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Competitive Relationships in Natural and Artificial Algal Communities

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Abstract—Modern data on competitive relationships and their role in the succession of natural and artificial algal communities are reviewed. The mechanisms of macroalgae competition and the factors that affect the competitive outcomes are considered. The conception of competitive interactions between seaweeds in the field and culture is suggested. (1) Competitive relationships are possible only between seaweeds which live together and are able to exchange signals. (2) Success in the competition for light is the basis for wins in the competition for space. (3) The competition for nutrients never results directly in the exclusion of the competitor from the community. It inhibits the competitor and allows the winner to overgrow, shade, act allelopathically, and to displace the inferior competitor in the community. (4) People, creating an artificial monodominant community, either increase the competitive potential of cultivated species by selection of growth conditions or exclude the competitors.

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ROLE OF COMPETITION IN THE NATURAL COMMUNITY

Among biological factors affecting the development of marine phytocenoses, the competition is of great interest and often is considered as the major selective force in the structuring of marine benthic communities [18, 27]. Competitive relationships between marine algae, together with natural and anthropogenic effects, are the most important factors that determine diversity of the species, their distribution (geographical distribution and distribution throughout different depths) and the biomass of algae in communities [78]. The role of competition in the succession of algal community increases when the effects of other biotic or abiotic factors come down. Competitive relationships between marine algae are important at all levels of their organization. The structure of an algal community might be affected by competition either directly or indirectly, via other structural factors, like grazing by herbivores, removal of certain species due to human activities, or the effects of typhoons [68]. At the population level, the competition can affect the size and age structure of the population. Finally, the competition is reflected on the physiological condition of certain plants and the reproduction of the latter.

THE ESSENCE OF COMPETITION

Competition is an active negative impact of some components in a community on each other in order to control certain resources which are in short supply. To such, resources could be referred to as space, substrate, light, and macro- and microelements indispensable to the life of the plants. In a wide sense, the competition boils down to the fact that one organism deprives another organism of a part of a certain resource; as a result, the latter organism grows slower, produces less offspring and has greater chances of dying. No competition arises, if the resources are sufficient enough or the plants are located far enough from each other, so no mutual effects are possible.

The competitive abilities of species depend on their capabilities to be injurious to the competitor or to counteract the negative impact of the latter. In competitive relationships it is a practice to distinguish winning species and vanquished species. If the final winning of any particular species in the competition is not obvious enough, we may speak of either great or small competitiveness of these species [69].

TYPES OF COMPETITION

The competitive relationships between algae could be intraspecific and interspecific [71]. In the case of intraspecific competition, the solidarity between individuals still retains; they are capable for reproduction, thus providing the transfer of genetic information that is characteristic of the population. The competitive relationships between the individuals of one and the same species turn more keen (strong), if the population density increases. The intraspecific competition in plants induced by increased density of vegetation causes significant changes in the morphology and physiology of certain individuals. When population density is great, the growth rate [87, 93] and reproductive potential of certain individuals [85, 87] fall down, whereas the mortality increases [24, 86]. The intraspecific competition is based, first of all, on the ontogenetic (physiological) differences between the plants coming into the competition, however, no less important is genetic heterogeneity of individuals in the population (if such a heterogeneity exists), which determines their competitive abilities [102].

Kenkel [59] suggests a two-phase pattern of intraspecific competition. First phase is a proportional consumption of available nutrients by all individuals, until the resources run out. Second phase is the development of asymmetrical competition, which begins at the point when a large plant takes up a disproportionate share of the light against the background of depleted nutrient resources.

The essence of interspecific competition lies in the fact that the growth rate, fecundity, and survivorship in the individuals of one species decrease as results of the impacts of specimens of another species, which can better use the resources, overgrow or allelopathically affect their competitors.

Most natural communities represent mixtures of numerous species. Therefore, the interspecific competition is usually observed between several species rather than between only two competitors. In marine benthic communities, the competitive relationships have been registered between algae and animals. Sometimes the competition between species is so strong that the weaker species can be totally excluded from the community. The winning species dominate communities either in biomass or the number of specimens or in both these indices at the same time.

Field and laboratory investigations showed that heterogeneity in environmental conditions, as well as the eating up of some plants by animals and avoidance of other plants could be the factors that change (decrease of increase) the competitive abilities of different species [26, 37, 58, 76].

Interspecies competition is considered as a kind of interaction that is harmful to both or several species; however sometimes it remains unclear, whether the organism has any real disadvantage as a result of the interaction [61, 111]. Moreover, the competing species can positively affect each other. For example, legumes, which compete with other grasses for substrate, light, and water, provide their competitors with mineral nitrogen. Competing algae, at certain stages of their life cycle, also can provide beneficial effects to each other. An example is better germination of spores or greater survival of the sporelings of some algae in thickets of a competing species compared with a naked substrate. For example, Worm and Chapman [108] have found that, in early stages of development, the density of minute sporelings of *Fucus* is greater in areas inhabited by encrusting algae or in the thickets of *Chondrus*, probably due to more favorable conditions for the attachment, preservation, and germination of spores (heterogeneity of substrate or absence of drying).

Two or more species of algae would compete only in the case where they are located in close vicinity to each other and can exchange signals. As for the exchange by signals, we would consider interactions of any type: chemical (exchange with metabolites or allelopathic effects), mechanical (contacts with thalluses or rhizoids, shading or overgrowing of some algae by others), etc. Therefore, the interspecific competitive relationships could arise only under conditions of symbiosis, which, in the wide sense of this term, is distinguished as the living together of two dissimilar organisms [1]. The symbiotic relationships between two or more species of algae become competitive when certain vitally important resources are in short supply, like space, substrate, light, mineral nutrients, etc. Moreover, according to this definition, the competing plants of the same species can also be symbionts, as being in different stages of life cycle (for example, sporophyte and gametophyte) or algal thalluses of different generations, as, in respect of ontogenesis, they represent different (and dissimilar) organisms. For example, native natural populations of the red alga *Gracilaria verrucosa (gracilis)* can comprise plants in different stages of development: male gametophyte, carposporophyte developing on female gametophyte and tetrasporophyte. Moreover, some scientists mentioned for *Gracilaria* the presence of mixed reproductive phases: carposporophyte and tetrasporophyte growing on a common sole; gametophyte developing on a tetrasporophyte; and male and female gametophytes located on a common thallus [5, 16]. Such organisms are symbionts and would compete for resources, if the latter are in short supply.

Effectual help in studies of competitive relationships is provided by mathematical models. The most well-known model has been proposed by two Italian scientists, independently of one another, Lotka [65] and Volterra [106]. This model suggests that the interactions between species are always negative and correlate linearly with their population densities; while the coexistence of competing species is possible, if interspecific competition is weaker than an intraspecific one. These tenets were also used in some other similar models [36, 89]. However, some scientists emphasized obvious pitfalls of the Volterra–Lotka Model. For example, Olson and Lubchenko [75] believe that this model does not bring to attention positive relationships between competing species, heterogeneity of the environment, as well as changes that take place in population structure and, as a consequence, the interaction forces between organisms. Taking into account the pitfalls of the Volterra–Lotka Model and using the latter as a basis, some more models of competition were proposed later on. For instance, Zhang [111] proposed a model taking into consideration possible mutualistic relationships between two competing species. It is pertinent to note that the role of mutualism in the maintenance of the coexistence of competing species in a community was, earlier on, neither studied nor evaluated. In summary, the author of this model provided the following conclusions: (1) mutualism is a possible mode of coexistence of competing species; (2) mutualism often benefits increasing size and density of populations that, for a long time, can coexist due to self-regulation, thus supporting the competitive abilities of the species. These conclusions suggest that not only mutualism, but also other biotic relationships (for example, parasitism, predatory, influence of herbivores) affect significantly the results of competition between species.

MECHANISMS OF COMPETITION

Schoener [94] and, later on, Olson and Lubchenko [75], proceeding from a few (in that time) papers dealing with the competition [30, 88], have distinguished at least four mechanisms of competition between algae. Depending upon how the algae affect each other (directly or indirectly, using resources that are in short supply), two types of competition are distinguished, exploitation and interference. The mechanisms of the exploitation comprise: (1) more intensive uptake and effective utilization of resources that are in short supply (light, biogens) by one of the species, which prohibits the utilization of these resources by competitors and (2) reservation or retention, i.e., unimpeded occupation of space (fast overgrowth of one species throughout a substrate that hampers attachment and germination of spores of the competitor). The interference also comprises two mechanisms: (1) overgrowth, displacement of competitor from a substrate or space including interactions with epiphytes and (2) chemical (toxic or hormonal) influence, i.e., allelopathic inhibition of growth and photosynthesis in associated species of algae by secondary metabolites, either at direct contacts or through the water column [75, 94]. Unfortunately, the studies performed in recent years did not add significantly to our body of knowledge about the mechanisms of competition. The authors emphasized the importance of competitive relationships for algal communities [2, 25, 29, 79, 99, 108, 109] and discussed possible mechanisms of interactions in algae that result in domination of one or several species, but did not corroborate these speculations with any experimental data [29, 99, 107, 108].

COMPETITION FOR SUBSTRATE AND SPACE

Most marine macroalgae follow a sessile mode of life, therefore they need an appropriate substrate for settlement and growth. This substrate can be either primary, like rocks, stones, coral skeletons or bottom sediments, or secondary, like other algae or animals. During the competition for a substrate, one of the mechanisms of interactions between algae is outgrowth. Such characteristics of the algae as fast lateral growth and the capability to raise the growing margins over the substrate determine the results of interferential relationships. Overgrowing usually results in the death of the competitor due to the compression of its tissues and striking decrease in illumination and the uptake of nutrients [40, 64, 108]. Santelices with coauthors [92] have mentioned in their paper the death of young (5–30 days old) tetrasporophytes and gametophytes of *Mazzaella laminarioides* due to their overgrowth of large adult (3 months old) plants of the same species. Such a mechanism of competitive relationships has been described for nonbranched coralline [72, 96] and turf-forming algae [11, 12]. Many marine macrophytes having specialized attachment organs (rhizoids) or developing stolons (like a creeping trunk), for example *Caulerpa*, can easily overgrow other benthic algae that are lacking these structures [83, 105]. Owing to fast growth and the ability to form multilayered (multilevel) mats [82], the stolons of *Caulerpa racemosa* overgrow rapidly the other species of *Caulerpa*—*C. taxifolia* (see [81]).

The area of a substrate really occupied with the attachment organs of adult thalluses often is not comparable with the area of projective coverage of the thickets of these algae. For example, Dayton [30] has found that the substrate proportion occupied with attachment organs of brown algae, which dominated the area, equaled less than 18% of the projective coverage. Therefore, the availability of a substrate for settlement in such thickets can be an important determinant for competition between species only during the settling of the plants on the substrate (spore, sporelings, juvenile plants). Major competitive interactions in adult plants would be confined to the interception of light and nutrients.

Occupation is also an important mechanism of competition that allows algae to occupy a dominating position in a certain part of a substrate and in space. In this case, such peculiarities of the algae, as great size, fast growth, and long vegetation period benefit the domination of competing species [75]. Some authors mentioned reservation (retention) of a free substrate and space by turf-forming algae followed by a decrease of disappearance there of other large morphological forms of algae [10, 22, 55, 66]. For example, it was found that substrate occupation by a red alga *Mazzaella cornucopiae* results in a significant decrease in the density of sporelings of brown algae *Fucus gardneri* and *Pelvetiopsis limitata* (see [62]).

It is not inconceivable that other mechanisms are also used by algae in their competition for a substrate. For example, we should not underestimate such a mode of interactions, as allelopathy. Apparently, a chemical impact is a universal mechanism, which can be used by algae in their competition for any limited (essential) resource. For a long time, the allelopathic effects in algal communities were considered as hypothetical, as their existence was not corroborated by convincing experimental data. Until recently, only a few studies have been performed dealing with marine macroalgae that produce substances inhabiting growth and photosynthesis in other marine macrophytes [35, 39, 41, 53, 100].

In the competition for a substrate or space, the allelopathic substances discharged into water by some algae can inhibit the release of spores, their attachment and germination, as well as the development of young sporophytes of other macrophytes species. It is found that some substances produced by *Delisea pulchra* inhibit germination of spores in the green algae *Ulva lactuca* (see [74]), while metabolites excreted by coralline algae suppress the maturation of female gametophytes, as well as formation and development sporophytes in *Laminaria*, especially under high temperatures [35]. Nelson with coauthors [73] have corroborated experimentally that extracts from *Ulva* and *Ulvaria* that show allelopathic properties negatively affect spore germination in fucoid algae. The authors believe that these substances could be dopamine and its derivatives blocking membrane proteins. In the other experiment, the extracts were isolated from a coralline red algae *Lithophyllum* spp., which destroyed zoospores of the brown alga *Laminaria religiosa.* The results of these studies showed that allelopathy can play an important role in the decrease of epiphyte growth of the surface of crustose coralline algae and, thus, benefit their growth and distribution in coastal areas of the northern Sea of Japan [100].

One would expect the intensification of competition for space in the case, when algae develop dense turf-like thickets (for example, algal turf on coral reefs) and also in the aggregations of nonattached algae that develop thick mats (for example, the fields of the Far-Eastern alga *Ahnfeltia*). It is known that algal mats of coralline and fleshy algae decrease the rate of restoration significantly in some species of large macrophytes, for example, the thickets of laminarian algae in Southern California [31]. Lubchenko [67] showed that dense thickets of *Chondrus* impedes the settlement of *Fucus vesiculosus* and *F. evanescens.* The turf-forming red alga *Phyllophora truncata* wins in the competition against the fast growing brown alga *Laminaria digitata* sinking in the turf of *Phyllophora* [22]. After the removal of the red alga turf from a hard substrate, the population density of laminarian sporophytes on the latter increased 10-fold. It is believed that in the latter case such interaction mechanisms, as occupation and allelopathy, turn to major ones in the competition for a substrate and space.

It is shown that the survival of sporelings (plantlets) of large fast-growing algae in dense mats can be greater than on naked substrates, probably due to the decreasing impact of such factors, as drying, wave effects and grazing by phytophages [15, 25, 108, 109]. For instance, the population density of *Cystoseira* spp. and *Fucus* on the mats of red algae was greater than on boulders, not inhabited by the algae. However, later on, the mortality in sporelings growing on the mats increased and the thickets of fucoids developed primarily on naked stones [14, 19]. The population density of sporelings plays an important role in the development of algal communities. Paine [77] has found that at a sporeling population density smaller than 25 plants for 1 m^2, a population of *Postelsia palmaeoformis* lost its ability to persist under the presence of mollusks competing with the alga for substrate and space. Thus, an increase in the population density of algae, on the one hand, necessarily causes the intensification of competition for substrate, space, and other environmental resources; however, on the other hand, the benefits of the high growing density, for certain species, sometimes are greater than these negative impacts. Among the benefits are, first of all, successful fertilization, decreasing impact of drying, wave effects, and grazing by phytophagous fishes [54, 67, 95, 103]. This is the reason why the high density of individuals in algal turf is important for long-term existence of thickets of this polydominant community.

Other, no less important factors have also been revealed affecting the opportunistic relationships of algae in their competition for a substrate and space. For example, a presence of herbivores allows *Fucus* to occupy the free substrate successfully, as *Enteromorpha*, its major competitor, is grazing by fishes and sea urchins. When these animals are absent, *Enteromorpha*, due to higher growth rate, takes the dominating position in the community and wins in the competition against the sporelings of *Fucus* [67].

We suppose that mutualistic relationships between some algal species can be reflected in the results of their competition with other macrophytes; mutualism can decrease negative effects of the competitor and provide benefits in the competition for a substrate. These speculations were partially corroborated by the results of experiments performed in the plant–animal system. According to Stachowicz and Hay [98], the "facultative mutualism" between a herbivorous crab *Mithrax* and a coralline alga providing a refuge for the crab provides for the algal host some advantages in competition with their epiphytes, filamentous algae that are eaten by the crab. In the other paper [70], the authors studied mutualistic relationships between a crustose alga *Ralfsia verrucosa* and an intertidal limpet *Patella longicosta*; the latter species protects the alga from fouling with a competing epiphyte, the *Ulva.* Thus, the mutualism between an alga and an animal can determine the result of competition for space between different algae.

COMPETITION FOR LIGHT

Light is a first priority resource, inevitable for life activities of all photosynthesizing organisms. The role of the light factor in the depth distribution of algae and the development of marine phytocenoses is difficult to be overestimated.

The competition for light in macroalgae is performed via the mechanism of consumption. The greatest rate of light consumption, the optimum utilization of the latter, and adaptation to a particular light regime provide in this case competitive advantages for one of the species [21]. Light consumption is often accompanied by such interferential mechanisms, as overgrowth and shading. For example, dense mats of fast-growing ephemeral algae (often blue-green algae) developing during algal blooms over the indigenous community can reduce the illumination significantly resulting in suppression and displacement of some algal species and even in the death of the initial community [17, 84, 104].

Large brown algae, victorious in the competition for space, develop dense thickets intercepting up to 90% of incident light and shading understory algae, thus entirely displacing light-requiring plants from the benthic community [32, 60, 88, 107]. The intensity of the competition for light in dense thickets can be reduced under strong wave movements of water, waving thalluses of thicket-forming species and, thus, favoring the penetration of light spots through the thickets [107].

When the light is in short supply, the competitiveness of a species is determined primarily by their ability to uptake and utilize efficiently the energy of absorbed light for growth and reproductive processes. In competition for light, if the latter were in short supply, more shade-resistant plants would be victorious. The shade resistance is determined, first of all, by genetic potential of the plant and its capability to realize this potential in the course of the life cycle via ontogenetic (physiological) adaptation [7].

In relation to their capability to live under different light regimes, higher terrestrial plants are divided into light-requiring, light-resistant, shade-resistant, and shade-requiring [9]. Long-term studies of ontogenetic adaptations of marine algae to light showed that almost all macrophytous algae of temperate and tropical latitudes are light-resistant or shade-resistant plants and may inhabit under illumination of 90 to 1% of photosynthetic active radiation coming onto the water surface (PAR_s) [6]. Marine algae that we have studied showed three major mechanisms of adaptation to a shortage in light: maximization of light uptake, rationalization of the utilization of absorbed light, and economization of a photosynthetic product [6–8]. Each of these mechanisms comprises several adaptation responses. Different algal species differ from each other in both a genetically inherited set of these responses and light ranges suitable for their realization. The most glowing example of the adaptive response for light shortage is accumulation of chlorophylls under reduced illumination in two species of green algae, *Enteromorpha linza* and *Ulva fenestrata* (see [4]). This response maximizes light uptake, mostly in the wave ranges of blue and red light. In *E. linza* it is initiated when illumination falls down to approximately 70% of PAR_s but is not revealed if the illumination falls down to 10% of PAR_s and beyond. In *U. fenestrata* the response appears when illumination falls down to approximately 50% of PAR_s and is not revealed at 2% of PAR_s and beyond. The concentrations of pigments in well-illuminated and extremely shadowed specimens of *E. linza* and *U. fenestrata* differ approximately 3-fold and 5-fold respectively. This example demonstrates that algae are species specific in their photoadaptive responses. Most macroalgae could adapt to very faint light, although the competition for light would, in all likelihood, be won by plants, which are capable, via adaptation responses, for fast and comprehensive adaptation to faint light, i.e., for maximum uptake of incident light and efficient utilization of the latter. In the latter example, at illumination lower than 10% of PAR_s, *Ulva* would obviously be a winner in the competition for light and, therefore, also for substrate (space), whereas *Enteromorpha* that have advantages against *Ulva fenestrata* under bright light might become a winner in competition for a substrate under these conditions.

In the competition for light, algae also use the mechanism of chemical (allelopathic) influence. Owing to the allelopathy, algae inhibit photosynthesis of the competitor and, therefore, can occupy the dominating position. For example, Varfolomeeva with coauthors [2] have mentioned the negative effects of metabolites of *Ahnfeltia* on photosynthetic function in *Chaetomorpha limum.* Other scientists have also found that metabolites of the green alga *C. taxifolia*, released into the water reduce significantly the primary production in the brown alga *Cystoseira barbata* f. *auranta*, but do not affect the red alga *Gracilaria bursa-pastoris*, which, in the opinion of the authors, demonstrates the species specific pattern of the effects of metabolites [39].

The victory in the competition for light becomes a background for the victory over competitors in competition for a substrate and space. The winner displaces its competitor from the substrate and space using the mechanisms of overgrowth and retention of resources.

COMPETITION FOR BIOGENS

Another first priority resource of the sea, for which the algae are competing, is water-dissolved nutrients containing such biogenic elements as nitrogen and phosphorus. Like it is in the competition for light, the major mechanism of interactions between algae is the consumption of the resource. The capability of some algal species to uptake nutrients more rapidly and to utilize them more efficiently, under conditions when these resources are in short supply in the environment, would evidently provide them the victory in competition for the resource and domination in phytocenosis.

In the competition for biogens, only allelopathy could play a significant role. The capability of some algae to inhibit the uptake of nutrients by their competitors [3] provides them certain advantages in the competition for resources.

Such environmental conditions are of great importance for competitors as the diversity of nutrient sources, their physico-chemical properties and availability for plants, as well as such characteristics of the plants, as uptake of different substances and capability to accumulate nitrogen and phosphorus for future use. All algae uptake nutrients from the water column, however, some species having well-developed rhizoids penetrating into the substrate are able to obtain nutrients directly from bottom sediments. The presence of such an alternative source of biogenic elements should improve the competitive abilities of these algae [21].

The availability of water-dissolved biogenic elements depends on their physico-chemical form and concentration in the environment, on the rate of their delivery to the thallus (wave effects, currents), and also from the morphology of algae and the physiological procedures of nutrient fixation. For instance, nitrogen could remain in the sea in either inorganic (ammonium salts, nitrates, nitrites) or organic (urea, amino acids, pyrimidines, proteins) forms. The inorganic form of nitrogen is more easily available for algae than the organic one. However, certain species show a high degree of organotrophy, i.e., they uptake and utilize water-dissolved organic substances (DOS) rich in nitrogen. Algae are known that grow well enough on both urea and inorganic compounds of nitrogen; these are *Codium fragile* and *E. linza.* For other species, for example *Pterocladia capillacea* and *Ulva fasciata*, organic nitrogen compounds remain more important sources of this element, especially in systems, where inorganic nitrogen compounds show small concentrations [53, 57]. It is shown that in periods when inorganic nitrogen in the environment is in short supply, the growth of *Gracilaria tikvahiae* is supported at the expense of uptake of organic nitrogen compounds coming into the sea with wastewaters [13, 50].

The inorganic forms of nutrients also demonstrate a different degree of availability for plants. It is known that algae uptake nitrogen easier and faster in the form of ammonium salts: they are followed by nitrates, and nitrites occupy only the third place [34]. However, some species of algae (*C. fragile, Goniotrichium elegans*, and *Nemalion multifidum*) still prefer nitrates [46, 49]. Macroalgae that are capable of uptaking different forms of nitrogen would obviously have advantages in the competition. In this case, the competitive abilities of algae in the competition for nitrogen would be determined by uptake rates for different nutrients.

The uptake kinetics of biogenic elements by algae depends on the concentrations of biogenic elements in the environment, which differ significantly in both space and time. Under conditions of low concentrations of nitrogen compounds, the species characterized with a small constant of semisaturation by nitrogen compounds would become competitive. For example, *G. tikvahiae* can uptake nitrogen compounds at rather small concentrations of these substances in seawater (the constants of semi-saturation for NO_3 and NH_4 equal 0.4 and 0.2 μm, respectively [33], thus leaving their competitors (filamentous and lamellate green algae) behind in terms of uptake rate, as the latter require greater concentrations of nitrogen in the environment [101].

Turbulence is one of the factors determining the availability of nutrients. The speed of water movement (exchange) in the layer boundary with thallus surfaces depends on both flow velocity and thallus morphology. For example, the brown alga *Macrocystis* has a morphologically complex thallus, which enhances water turbulence along the thallus surface and increases the rate of nutrient uptake by the plants [21]. Exactly the converse example is demonstrated by *Ulva* and *Enteromorpha* having a simple morphology and lamellate or filamentous thalluses.

The mode of how nutrients arrive to the plant can also determine the winner in the competition. Fujita [47] showed, in the example of relationships between *Gracilaria* and *Enteromorpha*, that under continuously great concentrations of nitrogen and phosphorus compounds in water, when the nutrients are always available, *Enteromorpha* is victorious in the competition over *Gracilaria*, due to a high rate of biogen uptake and fast growth. On the contrary, when biogenic elements came to the plants only in some periods and intervals between consecutive arrivals of the biogens were significant (14 days), *Gracilaria* attained advantages in the competition, as it could accumulate the nutrients for future use and grow under conditions of almost total absence of nutrients in the environment (the entire 14 days between the consecutive arrivals of nutrients) [48, 80]. The brown alga *L. religiosa* is able to accumulate nitrogen in amounts of up to 2.1% of its wet weight and to use it for growth for up to 2 months, if the concentrations of biogens in the environment fall down [23]. Thus, the mode of nutrient intake can provide algae some advantages in competition.

So, as it can be seen from the above discussed information, the competition between algae for nutrients in the sea is a common, but extremely complicated process. It is very difficult to predict the winner in the competition for nutrients, as the victory is determined by numerous external (natural) and internal (population, morphological, anatomical, physiological, and biochemical) factors. On the other hand, the available data provide evidence that the competition for nutrients never results in direct displacement of a competitor from the community; it can only weaken the latter, allowing the winner to overgrow, shade, or poison (negative allelopathic effects) the competitor and, finally, to force it out of the community.

COMPETITION DURING THE CULTIVATION OF ALGAE

The cultivation of such macroalgae as *Gracilaria, Chondrus, Laminaria, Eucheuma*, and *Kappaphycus* is common practice in many countries; however, the studies on competitive relationships in artificial algal communities are confined to a few papers, mostly dealing with competition with the epiphytes [20, 42–45, 101].

However, the competition of a cultivated species with weed algae at both plantation and intensive pond cultivation is of particular significance as the size and quality of the production depend on competitive abilities of all the species. Rapid development of associated algae (weeds) is one of the major problems in the cultivation of algae [44, 63]. In Chile the weediness of cultivated *Gracilaria* with green epiphytic algae sometimes reaches 60% of the dry weight of the *Gracilaria* [20]. Epiphytism represents a serious problem also in Taiwan, in cultivation ponds with stagnant water [28, 91]. For example, it has been found that, during the cultivation of *Gracilaria*, both the walls of the pond and cultivated species are fouling with fast-growing filamentous or lamellate algae *Cladophora pellucida, U. lactuca,* and *Enteromorpha compressa* (see [43, 44]).

Epiphytes decrease not only illumination [38], but also the intake the nutrients by the cultivated species [90]. They enlarge the total weight of the latter, which results in detachment of the plant from the substrate and, finally, they produce allelopathic substances inhibiting the growth of host algae [45, 53, 101]. Svirski with coauthors [101] noted the discoloration of growing tips of branches, inhibition of growth (1.5–2 times) and increased respiration in *Gracilaria* that grew in biculture with *Ulva.* They explained this effect primarily by influence of exometabolites produces by thalluses of *Ulva.* Friedlander with coauthors [53], who also performed some experiments, also revealed that the green epiphytic alga *U. lactuca* inhibits significantly the growth in the red marine alga *Gracilaria conferta*, probably by means of metabolites.

To avoid financial losses during the cultivation of algae, as a result of weediness with associated species and epiphytes, different methods of weed control are used. For example, in the intensive cultivation of algae, the development of a monodominant community and victory for the cultivated species in the competition are ensured via selection of environmental conditions (water, temperature, water exchange pattern) that are the optimum for this species. Moreover, physiological peculiarities of the cultivated algae are used to enhance their competitive abilities. For example, a temporary artificial shading (5–10 days) causes the death of less shade-resistant epiphytic algae, thus cleaning the thalluses of cultivated *Gracilaria.* Sometimes, prior to introduction into the culture, the *Gracilaria* is placed for several days into a medium with great concentration of biogenic elements; then it is cultivated in water with a small concentration of nutrients [52]. The shortage in biogens negatively affects the growth rate of associated algae, but is not reflected on the growth of *Gracilaria*, as the latter species is able to accumulate biogenic elements for future use.

The stocking density of algae could be increased to increase the competitiveness of the cultivated species in competition for the substrate and space [52]; thus limiting attachment of spores and growth of weeds. However, such a technique results in increasing intraspecific competition and, as a consequence, reduces the growth rate and production of the cultivated species. Moreover, to weaken the associated species of algae, methods are used such as chemical treatment (herbicides), mechanical removal of weeds, and cultivation of phytophages that selectively graze only the associated species of algae. The latter method is the most widely used in modern practice. For example, in Hawaii the fish *Poecilia* is cultivated to remove epiphytes in *Gracilaria* ponds (see [91]). The crustaceans *Gammarus laurencianus* and *Idotea baltica* selectively graze epiphytic algae *Enteromorpha* and *Ectocarpus* growing on the thalluses of *Chondrus crispus*, doing no harm to the red algae [97].

CONCLUSIONS

Our concepts on competitive relationships of macrophytous algae in nature and in culture, developed as results of the analysis of literature information and our original data on the physiology of marine algae are as follows:

(1) Competitive relationships are of crucial importance in the succession of marine communities.

(2) Competitive relationships are possible only among neighbor species capable of exchanging signals.

(3) The essence of competition among algae is competition for resources, i.e., substrate, space, light, and nutrients.

(4) The mechanisms of competition are as follows: overgrowth (displacing of competitor from a substrate or space); occupation of a free substrate or space; interception of light (shading) or nutrients (intensive uptake); and allelopathic effects (inhibition of life activities of competitor by metabolites).

(5) Long-term competition results in the development of algal communities dominated by one, two, or a few species of algae, but comprising much more species.

(6) The winners in the competition for resources dominate in the size of the occupied substrate or space and, often, also in biomass.

(7) The losers are either displaced from the community or survive in a suppressed condition.

(8) In competition for light, the algae become victorious, which are capable, via adaptation responses, to adapt, rapidly and comprehensively, to faint light. The victory in the competition for light appears to be the

background for victory over competitors in the competition for a substrate and space.

(9) Competition for nutrients does not result in direct displacement of a competitor from a community; it can only weaken the latter, allowing the winner to overgrow, shade, or poison (negative allelopathic effects) the competitor and, finally, to force it out of the community.

(10) Changes in environmental conditions can faithfully affect the competitiveness of a species and cause a structural reorganization of the entire community.

(11) On artificial cultivation of algae, people develop monodominant communities, or enhance artificially the competitiveness of cultivated species via selection of appropriate environmental conditions, or just artificially remove the competitors.

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