers of a series of quadrats of increasing area to draw a species/area curve. For that purpose two series of 11 relevés were made, using the "multiple plot procedure" (quadrats not overlapping); one series was at Banyuls and the other at Port-Cros (France), at 4 m depth, in "homogeneous"

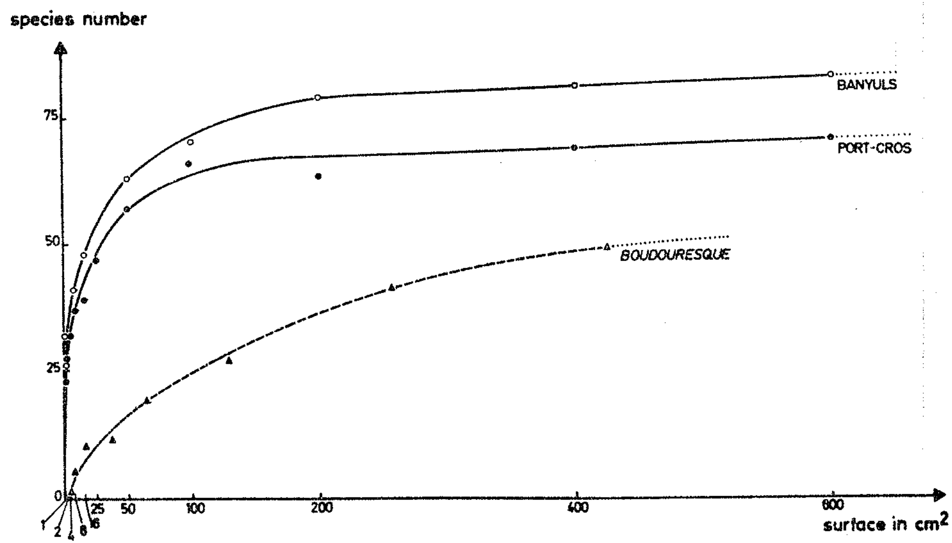

Fig. 4. Species/area curves of the algae of the photophilic biotope from Banyuls and Port-Cros (own observations) and of the sciaphilic biotope (Boudouresque, 1974b).

vegetation. Quadrat areas were 1 x 1 cm, 1 x 2 cm, 2 x 2 cm, 2 x 4 cm, 4 x 4 cm, 5 x 5 cm, 5 x 10 cm, 10 x 10 cm, 10 x 20 cm, 20 x 20 cm and 20 x 30 cm. After sorting the relevés and carrying out a Bravet–Pearson correlation analysis on the species numbers/relevé, a species/area curve was drawn. This is a parabolic curve (Fig. 4). According to the definition of Braun–Blanquet, the minimum area is reached where the curve becomes more or less horizontal; we can conclude that, for the vegetation studied, this area is reached between 100 and 200 cm^2. There are more accurate methods to determine objectively the minimum area on these curves. In the tangent-method of Cain and Castro (1959), the minimum area is reached when an increase of 10% of the surface results in an increase of 10% of the species number (method 1); for more precision, that area can be considered to be reached when an increase of 10% of the surface results in an increase of 5% of the species number (method 2). The following results were obtained:

	Banyuls	Port-Cros
method 1	115 cm^2	135 cm^2
method 2	250 cm^2	250 cm^2

Vestal (1949) developed another procedure, in which a semi-logarithmic plotting of the species/area curve (species-log area) is involved. On this curve, two points are determined such that the area at point 2 is 50 times larger than at point 1 and that the species number of point 2 is double that of point 1. Point 2 is then "the area definitive for composition" (Vestal, 1949). This was found to be 200 cm^2 at both Banyuls and Port-Cros.

Du Rietz *et al.* (1920) determined the minimum area by means of frequency/area or constant species/area curves (a constant species being a species present in 91–100% of the quadrats). According to these authors, the minimum area is obtained when the total number of constant species of the vegetation studied is achieved (Fig. 5). Values for this minimum area at Port-Cros and Banyuls were 100 cm^2 and 200 cm^2, respectively.

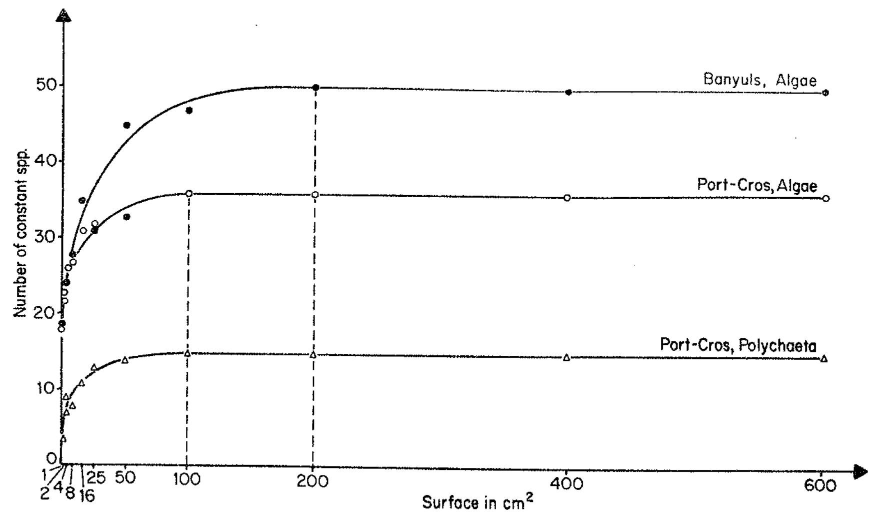

Fig. 5. Constant species/area curves of the algae (and Polychaeta) of the photophilic biotope from Banyuls and Port-Cros.

In conclusion, it is clear that the values of minimum area ((100)–200–(250) cm^2) depend on the method used, and that it undoubtedly is much smaller than the relevé area used (400 cm^2). This is the case for both sites, Banyuls and Port-Cros. Boudouresque (1974b) calculated the minimum area for circalittoral (sciaphilic) vegetation at 200 cm^2; Cinelli *et al.* (1977a) for vegetation dominated by *Cystoseira mediterranea* Sauv., at 150–200 cm^2; Cinelli *et al.* (1977b) for harbour vegetation, at 100–150 cm^2.

SPECIES DIVERSITY; EPIPHYTISM

Although the area of the relevé is so small (20 x 20 cm), the species diversity is very high within the taxonomic groups considered (Chlorophyceae, Bryopsidophyceae, Phaeophyceae, and Rhodophyceae); the average was 70 spp./relevé, with up to 109 spp. in some cases (Coppejans and Boudouresque, 1975). This is very high when compared with other biotopes studied using the same method. Superficial sciaphilic vegetation on exposed rocky coasts averaged 30–50 spp.; on sheltered coasts, 30–75 spp.; in harbours, 30–40 spp. (Boudouresque, 1971c). This high species diversity is partly due to the smaller algae of the underlying vegetation, partly to the epiphytes on the larger algae. The number of epiphytes can sometimes be quite impressive. Whilst Nasr and Aleem (1949) found 12 epiphytic spp. on one specimen of *Halopteris filicina* (Grat.) Kütz. in August along the Egyptian coast, 30 epiphytic taxa were once found on one specimen of *Stypocaulon scoparium* (L.) Kütz. (10 cm high), collected at Port-Cros in September at 20 m depth. The species included *Corallina granifera* Ellis et Sol.; *Jania rubens* (L.) Lamour.; *Jania corniculata* (L.) Lamour.; "*Falkenbergia rufolanosa*" (Harv.) Schmitz; *Spyridia filamentosa* (Wulf.) Harv.; *Plocamium cartilagineum* (L.) Dixon "var. *uncinatum*" J. Ag.; *Laurencia obtusa* (Huds.) Lamour.; *Dasya rigidula* (Kütz.) Ardiss.; *Wrangelia penicillata* C. Ag.; *Dictyota linearis* (C. Ag.) Grev.; *Ceramium byssoideum* Harv.; *Myriactula stellulata* (Harv.) Levr.; *Stilophora rhizodes* (Turn.) J. Ag.; *Giraudya sphacelarioides* Derb. et Sol.; *Antithamnion plumula* (Ellis) Thur. var. *bebbii* (Reinsch) J. Feldm.; *Lejolisia mediterranea* Born.; *Crouania attenuata* (Bonnem.) J. Ag. f. *bispora* (Crouan frat.) Hauck; *Discosporangium mesarthrocarpum* (Menegh.) Hauck; *Nitophyllum punctatum* (Stackh.) Grev.; *Rhodophyllis divaricata* (Stackh.) Papenf.; *Griffithsia barbata* (Sm.)

C. Ag.; *Ceramium diaphanum* (Lightf.) Roth; *Ceramium cingulatum* Web. v. Bosse: *Elachista intermedia* Crouan frat.; *Kuckuckia spinosa* (Kütz.) Kornm.; *Corynospora pedicellata* (Sm.) J. Ag. var. *tenuis* G. Feldm.; *Castagnea cylindrica* Sauv.; *Chondria mairei* G. Feldm.; *Bonnemaisonia* sp.; *Polysiphonia* sp.

Frequent epiphytes on other algae are: *Fosliella* spp.; representatives of the Chaetophorales (*Ulvella, Pringsheimiella, Phaeophila, Entocladia*); representatives of the Acrochaetiales; diverse Bangiophyceae (*Erythrocladia, Erythrotrichia, Chroodactylon, Goniotrichum*).

HOMOGENEITY; SIMILARITY

As mentioned in an earlier section, the relevés have to be taken from "homogeneous" vegetation; therefore, we checked if the impression of homogeneity agreed with the reality. Four contiguous relevés (of 20 x 20 cm) were made at Port-Cros and three relevés (of 10 x 20 cm) at Banyuls. After sorting them, the similarity coefficients were calculated by a series of formulae (Coppejans, 1977a, b). For mathematical background, the following references were used: Augarde (1957), Ceska (1966, 1968), Godron (1966), Goodall (1973), Gounot and Calleja (1962). The similarity tests fall into two groups; those that are based on the number of species present in the relevés and those based on the coverage of these species.

The similarity tests based on presence–absence of species (*vide*, for details, Coppejans, 1977a, c; those used were of Ceska, Kulczynski, Sørensen, Ochiai and Barkman, Jaccard and Sneath, Sokal and Sneath) all gave similar results. Those of Jaccard and of Sokal gave rather lower values, but when these were multiplied by a constant factor (Jaccard x 1.24; Sokal x 1.70) they became comparable with the other values. The average similarity value lies around 75%. This proves that the quadrat area used, 20 x 20 cm (and even 10 x 20 cm), is representative for the species-composition. These results are very high, compared with those of Boudouresque (1974b); for two relevés of 200 cm^2 made in a sciaphilic vegetation, he found the similarity coefficient of Sørensen to be 64.6%, whereas we found 77% for relevés of the same surface at Banyuls. This conflicts with the cautious conclusion of Boudouresque (1974b, p. 154): "L'aire minima varie d'un peuplement à l'autre. Son étude dans chaque type de peuplement et dans chaque région, est donc nécessaire, et il serait intéressant de rechercher si le seuil de similitude de 65% peut être considéré comme très général en milieu marin." According to our results this last supposition is not true, as the threshold value of similarity in photophilic vegetation is higher (75–80%, as in terrestrial vegetation).

The different similarity tests based on the coverage of the species (*vide*, for details, Coppejans, 1977a, b; those used were of Czekanowski, Kulczynski, Monthoux, Ruzicka, Spearman in Weber, 1972: 538) give rather divergent results.

As a general conclusion on this homogeneity study, we can say that the similarity-coefficients obtained by divergent formulae and based on different data (species number, percentage cover) are very high, much higher than those in marine sciaphilic vegetation, equalling those in terrestrial vegetation.

SAMPLING; STUDY OF THE SAMPLES

After the preliminary investigation of the photophilic infralittoral biotope, of the minimum area and of the homogeneity of the vegetation to be studied, the phytosociological investigation itself was commenced. So as to study photophilic algae at different depths and from different seasons and regions, sampling was done in homogeneous vegetation (see previous section) on horizontal or slightly inclined rocky surfaces, at depths of 2–25 m below C.D. The location of the relevés was taken at random by throwing away the chisel and taking the sample where it finally lay. This is important to provide the objective data needed for certain statistical methods. Date, depth, declivity and direction of the slope, coverage and maximum height of the vegetation were noted over a surface of 20 x 20 cm (see section on Qualitative Minimum Area).

The substratum was removed with hammer and chisel, to sample smaller and crustose algae of the underlying flora. All fragments were placed in plastic-bags, formalinized (4%) on arrival at the laboratory, and stored in the dark to reduce bleaching of the specimens. Over 100 relevés were recorded from March 1973 to July 1978; they were spread over winter and summer seasons at Banyuls (near the French–Spanish border); Marseille; the nature-reserve of Port-Cros, an island in front of Le Lavandou; and the bay of Calvi (Corsica).

Sorting through the relevés is extremely time-consuming, as each fragment in the samples is studied under a binocular microscope; the smaller algae and their epiphytes were also identified under the microscope (Cyanophyceae and Bacillariophyceae were excluded). Species diversity being very important (see that section), in total we identified 280 algal taxa, of which 40 were Chlorophyceae, 65 Phaeophyceae and 175 Rhodophyceae. These comprehensive species-lists are of great importance for later phytosociological analysis of the data. The presence, nature and frequency of the reproductive structures have also been noted and quantified. A reproductive coefficient and the reproductive density can be calculated from these data (Boudouresque, 1971a); these are, of course, time-linked. After the species list was completed, a percentage-cover was given to each species. We did not use the scale of Braun–Blanquet as it seemed too imprecise, especially for comparing the coverages of the epiphytes and of the smaller algae.

A sociability-factor could not be deduced as the samples consisted only of fragments of the original vegetation.

On the basis of the species lists, the ratios of different algal groups can be calculated; R/P (ratio of numbers of species of Rhodophyceae to Phaeophyceae) can be used to characterize the flora of a region. The ratios of the different orders within the Rhodophyceae can be used to characterize a biotope within a floristic province.

The distribution of the species present in the relevés over the different ecological algal groups ("groupes écologiques"; Boudouresque, 1970, 1971a) can also give important information about the population studied. All the above-mentioned data can be subjected to different ordination methods for identifying sociological units. For the photophilic vegetation, we still need more data so as to take the seasonal variation into account. From the species lists of the different quadrat-samples, it already seems that the depth where *Stypocaulon scoparium* is replaced by *Halopteris filicina* indicates the lower limit of photophilic algal vegetation in the western Mediterranean basin.

SYSTEMATICS

In sorting thoroughly the relevés, one is regularly confronted by identification and taxonomic problems. Boudouresque (1971c, p. 82) stated that:

> Contrairement à ce qui se passe dans le domaine terrestre (au moins dans nos régions) la systématique des végétaux marins reste extrêmement complexe. Est-il besoin de préciser qu'aucun ordinateur, qu'aucune méthodologie, si valable soit-elle, ne saurait remplacer une détermination exacte? Un travail de bionomie effectué sur des bases systématiques incertaines est une architecture compliquée bâtie sur des sables mouvants.

In the 100 relevés studied we identified, as stated above, 280 algal taxa (40 Chlorophyceae; 65 Phaeophyceae; 175 Rhodophyceae). Some of the specimens did not agree with any described taxon. *Polysiphonia banyulensis* Copp. has been described as a new species (Coppejans, 1976a, 1978a) and recorded since at Calvi (Corsica) and at Naples. For some other taxa, we either did not have enough specimens or did not find all the reproductive structures necessary for a complete description. We called them "species novae ineditae" and illustrated them (Coppejans, 1977a: *Sphacelaria papilioniformis, Lomentaria pennata, Myriogramme unistromatica, Peyssonnelia* sp. and a Ceramiacean belonging to the tribe Wrangelieae).

We also recorded taxa new to the Mediterranean Sea: *Ceramium cingulatum* Web. v. Bosse, described from the Indian Ocean and only found twice since the type collection, was present in our relevés at Banyuls, Marseille and Port-Cros (Coppejans, 1977b). *Ceramium taylori* Dawson, described from the North American Pacific coast and recently found by Verlaque at Marseille, was present in our relevés from the three areas studied. *Ceramium fastigiatum* (Roth) Harv. var. *flaccidum* (Børg.) Petersen has been described as an epiphyte on roots of mangrove-plants in the Caribbean Sea. We noticed it in relevés from Banyuls and Port-Cros. *Fosliella farinosa* (Lamour.) Howe var. *chalicodictya* Taylor had not been found since its type collection in the Caribbean Sea. We found it at Banyuls and Port-Cros (Coppejans, 1976b). It has also recently been collected by Boudouresque in Corsica. The record of *Lophosiphonia scopulorum* (Harv.) Womersley at Banyuls added this species to the Mediterranean flora (Coppejans, 1976b). Apart from these taxa new to the Mediterranean Sea, we also recorded species new to the French flora. *Myrionema liechtensternii* Hauck, described last century from the Adriatic Sea and never collected since, was found at Banyuls and, more frequently, at Port-Cros (Coppejans and Dhondt, 1976). *Dilophus mediterraneus* Ercegović, described from the Adriatic Sea, was frequently recorded at Port-Cros. Hitherto, *Griffithsia tenuis* C. Ag. was only known to occur in the Adriatic Sea and along the coasts of north Africa. It was a rare species in our relevés from Port-Cros. *Lophosiphonia cristata* Falkenb. has only been mentioned from Tobruk (Libya) since its original discovery at Naples, where it has not been found again. We recorded it at Port-Cros (Coppejans and Boudouresque, 1976a). *Sphacelaria fusca* (Huds.) C. Ag., already known from the Atlantic coasts of France, has been found along the Mediterranean French coast for the first time, at Banyuls, Marseille and Port-Cros. In total, we have added 15 taxa to the known French marine algal flora. A list of species rarely recorded for the Mediterranean has also been compiled; these included *Cladophoropsis modonensis* (Kütz.) Børg., *Siphonocladus pusillus* (Kütz.) Hauck, *Choristocarpus tenellus* (Kütz). Zanard. (Coppejans and Boudouresque, 1976b), *Colpomenia peregrina* Sauv., *Discosporangium mesarthrocarpum* (Menegh.) Hauck (Augier *et al.*, 1975), *Lobophora variegata* (Lamour.) Womersley, *Aphanocladia stichidiosa* (Funk) Ardré, *Chondria mairei* G. Feldm., *Lomentaria chylocladiella* Funk, *L. verticillata* Funk, and *Myriogramme distromatica* (Rodr.) Boud.

Some rare reproductive structures have also been observed. The gonimoblasts of *Antithamnion spirographidis* Schiffner were never seen in nature before. The propagules of *Fosliella farinosa* (Lamour.) Howe var. *farinosa*, figured in 1881 for *F. farinosa* var. *solmsiana* (Falkenb.) Foslie by Solms-Laubach, have never been observed since. We have recorded them in Corsica (Coppejans, 1978b).

On the basis of the species lists from the different relevés, we drew up an autecological and phenological "card" for each species. This information, combined with data from the literature, permitted the construction of an autecological, synecological and phenological image for each sampled species.

PHYTOSOCIOLOGY

Thus far, we have been unable to make winter observations at Banyuls or summer observations at Marseille. This makes it somewhat premature to give a phytosociological interpretation of our data. Nevertheless, we present a brief survey of previous bionomical groupings of the photophilic infralittoral algal vegetation. The zoologists, who give less importance to the algae, as well as those phycologists who adopt a simple solution, accept that the photophilic infralittoral vegetation is characterized by only one biocoenosis, the "Biocoenosis of the Photophilic Algae", ranging in depth from 2 to 25 (45) m. This oversimplifies the situation even when one distinguishes different facies, zones or populations within this biocoenosis. Other authors are over-influenced by the physiognomical diversity of the biotope. Using an imprecise bionomical method, they divide this zone into as many associations or communities as there are dominant algae. In this way, the infralittoral has been divided into:

different Associations: Feldmann, J. (1937); Zalokar (1942); Giaccone and Pignatti (1967); Giaccone *et al.* (1973); Nasr and Aleem (1949);
different Phytocoenoses: Giaccone (1965);
different Populations: Bellan-Santini (1962);
different Populations + facies: Pérès (1967);
different Communities: Ernst (1959);
different Biocoenoses: Molinier (1960); Boudouresque (1971a).

These latter authors divided the biocoenosis of the photophilic algae (*sensu lato*) into three: the Schotterion, as the underlying vegetation of the larger *Cystoseira* spp.; the Cystoseiretum strictae, at places with strong turbulence from just below the water-surface down to 50 cm depth; the Cystoseiretum crinitae, below that. We restricted our research to the study of the Cystoseiretum crinitae.

A third supposition is that the infralittoral vegetation forms a climax-cycle in which, starting from an initial association dominated by *Jania rubens* (L.) Lamour., eventually results a climax-association with *Posidonia oceanica* (L.) Delile (Potamogetonaceae, a marine phanerogam), with transitional associations (Molinier, 1954, 1955; Molinier and Picard, 1953, 1954; Pérès and Picard, 1955). All the latter authors based their interpretation on the data from a restricted area or from one season; they took only the "larger" algae into account to describe the above-mentioned groupings. Owing to this, they only mention a small number of "larger" species, not taking the smaller and (according to Boudouresque's results) often more characteristic ones into account, e.g. Giaccone (1965), 10 m depth, 1 m^2 quadrat, 7 spp; 4 m^2, 12 spp; Giaccone and de Leo (1966), 0.5 m depth, 8 m^2, 23 spp; 4 m, 1 m^2, 12 spp; 35 m, 6 m^2, 16 spp; Giaconne (1968), 60 m, 100 m^2, 23 spp.

The "transect-method" is rather physiognomical; by making such transects, one can distinguish different vegetation zones (as in Coppejans, 1970, 1972, 1974; Gamulin-Brida, 1965; Giaccone and

Pignatti, 1967; Huvé *et al.*, 1963; Larkum *et al.*, 1967). These authors again characterize the different zones by only a restricted number of larger algae. The results of such transect methods become absolutely useless (for bionomical interpretation) when all the noted algae are listed without recording the depth or the microbiotope (horizontal, vertical, overhanging rock-surface). Such lists are presented in Giaccone *et al.* (1972) for 0–38 m; in Giaccone *et al.* (1973) for 0–60 m; in Giaccone and Sortino (1974) for 0–50 m. Nevertheless these works have a positive value for the construction of species inventories for the area studied. The method of phytosociological relevés has been used only occasionally for studying photophilic marine algal vegetation, e.g., as in Cinelli (1969); Giaccone (1965, 1971, 1977); Giaccone *et al.* (1973); Molinier (1960); Pignatti (1962).

CONCLUSIONS

Our research aimed to contribute a better understanding of the phytosociological units within the photophilic vegetation in the Mediterranean sea. This was achieved by means of a rigorous bionomical method requiring the preliminary study of such factors as minimum area, homogeneity and species-composition. The fauna has been completely excluded from this study, as it had already been the subject of thorough studies by Bellan-Santini (1962, 1968, 1969); Gamulin-Brida (1965, 1974); Ledoyer (1968); Tortonese (1958). More winter observations are required fully to take into account the seasonal variation of the photophilic algal vegetation before our data are submitted to different ordination methods for identifying sociological units within the Cystoseiretum crinitae. It appears that the depth at which *Stypocaulon scoparium* is replaced by *Halopteris filicina* indicates the lower limit of photophilic algal vegetation in the western Mediterranean basin.

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