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ECOLOGICAL DISTRIBUTION OF *CAULERPA* IN THE RED SEA[1],[2]

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ABSTRACT

Species of *Caulerpa* occupy in the Red Sea a very wide range of habitats as compared to any other single genus. They appear from the partly exposed belts of intertidal zone down to the greatest depths from which benthic algae were obtained in the Red Sea, *i.e. ca.*, 120 m.

While an important group of species - those which are more robust-such as *C.racemosa* or *C. serrulata*, prefer soft substrate and are almost exclusive in sandy or muddy bottoms, the delicate species such as *C. webbiana* or *C. peltata* are exclusively found in rocky habitats or in coral reefs. A third group of species, such as *C. mexicana* may be found on both crumbly and firm substrates.

Morphological variations occur between populations of the same species which grow in different habitats, while parallel characteristics appear in variants of different species growing in the same habitats.

INTRODUCTION

THE ecological range of the genus *Caulerpa* in the Red Sea is very wide when compared with that of other genera of algae. Actually it was not equaled by any other genus found in that sea, including those represented by many species and thus are potentially capable of occupying a wide range of habitats.

Thirteen species of this tropical multispecific genus were found growing in the Red Sea. Papenfuss (1968) in summing up the published data concerning the algal flora of the Red Sea to date, lists 10 species : *C. cupressoides* (West) C. Agardh, *C. lentillifera* J. Agardh, *C. mexicana* (Sonder) J. Agardh, *C. racemosa* (Forsskål) J. Agardh, *C. peltata* Lamouroux (as *C. racemosa* var. *peltata*), *C. scalpelliformis* (R. Brown) C. Agardh, *C. selago* (Turner) C. Agardh, *C. serrulata* (Forsskål) J. Agardh, *C. sertularioides* (Gmelin) Howe and *C. webbiana* Montagne. Taylor (1967), listing the *Caulerpa* species collected by Professor G. F. Papenfuss at the Dahlak Archipelago off the Ethiopian coast during the Israel South Red Sea Expedition, 1962, added two species to those mentioned above, namely: *C. ambigua* Okamura and *C. fastigiata* Montagne. The thirteenth: *C. taxifolia* (Vahl) C. Agardh[3] was added in course of a study of the coast of Sinai Peninsula (Lipkin, in prep.).

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ECOLOGY OF *CAULERPA* IN THE RED SEA

The publications dealing with the *Caulerpa* species growing in the Red Sea refer mainly either to taxonomic relationships or to geographical distribution. As a result, data concerning habitats and plant communities in which these species live, is scarce. *C. lentillifera* was found "ad madreporas" at Koseir (Fig. 1) (Zanardini, 1858) and "occurs rarely on the coral reefs" in "Suez, Tor, Ghardaqa, Qoseir (=Koseir) and Jedda" (Nasr, 1947). *C. peltata* was collected by C. Crossland on coral reef at Khor Dongola (=Dongonab Bay) and at Suez (Harvey-Gibson, 1908). Nasr (op.cit.) writes that it "occurs on coral reefs below low water mark in the late spring and summer" at "Suez, Dongonab (- Bay). Ghardaqa, Daedalus (- Reef) and Port Sudan". It was found in the infralittoral fringe (Rhodophyta-*Serpulorbis* zone and Reef-forms zone), which is rarely or only exceptionally exposed, on rocky shores at Elat, associated with many other algae and animals (Safriel & Lipkin, 1964). Professor G. F. Papenfuss collected it at 3 meters depth at Cundabilu Island and at 1-2 meters depth at Nocra Island, both in the Dahlak Archipelago (Taylor, 1967). Concerning *C. scalpelliformis*, "few fragments were brought from a depth of 8m (Nasr, op. cit.). Ecological data concerning *C. racemosa*-which is very common in the Red Sea - is given by Harvey - Gibson (op. cit.) who writes that C. Crossland dredged it from a depth of 2 - 3 fathoms

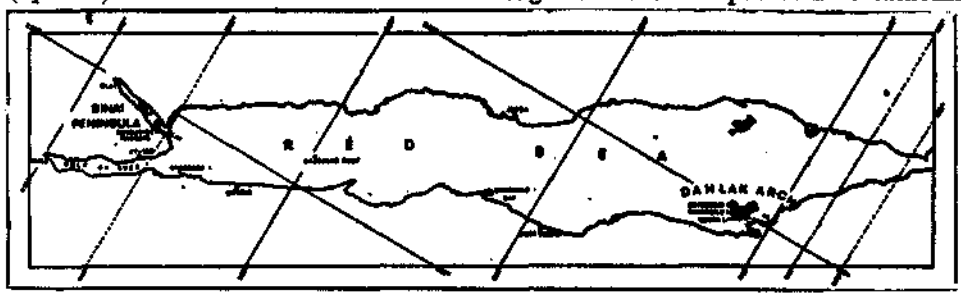

Fig. 1. Map of the Red Sea with localities mentioned in the text.

off Suez ; by Muschler (1908) who writes that it is to be found "sur divers substrata", in "Baie de Suez, Kosseir (=Koseir), el Tor"; by Aleem (1950) who writes that it " was collected at Suez and Ghardaqa in the summer... growing on dead corals" ; by Safriel & Lipkin (op. cit.) who found it in the infralittoral fringe at Elat, as mentioned for *C. peltata*; and by Taylor (op. cit.) who writes that it was collected at 1 m depth by Professor G. F. Papenfuss at Entedebir I., Dahlak Archipelago. The ecology of *C. serrulata* - which is also very common in the Red Sea - is refered to by Nasr (1947) as "very common in the environs of station (-at Ghardaqa), extending from the low water mark down to 5 fms or more". However, later in the text, describing the results of culture experiments, he mentions the depth of 10 fathoms as depth in which the alga was found and mentions crevices in coral reefs and lagoons as habitats in which the plant was found. Its ecology is refered to by Rayss et Dor (1963) also, who found it "sur les rochers madreporiques par la profoundeur de 1 metre a Eylath-Taba (=Elat)"; and by Safriel & Lipkin (op. cit.) too, who found it in the infralittoral fringe on rocky shore at Elat mentioned above, and who remark that it was "represented here by moderately developed individuals, while on sand of greater depths stolons may attain the length of more than 2 meters."

Nasr, in addition to observations, also cultured *C. serrulata* and *C. racemosa* in aquaria. By changing growth conditions from open sea to the laboratory, he obtained on one and the same plant assimilators which looked different from each

other. These differently looking assimilators which appeared on one plant, fitted into different taxonomic "varieties" and "forms" described previously. Thus he concluded that these "varieties" are the result of differences in external conditions and rejected the division of the species cultured by him into so many varieties as was done before. Tandy (1933, 1934), culturing species of *Caulerpa* from Florida - some of which appear also in the Red Sea - arrived at very similar conclusions.

During the last ten years, habitats and plant communities were studied in many places along the coasts of the Sinai Peninsula both on the Gulf of Elat and on the Gulf of Suez including the Suez Canal system (Lipkin, in prep.), and - during the Second Israel South Red Sea Expedition, 1965 - also in several islands in the Dahlak Archipelago. Ten species of *Caulerpa* are included in the present study, as *C. ambigua*, *C. cupressoides* and *C. fastigiata* - each reported from one Red Sea locality only - were not found in course of the study. [*C. prolifera* which is very common in the Mediterranean, is reported by Muschler (1908) from Suez. However, Papenfuss (1968) remarks that "the occurrence of this species in the Red Sea seems doubtful." This species too was not found in the course of the present study.]

The Red Sea, though extending very near to the latitude of N 30°, is a tropical sea and contains the typically tropical entities of coral reefs and mangroves. The first are found in all parts of the Red Sea, while mangroves are found extending only as north as Shurat - el - Manqata on the Sinaian coast of the Gulf of Elat (N28°12′). The biota of the Red Sea is of an Indo-Pacific origin. The Red Sea being geologically very young, the bulk of its biota entered it only recently and had no sufficient time to evolve new species in this sea. This is why almost all of the species found in the Red Sea, including those of *Caulerpa*, are to be found in other parts of the Indo-Pacific region as well.

The Red Sea is more saline than most other seas. It shows gradual increase in salinity from about 36°/₀₀ in the south, to about 41°/₀₀ in the north (Oren, 1964). Sea surface temperatures drop from a yearly mean of 27.7° C at the southern end - at the latitudes of N13° - N14° - to a yearly mean of 22.5°C at the northern end - the latitudes of N28° to N30° (Oren, 1962). Tides are conspicuous on both ends of the Red Sea, reaching an amplitude of more than 2 meters at the northern end and somewhat higher values at the south, but are almost negligible in its central part (Crossland, 1907). Wave-action as a rule, is moderate on most shores of the Red Sea, though there are differences between more exposed and less exposed shores. The vertical range of the intertidal zone, which depends on the amplitude of the tide on one hand, and on the intensity of wave action on the other, is nearly 2 metres at Elat in the northern end of the sea (Safriel & Lipkin, 1964) and about 4.5 meters in the Dahlak Archipelago in its southern part (unpublished).

Habitats inhabited by *Caulerpa* in the Red Sea, varies very much. Though *Caulerpa* is well known to be one of the few algae inhabiting soft substrates such as sand or mud, it is also well represented on the firm rocky or reefy substrates prefered by most of the algae. Concerning depth, populations of plants belonging to this genus were found growing from the lower part of the intertidal zone down to a depth of about 120 metres. However, they are typically plants of submerged habitats and are most abundant in the upper several meters of the subtidal.

Crumbly substrates in which *Caulerpa* grows are usually calcareous sands in shallow water - down to about 30 meters. These sands are, in its greater part, built of small fragments of eroded corals or shells of molluscs, foraminifers and other animals. At greater depth the substrates are built of finer particles and silts

or clays predominate. These substrates are the preferable substrates also for the sea-grasses growing in the Red-Sea, and *Caulerpa* is often found growing in association with them. As a rule, *Caulerpa* occupy only a small part of the total plant cover in these associations while the sea-grasses dominate. *Caulerpa* is found most frequently in meadows dominated by the very common *Halophila stipulacea* (Forsskål) Aschers., and *Halodule uninervis* (Forsskål) Aschers., and by the less common *Halophila ovalis* (R. Brown) Hook and *Thalassia hemprichii* (Ehrenberg) Aschers. Less frequently *Caulerpa* grows in stands dominated by *Syringodium isoetifolium* (Aschers.) Dandy or *Cymodocea rotundata* Ehrenberg & Hemprich; and is almost never found in stands of *Thalassodendron ciliata* (Forsskål) Hartog. Pure stands of sea-grasses on one hand and of *Caulerpa* on the other, are found too; but while the total plant cover is very high - reaching 100% - in those stands including sea-grasses (both the pure ones and those in which *Caulerpa* is found as well, those in which *Caulerpa* grows alone, are much less dense, with a plant cover of usually less than 15% of the total area. The habitats of soft bottoms are usually flat or gently sloping so that variations in light conditions and also in temperature are negligible or very moderate within small distances and vary only with depth.

Habitats on firm substrates vary much more, especially with regard to light conditions, due to its complex microtopography. These substrates range from pebbles or boulders scattered on sandy bottom, to gently sloping beach-rocks which appear along the coastline or to rocky flats situated at different depths, all well illuminated when at shallow water. Coral reefs, both dead and living - which are very abundant in the Red Sea - give, with its many cavities, cavelets, fissures and overhangings, a whole range of shaded habitats differing in the amount of light which penetrate into each. Rocks offer similar habitats. In these habitats *Caulerpa* grows in several different photophil and sciaphil plant communities, associated with many other algae. The communities here are very rich in species - in striking contrast with those of the sandy bottoms which are often dull, being composed of one, two or three species only. The plant cover of associations growing on solid substrates is usually very high and almost always is 100%, or very close to this level. The part of *Caulerpa* in these associations varies, but is often considerably high, reaching values of 30%-60% of the total plant cover. *Caulerpa* uses also organic substrates - though very rarely - and was found creeping on the vertical pneumatophores of the mangrove *Avicenia marina* (Forsskål) Vierb. in the upper part of the infralittoral fringe on the coast of Sinai, in association with other algal species which are more common in this habitat (Lipkin, in prep.).

The most common among the species of *Caulerpa* found in the Red Sea are *C. serrulata* and *C. racemosa*. Both are found in all parts of that sea and *C. racemosa* also succeeded in penetrating into the Mediterranean and was found in its western basin (Hamel, 1930) as well as in the eastern basin (Hamel, 1931; Lami, 1932; Rayss, 1941; Aleem, 1950; Huvé, 1957; Rayss & Edelstein, 1960; Lipkin & Friedmann, 1967 ; Lipkin & Safriel, 1971) of that sea. It is the only species of *Caulerpa* found in the Suez Canal connecting the two seas (Lyle, 1926 ; Lami, 1932 ; Lipkin, in prep.). *C. lentillifera*, *C. mexicana*, *C. peltata* and *C. scalpelliformis* are found too in all parts of the Red Sea but are less common. Two of these: *C. mexicana* and *C. scalpelliformis* penetrated into the eastern Mediterranean (Rayss, 1941). *C. sertularioides* and *C. webbiana* were not reported from the Gulf of Suez while being found in other parts of the Red Sea. Both may be common where appear. *C. selago* was found in the Red Sea proper, but was not found in the Gulf of Suez nor in the Gulf of Elat. The other four species found in the Red Sea were found only in one locality each: *C. cupressoides* on the Sudanese coast (Harvey-Gibson &

Knight, 1913), *C. ambigua* and *C. fastigiata* in the Dahlak Archipelago (Taylor, 1967) and *C. taxifolia* in the Gulf of Suez (Lipkin, in prep.). Of these, only the last was observed during the present study : at Et-Tor, where it was quite common.

The species of *Caulerpa* of the Red Sea may be grouped into four groups according to their preferance of substrates. The species of the first group: *C. selago* and *C. sertularioides*, were found growing in sand only, in shallow water in a community dominated by *Thalassia hemprichii* and *Caulerpa racemosa*. The species of the second group which includes *C. racemosa* and *C. serrulata*, are to be found on a variety of substrates, but both prefer soft substrates. On sand, both attain considerable size - the stolons may reach a length of a few metres each, with the assimilators well developed. They are also found in rocky habitats where the plants are much smaller. *C. racemosa* is usually found in well illuminated niches and thus usually in shallow water, while *C. serrulata* may be found in deep shade as well. The last is also the species among the caulerpas which was found growing deepest in the sea - it was dredged from a depth of about 120m in Museri Trough, Dahlak Archipelago (Lipkin, in prep.) where it grew on clay. These two species together with *C. scalpelliformis* were the only species found in lagoons (Lipkin, in prep.), while all others appeared only on open coasts. A third group includes *C. mexicana*, *C. taxifolia* and *C. scalpelliformis*. The species of this group are growing on both solid and crumbly substrates as do those of the former, but prefer the solid substrate. They all grow on dead coral reefs, on rock flats covered with a thin layer of sand or on pebbles and boulders. They may penetrate sandy areas from nearby rocky patches. *C. mexicana* was also dredged in several places in the northern end of the Gulf of Elat, from depths down to about 100m where it grew on mud (Lipkin, in prep.). Here it was found either in pure stands or in *Halophila stipulacea - Sargassum* community. In shallow water it may appear in *Laurencia papillosa* community or in *Sargassum dentifolium - Cystoseira myrica* community in well illuminated habitats; or in association with sciaphilic species such as *Udotea argentea* Zanardini, *Vanvoorstia spectabilis* Harvey, *C. webbiana* and *Peyssonelia rubra* (Gmelin) Decaisne, in crevices and overhangings. *C. taxifolia* was found growing in *Caulerpa racemosa - Digenea simplex* community with *Codium* spp., *Halimeda* sp., *Cystoseira myrica* (Gmelin) C. Agardh and *Turbinaria triquetra* (J. Agardh) J. Agardh as the most important accompanying species. *C. scalpelliformis* was found growing in a lagoon in a community of *Halodule uninervis* and *Caulerpa racemosa* and on open coast in a *Caulerpa racemosa-Digenea simplex* community. The fourth and last group of species: *C. lentillifera*, *C. peltata* and *C. webbiana*, grow exclusively on solid substrates. All prefer dim light and thus are found in crevices, cavelets, overhangings and any shaded cavities within coral reefs or rocks. However, the first appear usually in somewhat better illuminated habitats when compared with the later two.

Plants of many of the species that grow in more than one habitat, often show morphological differences when growing in the different habitats. *C. scalpelliformis*, *C. selago* and *C. sertularioides* were found in too few localities, which do not vary much ecologically, so that no morphological variations due to ecological variance were observed. However, along the Mediterranean coast of Israel, *C. scalpelliformis* do show such morphological variations which are probably found also in the Red Sea. In very highly illuminated habitats - such as rocky flats just below sea surface, in which there is, probably, an excess of light - its assimilators are very short, somewhat succulent, with the small teeth which are found on the margins of the much larger tooth-like lobes, being very prominent (- thus, the so called "var. *denticulata*"). Growing in less illuminated habitats, assimilators are much longer - reaching

lengths of up to 50 cms - and less fleshy. The tiny teeth on the lobes are less prominent but still conspicuous (-and thus still "belong" to the "var. *denticulata*). In deeper shade, the small teeth disappear, so that the so called "var. *scalpelliformis*, (=var. *typica*") is achieved. *C. mexicana* lives - as mentioned above - in highly illuminated habitats as well as in dim light, in deep water or in crevices in rock. The general appearance of the assimilators of this species is only slightly changed under the different light conditions of these habitats. Morhological differences somewhat parallel to those experienced in *C. scalpelliformis*, are found here. The assimilators which are short and somewhat fleshy under very strong light, become longer, thiner, and the teeth (=lobes) - which are very close to each other, or even overlap in the well illuminated plants - tend to depart so that distances appear between each other up to the width of the tooth itself, and even more.

Other species show more remarkable differences. *C. serrulata* which grow under similar range of light conditions as do *C. mexicana* bear assimilators composed of densely spirally twisted, very thick - almost cylindrical - ribbons, toothed on the margins, when growing under intensive illumination. In dim light the assimilators bear flat, very thin, and untwisted ribbons, here too with well developed teeth. This last fact is in contrast with the observations of Nasr (1947). The teeth in our material were found to be well developed even in depths several times those in which Nasr observed plants with poorly developed teeth (*ca.* 60 fathoms as compared with 10 fathoms, respectively).

C. peltata which bear the typical peltate discs when growing in shaded habitats, tends to bear thicker discs with smaller diameter in brighter light, and even spherical - *C. racemosa* - like - vesicles under direct sunlight. As the range of variations of morphology in *C. racemosa* is absolutely different from that here described, under the same range of ecological conditions (-only the forms of these two species which grow in strong light being similar-) it is assumed that the taxon bearing the peltate discs when growing in dim light, is a distinct species and not a variety of *C.racemosa* as it is sometimes treated. The similarity of morphology under certain conditions might be regarded as an atavistic phenomenon in *C. peltata*, hence pointing at a possible close evolutionary relationship between the last and *C. racemosa.*

C. racemosa and *C. lentillifera* show similar variations of morphology under differing light conditions. Normally, under favourable light conditions - which are good illumination for *C. racemosa* and somewhat less intense illumination for *C. lentillifera* - both bear many vesicles densely arranged around the axis of the assimilator giving it a cylindrical appearance. When growing in dim light both develop assimilators which bear much less vesicles that are arranged in one plane only, giving the assimilator a flattened looking ; this is the so called "var. *lamouroxii*" of *C. racemosa* and a parallel, very similar form in *C. lentillifera.* In heavy shade the assimilators of *C. racemosa* lack vesicles altogether retaining the axes only, hence creating the so called "var. *lamouroxii* f. *requienii*". This last shape of plants is also found in the well illuminated habitats at the beginning of the growing season - which was found to be the early summer (June-July) in the Red Sea- pointing at the possibility that apart of being an ecological form of poorly illuminated habitats, it may be a juvenile stage as well (Lipkin & Friedmann, 1967). *C. webbiana* shows similar patterns of variation to those exhibited by *C. racemosa* and *C. lentillifera.* Its cylindrically looking assimilators bear its three or more times dichotomously forked lateral brenchlets arranged all around its axis when growing in more light - and usually it means closer to the outside of the cavelets or the

crevices in which they live ; while in less light - deeper in the crevice or in other heavy shaded habitats, the assimilators look flat, bearing the lateral branchlets in one plane only, hence forming the so called " f. *disticta*". Often both forms are found on the same stolon if it extends from the well illuminated end of a crevice to less illuminated one.

C. taxifolia shows curious situation. Its plants normally bear flat plume-like assimilators. In the only locality in which it was found to date in the Red Sea,- at Et-Tor, Sinai - though most of the population was normal, a considerable amount of the stolons bear unusual, cylindrically looking assimilators, growing in many cases on the same stolons with the normally looking ones. In this case, no ecological difference could be detected between the patches in which the cylindrical form of the *C. taxifolia* (-which was not described yet) was found and the area covered by the normally looking plants, though such differences may occur.

A peculiar form of *Caulerpa* was dredged from depths between 45 meters to 80 meters at the northern end of the Gulf of Elat (Lipkin, in prep.). The plants are closely comparable to what was considered to be *C. freycinetii* var. *integerrima* Zanardini (Weber van Bosse, 1898) (=*C. serrulata* var. *integerrima*). However, they can not be considered as belonging to *C. serrulata*, as they do not exhibit the " depth form" attained by *C. serrulata* in the same, and even in greater depths ; though the assimilators of both branch similarly. It may be a form of a known species, simplified due to the deficiency of light, but it still may be a new species of *Caulerpa*.

The occurrence of the many morphologically different forms described above, which vary due to variations in external conditions, together with partial results of not yet completed studies on *Caulerpa* cultures (unpublished), show - in accordance with the conclusions of Tandy (1933, 1934) and Nasr (1947) - that the segregation of many species of *Caulerpa* in the subspecific levels is highly unjustified. Only further experimental work could enable the subdivision of species on more reliable grounds.

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