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SEAGRASS ECOSYSTEMS

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The seagrass ecosystem is defined as a unit of biological organization comprised of interacting biotic and abiotic components. The structural components are shelter and food and feeding pathways and biodiversity. Functional components include the rate of nutrient cycling, the rate of energy flow, and biological regulation. Healthy intact seagrass ecosystems provide services since they relate to the health, stability and well-being of the environment in which they live, but also to that of human populations.

Key words: seagrass, ecosystem, production, nutrient cycling, energy flow, biological regulation, ecosystem services

Дано определение экосистемы морских трав как единицы биологической организации, состоящей из взаимодействующих биотических и абиотических компонентов. К структурным компонентам относятся местообитания, пищевые цепи и биоразнообразие. Функциональные компоненты включают в себя интенсивность круговорота питательных веществ, скорость энергетического потока и биологическую регуляцию. Целостные экосистемы морских трав обеспечивают стабильность и благополучие не только своей собственной среды обитания, но и той, в которой обитает человечество.

Ключевые слова: морские травы, экосистема, поток энергии, биологическая регуляция, экосистемные услуги

Seagrasses are monocotyledonous vascular flowering plants that live in coastal and estuarine areas of the world. They are unique in that they are: 1) usually totally submerged in the water, 2) they possess a root system with stems buried within a soft substrate, 3) they have vegetative and sexual reproduction, and, 4) have flowers fertilized by water-borne pollen.

Seagrasses are not truly grasses. They belong to three families of monocotyledonous plants, but are called seagrasses since they usually form extensive underwater meadows, which re-

semble fields of terrestrial grasses. There are approximately 50 species of seagrasses in 12 genera. Seven genera are considered tropical, while the remaining five are more or less confined to temperate waters [35]. In almost all cases, seagrass communities are multispecific in the tropics, but tend to be unispecific in many parts of the temperate zones.

Seagrasses are found along most coastlines of all continents. They appear to be excluded generally north of the Arctic Circle and south of the Antarctic Circle [48]. *Zostera marina*

L. (eelgrass) extends north of the Arctic Circle only in northern Russia, presumably due to the warming influence of the Gulf Stream [47, 48].

Seagrass beds have long been recognized as critical coastal nursery habitat for estuarine fisheries and wildlife [2, 3, 19 – 21, 23, 26 – 31, 39, 40, 44, 46, 50, 56 – 60, 63, 65]. They function as direct food sources for fish, waterfowl, dugongs and manatees, and sea turtles. They are also participants in nutrient cycling processes, and are stabilizing agents in coastal sedimentation and erosion processes. In recent years, they have received attention as biological indicators of estuarine water quality and ecosystem health as a result of their sensitivity to nutrient enrichment and eutrophication [14].

Description of seagrass ecosystem. An ecosystem has been defined as a unit of biological organization comprised of interacting biotic and abiotic components [47] (Fig. 1).

Up to 1973, most seagrass research was either autecological or ecophysiological in approach. In 1973, the U.S. National Science Foundation sponsored an International Seagrass Workshop in Leiden, The Netherlands, attended by 38 scientists from 11 countries. This group assembled all known information on seagrasses, discovered what were the major gaps in our knowledge, and formulated recommendations as to future research. Among these recommendations was one to view the seagrass community as an ecosystem and that research on seagrasses be conducted from an ecosystem point of view.

Over a period of years, it was found, that even though water temperatures and adjacent communities were different in the tropics and temperate zones, e.g., mangroves, marshes, and coral reefs in the tropics, and marshes in the temperate zones, all seagrass communities displayed similar structures and functions.

Wood et al. [61] summarized the functions of the seagrass ecosystem: 1) relatively high organic production. For some species, this production rivals or exceeds that of subsidized crops; 2) high standing crops which produce large amounts of dissolved and particulate detritus which form the basis of important food chains, both within the seagrass ecosystem and shoreward and offshore as the materials are washed away from the seagrasses; 3) leaves and erect shoots present surfaces for epibiotic organisms to attach to. This increases both primary and secondary productivity, as well as providing a large amount of food sources for fish and invertebrates; 4) because the seagrasses are rooted in their substrate and produce shoots with leaf bundles, they stabilize their habitat. The leaves form a baffle, which slows and retards current and wave activity, which promotes sedimentation of particles as well as inhibiting resuspension of organic and inorganic materials. The roots and rhizomes also form a complex, interlocking matrix which binds the sediment and retards erosion; 5) the dense leaf baffle forms shelter for an extremely diverse fauna for all trophic levels; and, 6) since the leaf baffle generates and entrains autochthonous, as well as allochthonous organic material, an active environment is created for decomposition and nutrient cycling.

In this paper, we describe the seagrass systems in terms of their structural and functional components. The study of structural or functional components of a system alone is too static, since communities undergo change. The complex relations between the various components of an ecosystem have developed over long time periods and are the result of evolution, selection, and adaptational processes within each component [13].

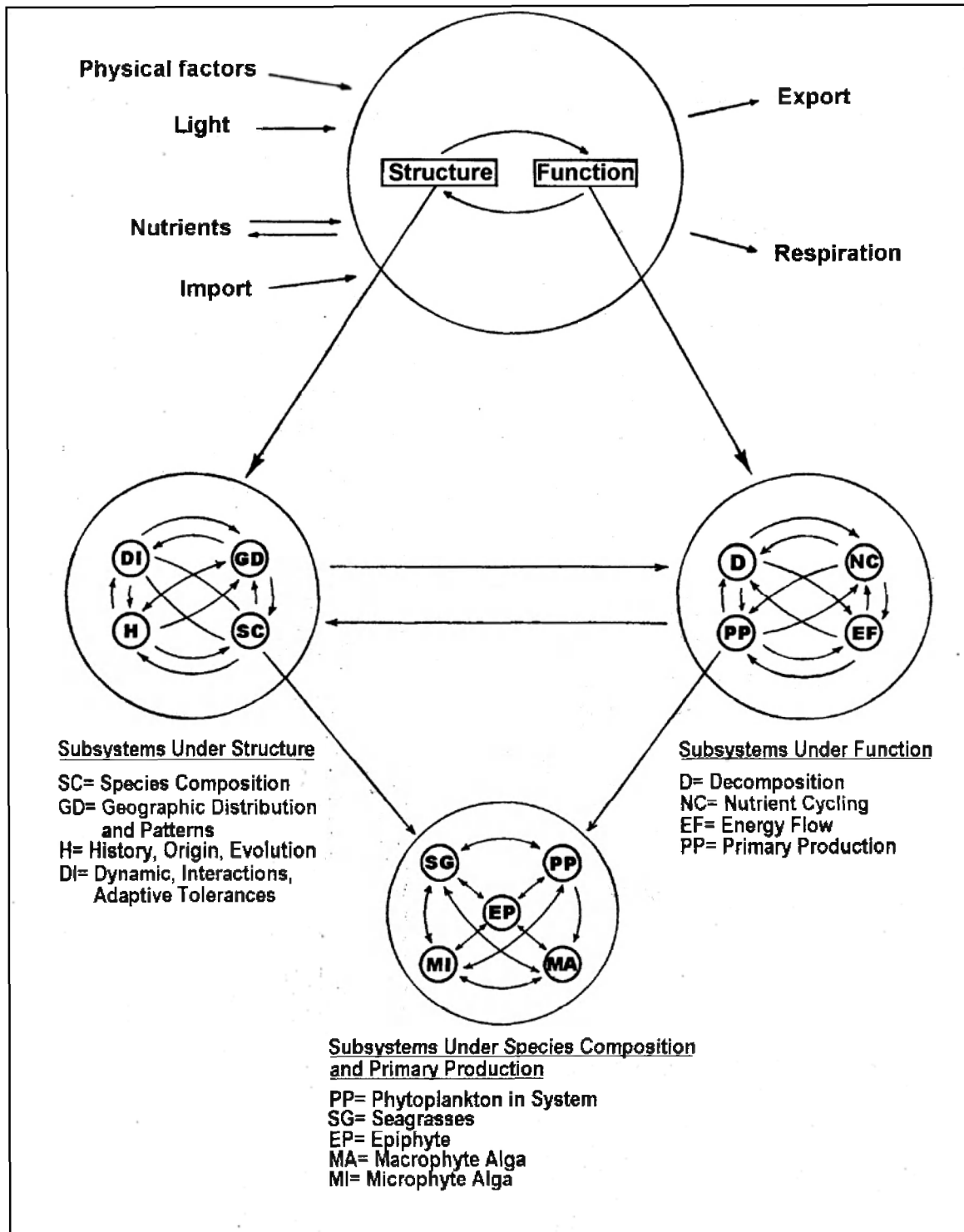


Figure. Conceptual model of a seagrass ecosystem

Рис. Концептуальная модель экосистемы морских водорослей

Structural Components. Structure consists of three major subcomponents that are inter-related: 1) floristic and faunistic composition; 2)

arrangement of the organisms in space and time; and, 3) interrelationships within the community and with the abiotic environment (Table 1) [47].

Table 1. Representative Seagrass Productivities
Таблица 1. Продуктивность некоторых видов морских трав

Species	Location	Productivity (gC/m ² /day)	Source	
<i>Cymodocea nodosa</i>	Mediterranean	5.5 – 18.5	[17]	
<i>Halodule wrightii</i>	North Carolina	0.5 – 2.0	[15]	
<i>Syringodium filiforme</i>	Florida	0.8	[unpublished, Zieman]	
<i>Thalassia testudinum</i>	Texas	0.6 – 9.0	[34, 38]	
	Florida east coast	0.9 – 16.0	[25, 62, 64]	
	Cuba	0.6 – 7.2	[7, 8]	
	Puerto Rico	2.4 – 4.5	[38]	
	Jamaica	1.9 – 3.0	[18]	
	Barbados	0.5 – 3.0	[41, 42]	
	Bermuda	5.6 - 7.2 (leaves - total plant)	[42]	
	<i>Zostera marina</i>	Denmark	1.72 - 0.45 (leaves- rhizomes)	[51]
		Rhode Island	0.4 – 2.9	[9]
North Carolina		0.9 – 1.23 (leaves)	[57]	
		0.9 – 1.04 (leaves) 0.15 – 0.28 (rhizomes)	[unpublished, Kenworthy]	
Washington		0.7 – 4.0	[45]	
Alaska		3.3 – 8.0	[32 – 33]	
Japan		0.3 – 1.8 (leaves)	[1, 37]	
France		1.06 - 0.5 (leaves- rhizomes)	[24]	

The spatial arrangement of seagrasses displays a number of characteristic patterns that can be divided into vertical, horizontal, and three-dimensional. Vertical patterns are characterized by zonation and stratification. Horizontal patterns may be observed over geographic distances or may be due to differences in bottom configuration or prevailing hydrodynamic conditions. The three-dimensional pattern is the way in which the species fill up the available space. This is probably the structural characteristic most decisive for the function of the community [13].

Not all seagrass communities contain all these structural elements. The pioneering communities, e.g., *Halodule wrightii*, are more simply

structured than are the climax communities. So far, no elaborate studies are available in which the framework consists of more than one species. It is not known whether the various coexisting seagrass species in a mixed community are sufficiently different in their anatomical and phytochemical properties to cause further differentiation in the form of development of species-specific epiphytic and epizoic associations [13].

A. Shelter.

The structural function of seagrasses is a result of the morphology of the seagrass plants. The seagrass plants possess an extensive underground rhizome/root system with erect shoots with bundles of leaves, which extend into the

water column. As a result, they create a highly structured ecosystem from a relatively unstructured one. Stauffer [55] classified the diversity of habitats within the seagrass bed as: 1) on the plants, 2) among the plants; 3) on the substrate surface, and 4) in the substrate. When the seagrass ecosystem is intact, the beds serve as nursery grounds, places of both food and shelter, for juveniles of a variety of finfish and shellfish of commercial and sportfishing importance [63].

Seagrasses receive material and energy inputs from the sun and surrounding ecosystems, such as riverine, marsh, and mangrove and offshore coral reefs (in the tropics), and tend to internalize their energy and material production. They export excess material in the form of dissolved and particulate detritus. Seagrass ecosystems can be extremely complex with high levels of biodiversity which function through herbivore as well as detritus food webs.

Seagrass beds are spatially positioned between the inshore mangroves and marshes and the offshore coral reefs, and/or open waters. Thus, a great variety of animals are permanent residents or find temporary shelter within the canopy at some time during the day or night or during seasonal movement at some part of their life cycle. There are seasonal finfish and shellfish that shelter and feed within the seagrasses during their migratory movements. There are also a great number of juvenile fish species which migrate from the inshore mangrove/marsh habitats inshore to the seagrass beds and refuge and feed before migrating offshore to deeper or deep waters [46, 56].

Kikuchi [26] enumerated the reasons for this sheltering function: 1) seagrass form a dense submerged meadow and increase the available substrate surface for epiphytic algae and fauna; 2) dense vegetation reduces the water movement

resulting currents and waves; 3) mineral and organic particles sink to the bottom in the less turbulent water, creating relatively clear water; and 4) the leaf mass reduces excessive illumination in the daytime which facilitates the refuge effect for prey species.

B. Food and Feeding Pathways and Biodiversity.

The photosynthetically fixed energy from the seagrasses may follow two different pathways: 1) direct grazing by organisms on the living seagrass, or, 2) the utilization of the detritus produced from decaying seagrass material, primarily leaves. The export of seagrass material either inshore or offshore allows for further distribution of energy away from its original source and helps to fuel other ecosystems [63].

Of the two pathways, the detrital pathway is overwhelmingly the most important within the seagrass ecosystem. In this pathway, bacteria form the basis of the food web. As they age, leaves release both particulate and dissolved carbon and organic matter, which the bacteria assimilate and transform into bacterial matter. The bacteria are consumed by a host of small organisms, which are then eaten by another larger group of organisms, and so on.

Detrital food webs are long and complex, and lead to commercially and recreationally important food animals. Direct or herbivore food webs are shorter, with perhaps two to three links. A relatively small number of animals feed directly on the plants, e.g., manatees in Florida and dugongs in the Indo-Pacific, a wide variety of waterfowl in the temperate zones, and green turtles, and a limited number of fish and sea urchins in the tropics [35]. In the Arabian Gulf, the valuable pearl oyster finds shelter and food in the extensive seagrass beds [2].

There exists a very large literature documenting the food webs and relationships within the seagrass ecosystems. Kikucki and Peres [27] subdivided the animal community in seagrasses into several components by microhabitat structure and mode of life: 1) biota on the leaves, e.g., mobile epifauna, and swimming fauna which often rest on the leaves; 2) biota attached to the stems and rhizomes, e.g., nest-building polychaeta and amphipods; 3) highly mobile animals swimming through and under the leaf canopy, e.g., fishes, cephalopods, decapods; and, 4) the biota living on or in the sediment [26].

Fonseca et al. [16] concluded that the high biodiversity was the result of the high productivity of the seagrasses coupled with the physical stabilization, which the plants exert on their physical environment. The three-dimensional space created in the water column by the seagrasses is also a decisive factor in the high biodiversity [47].

Functional Components. A study of the functions or processes of a seagrass ecosystem is an analysis of what the various components do. There are three major functional components: 1) the rate of energy flow through the system, including primary and secondary production and respiration; 2) the rate of material or nutrient cycling within the system, including decomposition; and, 3) the degree of biological or ecological regulation in the ecosystem, including the regulation of organisms by the environment and vice versa.

A. Rate of Nutrient Cycling

The production of detritus and promotion of sedimentation by the seagrass leaves provide organic matter for nutrient cycling [63]. Epiphytic algae on the leaves fix nitrogen, thus adding to the nutrient pool of the region [63]. Seagrasses assimilate nutrients from the sediments, transport-

ing them through the plant and releasing them into the water column through the leaves, thus acting as a nutrient pump from the sediment [63]. Seagrass blades, epiphytes, and macroalgae also pick up water column nutrients [16].

Many process-oriented investigators give much attention to turnover rate in seagrasses, the quotient between net primary production and average biomass. Turnover rates of above- and below-ground parts may be different on the same seagrass plant [13]. In order to give turnover values a more functional meaning, it is necessary to study decomposition processes in more detail [47].

Decomposition rates of the various plant and animal substances show great variation from almost no decomposition to instant decomposition. These rates determine whether nutrients will be returned quickly to the system or held in reserve. These rates could also influence the relative predominance of feeding types in a system (particulate feeders, grazers, etc.). If detritus is removed by suspension or deposit feeders, nutrient relationships in the sediment will be altered. On the other hand, if grazers are numerous, a significant amount of energy will be transported away from the system [47].

In an intact, relatively dense seagrass bed, the leaves act as a baffle for wave and current action. This baffling effect effectively reduces water motion within the leaf canopy, allowing incoming and resident particulate matter to settle to the bottom and remain there. This allows water within the seagrass bed to be clearer than water over unvegetated sediments, thus improving water quality for resident plants and animals [16, 63].

B. Rate of Energy Flow

The physical stability, reduced mixing of different water masses, and shelter provided by

the complex seagrass structure provides the basis for a highly productive ecosystem [16, 61]. The ability of seagrasses to exert a major influence on the marine seascape is due in large part to their extremely rapid growth and high net productivity. Leaves grow at rates typically 5 mm/day, but growth rates of over 10 m/day are not uncommon under favorable circumstances [5, 49, 63].

Primary production is the most essential function of the seagrass ecosystem [47]. Production rates are remarkably high. Seagrass primary production rates in Australia vary from 120 gC m² yr⁻¹ to 690 gC m² yr⁻¹, depending on the species [22]. Elsewhere, rates for tropical species vary from 280 gC m² yr⁻¹ (*Halodule wrightii* Aschers.) to 825 gC m² yr⁻¹ (turtlegrass, *Thalassia testudinum* Banks ex König), while the temperate seagrass species vary between 180 gC m² yr⁻¹ (32) to 400-800 gC m² yr⁻¹ [52], (Table 1).

These rates compare with the maximum values for terrestrial plants, but are somewhat lower than the very high rates of the highest agricultural crops or of mangroves (3,000 gC m² yr⁻¹ for sugar cane and sorghum and ~2,000 gC m² yr⁻¹ for mangroves; [22]).

Few data exist on the primary production of seagrass epiphytes and the benthic macrophyte and microphyte components within the seagrass ecosystem. Production of epiphytes can reach 50% of the seagrass production (4, 6, 25, 36, 43). Loose-lying and attached macroalgae within the seagrass ecosystem may account for 2% to 39% of the total above-ground seagrass biomass at times and various places, ranging to almost 75% [12]. Thus, the total primary production of any given seagrass ecosystem may be extremely high.

C. Biological Regulation

Species composition affects biological regulation. Blue-green bacteria on or in the plant or substrate fix nitrogen for seagrass or epiphyte

use. Owing to the high rate of use, nitrogen is considered a rate-limiting factor in the seagrass ecosystem. Seagrass density and biomass variations on spatial and temporal scales are reflections of the nitrogen pool [53]. These parameters in turn affect sediment accretion and stabilization, water clarity (which affects primary production), and further nutrient cycling. Features of the abiotic environment, viz., daily and annual ranges in temperature and salinity, wave activity, and tidal currents, regulate species composition and productivity values. In a holistic sense, at least one major ecosystem property emerges when the system is intact, e.g., the nursery function of a seagrass meadow. The vast interplay of structural and functional characteristics results in a dense, stable environment that forms refuge and shelter as well as food for a myriad of organisms.

Dynamics. Many authors have used the term “seagrass dynamics” to mean everything from density and biomass changes to growth parameters and to normal functions such as primary production and phenological changes. As it pertains to the ecosystem, seagrass dynamics refer to changes in the system in time. The main emphasis is on changes in the structure of the ecosystem. However, changes in structure bring changes in function. The major process involved in ecosystem dynamics is succession.

In structural succession, the seagrass system increases in differentiation, which is associated with changes in floristic and faunistic composition. These changes lead to a structure in which maximum diversity is coupled with the most efficient organization [13]. It is also true that changes occur in system functions, e.g., primary production and respiration increase as structure changes, more dissolved organic matter and detritus are formed, and biological regulation increases as more species are added and as the

plants have a greater effect on modifying the physical environment in which they live.

Succession is a long-term process. Temporary disturbances due to weather or population explosions of grazers may cause quantitative and qualitative changes in the floristic and faunistic composition that may take more than a year to recover from [47]. In many parts of the world where anthropogenic activity is found, e.g., eutrophication in estuaries adjacent to large cities, dredging activities, mining activities, seagrasses have been documented to disappear in great amounts [54]. These disturbances have led in some cases to permanent loss of the seagrasses. Succession may be obscured by long-term cyclic phenomena. There is a possible rhythm in the decline and increase of eelgrass vegetation in the North Atlantic, suggesting that the "wasting disease" of 1931-1933 was an extreme pulse in this rhythm [13].

Ecosystem services. The functions and processes of seagrass ecosystems can be de-

scribed as ecosystem services, since they directly relate not only to the health, stability, and well-being of the physical environment in which they live, but also to that of human populations as well (Table 2) [14; Short., personal communication].

Various agencies and groups have worked on placing financial values on either the seagrass ecosystem or on the estuarine habitats of which seagrasses are a very large part.

Costanza and other authors [10, 11] stated that, for the entire biosphere, the economic value of all the ecosystem services [17] for 16 biomes was estimated to be in the range of 16 to 54 trillion US\$/year, with an average of 33 trillion US\$ / year. He considered this to be a minimum estimate. Coastal environments, including estuaries, coastal wetlands, beds of seagrasses and algae, coral reefs, and continental shelf were of disproportionately high value. They cover only 6.4% of the world's surface, but are responsible for 43% of the estimated value of the world's ecosystem services.

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