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Marine Plants in Coral Reef Ecosystems of Southeast Asia

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I. CORAL REEF ECOSYSTEMS

The coral reef ecosystem is a collection of diverse species that interact with each other and with the physical environment. The latitudinal distribution of coral reef ecosystems in the oceans (geographical distribution) is determined by the seawater temperature, which influences the reproduction and growth of hermatypic corals – the main component of the ecosystem. As so, coral reefs only occupy the tropical and subtropical zones. The vertical distribution (into depth) is limited by light. Sun light is the main energy source for this ecosystem, which is produced through photosynthesis of symbiotic microalgae – zooxanthellae living in corals, macroalgae, seagrasses and phytoplankton. Therefore, hermatypic corals are able to win in competitive struggle for the substrata and resources with other autotrophic organisms even under light about 1% of the surface photosynthetically active radiation (PAR₀). The hard substratum for the majority of recent coral reefs is limestone basis, which is formed from remnants of historical reefs (fossil) appeared on the earth in the middle Triassic period (225–200 million years ago). The other hard substrata colonized by hermatypic corals are underwater rocks and stones, which will further form coral reefs. Moreover, coral reef can also be built on the basis of artificial substrata (e.g. oil towers or underwater constructions of mariculture farms in tropical regions of the oceans) (Titlyanov, Titlyanova, 2012a). The main difference between coral reefs and other underwater ecosystems is the formation of hard substratum, which is based on hermatypic coral colonies dying off and subsequent colonization by animals including corals and seaweeds. Coral reefs are the most diverse ecosystem and provide the largest primary production among all the underwater ecosystems on the coastal shelf. They occupy less than 0.1% of the world's ocean surface, but provide habitat and refuge for 25% of all marine organisms, including fish, mollusks, worms, crustaceans, echinoderms, sponges, tunicates, etc. Competition for resources such as food, space and sunlight are the primary determining

factors for the organisms' abundance and diversity on a reef.

Coral reefs have calcium carbonate based structures that are constructed by communities of reef building stony corals or scleractinian corals. Coral reefs are generally divided into four main types (Littler, Littler, 2003): (1) fringing reef is the most common type that develops adjacent and parallel to the shoreline; (2) barrier reef is an actively growing type that also occurs parallel to the coastline but relatively further away from the shore; (3) atoll is a ring of calcareous reefs that is often interspersed with low sandy isles and a relatively shallow, sheltered lagoon; (4) patch reef occurs as small mounds or cup-shaped structures growing on hard substrates that cast into the lagoons of barrier reefs or atolls (Figs 1–4).

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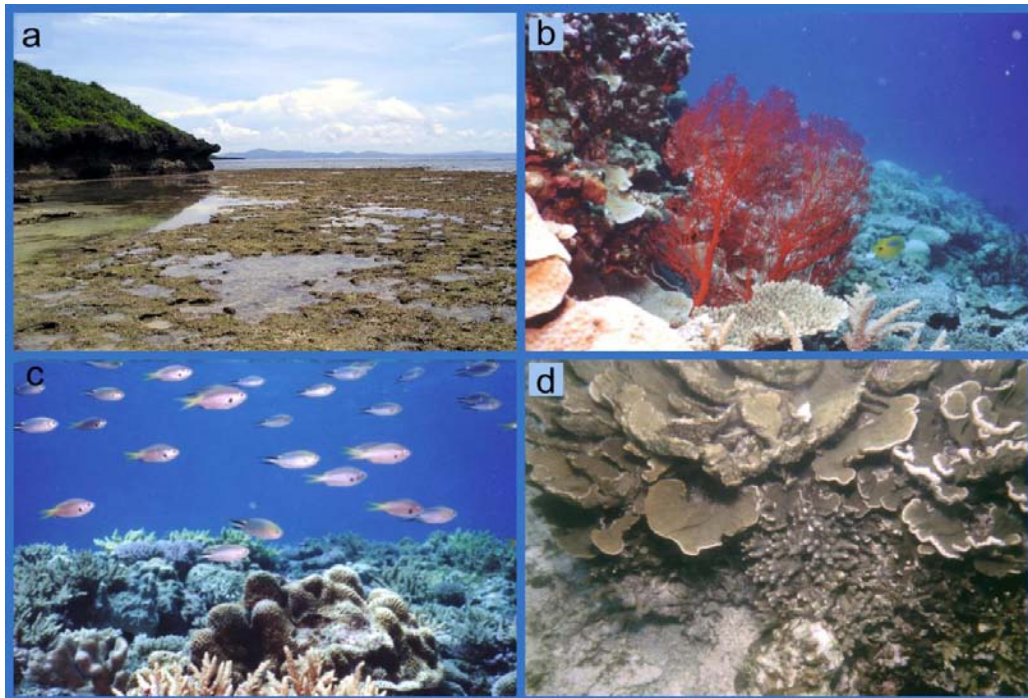


Fig. 1: Fringing reef located along the East coast of the island Sesoko (Okinawa Prefecture, Japan). Sesoko Island ($26^{\circ}39'N$, $127^{\circ}51'E$) is situated not far from the coast of Motobu Peninsula of Okinawa Island and it should seem similar to large number of islands of the Ryukyu Archipelago, June 1995: a – coral reef at low tide; b – coral and calcareous algal communities on the reef slope; c – coral and algal communities on reef flat; d – coral community in lagoon.

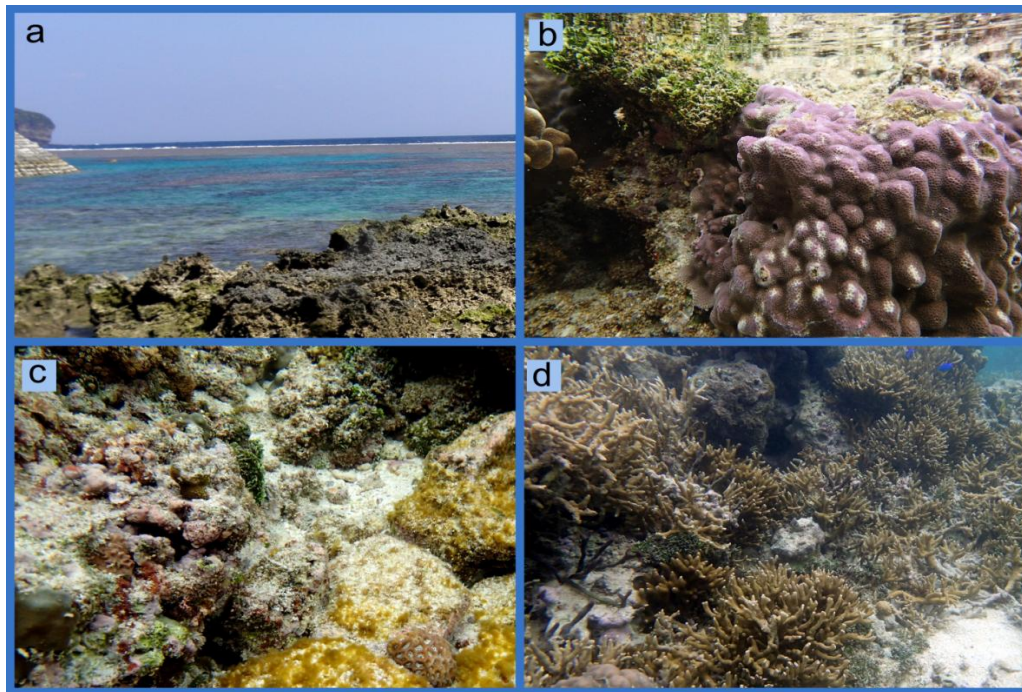


Fig. 2: Fringing reef located along the southern coast of Yonaguni Island ($24^{\circ}27'N$, $122^{\circ}57'E$), which is situated at the tropical northern periphery of the Indo-Pacific Ocean. The island is one of the Yaeyama Islands and the last southwest island in the Ryukyu Archipelago chain (Okinawa Prefecture, Japan), March 2013: a – coral reef in Higawa Bay (in the foreground fossil reef; in the background of live coral reef at high tide); b – coral and algal communities on reef crest; c – coral and algal communities on reef flat, d – community of branched hermatypic corals in lagoon.

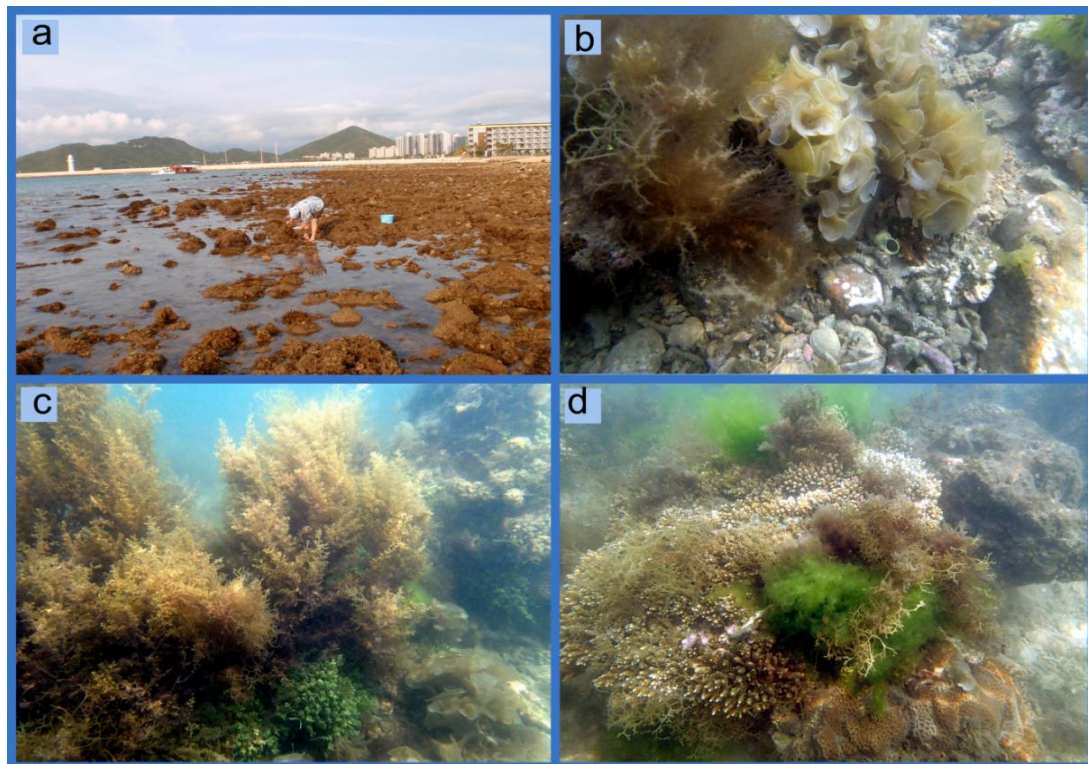


Fig. 3: Heavily damaged coral reef located along the southern coast of Hainan Island, China (Luhuitou Peninsula, 18°13'N, 109°34'E), March 2012: a – fringing coral reef at low tide; b – algal community in the middle intertidal zone; c – algal community in the low intertidal zone; d – coral-algal community in the upper subtidal zone.

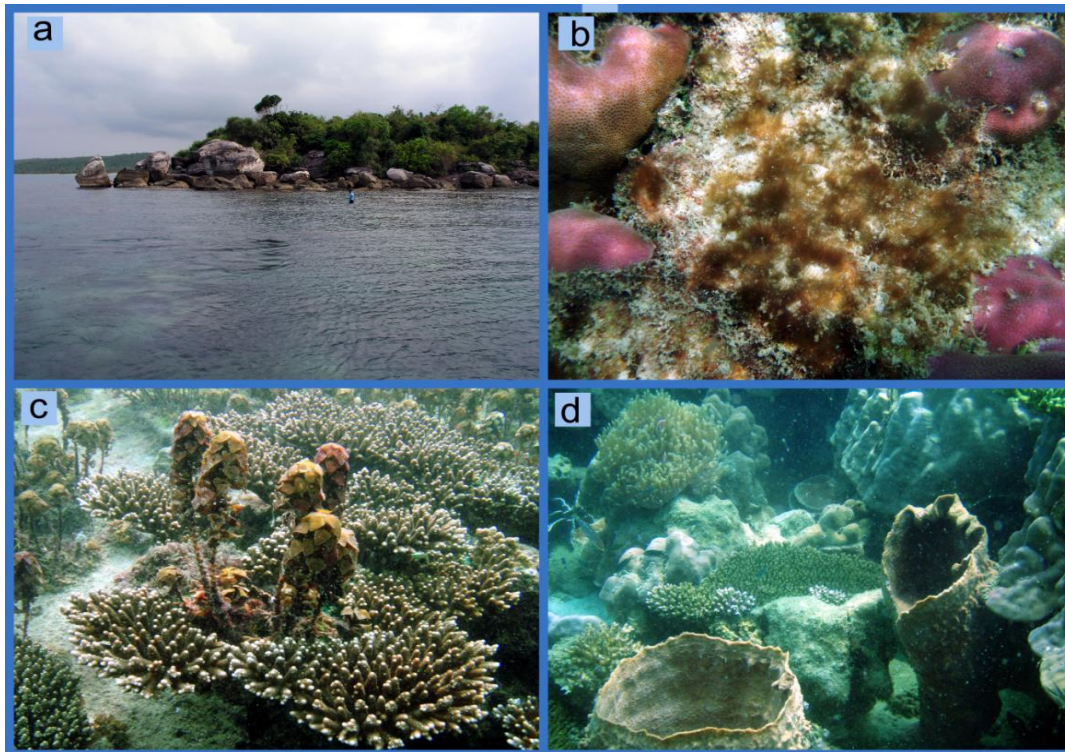


Fig. 4: Coral reef along the coast of Thom Island (9°59'N, 104°01'E), one of group of the An Thoi Islands and the Phu Quoc Archipelago (Vietnam) in the Gulf of Thailand, March 2009: a – reef at high tide; b – coral-algal community in the intertidal zone; c, d – communities in the upper subtidal zone.

The first encountered zone of reefs is on the beach or rocky intertidal. It occurs adjacent and parallel to the intertidal shoreline, consisting of a shallow reef platform followed by a lagoon. The depth of the lagoon varies from less than a meter to 10–30 meters. The lagoon with a sediment bottom is protected from intense wave actions by the offshore barrier reef. Channels that connect the lagoons with the open waters provide fresh and cold water for the lagoons. The channels enter lagoons via reef flat, a broad, shallow and flat part of a reef, which is protected from heavy surf by reef crest. Reef crest is the top of the reef slope, which descends as deep as 5–30 meters (Littler, Littler, 2003).

Coral reefs are less resistant to natural and anthropogenic catastrophes, which disturb Previously established balance for primary production between producers and consumers, predators and tolls, and symbionts and their hosts. This notion indicates that fluctuations in the abundance of one species can drastically alter the diversity and abundances of the others. Hurricanes and other large storm events can be the stimulus for such alterations, but anthropological forces are actually more common for influencing the ecosystem. For example, overfishing of herbivorous fish often results in increased growth of algae and seagrasses. The disturbance of symbiotic interactions between corals and algae-zooxanthellae leads to coral bleaching and their subsequent mortality. Dead coral colonies are rapidly colonized with algae, which causes the biodiversity of coral reef shift to plant reef with the predominance of macrophytes in the ecosystem. The damaged coral reef may completely recover, or recover to a different state, which is dominated by other species and forms of corals, or turn into “plant” reef. After decades, this “plant” reef can be destroyed by waves due to the mortality of hermatypic corals and the loss of the main and unique property to build carbonate calcium for reef formation.

II. MARINE PLANTS OF CORAL REEFS

All the marine plants are autotrophic organisms (in independence of their systematic status). They contain chlorophyll a and execute photosynthetic process, which produces organic matter and oxygen by absorbing sunlight, carbon dioxide and water. Marine plants belong to three groups of organisms: microalgae (blue-green, diatoms, dinoflagellates, zooxanthellae), macroalgae (green, brown and red) and higher plants or seagrasses. The latter two groups are

- a) *Identifying the characteristics of representatives from different Phyla*
 - i. *Phylum Tracheophyta, order Alismatales (sea-grasses)*

Seagrasses (marine flowering plants), inhabiting sandy and silty-sandy areas of the bottom, are one of the main components of reef ecosystem. Some of them

are able to attach to the hard base of the reef (e.g. *Thalassodendron ciliatum*). Seagrasses can form extensive beds or meadows in shallow sheltered coastal waters. Similar to the terrestrial higher plants, seagrasses have roots, stems, leaves and flowers (Fig. 5a).



Fig. 5: Identifying the characteristics of representatives from different phyla: a – the seagrass *Cymodocea serrulata* (R. Brown) Ascherson and Magnus (Phylum Tracheophyta, Order Alismatales), Phu Quoc Island (Vietnam) in the Gulf of Thailand, April 2009; b – *Ulva linza* Linnaeus (Phylum Chlorophyta, Order Ulvales), plants growing on the nylon cord, Hainan Island, Luhuitou, April 2012; c – *Sargassum polycystum* C. Agardh (Phylum Ochrophyta, Order Fucales), in habitat, the upper subtidal zone, Hainan Island, Luhuitou, April 2012. Insets: details showing air bladders and phylloids; d – *Dichotomaria marginata* (J. Ellis and Solander) Lamarck (Phylum Rhodophyta, Order Nemaliales), in habitat, the upper subtidal zone, Hainan Island, Luhuitou, April 2012; e – community of Cyanobacteria in the low intertidal zone (Sanya Bay, Hainan Island). Insets: 1 – *Planktothrix agardhii* (Gomont) Anagnostidis and Komárek; 2 – *Lyngbya majuscula* Harvey ex Gomont (Phylum Cyanobacteria, Order Oscillatoriales), the upper subtidal zone, Hainan Island, Luhuitou, April 2012; f – the diatom alga *Licmophora* sp. (Phylum Bacillariophyta, Order Licmophorales) – epiphytic on the red alga *Amphiroa foliacea*. Sanya Bay, March 2012.

ii. *Phylum Chlorophyta (green algae)*

The green algae (Fig. 5b) are named for their green chloroplasts. They are characterized by the predominance of the green pigments (chlorophylls *a* and *b*), which mask carotenes, xanthophylls (such as lutein, zeaxanthin and siphonoxanthin) and other pigments. These photosynthetic pigments are located in chloroplast's thylakoids that are grouped into stacks. The green algae's cell wall is composed of a layer of pectin and an inner cellulose layer. Starch is their storage nutrient. Most green algae reproduce both sexually and asexually. The reproduction involves the formation of flagellated spores and the production of non-flagellated spores to a less degree. Alternation of generations, where the algae alternate between gametophyte and sporophyte, is common in the multicellular green algae. Vegetative reproduction through the fragmentation of thalli is also common, especially in filamentous forms (Dawes, 1998).

iii. *Phylum Ochrophyta, Class Phaeophyceae (brown algae)*

The brown algae (Fig. 5c) contain large amounts of carotenoids in their plastids, which are brown and golden pigments that give the plants their characteristic color. The most important carotenoid in the phaeophytes is fucoxanthin. Besides, their plastids also contain other pigments such as chlorophylls *a* and *c*. The chloroplasts have thylakoids and 3 of which are grouped into a stack. Their cell walls are mainly composed of cellulose and alginic acid. Laminarin and mannitol are the main forms of nutrient storage of phaeophytes. Laminarin is a polymer of glucose and mannitol is a six-carbon sugar alcohol. The life cycles of brown algae vary greatly. They have both sexual and asexual reproduction. Vegetative propagation can also happen through the fragmentation of thalli. Additionally, there is a formation of special reproductive branches known as propagula present in species of *Sphacelaria* (Dawes, 1998).

iv. *Phylum Rhodophyta (red algae)*

The red algae (Fig. 5d) are characterized by dominant pigments phycoerythrin and phycocyanin, which give this group their red coloration and mask the color of the chlorophylls *a* and *c*. Other pigments found in their cells are carotenes and xanthophylls (lutein, zeaxanthin, etc.). Chloroplasts of the red algae have thylakoids that occur individually (not in stacks as in the green and brown algae). Their cell wall contains less cellulose and more of gelatinous or amorphous sulfated galactan polymers, such as agar, carrageenan, etc. Their storage nutrient is floridean starch. The red algae are reproduced in various ways. Their reproduction methods and life histories are the most complicated which include both sexual and asexual modes. The majority of advanced genera have one gamete-producing phase (sexual phase) and two spore-

producing phases (asexual phase). Vegetative multiplication also occurs in the Phyla (Dawes, 1998; Abbott, 1999; Lee, 2008).

v. *Phylum Cyanobacteria (the blue-green algae)*

Blue-green algae, known as Cyanobacteria, are named for the blue-green pigment phycocyanin, which gives them the blue-green appearance along with chlorophyll *a*, carotenoids and phycobiliprotein (Fig. 5e). They are oxygenic photosynthesizing organisms and have unicellular, colonial or filamentous-like forms: the gelatinous sheath of individual cells either remain distinct or fuse into gelatinous matrix; the colonial forms are flat, spherical, elongated, or amorphous; the filaments consist of one or more chains of cells, and each chain is termed as trichome. The blue-green algae have no organelles for locomotion. However, some genera, such as *Oscillatoria*, can move forward, backward or oscillate. The reproduction of Cyanobacteria is vegetative and asexual. Unicellular cyanobacteria divide and reproduce by fusion. Some colonial and filamentous species produce specialized vegetative fragments called hormogonia, which develop into new filaments; other filamentous members form heterocysts, which are larger than vegetative cells. Some genera produce endospores and exospores by internal division of the protoplast. Resting spores called akinetes are also produced by certain species in response to unfavorable conditions (Lee, 2008).

vi. *Phylum Bacillariophyta, Class Fragilariophyceae*

The diatoms are one of the largest and important groups of freshwater or marine organisms. They are oxygenic photosynthetic organisms. Most benthic diatom algae are delicate unicellular organisms or multi-shaped colonies. Many species of diatoms stay connected after cell division and form colonies or long chains in the shape of filaments or ribbons. Sometimes only the tips are connected, so they form a zigzag pattern, or in the shape of stars and fans (Fig. 5f). Their chloroplasts contain pigments such as chlorophylls *a* and *c*, beta-carotene, fucoxanthin, diatoxanthin and diadinoxanthin. Diatom cells are enclosed within a siliceous cell wall (also called frustule) that is coated with a layer of organic material. Diatoms can be divided into two main orders: centric diatoms (Centrales), which are generally radially symmetrical, and pennate diatoms (members of the Pennales), which are bilaterally symmetrical. They reproduce both sexually and asexually (vegetative cell division). Diatoms are the major components of plankton, while many of them are benthic plants.

vii. *Phylum Miozoa, Class Dinophyceae*

Zooxanthellae, usually called symbiotic microalgae, mainly live in the endoderm of tropical marine cnidarians (e.g. corals, sea anemones and jellyfish), nudibranchs, sponges, flatworms, hydroids and mollusks (e.g. the giant clam *Tridacna*, some

species of radiolarians and foraminiferans). Generally, zooxanthellae are intracellular symbionts living within a host cell and staying in coccoid (non-motile) stages (6–13 μm in diameter) with thin cell wall (Fig. 6). They are reproduced inside of host cells and transferred from

parents to progenies by sexual or asexual (planulae) products. Distant in systematic state hosts are harbored by various species or even genera of symbionts. Various species of reef-building corals are usually harbored by *Symbiodinium microadriaticum*.

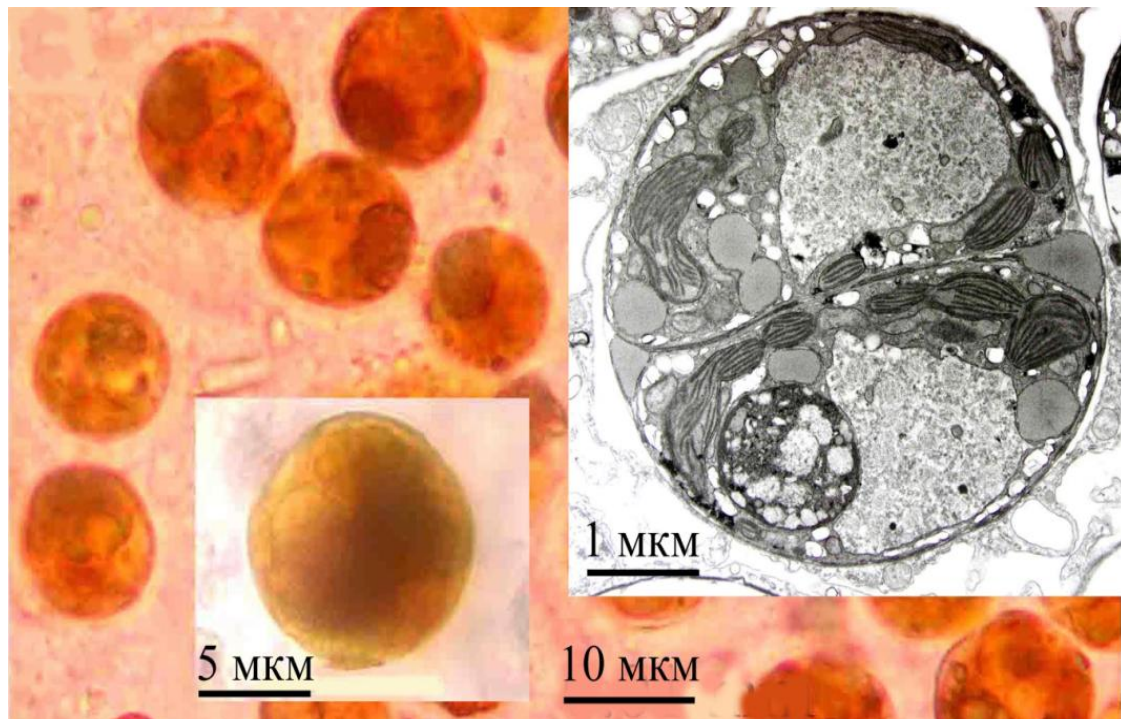


Fig. 6: Endosymbiotic algae-zooxanthellae in the tissue of the scleractinian coral *Porites lutea* (Titlyanov, Titlyanova, 2012a). Insert: dividing zooxanthella under an electronic microscope (photographed by Junzo Tsukahara).

b) Life forms of benthic marine plants

Marine plants inhabiting coral reefs live in different life forms. For example, epilithic algae inhabit hard substrates, anchored to stones, mollusk shells and dead coral skeletons; endolithic algae settle within hard substrates, e.g., in the skeletons of alive and dead coral colonies, in mollusk or other animals' shells, and in the carbonate base of coral reefs (Fig. 7).





Fig. 7: Life forms of benthic marine plants: a – community of epilithic algae (*Asparagopsis taxiformis*, *Padina* sp., *Sargassum* sp. et al.), Cape Bang La (Vietnam), April 2009; b – the green *Halimeda simulans* growing on sandy bottom, Yonaguni Island (Japan), March 2013. Inset: habit, showing bulbous rhizoidal mass binding sand particles; c – fouling algae (crust red algae and the green alga *Ulva papenfussii* on artificial substratum, a car tire, Mot Island (Vietnam), lobster farm, 0.7 m deep, 9 April 2006; d – *Pseudocladophora conchopheria*, overgrowing sea snail, the marine gastropod mollusk *Turbo* (*Lunella*) *coreensis* Récluz, 1853, Amakusa Island (Japan), April 2013. Inset: habit; e – *Ceramium cimbricum*, epiphytic on the red alga *Grateloupia filicina*. Sanya Bay, April 2012; f – the endolithic green alga *Ostreobium quekettii*, living in the skeleton of the scleractinian coral *Porites lutea* (Titlyanov, Titlyanova, 2012); g – two types of blue-green algal films were found on the surface of the holes of dead coral block in the splash zone. *Oscillatoria limosa* (inset) was dominant (Titlyanov et al., 2014); h – the endophytic green alga *Ulvella leptochaete*, living under cuticle of the red alga *Hypnea spinella*. Sanya Bay, Hainan Island, April 2009.

Endolithic algae have two well-defined life forms: colonizing existing cavities within the substrate, and actively penetrating into hard substrates (Fig. 7g, h).

Marine plants can live as symbionts with animals. Among the plants we mentioned above, for example, there are unicellular algae, zooxanthellae, intracellular symbionts of coral endoderm (endosymbionts) (Fig. 6), and symbiotic green and blue-green algae inhabiting skeletons of alive scleractinian corals (ectosymbionts) (Fig. 7f).

Epiphytic algae are attached to thalli of large macroalgae or leaves of seagrasses (Fig. 7 e); epibionts live on hard or soft body surface of animals. Multicellular and unicellular algae can live in intercellular spaces of other plants (endophytes) or be parasitic on marine animals or other species of algae (Fig. 7 h).

c) *The main algal communities on coral reefs*

In reef ecosystem, both short-lived and long-lived algal communities are formed depending on environmental conditions and competitive abilities. As a rule, the short-lived algal communities are fast growing. These communities are commonly formed on newly-formed substrate after natural or anthropogenic catastrophes. It has been shown that the short-lived communities are mostly developed under dramatic changes of temperature, light intensity, salinity, seasons, and tides, especially in the intertidal zones (Fig. 8a). The short-lived communities are mostly blue-green algae, diatoms, filamentous or membranous green algae. They often only consist of one or two algal species. The algal "bloom" is an example of short-lived algae formation on unhealthy coral reefs (Fig. 8b).



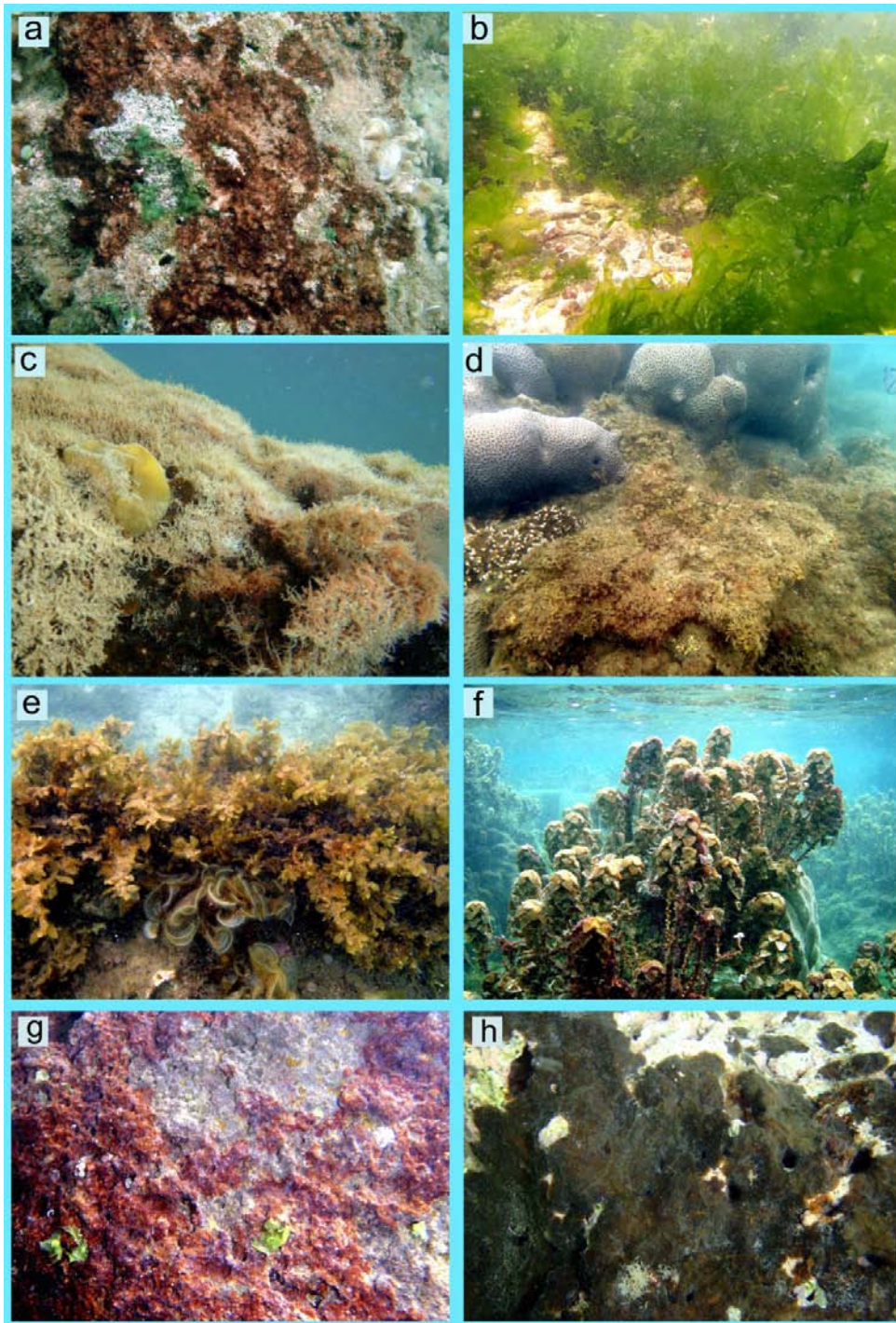


Fig. 8: The main algal communities on coral reefs: a – temporary community of *Cyanobacteria* in the low intertidal zone, Hainan Island, Luhuitou, April 2012; b – the algal “bloom” of green algae *Ulva* spp., Hainan Island, Luhuitou, March, 2012; c – dense algal turf community composed of dominant species such as *Acanthophora spicifera*, *Palisada papillosa*, *Tolypocladia glomerulata* in the low intertidal zone, Luhuitou, Hainan Island, April 2009; d – algal turf community (predominant species: *Hypnea pannosa*, *Spyridia filamentosa* overgrown with *Gayliella flaccida*) in the upper subtidal zone, Luhuitou, Hainan Island, March 2012; e – macroalgal community with upright foliose morphology (the bidominant community comprised of brown frondose algae, *Sargassum polycystum* and *S. sanyaense*), Hainan Island, Luhuitou, February 2012; f – monodominant community of the brown alga *Turbinaria decurrens* (Dam Trong Islet, south coast of Phu Quoc Island, Vietnam, March 2009; g – monodominant community of the red crust alga *Hildenbrandia rubra* in the upper to middle intertidal zone, Meixia, Hainan Island, March 2012; h – monodominant community of the brown alga *Neoralfsia expansa* in the middle intertidal zone, Luhuitou, Hainan Island, March 2012.

In the subtidal zone, the absence of sharp environmental changes promotes the formation of long-lived communities. In general, the macroalgal community in the subtidal zone includes multiple algal species characterized by several dominant ones. Algal composition and biomass of some species in such community change from season to season. Sometimes, the long-lived communities can also contain only one or two algal species when the conditions are favorable for them.

i. Algal Turf Community

Turf, turf-forming, or mat-forming algae occur in coastal waters worldwide, and they have unique importance for coral reefs. However, they are not considered as the most important group of free-living algae regarding the primary production and serving as food source for the herbivorous reef animals (Price, Scott, 1992). Turf algae represent a particular life form of algae, with characteristic biological structure and function. Taxonomically it is a diverse group containing organisms that represent various algal divisions. Members of these different divisions are commonly found on reefs and closely intermixed in multiple assemblages. The turf algae are densely growing, attached to the substratum at numerous points, and their erect branch systems arise from the prostrate axes. Some of the algae form filamentous, cushion-like tufts, bushy clumps, or tangled mats. The general morphological characteristics of turf algae are small size (to about 3 cm in height) at maturity, and slender branches. Juvenile or suppressed individuals of larger macroalgae frequently occur in algal turfs (Fig. 8c, d).

Turf-forming algal communities are resistant to wave actions and very often colonize rocky substrate where the turbidity is higher in the intertidal zone (Carpenter, 1986). Many turf algal species have creeping habit, which makes them well adapted to the intense grazing pressure in 15 coral reef ecosystems. They can regenerate from the remaining branches, creeping axes or basal parts after being destroyed by grazing.

ii. Macroalgal communities with upright foliose morphology

Upright macroalgal communities with foliose and fleshy morphology are widely distributed on coral reefs in the low intertidal and upper subtidal zones. These communities usually occupy stony substrata, carbonate base of coral reefs (Fig. 8e, f); some species of them grow on sandy bottom. They are distributed along the border between the low intertidal and upper subtidal zones, forming dense bed comprised of mono- or bidominant communities (e.g. *Sargassum* spp. densely overgrown by epiphytes such as *Chroodactylon ornatum*, *Erythrotrichia carnea*, *Acrochaetium robustum*, *A. microscopicum*, *Colaconema gracile*, *C. hypneae*, *Jania unguolata* f. *brevior*, *Gayliella mazoyeriae*,

Neosiphonia sphaerocarpa (Rh), *Kuetzingiella elachistaeformis*, *Sphacelaria novae-hollandiae*, *S. rigidula* (Ph) and *Ulva clathrata* (Ch).

iii. Communities of calcareous crust algae

These communities are distributed on hard substrates in the intertidal and upper subtidal zones. The red crust alga *Hildenbrandia rubra* and the brown crust alga *Neoralfsia expansa* are common on flat stones in the upper and middle intertidal zones (Fig. 8g, h).

d) Distribution of algae on coral reef and factors regulating their expansion

Both on coral reefs and in other ecosystems marine plants are distributed within the euphotic (epipelagial) zone or illuminated seawater column, where the light conditions allow photosynthetic organisms to complete their life cycles. The light condition in the shallow part of euphotic zone is different and mostly depends on the water transparency. In clean oceanic waters the euphotic zone can extend down to 200 – 250 m deep (Littler et al., 1986).

Light is one of the major factors limiting the expansion of algae into depths. Algae usually do not grow in depths, where the light intensity is smaller than 1% of PARS, i.e., approximately 10 – 15 $\mu\text{E}/(\text{m}^2 \text{ s})$ if measured at the noon of a sunny day (Titlyanov, 1999). However, red coralline algae of the genus *Lithothamnion* are widely distributed in deeper sites in subtropical areas, where the illumination level ranges within 0.05 – 0.1% of PARS (Molinier, 1960; Lang, 1974; Littler et al., 1986).

If interspecies competition is absent, almost all algae can survive with the light intensity ranging from 1 to 100% of PARS, despite some species are vulnerable to ultraviolet so that they cannot live in the intertidal area under the direct sunlight (Fong, Paul, 2011).

Unlike higher plants, marine algae can adapt to an extremely wide range of light intensity. The process of adaptation involves the initiation of certain mechanisms that is associated with numerous adaptive responses. For example, the mechanisms, such as maximization of light absorption, efficient utilization of absorbed light and saving consumption of nutrients, can help plants adapt to extremely low light level. Maximization of the light absorption will mainly lead to the accumulation of photosynthetic pigments. Efficient utilization of absorbed light can boost the quantum output of photosynthesis in shaded plants. Saving consumption of reserve and structural substances is achieved through slowing down the respiration and the excretion of assimilated substances (Titlyanov, 1999).

Depending on their physiological capabilities, marine plants can inhabit in three different ecological reef zones (Fig. 9). The first zone is located at the border between the sea and the land, which is supratidal fringe

or splash zone (Fig. 9a, b). Most of the time, this area is above water level and is only moistened by strong storms or extremely high tides. The marine plants in

supratidal area usually settle in shaded rocky crevices, small cavities (grottoes) on vertical walls, or under the rocky ledges.

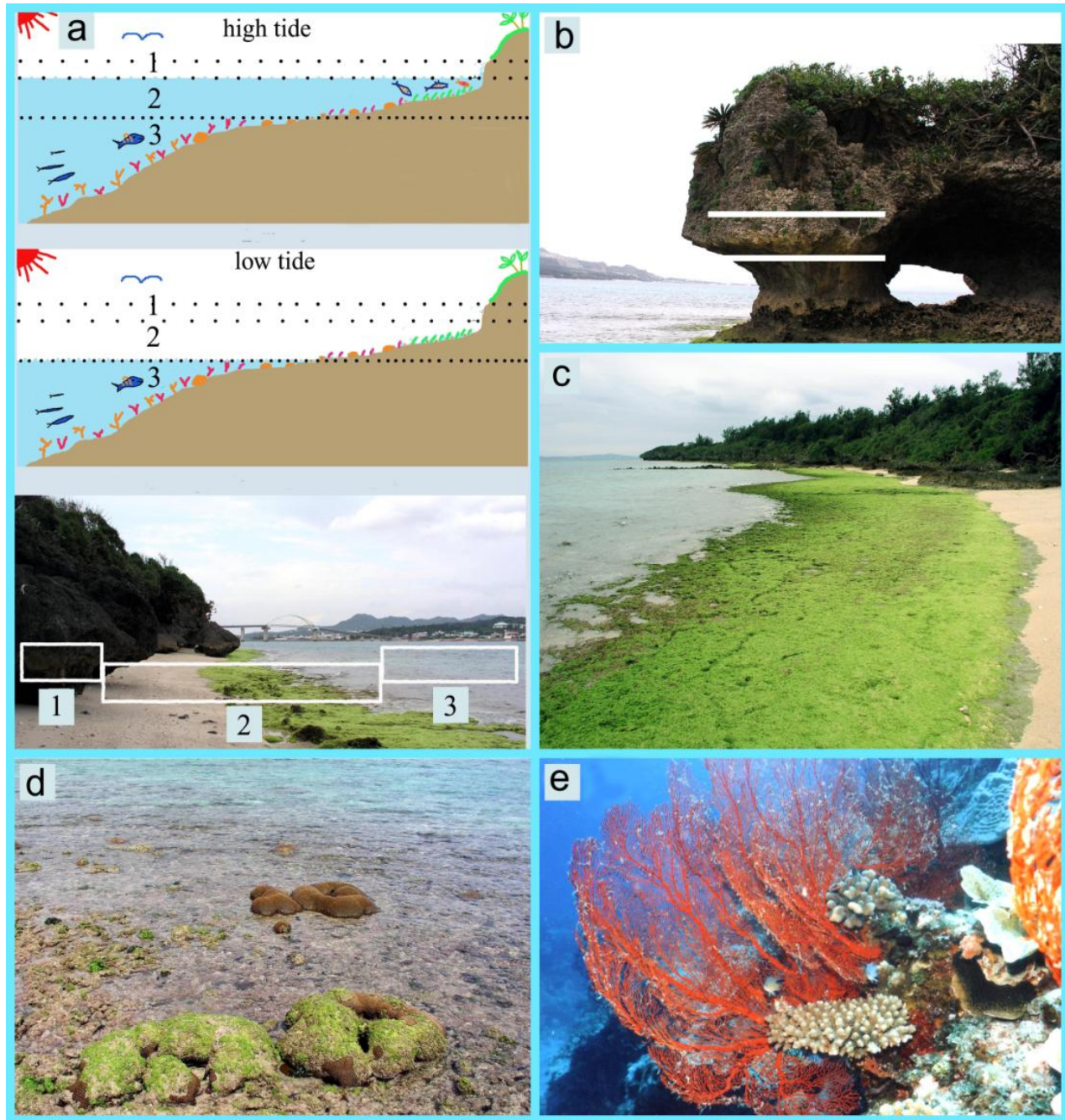


Fig. 9: Different ecological reef zones (coral reef of Sesoko Island, Okinawa Prefecture, Japan: a – scheme of the distribution of tidal zones (1 – supratidal fringe or the splash zone, 2 – the intertidal or littoral zone, 3 – the upper subtidal zone); b – supratidal fringe; c, d – the intertidal zone; e – the upper subtidal zone.

The second ecological zone is the intertidal or littoral area. Marine plants inhabiting this zone are dipped in water during high tides and drying up during low tides. Algae living in intertidal pools (depressions in rocky or boulder-blocky grounds) are permanently covered by water (Fig. 9a, c, d).

The third zone is the upper subtidal zone. Marine plants and animals in this zone mostly remain submerged (Fig. 9e).

The environmental conditions are strikingly different in different zones. Temperature conditions are especially varying in the supratidal fringe and upper

intertidal zone. In these zones, algae are often exposed to air and can even desiccate without losing viability, where as subtidal algal species are less tolerant to desiccation. During the rainy seasons the algae are prone to desalination. The unfavorable conditions for algae in supratidal zone are also harmful for intertidal algae during low tides. Supratidal and intertidal organisms are adapted to rapid and dramatic fluctuations of temperature, illumination, salinity, humidity, pH, oxygen concentration, and carbon dioxide concentration (Fong, Paul, 2011).

The algae in the subtidal zone live under more favorable and more stable conditions. In tropical reef ecosystems, the water temperature usually ranges from 24°C to 30°C, and its fluctuations related to different depths and winter/summer transitions are very small. Therefore, the temperature, in all likelihood, does not belong to factors that limit the distribution of marine plants in the subtidal zone.

The salinity of water in coastal ecosystems of continents and large islands depends on the amount of precipitation and ranges within 24 – 34‰. Due to the natural resistance of marine plants to salinity fluctuations, temporary small changes of water salinity on coral reefs exert almost no effect on their viability and the structure of their communities. The desalination of seawater that happens close to estuaries of large rivers affects symbiotic corals much more than marine algae. The corals could suffer from osmotic shock and lose their zooxanthellae partially or entirely. If they cannot recover after the shock, they will die and then get occupied by epilithic algae (Titlyanov et al., 2000, 2008a; Diaz-Pulido, McCook, 2002).

Dissolved inorganic nitrogen (ammonium, nitrates and nitrites) is one of the major factors that ensure the growth of algae on coral reefs. The concentrations of mineral nutrients in the water around coral reefs are usually greater than that in neighboring ocean waters, but are lower than that in coastal estuaries and lagoons (Crossland, 1983; D'Elia, Wiebe, 1990; Szmant, 2002; Atkinson, Falter, 2003; Atkinson, 2011). Nitrogen-fixing blue-green algae can increase nitrogen concentration and benefit the balance of nitrogen-containing substances in coral reef ecosystem (McClanahan et al., 2007). On coral reefs there is enough phosphorus due to its turnover within the ecosystem (Atkinson, 2011). However, some studies showed that phosphorus can be removed from the ecosystems as a result of calcium binding to phosphate ions; if so, the algae will also suffer from a phosphorus shortage (Fong et al., 1993).

The upper subtidal zone is inhabited by algae that are most tolerant to high water turbulence. For example, gulfweeds and coralline algae can grow and withstand surf actions in the surf areas of coral reef, on the outer side of reef flat, and within the reef crest. In dense communities of fleshy algae (e.g., *Sargassum* spp.), as well as in algal turf, the mild water turbulence

helps the inflow of nutrients to the plants (Sousa, 1984; Hurd, 2000).

The ecological zones described above vary a lot in the effects of certain biotic factors on marine algae. For example, in the supratidal zone the grazing of algae by fish and invertebrates is almost excluded. However, in the intertidal area, grazing is determined by tides and water turbulence associated with tidal currents and surf. Grazing by herbivorous animals is an important factor of succession control for algal communities. It regulates the rate of biomass accumulation, frequency and intensity of reproduction in individual plant. The major herbivorous animals on coral reefs are fishes, sea urchins and gastropod mollusks (Glynn, Enochs, 2011; Montgomery, 2011).

On a healthy coral reef with unpolluted water, the competition for substrate and resources utilization between marine algae and corals is insignificant and not so important for development of plants and coral communities. On these reefs, the percentage of bottom covered by coral is around 80 – 90% without changing for years. However, after damages to coral reefs, especially after massive mortality of scleractinian corals, the competition between algae and corals for newly available substrates becomes crucial for restoring and maintaining the reef ecosystem. Dead and damaged coral colonies are occupied by benthic micro- and macroalgae during the first year after the ecological disaster. The coverage of carbonate reef base by living corals decreases, whereas the degree of algal coverage rises up (McCook et al., 2001; Titlyanov, Titlyanova, 2008; Chadwick, Morrow, 2011).

Littler and Littler (1984) came up with a hypothesis that the distribution of corals and different algal communities on coral reefs depends on the effects of major abiotic and biotic factors (Fig. 10). According to this hypothesis, hermatypic corals containing zooxanthellae usually successively occupy substrate and space under the conditions of intensive grazing of macrobenthic algae by animals, moderate levels of wave actions, and low concentration of nutrients in seawater. Coralline algae will dominate in areas with moderate or strong grazing of non-calcified algae, strong wave effects, and moderate or high concentration of nutrients. Communities of algal turf develop under low concentration of mineral nutrients and small level of grazing. The beds of large fleshy and foliaceous (frondose) macrophytes occupy ecological niches that are rich in nutrients and free of pressure from herbivorous animals (Littler, Littler, 1984). Fig. 10. Modified Littler and Littler (1984).

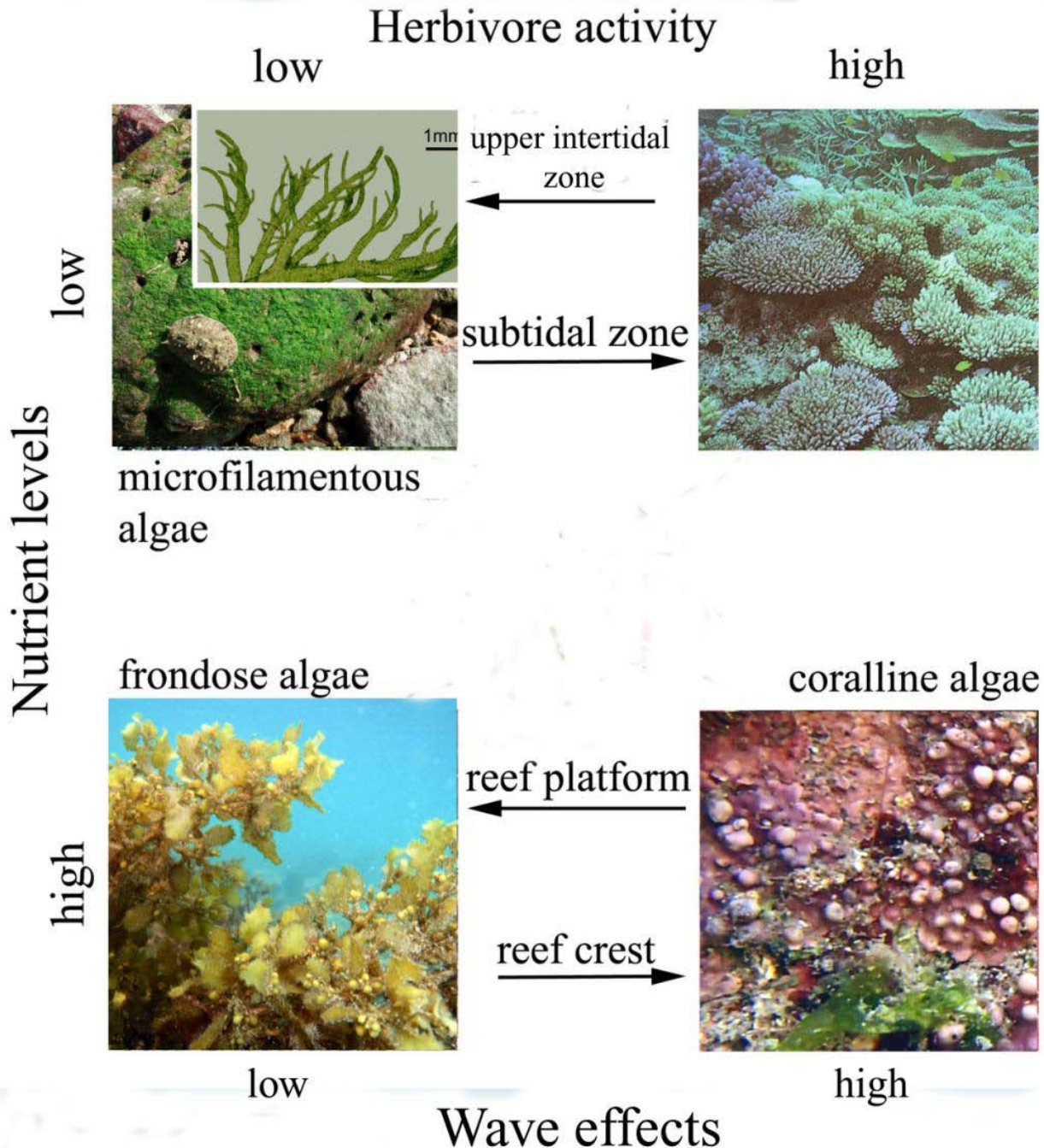


Fig. 10: Modified Littler and Littler (1984) representation of the relative dominance paradigm

e) *The role of marine plants in coral reef ecosystem*

i. *Primary production of organic matter and its turnover*

Coral reefs are one of the most diverse and productive ecosystems on Earth. They form heterogeneous habitats that serve as important sources of primary production within tropical marine environments (Odum, Odum, 1955; Connell, 1978). The total coral reef coverage amounts to 600,000 km², which is about 0.17% of the ocean surface. The gross

fixation of carbon by coral reefs is 20×10^{12} g per year, 15% of which is consumed by the reef system, 10% is used by human, and the remaining 75% is exported into adjacent areas in the ocean (Crossland et al., 1991).

The massive production of coral reefs is determined by several factors: efficient absorption of incident light by reef photosynthesizing organisms, complete structure of coral reefs, and high degree photoacclimation of reef photosynthesizing organisms

(Titlyanov, 1991; Titlyanov, Titlyanova, 2002a, b; Dubinsky, Falkowski, 2011). On coral reefs, the illuminated bottom surface in the upper subtidal zone is almost entirely covered by photosynthesizing organisms, and the most illuminated areas are occupied by the most productive organisms, the scleractinian corals (Fig. 11a). The primary production of the

scleractinian corals is made up by the production of endosymbiotic unicellular algae, zooxanthellae (Fig. 6), and ectosymbiotic green and blue-green algae (Fig. 7f). The communities of finely lamellar and finely filiform macroalgae are also very productive (Fig. 11b), which occupy brightly illuminated ecological niches in the intertidal area.

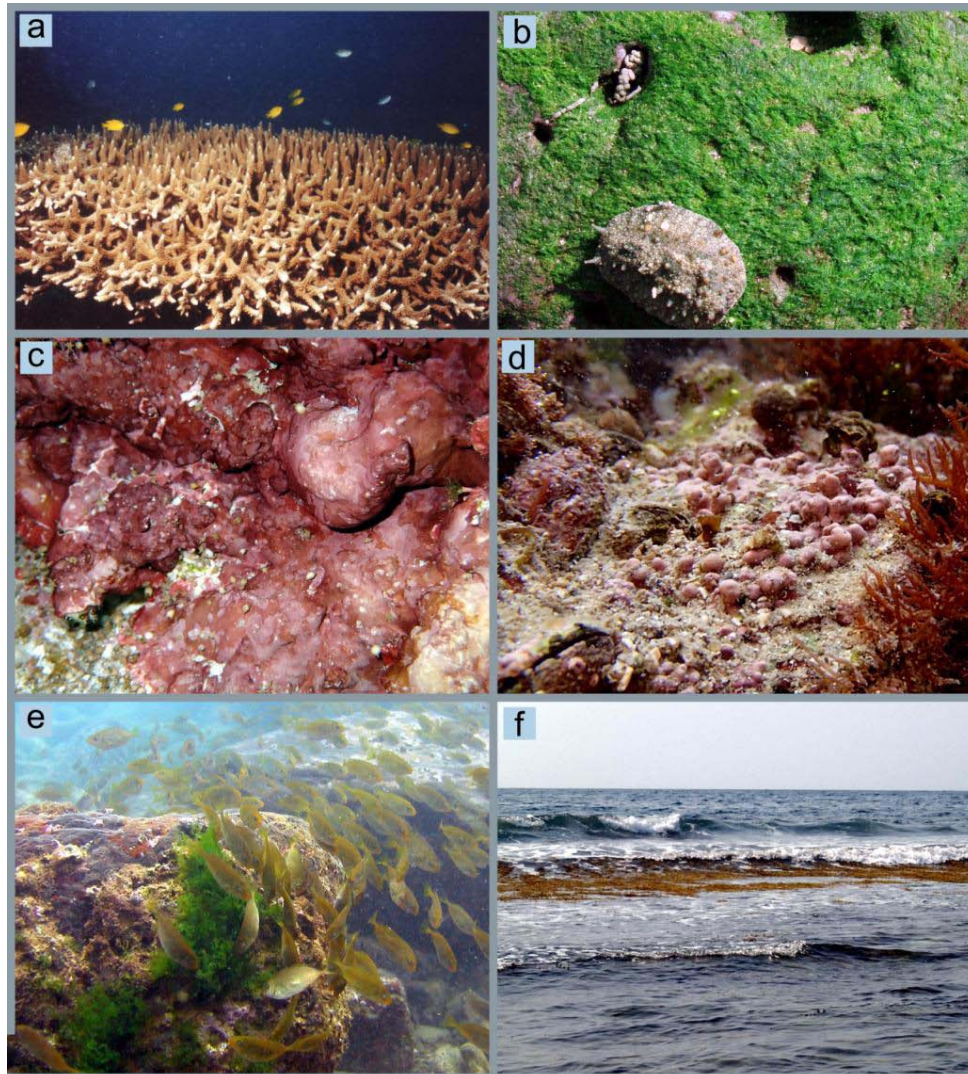


Fig. 11: The role of marine plants in coral reef ecosystem: a - on healthy reef the illuminated bottom surface in the upper subtidal zone is almost entirely covered by the most productive photosynthesizing organisms, the scleractinian corals; b - in the intertidal zone the most illuminated areas are occupied by very dense communities of fine filamentous, high productive green algae (for example, temporary monodominant community of the green alga *Ulva clathrata* in the upper intertidal zone of the Luhuitou coral reef in Sanya Bay, October 2008; c - the shaded deep-sea areas and strongly shaded grottoes of reefs are mostly inhabited by low-productive long-lived red coralline algae (e.g. the shadowed niche in the subtidal zone of coral reef of Yonaguni Island in the Ryukyu Archipelago chain (Okinawa Prefecture, Japan), March 2013; d - the communities of calcareous crustose algae connect together the neighboring areas of carbonate reef base, dead skeletons of colonies, they protect the reef from erosion and build a new carbonate layer on the base of the coral reefs. The red calcareous alga *Lithophyllum okamurae* on damaged coral reef of Yonaguni Island (Ryukyu Archipelago, Japan, March 2013); e - marine macrobenthic algae are the major food of herbivorous animals inhabiting coral reefs, Vietnam, Nha Trang Bay; f - frondose algae of the genera *Sargassum*, inhabiting the lower intertidal zone and the uppermost part of the subtidal zone and forming extensive beds protect reefs from wave action and erosion.

Planktonic microalgae and symbiotic algae of sponges, soft corals and mollusks are also producers of organic substance on coral reefs, but their contribution is insignificant (Crossland et al., 1991; Fong, Paul, 2011). The shaded deep-sea areas of reefs are mostly inhabited by low-productive long-lived red coralline algae (Fig. 11c). On undamaged coral reefs (percentage of substrate covered by corals exceeds 50%); the major primary production is provided by unicellular symbiotic algae, zooxanthellae. While on damage coral reefs, macrophytes can become the major producers (Titlyanov, Titlyanova, 2008; Stambler, 2011).

Dying algae are washed up on the coast or gravitate to the bottom, where they are held among patch reefs. In both cases they become food for animals (consumers) and bacteria (reducers). Bacteria can transform organic substance into inorganic compounds, which increase the concentrations of dissolved nitrogen and phosphorus (especially in lagoons) up to the level that is enough to support high productivity of marine plants (Fong, Paul, 2011).

ii. Reef-Builders

The communities of calcareous crustose red algae of the genera *Porolithon*, *Peyssonnelia*, *Lithothamnion* and *Lithophyllum* are reef-builders. They connect together the neighboring areas of carbonate reef base, dead skeletons of colonies, coral pebbles, cement carbonate sand, and other sediments located in-between coral colonies. Therefore, they protect the reef from erosion and build a new carbonate layer on the base of the coral reefs (Fig. 11d). Calcium carbonate is deposited within the tissues of crustose calcareous algae at the rate of more than 10 kg CaCO₃/m² per year. In the subtidal zone, these algae can build up carbonate structures down to 50 – 100 m deep (Molinier, 1960; Lang, 1974; Littler et al., 1986; Chisholm, 2003). The communities of large calcified green algae (the genera *Halimeda* and *Udotea*) and red algae (the genera *Amphiroa* and *Galaxaura*) also produce calcium carbonate (Macintyre et al., 1987; Hine et al., 1988, Marshall, Davies, 1988, Roberts et al., 1988, Hillis, 1997, Merceron et al., 2007; Nelson, 2009). The remnants of thalli from these algae transform into carbonate sands, which fill up gaps between coral colonies on the bottom and serve as building materials for coral reefs.

iii. Nitrogen Fixation

An important function of marine plants on the reef is nitrogen fixation. It is performed by cyanobacteria (members of the genera *Lyngbya*, *Oscillatoria*, *Calothrix*, *Anabaena*, *Entophysalis*, *Nodularia*, etc.) inhabiting soft sediments in-between coral colonies. They live also on stones and dead coral colonies, being epiphytic on seagrasses and endolithic inside of coral skeletons (Fig. 5e). The rate of nitrogen fixation by blue-green algae

depends on factors as light intensity, availability of dissolved nutrients and water temperature (Bergman et al., 1997; Welsh et al., 2000; Dong et al., 2002a, b, 2006, 2008; Lugomela, Bergman, 2002; Hamisi et al., 2004).

iv. Marine plants are the initial link of food chains

Marine macrobenthic algae and epiphytic microalgae are the major food of herbivorous animals inhabiting coral reefs (Fig. 11e). Experiments have shown that herbivorous animals can consume up to 100% of daily production of macroalgae during one day (Carpenter, 1986; Duffy, Hay, 1990; Hay, 1997; Burkepile, Hay, 2006; Hughes et al., 2007). Fishes from families like *Blenniidae*, *Kyphosidae* and *Siganidae* are selectively grazing filamentous and fleshy algae from turf community, thus helping calcareous coralline and other crustose algae to grow.

Some fish species are grazing green algae of the genera *Cladophora*, *Enteromorpha* and *Ulva*; other fishes are foraging on brown algae of the genera *Sargassum* and *Dictyota* (Hay, 1997). Besides fishes, marine algae are also eaten by sea urchins, mollusks, crabs and amphipods. Seagrasses are consumed only by animals that can digest cellulose, such as sea green turtles, manatees and dugongs.

v. Communities of marine plants provide environment for marine animals

Communities of algal turf (especially in the subtidal zone), large densely branching gulfweeds, and seagrasses provide good refuges for fish, crustaceans and mollusks, as well as their larvae. Articulated coralline algae provide refuges for many species of small invertebrates (Nelson, 2009; Fong, Paul, 2011). Some scientists distinguish specific fauna of these algal communities (Kelaher, 2002; Kelaher et al., 2004; Chapman et al., 2005; Liuzzi, Gappa, 2008).

Large macrophytes and crustose calcareous algae are good substrate for some sessile marine animals to settle down, like hydroids, spirorbids, polychaetes, bryozoans and foraminiferans. Coralline algae serve as substrate for scleractinian coral planulae (Vermeij et al., 2009; Ritson-Williams et al., 2010). Coralline algae are utilized by marine farms specialized on abalone (*Haliotis* spp.) growing, serving as a substrate for settlement and development of abalone larvae (Morse, Morse, 1991).

Additionally, old thalli of macroalgae and leaves of seagrasses are populated by numerous epiphytic and endophytic algae, as well as saprophytic marine fungi. Therefore, marine plants ensure one of the major conditions for coral reef to exist, its high biodiversity.

vi. Protection of reefs against deleterious effects from surf

Coralline algae are highly resistant to surf. They settle on reef crest and develop a stout ridge that functions like a breakwater, which protects delicate algal forms and animals inhabiting the upper part of reef

slope from damages. The coriaceous and frondose algae of the genera *Turbinaria* and *Sargassum* (Fig. 11f), inhabiting the lower intertidal zone and the uppermost part of the subtidal zone, also play the similar roles (Littler, Littler, 1988).

III. REEFS UNDER DISTURBANCES

a) *Natural and semi-natural disturbances*

Coral reef ecosystems are susceptible to natural and semi-natural disturbances which, if their magnitude is such that the threshold of system tolerance/resilience is exceeded, may lead to major changes in ecosystem functioning (Steinberg, 2012). Throughout the evolutionary history of coral reefs, they have been exposed to various forms of natural catastrophes including super-typhoons, tsunamis, volcanic activities, sea temperature fluctuations and sea level changes that have led to major shifts in reef communities.

b) *Possible role of marine plants in damages, mortality or recovery of coral reefs*

Severe physical disturbances such as typhoons/hurricanes/cyclones and tsunamis cause extensive damages (e.g., fragmentation and dislodgment) in coral colonies (Woodley et al. 1981; Glynn 1990). Death of hard corals leads to the loss of architectural complexity and reef flattening through the collapse of coral skeletons. As such, disturbance is a well-known modifier of reef seascapes. In marine systems stormy conditions may not only remove or bury subtidal organisms but they may also help form new substrate patches. In the wake of a strong disturbance, newly formed substrates appear as bare rocks and banks formed of sand and coral fragments, with dead/damaged coral colonies providing space for sessile organisms (Rogers et al., 2008; Massel, Done, 1993; Trenberth, Shea, 2006; Manzello et al., 2007; Alvarez-Filip et al., 2009).

Coral bleaching is often caused by unusually high sea temperatures (>30°C) combined with periods of slack wind, calm seas, cloudiness, high solar radiation, and in some areas, reduced salinity due to extreme weather events, such as typhoons, storm surges, storms, or floods. Bleaching leads to reduced photosynthesis, a tissue growth, regeneration, calcification and subsequently to the death of corals (Lesser et al., 2007). On some reefs, up to 100% of corals died within few months after a bleaching event (Baker et al., 2008). Elevated seawater temperatures that result in coral bleaching may also negatively affect algae. It is well known that some Corallinaceae species (e.g., *Corallina officinalis*) are bleached (Latham, 2008), but to date there has been no documented record of mass bleaching of seaweeds or their destruction due to a bleaching episode.

The speed of recovery often depends on the severity of bleaching disturbance, and on the amount of coral cover remaining after the disturbance (Loch et al., 2002; Stobart et al., 2005; Guzman, Cortes, 2007; Glynn et al., 2011). A decline in live coral cover may not follow a single bleaching episode but often depends on accompanying coral diseases, *Acanthaster* predation and the occurrence of repeated bleaching episodes. Eventually, bioerosion and mechanical fragmentation of reef materials generate unstable rubble- and sand-substrates which are unfavorable for coral recruitment (Szmant, 2002; Baker et al., 2008; Rogers et al., 2008). Patterns of loss and recovery in coral cover at several eastern Pacific sites ranged from total elimination to total recovery with periods spanning 10 – 28 years (Wellington, Glynn, 2007). Recovery of undisturbed and slightly affected coral reefs was recorded at annual rates of 1 – 10%, while gradual decline in live coral cover ensued at sites experiencing severe anthropogenic stresses (Connell et al., 1997; McClanahan et al., 2007; Baker et al., 2008).

Severe natural catastrophes on coral reefs result in the formation of new substrata, changes in the relative abundances of surviving hermatypic corals and the dominance of non-coral taxa associated with reef assemblages. The fate of a damaged reef depends on factors such as the degree of coral reef damage, the presence of coral and non-coral taxa on the reef and sources of planulae supply for recolonization and restoration of coral populations (Harrison, 2011). A damaged coral reef may completely return to its initial state or attain a changed state with the predominance of other species and forms of corals or turn to non-coral taxa reef (Baker et al., 2008; Titlyanov, Titlyanova, 2012b) (Fig 12).

Possible fate of the damaged coral reef

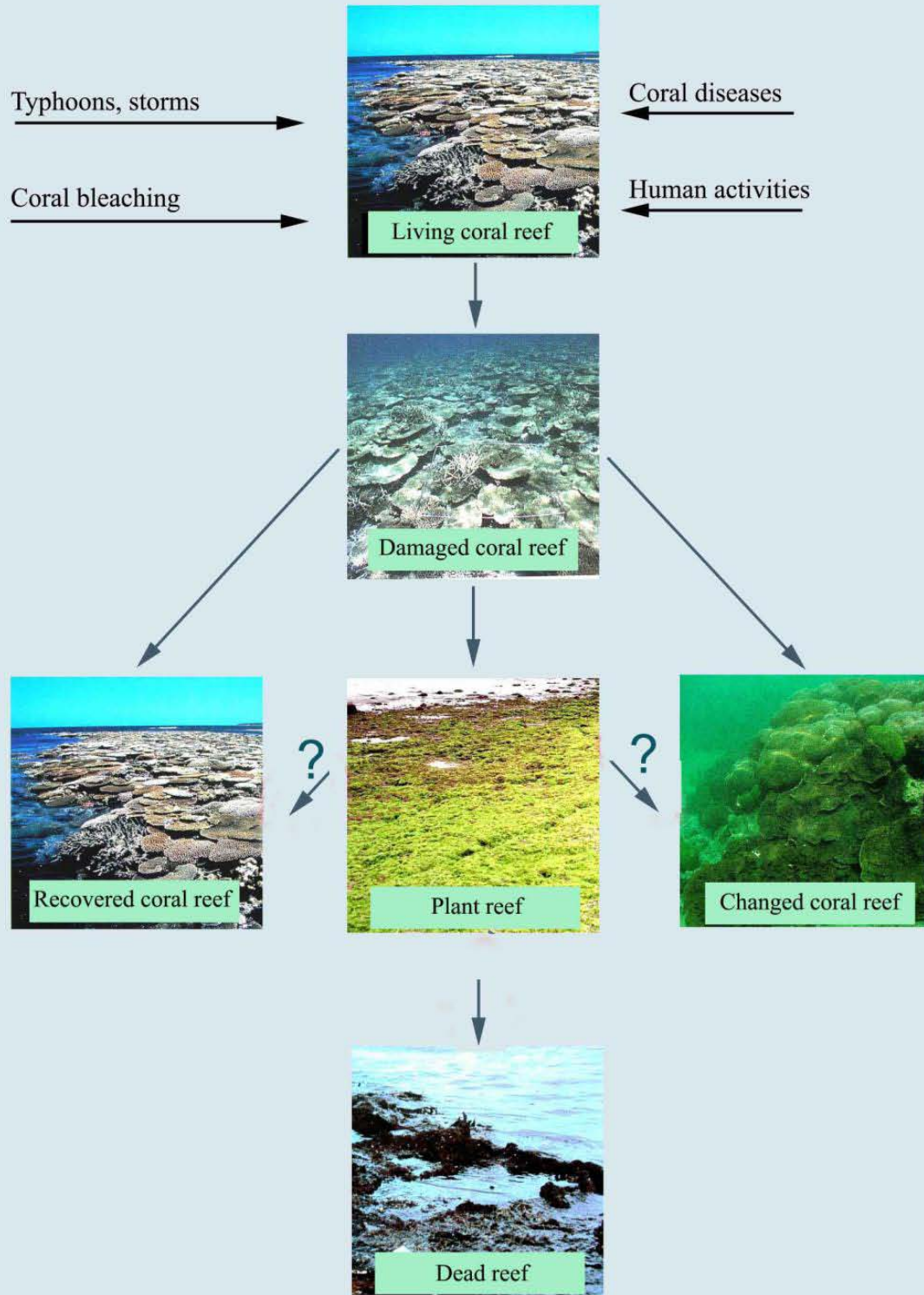


Fig. 12: Possible fate of the damaged coral reef

i. *Possible fate of the damaged coral reef*

A number of studies reported that severely damaged coral reefs were subsequently transformed into a seaweed-dominated state ("phase shifts") (Done, 1992; Knowlton, 1992; McManus, Polsenberg, 2004). Bruno et al., (2009), however, indicated that the replacement of corals by macroalgae as dominant benthos was less common and less geographically extensive than assumed, based on a meta-analysis of 3581 quantitative surveys conducted in 1996 - 2006 involving 1851 reefs around the world. These give credence to the view that such a "phase shift" represents a temporary state of coral reefs on their way to recovery to an initial or changed state (Titlyanov, Titlyanova, 2012b).

ii. *Colonization of newly formed substrates*

Newly formed substrates (after bleaching events, etc.) made of dead or damaged colonies of hermatypic corals are rapidly colonized by sessile organisms such as sponges, hydroids, gorgonians as well as various algae. As was shown by field and laboratory studies (Diaz-Pulido, McCook, 2002, 2003, 2004; Diaz-Pulido et al., 2007; Mumby, 2009; Chadwick, Morrow, 2011), microscopic diatoms, fine filamentous blue-green and green algae, tunicates, foraminifera, small-sized polychaetes are the first colonizers on both dead and wounded coral colonies.

Studies involving mechanically damaged colonies (with various types of injuries) and dead coral debris (pebbles) of massive and branched corals (Titlyanov et al., 2005, 2006, 2008b) showed that the injuries and pebbles were immediately overgrown by algae and cyanobacteria. After the first month of colonization, algae occupied 1 – 7% of the injured surfaces and 1 – 4% of the surface of pebbles. Algae settled only on the skeleton surfaces not covered by live coral tissue. The first settlers were microscopic, micro-filamentous, fine filamentous and filamentous-tubular forms (Fig. 13a, b). By the third month, algal cover significantly increased to 30 – 50% on the injuries and to 25 – 60% on coral pebbles. The composition of dominant species on the lesions had changed, but ephemeral algae still dominated (Fig. 13c, d). During the 6 – 8 months of the experimental period, the projected cover of algae amounted to 80 – 100% on the lesions and 60 – 90% on coral pebbles, where an algal turf community with the dominance of ephemeral as well as long-lived species was formed (Fig. 13e, f). Algal communities on new substrata lasted from 6 – 8 months (algal turfs) to some years and subsequently species composition, biomass and density of these communities changed seasonally and depending on competitive abilities of different settlers.



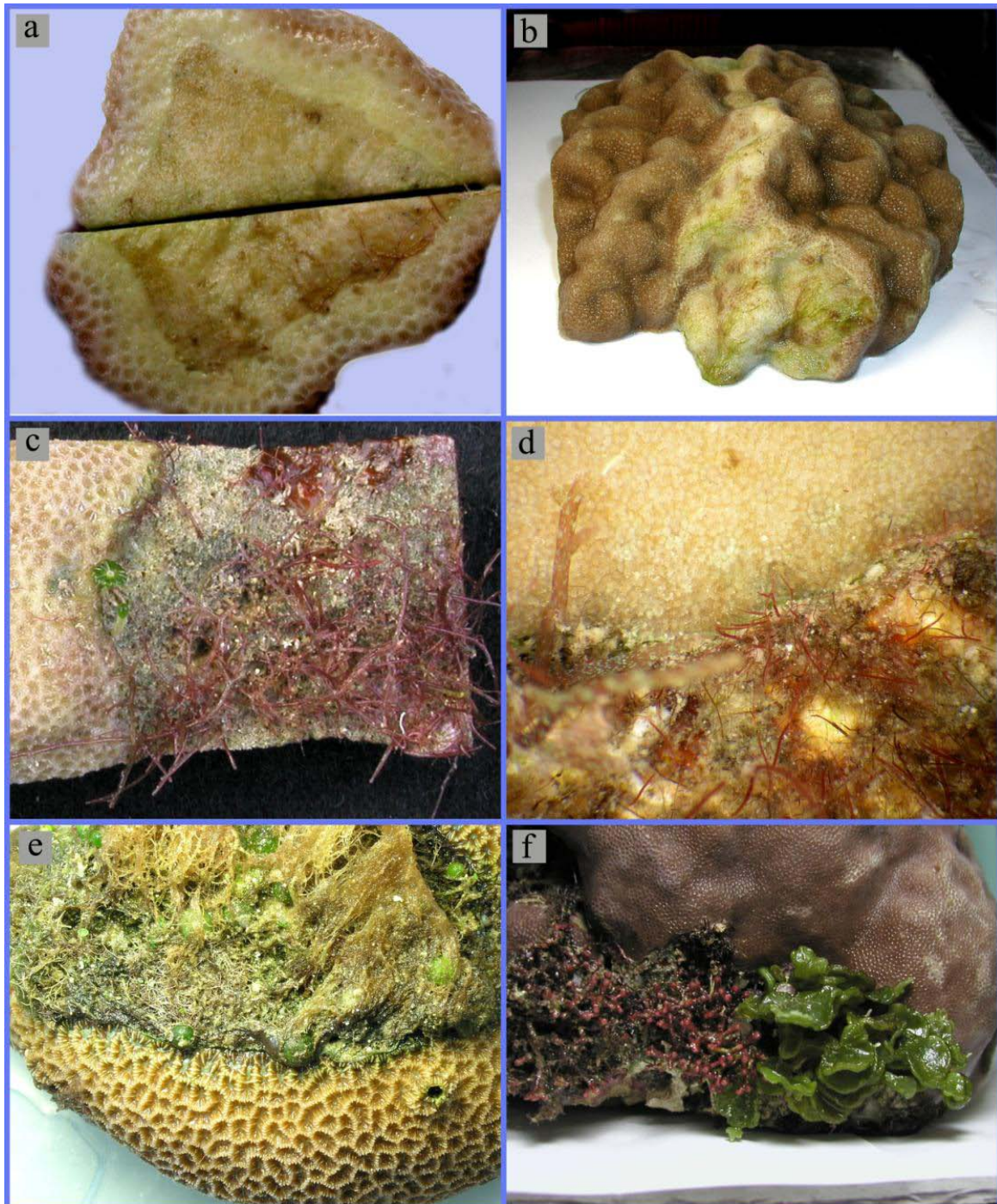


Fig. 13: Polyp regeneration and algal settlement onto inflicted damages on coral colonies: a, b – algal settlement onto inflicted damages on *Porites lutea* colonies, after the first month of colonization, c, d – algal settlement onto inflicted damages on *Porites lutea* (c) and *Porites cylindrical*; d – colonies after three months of the colonization; e, f – the formation of algal turf on inflicted damages on *Platygyra verweyi* (e) and *Porites lutea* colonies (f) after 6 – 8 months of the colonization

iii. Coral-algal relations

As discussed above, algae occupy newly-released substrata within some months and are involved in competitive relationships with survived and newly settled corals and other invertebrates. Successional interactions begin from the first stages of algal

community colonization and complete with the transition of a reef into one of the stable states where either hermatypic corals or algae become dominant. With the transition of a damaged reef into a stable state, competitive relationships are generally replaced by symbiotic (mutualistic) relationships that contribute to

the maintenance of ecosystem stability or homeostasis (Petraitis, Dudgeon, 2004).

At early stages of colonization, competition between corals and algae is characterized by overgrowth of competitors and allelopathic influences (McCook et al., 2001), where coral polyps that survived a catastrophe tend to be competitively superior (Titlyanov, Titlyanova, 2008). In an experiment on the regeneration of adult colonies of *Porites lutea* and *P.*

cylindrica from artificially-inflicted injuries, coral polyps were able to overgrow more than 100 algal taxa (but not toxic blue-green algae such as *Lyngbya semiplena* and *L. majuscula*). Injuries up to 20 cm² in area healed within 6 months, i.e. the algal-turf community formation was not a serious impediment to the recovery of damaged corals, although the rate of recovery slowed down (Figs. 14, 15, 16).

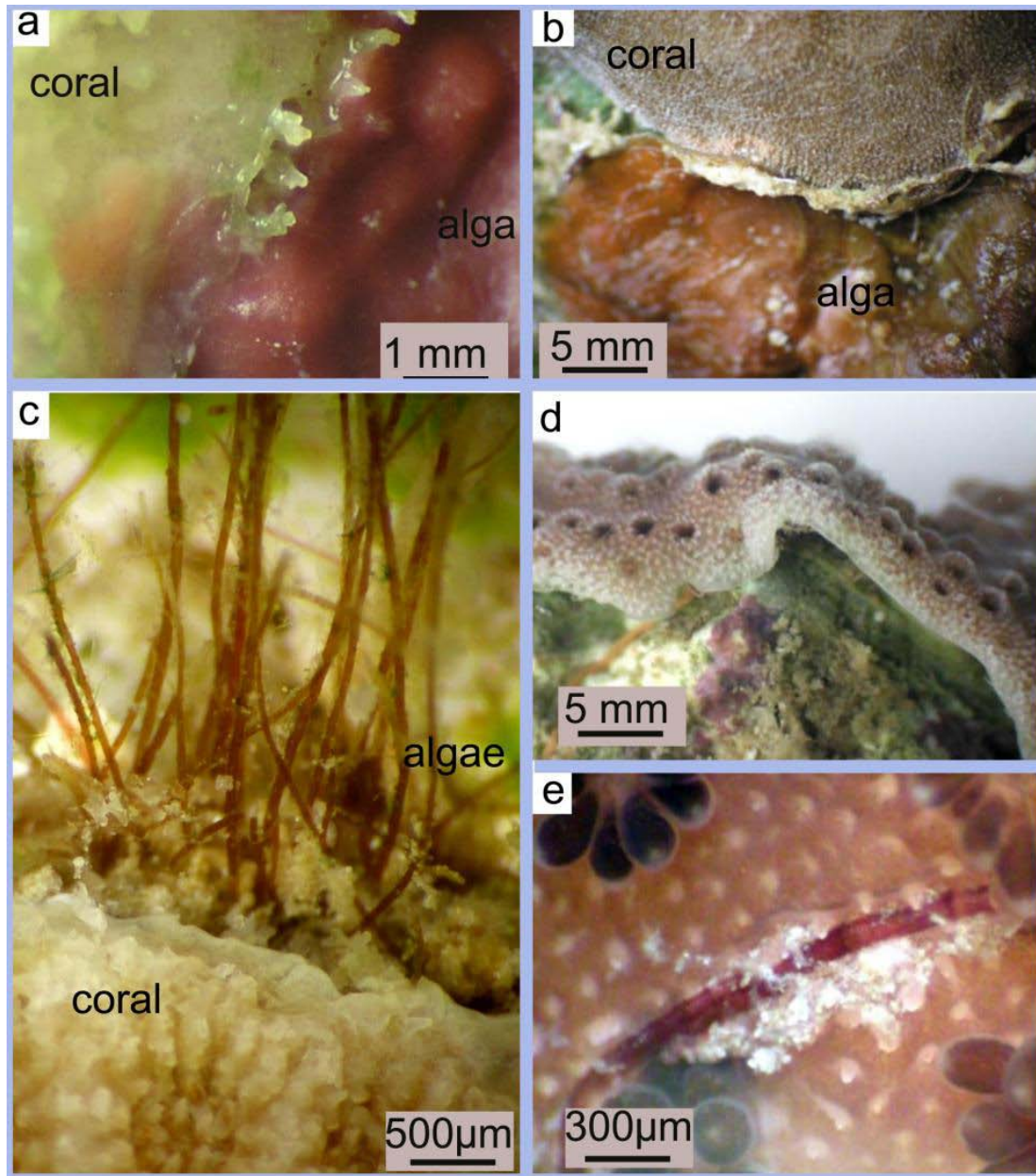


Fig.14: Various ways of overgrowth of algae by corals under moderate light (20 – 30% PAR0) (Titlyanov, Titlyanova, 2008; Titlyanov et al., 2009): a – coral-algal competition for substratum of the coral *Porites lutea* and the red crust alga *Peyssonnelia conchicola*. Polyps overgrew algal thalli with thin, transparent, azooxanthellate tissue (50 – 200 μm wide); b – overgrowth of the brown alga *Lobophora variegata* by the coral *Porites lutea* (by the release of mucus by the coral); c – coral expansion on algal turf (coral tissue produce skeletal crystals); d – overgrowth of blue-green and red crust algae by encrusting coral (forming canopy above algae); e – entombing into skeleton of the red alga *Centroceras clavulatum* by the coral *Acropora* sp. (Titlyanov, Titlyanova, 2008).

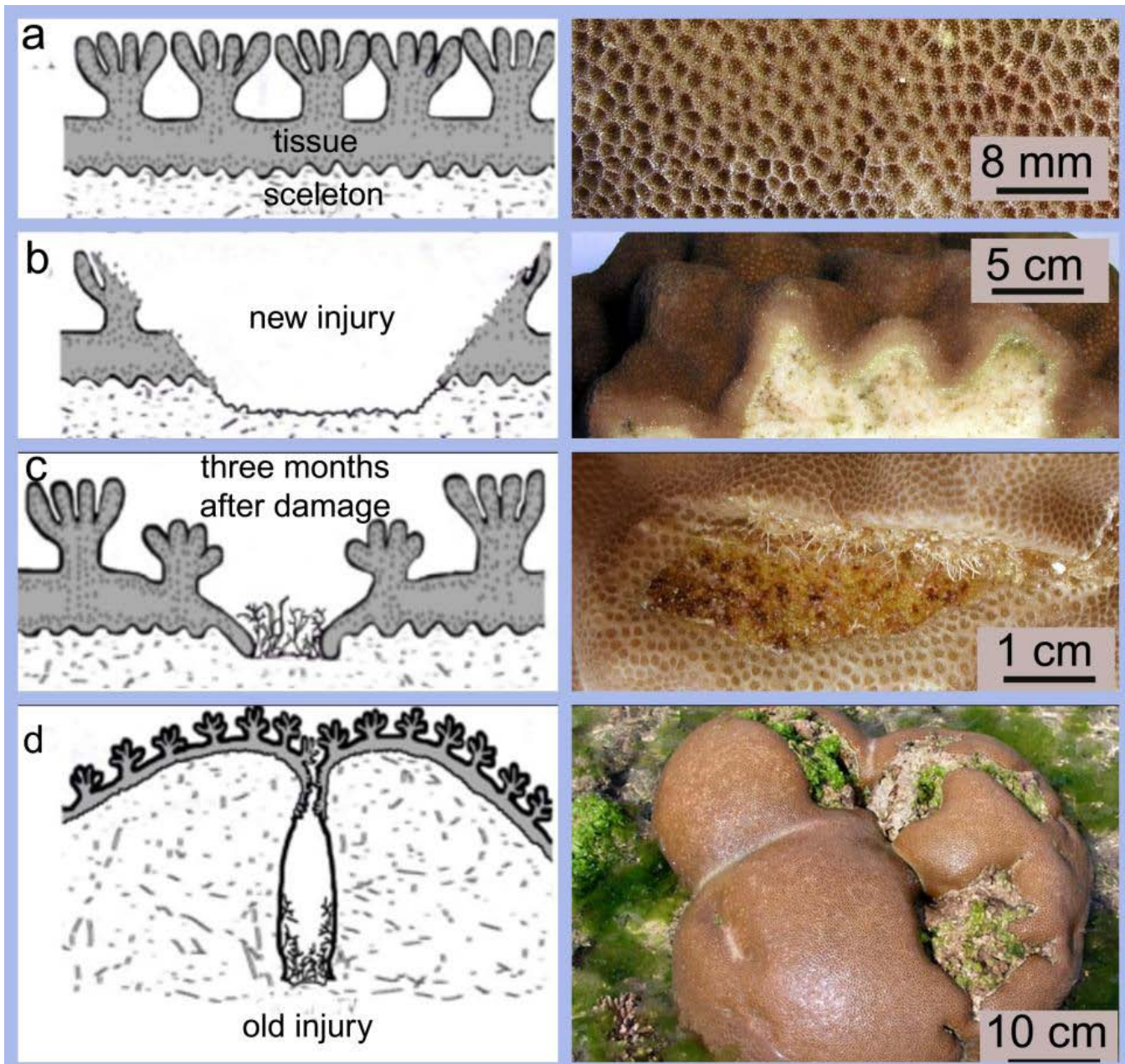


Fig.15: Scheme of stage-by-stage regeneration of damaged colony of the hermatypic coral *Porites lutea*: a – polyps of healthy (undamaged) coral; b – injury (one week old); c – injury (4 month old) overgrowing by polyps; d – old wound (4 years old) of recovering coral colony (Titlyanov, Titlyanova, 2008).

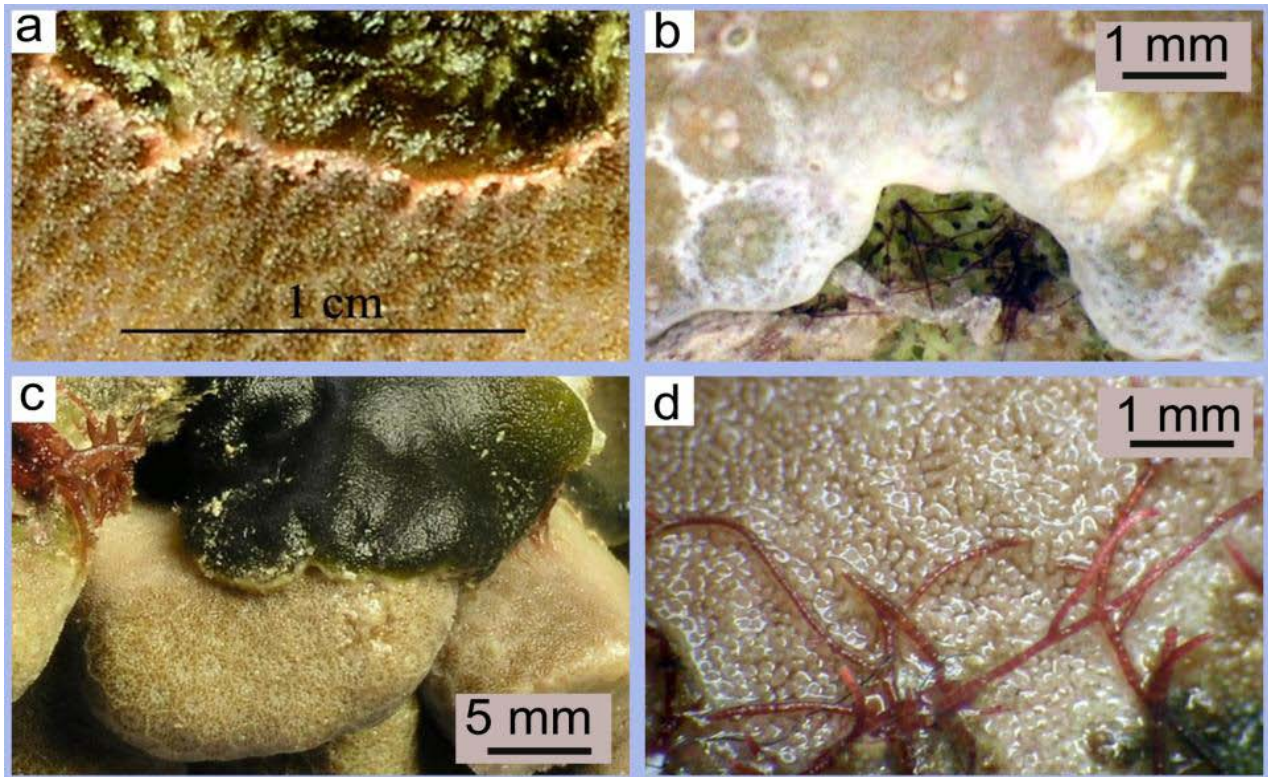


Fig. 16: Allelopathic influence of Cyanobacteria on corals and overgrowth of corals by macroalgae: a – The coral *Porites lutea* under allelopathic contact with the blue-green alga *Lyngbya semiplena* (coral changing growth form in upright direction); b – bleaching and inhibition of polyps' growth of the coral *Porites lutea* under allelopathic contact with the blue-green alga *Lyngbya majuscula*; c – overgrowth of the coral *Porites cylindrica* by the green alga *Codium arabica* under low light (2–1% PAR₀); d – overgrowth of the coral *Porites lutea* by the red alga *Centroceras clavulatum* under low light (Titlyanov et al., 2005).

After the formation of algal communities on vacant substrata, competition between coral colonies and algal settlers continue with different modes of competition being involved. These include direct physical interactions such as overgrowing, overtopping, smothering (McCook et al., 2001; Box, Mumby, 2007; Titlyanov, Titlyanova, 2008; Titlyanov et al., 2008b) and indirect ones such as environmental modification and space preemption (Dobson, Hudson, 1986; Hudson, Greenman, 1998), production of allelochemicals (Bak, Borsboom, 1984; Paul, Puglisi, 2004; Gross, 2003; Titlyanov et al., 2007) and the stimulation of pathogenic bacteria (Nugues et al., 2004; Smith et al., 2006). Further, there have been reported cases of macroalgae directly killing and overgrowing neighbouring corals (McCook, 2001; Jompa, McCook, 2003; Nugues et al., 2004).

Not all algal species on coral reefs compete with corals for space (e.g., endophytic and epiphytic algae). Corals' main competitors for space include brown algae with large upgrowing thalli (the genera *Sargassum*, *Padina*, *Dictyota*, etc.), dense communities of algal turfs and toxin-producing algae. With the formation of algal communities on a damaged coral reef, the recovery of coral colonies and their expansion

over hard substrata may largely be impeded (Titlyanov, Titlyanova, 2008), depending on species-specific competitive abilities of algal thalli and coral colonies (Jompa, McCook, 2003; Birrell et al., 2005) and also on environmental conditions. However, even at this stage of coral/algal competition, adult coral colonies may still remain superior competitors in the absence of strong anthropogenic stresses.

It should be noted that algae can overgrow coral polyps only when they are damaged, weakened or under stressed conditions in general. In an experimental study involving algal species such as *Peyssonnelia conchicola*, *Corallophila kleiwegii*, *Centroceras clavulatum*, *Anotrichium tenue*, *Polysiphonia* spp. (Rh), *Lobophora variegata*, *Sphacelaria novae-hollandiae*, *S.tribuloides* (Ph), *Codium* spp., *Dictyosphaeria* spp. (Ch), these could overgrow colonies of *Porites lutea* only under the light intensity of less than 5% PAR₀ (Titlyanov et al., 2009a). This is related to the differences in light adaptation between algae and corals. It has been demonstrated that the majority of scleractinian coral species are associated with light levels of 1 - 80% PAR₀ (Titlyanov, Latypov, 1991), while red coralline algae can tolerate down to 0.1% PAR₀ (Littler, Littler, 1988).

Early life stages of many sessile species including hermatypic corals are typically competitively inferior to older and larger individuals (Sebens, 1989; Maida et al., 2001; Vermeij et al., 2009). In similar vein, large-sized, fleshy, coriaceous and foliaceous forms of marine plants as well as algal turfs can limit the success of smaller competitors (e.g., coral planulae, larvae of other sessile organisms, young coral colonies (Grant, 1977; Grizzle et al., 1996). It has been suggested that the effect of algae on corals is strongest during the coral's earliest benthic stages (Hughes, Jackson, 1985; Hughes, 1989, 1996; McCook et al., 2001; Vermeij, Sandin, 2008). Coral recruitment commonly declines when benthic algae become abundant in experimental (Rogers et al., 1984; Birrell et al., 2005; Hughes et al., 2007) and natural settings (Hughes, 1989; Birkeland, 1996; Edmunds, Carpenter, 2001; Vermeij, Sandin, 2008). Benthic algal assemblages have direct negative impacts on coral recruitment mainly through the preemption of settlement space (Birrell et al., 2005; Mumby et al., 2007; Vermeij et al., 2009). Additionally, algae can have indirect negative impacts on coral recruits through allelopathy (Gross, 2003; Kuffner et al., 2006).

Abundance of macroalgae is often attributed to their ability to actively overtake space previously occupied by corals, i.e. their presumed greater competitive capacity than corals, although there is little direct evidence supporting this hypothesis (McCook et al., 2001; Fong, Paul, 2011). Indeed, we argue that passive colonization of space previously occupied by stony corals that died from causes other than competition with algae (e.g., disease, bleaching) might often have been mistakenly interpreted as evidence of active competition between corals and algae (Vermeij et al., 2009). On the other hand, under certain circumstances macroalgae do seem to restrict the growth of coral colonies. In subtropical, high-latitude coral assemblages, polyps on the edges of acroporan (*Acropora*) colonies are often injured and killed by whipping movements of neighbouring macroalgae such as *Gelidium elegans*.

iv. Corals as superior competitors in coral reef recovery

Recovery rates of coral reefs can reach 10% per year, according to experimental ecophysiological studies conducted on healthy and damaged coral colonies (Titlyanov et al., 1998, 1999, 2000a, 2001a, b, c, d, 2005, 2006, 2007, 2008a, b, 2009a; Titlyanov, Titlyanova, 2002a, b, 2008, 2009, 2012a, b) and the monitoring of coral reefs after natural catastrophes in different regions of the world (Loch et al., 2002; Stobart et al., 2005; Guzman, Cortes, 2007; Wellington, Glynn, 2007; Baker et al., 2008; Rogers et al., 2008). During coral reef recovery, hermatypic corals are often superior competitors to macrophytes and cyanobacteria which do not impede coral recruitment. High competitive

abilities of hermatypic corals are related to various morphological and physiological aspects:

- (1) Long-term (tens to hundreds of years) presence and growth of certain coral colonies (Veron, 1986), while marine plants exist from days to a few years at most (Loban, Harrison, 1994). Corals are permanent (long-living) settlers on hard substrata and gradually overgrow other non-toxin producing organisms. At the same time, algae (toxic or large forms) constitute only a temporary impediment to corals as they may be replaced by other, non-toxic forms which cannot impede coral growth. This replacement may occur during seasonal changes in species composition of algal assemblages or under stressful conditions (disturbances by storms, grazing by animals, etc.). After disappearance of harmful algae, bleached polyps (which were under direct contact with toxic or large algae) could recover in 2 – 4 weeks and continue to occupy the substrate.
- (2) High regenerative capacity of corals. Newly-formed live tissues of corals can gradually overgrow the dead parts colonized by algae. Corals' ability to recover from damages, depending on the position, size, shape and type of the damage, has been well documented (Bak, Steward-van Es, 1980; Bak, 1983; Wahle, 1983; Rinkevich, Loya, 1989; Meesters et al., 1993, 1994; Meesters, Bak, 1995; Hall, 1997, 2001; Oren et al., 1997; Marshall, 2000). For example, the newly-formed tissues of the corals *Porites* spp. and *Montipora grisea* tightly adjoined to the substrate with the exception of the front line (Titlyanov et al., 2005). This portion of the live tissue edge (probably not calcified or slightly calcified) had no zooxanthellae and appeared as transparent stripes between live polyps and dead skeleton of the lesion. The width of the tissue stripe depended on coral species, e.g. 100 – 300 µm wide in *Porites lutea*, 50 – 100 µm in *P. cylindrica* and 50 – 200 µm in *P. rus*. The newly-formed coral tissue was able to go round impediments (Fig. 14) or rise above the impediments to overgrow. In the latter case, the impediment (live or lifeless object) was entombed into the coral skeleton.

A branched coral *Acropora* sp. and a foliaceous coral *Pavona divaricata* demonstrated different processes of lesion healing. After fast recovery (4 – 6 days) of damaged tissues, polyps began to occupy dead areas of the lesion by spreading and overgrowing with a thin blade-like formation consisting of soft tissue and hard skeleton. Sharp crystals (like spines or teeth), sometimes covered by live tissue (bearing zooxanthellae), and projected along the front line of the "blade". The blade did not adjoin firmly to the substratum and could rise above the lesion at a distance of 1 mm or more. As the blade expanded over

the substratum, its back portion fixed newly formed skeleton to the lesion, entombing all sessile organisms into the skeleton. Our research to date suggests that this mechanism of substrate colonization is characteristic of many encrusting coral species and widely observed on coral reefs.

Expansion of massive corals may be temporarily hampered by obstacles such as tall and dense algal turfs, large fleshy algal thalli or large sessile animals. In such cases, new polyps may form "bolsters" in front of and above the impediment (Titlyanov, Titlyanova, 2008) and these may eventually close up, entombing algae into the coral skeleton.

On damaged reefs, coral polyps coming into direct contact with algae tend to become bleached by allelopathic substances, abrasion, smothering or shading. However, bleached polyps may remain alive for a long time and recover after cessation of negative algal influences. For instance, experiments on the physical contact of *Porites lutea* colony fragments with a mat of the blue-green alga *Lyngbya bouillonii* demonstrated that the contact during one month inhibited growth and photosynthesis of the coral and bleached its polyps, due to a significant decline in zooxanthellae density and their total chlorophyll content (Titlyanov et al., 2007). These bleached fragments completely recovered in the absence of *L. bouillonii* under the light intensity of 30% PAR0 for two months. Similarly, our observations in Amakusa, Japan, showed that a colony of encrusting *Acanthastrea* sp. was observed to recover after having been covered by algae for several months and suffering from partial discoloration.

- (3) Advantage of size. In tropical and subtropical waters, healthy adult coral colonies of all growth forms except encrusting ones do not generally compete with algae because of their large sizes (height) surpassing algal assemblages, conceding only to Sargassaceae species on rare occasions. Coral colonies shade the bottom space immediately underneath and deprive fast-growing algae of necessary light. On shaded substrates under coral colonies, mainly slow-growing coralline algae settle, which in turn promote the attachment of hermatypic corals' planulae (Fong, Paul, 2011).
- (4) Different ways of feeding in corals, including photosynthesis of zooxanthellae, predation, consumption of particles of organic (animal) origin and digestion of own zooxanthellae (Titlyanov et al., 1996; Titlyanov, Titlyanova, 2002a). These allow corals to survive under unfavorable conditions such as low light conditions and waters poor in nutrients. For instance, the branched coral *Stylophora pistillata* was shown to survive and acclimate to a wide range of light intensities from 0.8 to 95% PAR0. Acclimation to low light conditions (8 and 30%

PAR0) involved maximizing the light harvesting capacity by increasing photosynthetic pigment concentration in zooxanthellae and zooxanthellae population density in coral branches. Under the extremely low light level (0.8% PAR0), the coral lost zooxanthellae by digestion and retained zooxanthellae-accumulated high concentrations of chlorophyll. The photoacclimation process is dynamic and immediate. Changes in pigment concentration in zooxanthellae occurred within 2 - 4 days and changes in zooxanthellae population density within 40 days. Zooxanthellae population densities were regulated by changes in the rates of division and degradation (digestion) of symbiotic cells (Titlyanov et al., 2001c).

Predation may be interpreted as adaptation to low light levels. Under the illumination of 2% of PAR0, capture and ingestion of *Artemia salina* nauplii by the coral *S. pistillata* were stimulated, with increasing ratios of ingested to killed nauplii; i.e., predation became more efficient than under 20 or 90% PAR0. It has been mentioned that under high/moderate light, corals most actively hunt in early morning hours, whereas under conditions of shading, they hunt throughout the day. When light is deficient, predation appears to be the major source of obtaining food in corals (Titlyanov et al., 2000 b, c). A decrease in photosynthesis of *S. pistillata* under light limitation also induced an increase in both chlorophyll concentration and zooxanthellae population density. Both responses require nitrogen that is generally insufficient in seawaters above coral reefs. For maintaining these responses the coral is capable of using nitrogenous compounds derived from captured zooplankton prey (Titlyanov et al., 2000c).

- (5) Corals' capacity to clean off organic and inorganic sediments from colony surfaces. Corals exhibit both active and passive removal of sediment particles (Lasker, 1980). They have a variety of mechanisms for coping with sediments including the use of their tentacles and cilia, stomodeal distension through water uptake, and entanglement of particles in mucus which later sloughs off the colony surface (Hubbard, Pocock, 1972). Where currents are strong, water movement will help keep sediment particles from settling on colony surfaces, and corals will have to spend less energy in sediment rejection. Species differ in their ability to reject sediments, colony and polyp morphology playing an important role (Hubbard, Pocock, 1972). The amount and type of sediment will influence the ability of a coral to maintain its surfaces free of sediments.

Colonies of some genera of hermatypic corals exhibit changes in orientation and morphology, which appear to occur in response to sediment stress (Bak, Elgershuizen, 1976). This would reduce the possibility of

settlement of spores and planulae on colony surfaces and help corals survive under conditions of high sedimentation. Macroalgae under such conditions become covered with sediments that limit their production and absorption of nutrients (Titlyanov et al., 2011a, b). Only crustose calcareous algae have a mechanism of surface cells' sloughing (Keats et al., 1994).

(6) The ability of coral planulae to attach to and grow on the thalli of competitors. Calcareous algae are considered the preferred substrate for attachment and development of coral planulae. When planulae receive certain chemical triggers secreted by crustose coralline algae, they stop swimming, attach to the substrate and develop into the primary polyps (Harrison, Wallace, 1990; Harrington et al., 2004; Golbuu, Richmond, 2007). It was shown that this induction effect of settlement is species-specific (Heyward, Negri, 1999; Golbuu, Richmond, 2007). Microbes living on algae may also induce/stimulate planula settlement and metamorphosis (Neumann, 1979; Richmond, 1987; Morse et al., 1988; Zaslou, Benayahu, 1996; Heyward, Negri, 1999). Moreover, settlement and survival of coral planulae may be influenced by independent as well as synergistic effects of macroalgae and microbes (Vermeij et al., 2009).

These suggest that not only red calcareous algae but also other representatives of algal turfs may serve as substrata for planula settlement. When 11 macroalgal species were tested on their effects on the swimming and settlement of *Platygyra daedalea* larvae, algal turfs and crustose calcareous algal groups had minor effects on coral settlement, while upright calcareous and fleshy macroalgae inhibited settlement (Diaz-Pulido et al., 2010).

(7) Coral fragments' capacity to attach to and grow on hard substrata and also the possibility of their non-attached existence. This feature is considered of importance in coral reef restoration after strong typhoon/tsunami damages. Coral fragments or even colonies could be dislodged, transported by water movements and relocated in new habitats. Under certain conditions, coral fragments may successfully attach to hard substrata or grow together with live colonies. Unattached fragments may survive for a long time on soft substrates, often acquiring a spherical form due to rolling (Veron, 1986; our own observations). In contrast, algae detached from the substrate are most likely to perish.

(8) Mobility of corals. Some coral species, most notably of the Family Fungiidae, are capable of actively moving over hard and soft substrata (Veron, 1986), which allows them to aggregate in favorable microhabitats where competition with algae may be reduced.

Thus, hermatypic corals tend to be competitively superior to macroalgae under natural/semi-natural conditions of reef ecosystems. While the competitive capacity of some macroalgae is enhanced under the advanced states of seawater contamination (Rosenberg, 1985; Doering et al., 1995; Harlin, 1995; Fletcher, 1996; Raffaelli et al., 1998; Taylor et al., 1999; Thornber et al., 2008; Nixon, Buckley, 2002), the combination of traits described here gives credence to the view that in the majority of cases corals outcompete algae on coral reefs damaged by natural catastrophes.

IV. CONCLUSION

In conclusion, we draw attention to the positive roles of algae in first colonizing newly-formed substrata after disturbance events and in contributing to the restoration of coral-dominant states of undamaged reefs. It may be argued that damaged coral reef ecosystems can regain homeostasis that has been lost during a natural catastrophe. We suggest that this is mainly achieved through the colonization of newly formed substrates by marine algae, with the following characteristics:

- (1) Maintenance of high ecosystem productivity through settlement of highly productive morpho-functional algal forms such as fine filamentous, filamentous and lamellar green and red algae (Sergeeva et al., 2007). While in healthy coral reefs symbiotic microalgae-zooxanthellae are the main primary producers, multi-cellular algae and cyanobacteria may often become the main primary producers that occupy denuded substrata after a catastrophe. Photosynthetic rates (per unit area of substrate) of algal communities may be equal to or greater than that of zooxanthellae in hermatypic corals (Littler, Littler, 1988; Littler et al., 1991; Titlyanov et al., 2007). Algal communities temporarily become the main supplier of organic matter and energy in a damaged reef ecosystem.
- (2) Protection of coral reef basis and newly formed carbonate substrata (dead coral colonies) from erosion and continuation of carbonate reef base building. Calcareous algae (Littler, Littler, 1988) help cement dead colonies and their debris into the carbonate reef base.
- (3) Colonization of Vacant substrates by algae enhances the biodiversity of an entire reef assemblage (Sergeeva et al., 2007; Baker et al., 2008; Fong, Paul, 2011).
- (4) Symbiotic relations between algae and corals also promote homeostasis and coral reef recovery in damaged reef systems through transport of assimilates from endolithic symbiotic algae (e. g., *Ostreobium quekettii*) to coral tissue (Fine, Loya, 2002; Titlyanov et al., 2008b, 2009b), which

- intensifies during a bleaching episode (Fine, Loya, 2002), or by coral digestion of own zooxanthellae that intensifies under extreme conditions (low light, starving, osmotic shock) (Titlyanov et al., 1996).
- (5) Release of secondary chemicals by encrusting calcareous algae (or their bacterial biofilm) promoting planula settlement and growth on their surfaces (Hadfield, Paul, 2001; Negri et al., 2001; Vermeij et al., 2009; Ritson-Williams et al., 2010).
- (6) Planulae and young colonies attached to calcareous algae at the base of algal turf are protected from predatory/grazing organisms and from desiccation and bleaching in the intertidal. Coral growth is enhanced by the accumulation of zooplankton and other organisms in algal turfs (Sorokin, 1990).
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