DECENTRALIZED ORGANISM EXEMPLIFIED WITH COLONIAL HYDROID SPECIES

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Colonial hydroids, corals, bryozoans, ascidia, and some other aqueous species look as numerous interconnected bodies. However, they are not communities; rather, they are manifold individuals adapted to capturing food particles from flowing water, which is what makes them looking similar to plants organized to capture sunlight. The colonial type of organization is believed to emerge as the result of an incomplete vegetative proliferation associated with that young unit bodies stay connected with their mother. Such manifold or modular organisms are less integrated or centralized compared with their solitary (unitary) ancestors. The structure of such decentralized organisms provide opportunities to study the integration of parts into a whole involving no central organizers. Such relationships between a whole and its parts are featured by many natural and social systems but are still poorly studied. The specialized organizing means, such as the nervous and endocrine systems, are but superstructures built upon the more simple way of inner coordination featured by decentralized organisms whose integrity is based on interactions between numerous equipotent parts. Among the decentralized organisms, colonial hydroids are most convenient for studying and thus may serve as paragons of the decentralized biological organization as such. The salient features of the decentralized organization are: multiplication or polymerization of parts; the absence of regulatory organs; a significance degree of self-sufficiency of parts; a high resistance of the whole to impacts on its part; the plasticity of the shape and a broad variation of the sizes of the whole; ingrowth into the environment; network organization; a cyclic mode of morphogenesis; and indeterminacy of age limits. The implications of the results obtained in studying decentralized organisms for supra-organismal systems, such as populations, ecosystems, or biosphere, are discussed.

***Keywords**: colonial organism; Hydrozoa, modular organization; decentralized system.*

INTRODUCTION

Centralized, Non-Centralized and Decentralized Systems

The two alternatives of system organization, centralized and non-centralized, have been avidly discussed in the scientific literature for more than half a century, but mainly with regard to the social systems, collective management bodies, economy, and information flows, without even minor attempts of system-wide generalizations [67, 98, 138, 153, 162]. However, the conceptual possibilities to analyze the degrees of centralization are much broader, and they can be applied to any systems, including biological ones [148].

The two opposite ways of organizing a complex system are centralization and decentralization.

Centralization means strengthening the role of a coordinating center, i.e. increasing the coherence of processes within a system and their subordination to a certain order or certain signals. This is associated with the specialization of the parts and processes within a system, the restriction of freedom of the parts, and the reduction of uncertainty, both functional and structural, within the system.

Decentralization is increasing the independence of system parts and parallel processes, decreasing the frequency of commands from a center (if it exists), enhancing the variability of the whole and the uncertainty of all its features and, ultimately, making the algorithms of vital processes more flexible.

The decentralized system concept is often applied in the literature to non-centralized systems. However, it is reasonable to distinguish the two types of systems according to their origins. In the first of the types, all elements of a system are the parts of a single organism, which are not disengaged because they have originated from a single "root", as e.g. zooids in a colonial organism. The non-centralized systems that result from decentralization may be called decentralized systems. In the second type, a system is composed of heterogeneous elements, which originate, e.g., from independent organisms of the same species or even different species. Such systems are non-centralized by their origin; they have not been decentralized, i.e., did not undergo a reduction in the degree of their centralization. Differences in the degrees of keenness affect the degrees of integrity of systems and the modes of their self-organization; however, the present article is not concerned with that. Therefore, we will use the terms "decentralized" and "non-centralized" as synonyms, although their scopes are different. The concept of "non-centralized" organization is broader than that of "decentralized" organization, the latter being a particular case of the former. With all that, the present paper mostly addresses their common features as they may be exemplified with decentralized systems.

Non-centralized systems, including decentralized systems, are entities that consist of interacting parts whose functions are not controlled by any individual specific body.

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In any natural system, there are signs of centralization and decentralization. The least centralized biological systems are ecosystems, and the most centralized ones are organisms. The simultaneous effect of the environment on all ecosystem components is an analogue of the centralized regulation. Such "control" has very little in common with the internal regulation carried out by the nervous system of multicellular organisms.

The non-centralized mode of integration appears to be inherent in all natural systems and makes the base of their integrity. However, centralization imposes significant constraints on the manifestations of the non-centralized integration.

Rigid control mechanisms have long attracted much more attention of researchers than coordination mechanisms based on the freedom of the parts (components) of a system. In recent decades, the situation has begun to change due to studies and conceptual generalizations related to the non-centralized organization of complex social, biological and technical systems [52, 53, 65, 83, 120, 121]. Knowing the optimal relationships between centralization and freedom is especially in demand in politics, economics, state security, sociology, pedagogy, etc. [81, 92, 143]. This is what makes it important to study other systems based solely on non-centralized coordination.

Decentralized Organisms

In a non-centralized organism, no central control organ is responsible for coordinating the processes that take place in its various parts. The integrity of such an organism is ensured only by the unity of its body, in which all its parts have the same origin, such as a fertilized egg or a fragment of the parent organism, while differentiation and specialization are achieved automatically due to the so-called "positional information", i.e., responses to the specific positions of the emerging parts of a developing body relative to the rest of the body and to the environment [70, 82, 159].

The central control organs include the nervous and endocrine systems. Hence, fungi, plants and animals that lack neuroendocrine regulation can be referred to non-centralized organisms.

The lack of the centralized management of vital activities is especially apparent in the so-called modular organisms, which will be discussed in the next section. They have undergone genuine decentralization, i.e., transition from the centralized organization to the non-centralized one. The centralized organization is featured by unitary (non-colonial) organisms, e.g., hydra or actinia, whereas vegetative reproduction not associated with the separation of individuals results in the decentralized organization (Fig. 1).

The nervous system of a hydra or actinia is underdeveloped, but is sufficient to control the movements of an individual. For example, a hydra or actinia reacts to irritation by shortening its body length and contracting its tentacles. Similar responses are observed in the individual hydranths of a colonial organism. However, in many colonial species, a hydranth does not influence its neighbors [99].

Modular Organisms

All organisms can be referred to the categories of unitary and modular [76, 119, 139].

A unitary organism is characterized by a specific shape and size of its body, minimal variations in its individual development, and a limited number of repetitive organs or parts of its body.

A modular organism is characterized by multiple repeats of its body parts due to a special form of its individual development, which involves *morphogenetic cycles that results in the* polymerization of its organs, the absence of non-repeated (singular) parts able to function as operating organs, and a highly variable body shape and size [35, 39, 48].

In both cases, the individual development starts from a single source, i.e., a fertilized ovum whose division produces a multicellular organism or, upon the asexual reproduction (division, budding, parthenogenesis), from a part of a single initial (maternal) organism. At the early stages of ontogenesis, the unitary and modular organisms are similar by their organization. However, after their individual ontogenies are completed, their subsequent developmental pathways diverse. The modular organisms under favorable conditions can grow indefinitely by reproducing their individual parts: they ramify and form branched or monolithic bodies, which can later disintegrate or retain their integrity. Such unlimited growth is a feature of primitive organization.

At difference from the modular organisms, the unitary ones slow down their growth rate as they age, and the shapes of not only their individual parts, but also their whole bodies become strictly defined[1]. Any constraints imposed on morphogenesis is a manifestation of increasing the complexity of the respective development program. Unitary and modular organisms may relate to the same taxonomic unit. Since the module of an invertebrate animal often resembles a unitary organism, it is believed that unitary organisms are primary, and colonial ones (which are essentially modular) are secondary. If this is so, this means that the formation of a colonial organism is associated with decentralization.

The modular organization is widespread in wildlife. Fungi, many plants and many colonial invertebrates are modular [35, 48, 119]. Sponges, corals, hydroids[2], bryozoans, camptozoids,

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[1] There are numerous examples of growth during virtually the whole life of a unitary organism, but growth gradually slows down in each of such cases, which is not typical of modular organisms.

[2] Although included into the class Hydrozoa, siphonophores do conform to characteristics of a modular body, except for that: (1) they have a non-polymerized organ, i.e. pneumatophore, (2) their stolon virtually does not branch; (3) there exists a common, albeit underdeveloped, colonial ner-

and ascidians represent the contemporary fauna. Modular organisms are a convenient object for studying the characteristic features of decentralization, as well as the regularities of biological systems integrity [35, 49-51, 125].

Decentralization as a Consequence of the Modular Organization

Multiplication of all body parts and the absence of a coordinating organ result in the genuine decentralization, i.e., not just the absence or underdevelopment of a central control system, but the complete elimination of such coordination between modules. "Rudiments" of possible coordination remain in individual modules. This phenomenon can be illustrated with unitary and colonial Cnidarian species. There is a cluster of nerve cells around the oral opening of a hydra or actinia, and the movements of its tentacles, body and mouth are coordinated in some cases. By contrast, colonial hydroids and six-ray corals feature no coordination between zooids, while in their common body (cenosarcum), nerve cells are scattered and do not form plexuses[3].

The individual development clearly shows the stages of transition from a singular species to a colonial one. At all of the stages, the maternal entity is not accreted by a new daughter entity, but is expanded into a new structure: zooid → zooid with a protrusion of its wall → zooid with an underdeveloped daughter zooid, combined with it by their common cavity and body walls → two zooids that have retained their connection. Being multicomponent, the colonial individual loses its inherent centralization, which remains limited to only a part of its organism.

Relatively low integrity of the colonial organisms compared with the unitary ones is manifested in the ability of the former to continue normal life after losing a considerable part of the body. Unitary organisms survive in such cases due to the regeneration of the lost body part. Colonial organisms are also capable of regeneration, but they continue to function normally without it too. An organism that is modular both anatomically and functionally is simpler than a unitary one. Although it may consist of a much larger number of parts, in some cases different from each other and altered compared with a single analog, neither of the colonial organisms used above as examples has reached the degree of integration characteristic of its single analogue. This is most clearly demonstrated by the level of morphogenetic regulation, which is always higher in single organisms than in colonial ones.

Decentralization appears to be conformable to nature. Because a whole body is the sum of numerous modules that develop in accordance with the carrying capacity of their habitat, the plasticity of the shape and size of the whole body is enhanced, which may be ecologically advantageous over the strictly defined shapes and sizes of unitary organisms. The centralized control of growth and other vital functions turns out to be meaningless and even harmful in the context of adaptation of a sessile organism to an anisotropic (asymmetric) medium.

Nevertheless, there are examples of secondary centralization, e.g. in *Octocorallia*, when a colonial organism acquires an orderly organization, such as is the case of the structure of sea feathers (the order *Pennatulacea*), and becomes capable of synchronized responses of the whole body to irritation [144]. The achievement of integrity level similar to that of unitary organisms is an adaptation to specific living conditions and is rare among colonial organisms. Charles Darwin described long ago the amazing ability of sea feathers to dig themselves quickly into silted sand [11]. G. Spencer believed that in the course of phylogeny this could lead to a super-organism consisting of multicellular organisms that have undergone progressive integration along within increasing specialization of multicellular individuals comprising it [55].

Colonial Animals

Considering the decentralized organisms will be confined below to colonial organisms, most of which are invertebrates.

Organismic colonies (cormuses) or, more accurately, colonial organisms are found among metazoans, including sponges (*Porifera*), corals (*Anthozoa*), hydroids (*Hydrozoa*), bryozoans (*Bryozoa*), camptozoans (*Entoprocta*), and tunicates (*Ascidiacea* and *Thaliacea*).

Colonial hydroids are the most suitable biological model to study the non-centralized self-organization.

The objective of the present article is to sum up scattered information about functioning of colonial hydroids as decentralized organisms and to determine the possibility to extrapolate the established regularities to other non-centralized integrated systems. The article is based on studies supported by Grants Nos. 11-04-00994-a, 07-04-00736-a, 98-04-49342-a, and 95-04-12071-a from the Russian Foundation for Basic Research

The Original Studies of Decentralized Organization at the Base of the Present Discussion

Among several dozen species of colonial hydroids available for our studies, the two species most suitable for examining the patterns of decentralized organization are *Gonothyraea loveni* (Allman, 1859) and *Dynamena pumila* (L., 1758). Both species, which belong to the order Leptothecata of the class Hydrozoaof of the type Cnidaria, are

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vous system, despite the absence of an integrating organ. Nevertheless, the sum of characteristics makes it possible to regard siphonophores as modular non-centralized organisms.

[3] The only exception are siphonophores whose nervous system is developed better. Siphonophores are integration champions among modular organisms. Once, siphonophores were viewed as the crown of the evolutionary integration of a colony. However, nowadays another hypothesis is accepted: siphonophores results from neoteny, whereas their high integration is a direct consequence of the underdevelopment of their zooids and the preservation of the original integrity of the respective single organism.

referred to the two families, Campanulariidae and Sertulariidae, respectively, of highly organized animals, which differ in the morphogenetic pathways of shoot formation.

The advantages of these species as objects for studying the functioning of non-centralized colonial organisms are as the following:

– Highly transparent tissues and integuments allow examining the flows of fluids within the cavities of intact colonies, the harvesting of food particles by gastrodermal cell, the movements of specialized cells (e.g., cnidocytes), and the pulsations of cell layer.

– Growth rate is sufficient to study changes in the shape and size of a colonial organism during several days or weeks.

– The sizes of zooids, shoots and colonies make it possible to study them with conventional optical microscopes at a ×8 to ×80 magnification.

– Easy handling under laboratory conditions at temperatures 15-18 °C, which are close to the room temperature, upon feeding with *Artemia salinalarvae*.

– The ability to grow on glass plates is convenient for live colonies microscopy.

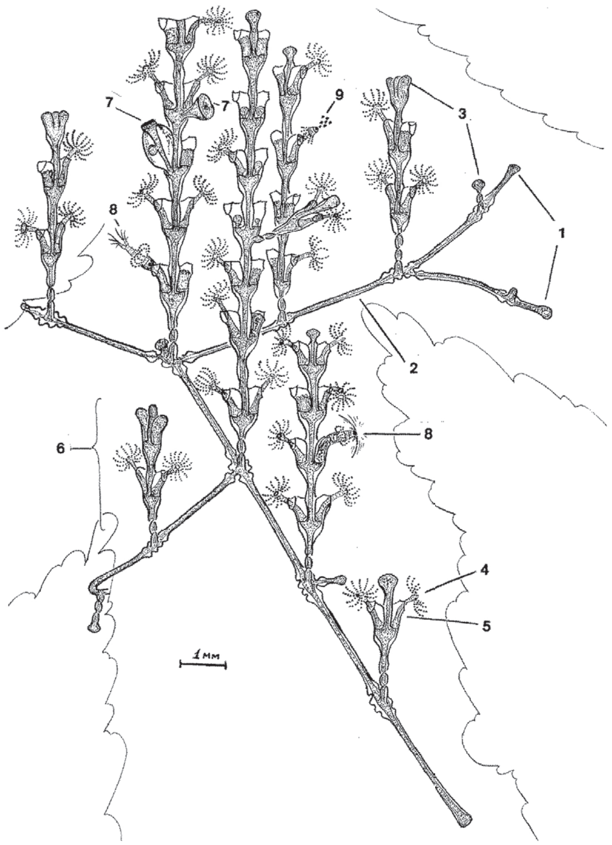

Fig. 1. A schematic drawing of the colonial hydroid *Dynamena pumila* (L.) (reproduced from [33]). 1. The growth apex of stolon. 2. Stolon. 3. The top of a growing shoot. 4. Hydranth. 5. Calicle. 6. Offshoot. 7. Gonangium. 8. Hydranths that capture prey. 9. Hydranthsexcretions.

To clarify some specialized features of the structure and functioning of colonial organisms, nine more species were used besides the above two:

Clava multicornis (Forskal, 1775) (Clavidae);
Ectopleura larynx (Ellis et Solander, 1786) (Tubulariidae);
Abietinaria abietina (Linnaeus, 1758) (Sertulariidae);
Hydrallmania falcata (Linnaeus, 1758) (Sertulariidae);
Sertularella gigantea (Mereschkowsky, 1878) (Sertulariidae);
Sertularia mirabilis (Verrill, 1873) (Sertulariidae);
Laomedea flexuosa (Hincks, 1861) (Campanulariidae);
Obelia geniculata (Linnaeus, 1758) (Campanulariidae);
Obelia longissima (Pallas, 1766) (Campanulariidae).

Experimental techniques have been described in earlier publications [20, 23, 26, 27, 29-31, 40-43].

The branched tubular body of a colonial hydroid is formed by the *stolon*, which adjusts to a substrate, and by *hydranths*, which branch from the stolon, or *shoots*, which bear hydranths (Fig. 1).

Body wall is composed of two layers of myoepithelial cells (MEC) with a thin non-cellular mesogloea *(basal membrane*) between them. A two-layered body structure is featured by both, the hydranths and the *coenosarc*, which connect hydranths. In addition to MEC, the outer layer of cells (*epidermis*) comprises several types of specialized cells, including glandular, urticant, nervous and undifferentiated cells (i-cells). The epidermis secretes the chitin-like envelope (*perisark*), which serves for protection and support. The inner layer of cells (*gastrodermis*) contains glandular cells in addition to MEC. The common cavity of the tubular body is filled with a liquid (*hydroplasm*), containing food particles derived from prey partially digested by hydranths. Growth is confined to certain areas of the body, i.e. to the *growth zones*. The growth zones are usually located directly after the terminal sections of the stolon and shoots, which are called *growth apexes*. Branching is of the budding type that is the initiation of new growth apexes is confined to certain areas, i.e. *budding zones* [33].

Analysis of Findings obtained in Studies of Hydroids and Other Colonial Organisms

In the past, a unitary organism was considered as an individual, whereas a modular organism, as a colony of individuals. However, this assumption proved to be erroneous [33]. A colonial organism originates from the zygote or a part of the body of the maternal organism, and all its modules are the parts of the same whole having common metabolism, whereas organisms that coexist in a genuine colony originate from different ancestors and do not constitute a single organism having its own metabolism. A unitary and a modular organism are both individuals, but they represent two opposite strategies of morphogenesis: any repetition (multiplication, polymerization) is attenuated according to one of them or is enhanced according to the other. It is believed that the vegetative reproduction represents an intermediate strategy of morphogenesis or, possibly, a transitional stage between the unitary and the modular organization.

Vegetative Reproduction

The vegetative reproduction is widespread in all kingdoms of life, including invertebrates [19]. This mode of reproduction provides for cloning of individuals, increasing of population size rapidly under favorable conditions, and recreating a population from a particular individual. At the same time, the vegetative reproduction often results in overpopulation and increased intraspecific competition [68, 90]. Therefore, the vegetative reproduction is most beneficial under conditions of high mortality and least beneficial under stable conditions characterized by low mortality [33].

The transition from the vegetative reproduction of unitary individuals to the modular organization of decentralized organisms is theoretically possible in cases where, for some reasons, the daughter individuals do not separate from the maternal one. As early as in 1744, Abraham Trembley described a hydra, in which offspring separation occurred with a delay sufficient to allow budding and the appearance of second-order offspring on buds (Fig. 2) (see [56]).

This phenomenon was studied in more detail in *Moerisia maeotica* (“marine hydrae”) in which the delayed separation of daughter zooids develop upon food deficiency [27]. The daughter species that remain connected with the maternal organism can get food from a temporary colony (Fig. 3).

According to G. Spencer [55], a delayed separation of individuals during vegetative reproduction may be fixed in evolution if it is beneficial in some way. This eventually may result in temporary to permanent colony transformation. This assertion seems so logical that it has never been checked. There was a theory of gradual strengthening of individuality of a colony associated with decreasing the individuality of individuals therein [1]. However, closer examination of various examples revealed internal contradictions in this concept [33]. Some large taxa, such as the type Bryozoa and the subclass Octocorallia were found to have no primary single organisms. Instead, colonial and secondary single individual organisms developed only upon the reduction of coloniality [1].

The hypothesis that coloniality results from vegetative reproduction is inconsistent from the morphogenetic point

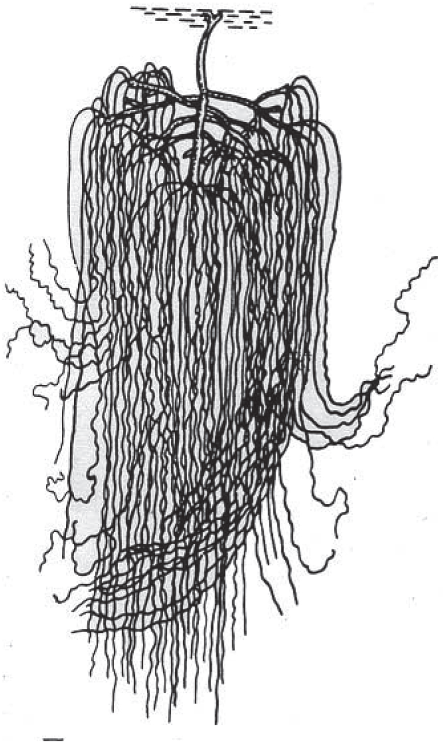

Fig. 2. Temporary colony of hydras developed as a result of delayed separation of the daughter organisms from the maternal one (see [56])

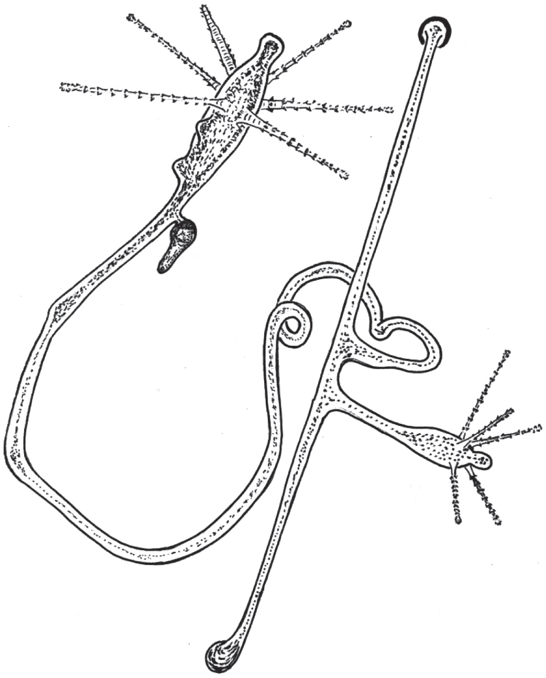

Fig. 3. Temporary colony of *Moerisia maeotica* (“marine hydrae”) developed under food deficiency conditions (see [27])

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of view too. Vegetative reproduction can be subdivided into three types based on the localization of the sites of the formation and separation of daughter individuals: 1) transverse division of the maternal body; 2) longitudinal division of the maternal body; and 3) lateral budding from the maternal body (Fig. 4).

If coloniality was preceded by separation of daughter zooids from the maternal body, it is reasonable to expect that a delay of this process would result in the formation of colonies of zooids separating directly from other zooids (Fig. 4, *1*). Indeed, in primitive six-ray corals, colonies develop by the longitudinal division of corallites so that two daughter zooids extend the maternal one to from a bifurcation (Fig. 4, *2*). However, this is not the case in Octocorallia and Hydrozoa. Their zooids are connected to each other indirectly via the coenosarc, i.e., the common body of the colony. In Octocorallia, zooids are formed from the collenchyma (Fig. 4, *4*); in hydroids, they are formed from the stolon (Fig. 4, *3*) [33].

In the case of, e.g., hydroids, it is reasonable to assume that at first there could be a single ancestor, then a polyp with a stolon, and thereafter a colony. In this sequence of events, the vegetative reproduction occurs at the final stage: the formation of the daughter individuals take place not on the maternal individual, but on new structures not featured by unitary individuals, i.e., the coenosark and the stolon. The mode of initiation and arrangement of zooids in the simplest colonies of hydroids suggests the leading role of the proliferation of the basal part of polyp body without the direct budding and separation of the daughter polyps.

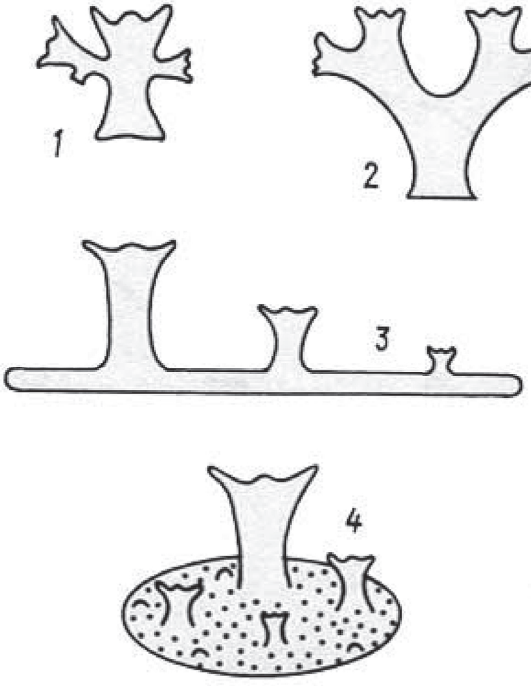

Fig. 4. Variants of zooids positions relative to each other during colony formation: 1) upon lateral division; 2) upon longitudinal division; 3) upon budding from the stolon; and 4) upon budding from the collenchyma (reproduced from [33])

If zooids of the colonial hydroids are formed on the common body rather than on other zooids, then coloniality could not result from the vegetative reproduction of non-colonial ancestors, which did not yet have a common body, and thus their budding or division occurred directly on their zooid. This contradiction casts doubts on the hypothesis that coloniality evolved via vegetative reproduction.

The above contradiction may be resolved upon the assumption that the unitary organization, vegetative reproduction and modular organization are the three components of the same phenomenon, which are expressed differentially depending on the morphogenetic capabilities of a taxon and the ecological strategy. This phenomenon is polymerization. The absence, or rather the blocking of polymerization, is a prerequisite of the unitary organization. Polymerization associated with the formation of detachable units is vegetative reproduction. Polymerization associated with preserved connections between the units formed is a way to increase the size of a body. Each of the three variants of the polymerization process has its own specific morphogenetic and ecological features.

Polymerization as the Basis for the Formation of a Modular Organism

Polymerization and oligomerization are two opposite mechanisms for changing the organization of any system [12]. Polymerization is multiple repetition of a certain structure [16]. The emergence of multicellular organisms also fits the concept of polymerization [17]. Daughter cells, which remain being connected with both the maternal cell and other daughter cells, become not just a community of cells, but rather an integral structure of a higher level than that of an individual cell [18, 62]. Polymerization can also take place in a multicellular organism in the form of repetitions of certain parts of its body or organs [14, 15, 57]. Multiple repetitions of the same structures result in the development of metameric animals (polychaetes, arthropods) and all modular organisms, no matter what type they belong to [39].

Oligomerization is a reduction in the number of repeated structures, i.e., cells, segments, organs, or zooids. Oligomerization occurs in parallel with increasing the centralization and integrity of abody.

Oligomerization is one of the mechanisms of the evolutionary complexification of organisms. There are many examples of the initial multiplication of an organ, e.g., the limb in arthropods, followed by the specialization of the emerged repeats and reduction in their number in the course of subsequent evolution [13]. Biological evolution as such is a consequence of increasing the number and diversity of features, individuals and populations, and of subsequent natural selection and specialization.

Polymerization and oligomerization take place not only in nature, but also in society. Polymerization may be exemplified with the increasing number of workers employed in some production as well as with the growth of network institutions, the construction of unified multi-apartment houses, and the expansion of urban areas. Oligomerization may be illustrated with the reduction in the number of employees due to the specialization and increased productivity of the remaining staff, with complex shopping centers instead of numerous small identical shops, and with increasing the diversity of services and entertainments instead of their multiplication by replication.

In management, polymerization is the predominance of quantity, whereas oligomerization is a qualitative innovation, i.e., improvement.

Polymerization at the level of multicellular organisms is most clearly seen in two the variants of individual structure, i.e., metameric and modular. They are often unreasonably considered sub-variants of the modular organization.

The *metameric* structure of an animal organism is expressed as multiple linearly arranged segments, which are the stereotype parts of the body. In the simplest case, they all are identical, except for two segments, the head and the tail, which differ from the other segments. This makes the metameric structures different from the modular ones. As a rule, metameric animals, such as annelids and arthropods, are unitary and mobile. Metamerism facilitates nervous system centralization and the subsequent segments specialization (oligomerization). For plants, "metameric" is essentially the term used to designate their modular organization [48, 58, 60]. This parallelism stems from the fact that the term "metameric structure" was introduced in botany earlier than the term "modular structure". This resulted in a superficial analogy between body parts repetition in a non-centralized plant organism and segments repetition in a unitary animal organism featuring all attributes of centralization.

The *modular* structure of an organism is expressed in the multiplication of absolutely all of the parts of its body, without exceptions [36, 39]. Modules can be found in colonial hydroids: zooids, segments (internodes) of a shoot, segments of the stolon, shoots themselves, branch shoots, and growth apexes. As a rule, the modular structure is accompanied by branching, i.e., the linearity of such structures is not typical for them.

Whereas the metameric structure is in animals an example of the polymerization of body parts upon preservation of the centralized organization of an organism, the modular organization is an example of the polymerization of body parts upon the loss of the centralized organization of an organism [39]. Therefore, *metamerism is only a variant of the structure of a unitary organism, whereas coloniality, such as of a modular organism, is a variant of an alternative to the unitary organization*. The difference is rooted in the different ways of adaptation to the environment (see below).

Cyclic Morphogenesis as the Basis of Modular Organization

Cyclic morphogenesis is the basis of the formation of a modular organism. Shoots and stolon segments are formed by a certain sequence of morphogenetic changes, which ends to form starting points for the next segments [36, 44]. With regard to plants, this phenomenon is called the "open growth" [25, 48, 59].

Fig. 5 shows the formation of a next segment in a shoot of the colonial hydroid *Gonothyraea loveni*. First, a segment having several identical constrictions is formed on the tube of a shoot, then a smooth segment is formed, then a segment with constrictions is formed again, its beading, however, being narrowed, then a dilation is formed, and finally a zooid emerges and growth discontinues. Simultaneously, a swelling, which is the germ of the next segment of the shoot, appears in a strictly defined place on the boundary between a smooth and a beadlike segment.

Repeated stereotyped segments of a shoot and the stolon of a hydroid are called *interstices*, by analogy with plants [47]. In morphological terms, an interstice is a segment between consecutive branching sites; however, in essence it is the product of cyclic morphogenesis, multiple repetitions of the same growth algorithm resulting in the formation of stereotyped modules of a colonial organism or a plant.

The cyclic morphogenesis is characteristic of modular organisms [39, 48]. Instead of growing in size and becoming progressively differentiated, as it is inherent in unitary organisms, the modular ones grow predominantly outside the formed parts of their bodies (their modules). The next growth zone is laid, the next segment of the body is formed, and a new zooid develops. The cyclic morphogenesis in hydroids and bryozoans is usually brought about by branching of the longitudinal chains of modules, such as the longitudinal division of an acrescent corallite of a coral.

As a variant, cyclic morphogenesis may be realized as a permanently functioning growth zone, on which the rudiments of hydranths or shoots are regularly formed (Fig. 5). That is how the stolon in hydroids, complex shoots [32] and marginal growth zones in some corals, the apical growth zone in *Acroporacorals* [28], and the growth apexes in highly organized hydroids, e.g., *Dynamenagenus* [34], function.

Once started, a morphogenetic cycle usually continues even under unfavorable conditions, as for example in the case of food deficiency, until the completion of an internode or zooid formation, after which growth may stop until the conditions become favorable again. Therefore, the number of growth zones in a modular organism can be not only increasing, but also decreasing in accordance with the amount of food received [2-5, 41]. Thus, *cyclic morphogenesis turns out to be a part of feedback in self-regulation of modular organism growth, so that a change in the number of growth zones is proportional to the amount of food received.*

Proportionality in the Modular Organisms

Almost all unitary organisms have definite body shapes, which maybe expressed as the ratios of the lengths and widths of their body segments, limbs, organs, etc. Certain proportions of the linear dimensions or volumes are characteristic for each stage of life cycle and may be expressed as indices. In the process of growth, proportional relationships between body parts may be constant (the isometric growth) or may change (the allometric growth). In any case, the proportionality of body-build is an indispensable characteristic of unitary organisms.

In modular organisms, the concept of proportionality of the body shape is applicable to its separate parts, for example, to zooids, leaves or modules. However, the shape of a modular organism, especially a branched one, is so variable and unstable that for long no attempts have been being made to find proportions in the colonies of hydroids, corals or bryozoans. It was believed that any colony, being an association of individuals, is not subject to restrictions applicable to organisms.

Nevertheless, the morphological integrity of colonies has been found, at least in hydroids [23, 26, 33]. The proportionality of a colonial organism is expressed as the ratios of its modules: the number of hydranths vs. the number of growth apexes (H/T); the number of hydrants vs. the length of the cenosarcum of the entire colony (H/L); and the number of growth apexes vs. the length of the cenosarcum (T/L). The ratios between the numbers of colony modules are maintained within certain limits during colony growth. This is an indirect confirmation of a feedback between the number of zooids and the number of growth apexes, as well as the rate of growth.

Such feedback is realized through cyclic morphogenesis. When food is in excess, branching of shoots and stolon takes place, i.e. there appear additional growth zones that consume the available cellular material. Upon food shortage, some of growth apexes cease functioning at the stage of morphogenetic cycle completion. As a result, cell material necessary for growth is reallocated to the remaining growth apexes and, primarily, the stolon. This means that *the structural proportionality of a colonial organism is realized through changes in the number of different types of modules in it* [40].

Limitations to the Morphogenesis of the Parts of a Modular Organism

Even though the shape of a modular organism varies widely, the shape of its individual parts may be quite stable,

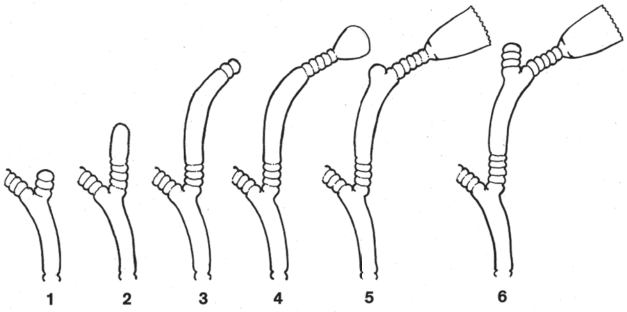

Fig. 5. Cyclic morphogenesis of a shoot in the colonial hydroid *Gonothyraea loveni* is an example of a temporarily functioning growth apex (see [33]): 1 to 6: the successive stages of shoot growth (the formation of a module)

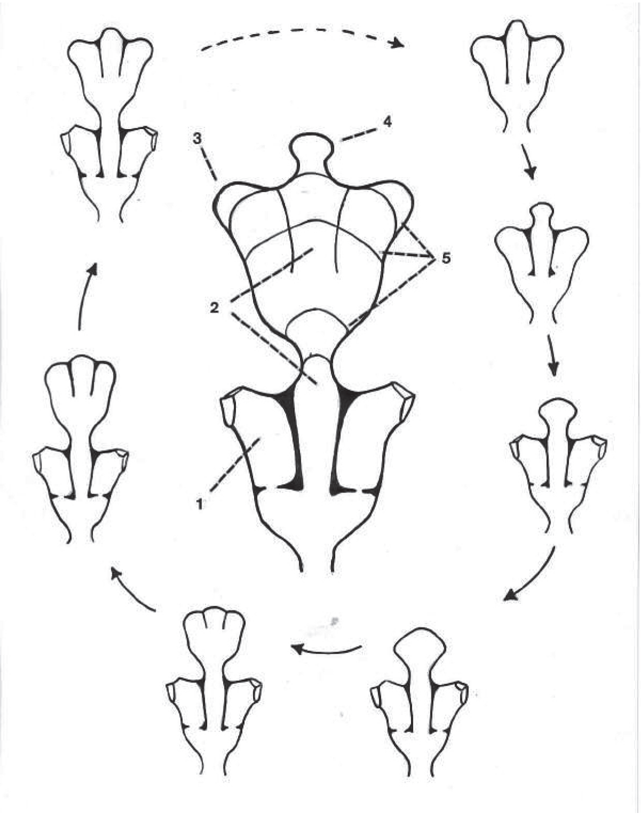

Fig. 6. Cyclic morphogenesis of a shoot of the colonial hydroid *Dynamena pumila* is an example of the constantly functioning growth apex (see [34]): 1) hydrotheca; 2) shoot stem; 3) the rudiment of a nascent hydranth at shoot tip; 4) shoot tip; 5) contours of successive stages of shoot tip growth

i.e. comparable to that of a unitary organism. This applies to both, individual modules and supra-modular levels of organization, e.g., to the shape of a shoot and of its branches. There exist feather-shaped shoots, in which the lateral branches are located in the same plane and in a certain order. Shoot morphogenesis in such cases includes lateral shoots initiation in the course of an intermodal development cycle (Fig. 7). This is a more complex variant of morphogenesis, which differs from a simpler one by considerable constraints on budding (lateral buds initiation). In the case of the unlimited growth of lateral branches, shoot shape is not just feather-like but triangular. If the growth of the lateral branches is constrained by a certain number of morphogenetic cycles, then the shape of the shoot is more feather-like, since all of the lateral branches that extend from the shoot stem are of the same length, except for the youngest ones. In all cases, instead of the free initiation of lateral shoots or the unlimited growth of branches and zooids, morphogenesis becomes increasingly constrained as to the patterns or durations of processes implicated in it [23, 32, 104, 111].

The Ecological Importance of the Colonial Organization

The modular structure of an organism is an adaptation to its sessile mode of life associated with that it has to obtain vital resources from the environment that is moving relative to its position.

In animals, the modular organization is always associated with increasing the number of organs for grasping food: "poly-mouthness" or "multi-headedness". Poly-mouthness, i.e., an increase in the number of zooids, allows a sessile organism to capture food particles or prey suspended in moving water. Poly-mouthness[4] corresponds to the ecological strategy of filtration, i.e., capturing of nutrient objects from water flow, as opposed to the search and hunting strategies. This is true for all colonial invertebrates featuring a common body (cormus), such as sponges, hydroids, corals, siphonophores, bryozoans, and colonial ascidians. The effectiveness of poly-mouthness increases due to specialization in capturing of small prey, its concentration in the environment being much higher than that of large prey. This is easily seen in the evolution of the colonial organization within a class, i.e., from primitive colonies with large zooids to complexly organized colonies with small zooids [32, 47]. The progressive decrease in the size of hydranths is a manifestation of miniaturization, which is a widespread phenomenon in wildlife [54, 71, 132].

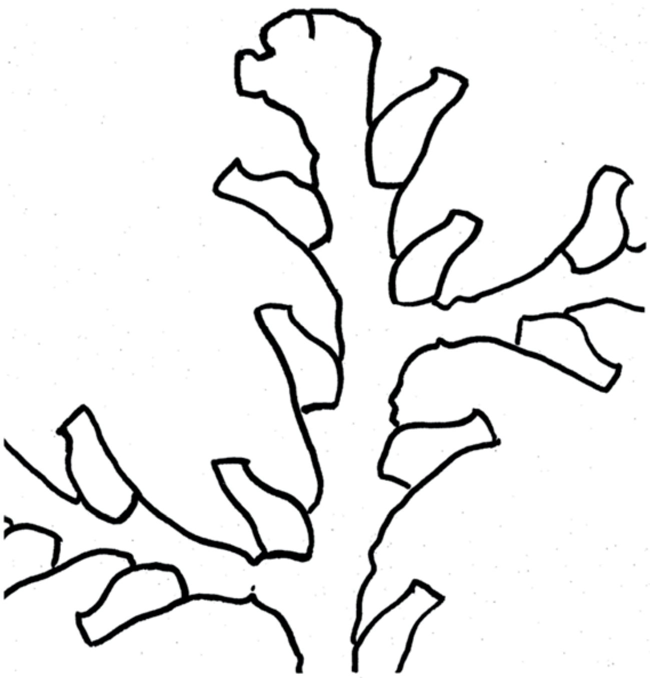

Fig. 7. A feather-shaped shoot of the hydroid *Abietinaria abietina*with a lateral shootinitiated at its growth apex

Miniaturization

In colonial hydroids, miniaturization as an evolutionary trend is manifested in the order Leptothecata, which differs from the order Anthoathecata by smaller zooids and the presence of the perisark not only around the coenosark but also around the zooids. Because the shape of the perisark around the zooid is significant in taxonomic terms, this structure is termed specifically as "hydrotheka". At difference from all Leptothecata hydranths, which stop growing after the completion of their morphogenesis, Anthoathecata zooids continue to grow after their morphogenesis is completed, i.e., after tentacles and oral opening have developed and independent capturing of food has become possible. Underdeveloped hydrants are able to capture prey, hold it with tentacles, swallow and partially digest it. However, they do not form the reproductive organs, gonophores, where the baby medusas with sex gonads or the gonads themselves develop. Growth cessation in zooids is associated with blocking of cell proliferation within their bodies [40].

The above affects not only the growth of zooids, but also the duration of their life cycle, because the insufficient replenishment of cells results in the depletion of the originally available reserves of the most readily spent cells, i.e., urticant and glandular cells. That is why hydranth lifespans known from the literature are shorter in the order Leptothecata than in Anthoathecata [27, 29, 30, 42, 80].

Filter Feeding

Filtration of small particles from water is a mode of feeding common to both, unitary and modular aquatic

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[4] Environmental strategy [150] is a convenient and capacious concept not limited to nutrition, behavior, reproduction or life forms. For example, the evolutionary adaptation of hydroids to feed on small prey is accounted for by at least three specializations: attachment to the substrate, a branched body shape, and a small size of zooids (miniaturization).

invertebrates [83]. The specific feature of adaptation of modular invertebrates to capturing of water-borne food particles is their attachment to the substrate and formation of a kind of net by their branched body. Within the class Hydrozoa, this environmental strategy is clearly expressed in the orders Anthoathecata and Leptothecata. Other modular animals not referred to the class Hydrozoa are also specialized in consuming small food particles from the surrounding water mass [82, 106, 136]. Only the most primitive representatives of modular organisms, such as some corals that have large and innumerous corallites, are able to feed on large prey [158].

Hydroids and corals capture food objects with their specialized harpoon cells, cnidocytes. Bryozoans and camptozoans filter out small particles with cilia on tentacles located outside of zooid body. Sponges and ascidians also filter water with cilia, but by passing it through the cavities of their bodies.

The transition from the unitary to the modular organization ensures the formation of a networked body without significant rearrangements of the primary structure.

With increasing the number of organs for food capturing, the success of each individual attempt to retain prey becomes less significant, whereas *the size of the "net" and the way of its optimal spatial organization become the main factors of successful feeding*. Therefore, of paramount importance are the order of body branching and the distance between zooids.

This trend is clearly seen in every group of modular animals. In hydroids and eight-ray corals (Octocorallia), the most perfect are the feather-like shoots that are oriented across the prevailing water current [87, 105, 133, 151, 156]. The formation of such a structure is accompanied by ordering of its branching and restricting of the growth of zooids and higher-order branches [43, 103]. The effectiveness of filtration [45] and, therefore, of growth and reproduction depends on the ability to withstand the flow of water. A number of features of shoot morphology determine the ability to withstand bending, i.e. the ability to stay across the flow of water [108]. The shoots of hydroids become stronger when shoot stem diameter and walls thickness increase, several trunks are fused (polysiphonism), the inclination angles of hydranth axes relative to trunk axis are decreased, the calycles are fused with the trunk, hydranth and calycle size is decreased to the extent that calycles become constrained inside the trunk, etc.

Modular organisms of plants have a similar arrangement. Leaves are analogous to zooids. The size of the leaves and their optimal distribution in space are important for capturing sunlight. In the evolution of the modular organization of plants, the importance of the optimal arrangement of light-capturing leaves rather than of their size increased.

Ingrowth into the environment

Sessile organisms usually dwell in a complexly organized space among other organisms, both modular and unitary. Being unable to change their position by movements and other behaviors, modular organisms, nevertheless, can perfectly conform to the spatial heterogeneity of their environment [93]. The simplest form of ingrowth into the habitat is manifested as the dependency of the form of a colony on the form of its limiting substrate. Thus, the stolon of the hydroid *Orthopyxis crenata* grows mostly longitudinally [6] on the long and narrow leaves of the alga *Phyllospadix iwatensis.*

The shape of a coral colony often depends on the environmental anisotropy, which manifests itself, e.g., in uneven illumination or horizontally stratified water flow [77, 120, 155]. In densely packed communities of corals, any colony turns out to conform exactly to the intricate shape of free space between the neighboring colonies. Coral branch growth stops when adjacent sessile organisms are approached. Stinging cells shoot at dangerously approaching objects. Such combats and their consequences are amply described in the literature [135]. The same maybe seen in the case of plants [72, 127, 147]. Fir trees that grow on open space are symmetric, whereas those that grow in a forest close to other trees are asymmetric. Such asymmetry of an individual tree is determined by the proximity of the neighboring trees on its one side and of free space on its other side.

The shapes of all modular organisms are very diverse, vary in the course of their development and correspond to the area occupied by them in the environment. In plants, the growth of branches is inhibited in the shade, including the shade of a neighboring plant crown [127]. At the same time, branches grow faster on the illuminated side. In the case of hydroids, the growth of the pivot of a colony, i.e. its stolon, and of the outgoing side stolons and shoots depends on the amount of food received by zooids in a particular part of the colony [3]. Growth in the direction where food is most limited slows down or discontinuer. Growth in the direction where food is ample is accelerated, additional shoots are formed there, and lateral branches of the stolon, shoots on them, and lateral branches of the shoots develop. A colony sort of "grows into the available space" and, as a result, closely conforms to it spatially due to branching. The planes of feather-like shoots of hydroids (Abietinaria, Sertularia, etc.) and eight-ray corals (e.g., Gorgonaria) always stand across the predominant direction of water flow [133].

Modular organism "ingrowth" into the surrounding anisotropic space is based not only on a certain degree of independence of processes in the different parts of an organism, but also on the mandatory general organismal integrity. The integrity manifests itself, first, in allocating food resources to those parts of an organism that cannot feed themselves, primarily to the growth zones, and,

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second, in the termination of growth zones functioning in the inefficient body parts and in the orderly resorption of zooids and coenosarc where food is chronically deficient, followed by digesting the cells of these zooids and by transporting the nutrients thus released to the other parts of the colonial organism [5].

Overcoming of Age Restrictions

Changes in the shape of a colonial organism are facilitated by not only the uneven growth of its various parts, but also by the short "lifespan" of zooids. The duration of functioning of food-producing zooids in the hydroids of the order Leptothecata, e.g. in a *Gonothyraea loveni* colony, ranges from two to nine days, whereas the colonial organism itself lives for more than a year [42]. Zooids in hydroids referred to this order grow old and dissolve due to depletion of some cells [80, 40] that are spent in the course prey catching (cnidocytes) or digesting (gastrodermal cells). This is the price for miniaturization and specialization in feeding on small prey.

The cells that make up a zooid do not just disappear for nothing by the end of its life cycle. Instead, they become digested, i.e., absorbed by their colonial organism not only where an aged hydranth dissolves, but by other parts of the body too. During resorption, a zooid undergoes successive stages of dedifferentiation, similar to the reverse development, i.e., tentacles become shorter and then disappear, and the body of the zooid rounds up and shrinks [98]. At the same time, cells from zooid walls enter the gastrovascular cavity where they disintegrate, and their fragments are transported by hydroplasm to other parts of the colony [73].

If there is enough food in the colony, new zooids form within 24 hours at the site of the dissolved zooids, but this does not happen if food is scarce [33]. Upon a more severe starvation, the oldest part of the colony body, its coenosarc, undergoes resorption [3, 5]. Thus, the form of the colony changes not only due to its growth, but also due to involution depending on the availability of food. Old zooids and shoots resorption associated with the continuing growth of stolons slows down colony movement on its substrate.

Repeated events of zooids formation or coenosarc restoration is an amazing example of rejuvenation of an organism [42]. Young zooids replace the resolved ones thus making it possible to overcome age limitations.

Body decentralization is the main prerequisite for significant changes in body shape, as well as for rejuvenation of the components of a colonial organism.

The Size of a Modular Organism

The size of a modular organism, i.e. the number of its zooids and the extent of their control over the surrounding space, determines the prosperity of the respective species. Whereas in the unitary organisms their body weight and strength and the size of their mouthpiece determine the maximum size of their prey, in the modular organisms their body size primarily determines the size of the "trapping network", which is a set of small trapping organs distributed in space.

Since the bulk of food captured by individual zooids is consumed not by those zooids that have acquired it, but, instead, is assimilated by the other parts of the colonial organism [24], the growth, branching, and eventually the rate of further increase in the colonial organism depend directly on the number of zooids.

Theoretically, there are no limits to body size and age in the modular organisms. The most striking findings to illustrate this assertion have been obtained in studies of the aspen-poplar (*Populus tremuloides*), which produces shoots from a system of branched rhizomes. The estimated weight of this huge branched organism, which has been growing for more than 80,000 years over a large area in the Fishlake forest (the USA), is about 6,000 tons [118].

Colonial animals, so as trees, could grow indefinitely, if not for external circumstances. Many hydroids die under layers of precipitates or of sediments formed by new organisms or die after the death of the algal substrate on which they grow. Corals can reach enormous ages, up to hundreds and even thousands years [129, 137], but most of them live in an overcrowded space where continuous growth is impossible. Corals may also die because of the impacts of intense waves able to break calciferous colonies or because of fouling organisms or environmental changes, e.g. in temperature regimens. Modular organisms usually do not die of old age; however, simultaneously with their body growth, there may take place their spontaneous auto-fragmentation into parts that continue to grow further [95]. Auto-fragmentation makes it possible to avoid excessive concentration of zooids in the space occupied by them and at the same time to continue their vegetative proliferation.

The larger a colony of hydroids is, the longer it is able to withstand starvation. The physiological integration of the colony provides for the use of the available cellular material for nutrition under nutrient deficiency. Whereas unitary organisms have certain tolerable emaciation limits, beyond which their organs lose the ability to perform their functions, a modular organism, by contrast, reduces the size of its body by decreasing the number of identical modules [34, 80]. In doing so, the organism remains viable and can recover even from a single zooid or a fragment of its coenosarc. The simplicity of organization and multiplication of all vital organs of colonial organisms is what ensures their high viability.

The larger a colony, the more prolific it is. The number of reproductive units produced (medusas, planulas, or frustules) depends on the size of the colonial organism and can vary within very wide limits. There are many examples of high fertility of unitary organisms. The number of germ cells in one unitary individual may amount to thousands.

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However, this does not mean that the fertility of a unitary organism can increase thousand times in a favorable year. The fertility of a population of unitary organisms depends on not only living conditions, including the abundance and availability of food, but, also, on the size of the fertile population, which is determined by the previous breeding cycles and habitat conditions. No matter how optimal conditions for reproduction develop in a given year, the number of breeding individuals usually increases only slightly (mainly due to reduction in their mortality).

In this regard, the modular organisms are different, especially those that feature a high growth rate. Under favorable conditions, a modular organism increases in size many times before it begins reproduction. Thus, the modular arrangement is better adapted to rapid changes in body size and makes it possible to use favorable growth and propagation seasons more efficiently than it is possible for the unitary organisms. There is still no direct evidence in favor of this assertion, but simple calculations show that the growth and fecundity of fast-growing modular organisms are much more variable than of the unitary ones. Only the unitary organisms that are capable of vegetative reproduction can respond to growth of food resources as effectively as the modular ones can [10].

The growth rate of a modular organism is determined by the specific features of its configuration. The slowest growth rate is featured by massive colonies and the fastest growth rate, by branched colonies that feature thin branches. This has been shown in corals [75, 79]. Branched colonies attributed the genus *Acropora*can grow at a rate of 5 to 20 cm per year, while massive colonies, for example referred to the genus *Montastrea*, at a rate of only 1 to 5 mm per year.

In many colonial hydroids, the daily growth rate of individual branches reaches 1 to 2 mm or more [41, 160]. It is meaningless to calculate their growth per year, since the time of branches and shoots growth is limited, and the increase in the length of the entire branched body of a colonial hydroid depends on its branching. Nevertheless, it seems worthwhile to cite the following data to compare colonial hydroids and corals: the length of one stolon of *Gonothyraea loveni* or *Obelia longissima* colony increases by 5 to 10 cm per month upon moderate uninterrupted feeding at a temperature of 14 to 16 °C.

Such high growth rate is accounted for by the fact that stolons and shoots bodies in the colonial hydroids are tubular, that is almost cylindrical, and the thin walls of the tubes consist of only two layers of small cells separated by the basal membrane. Wall thickness of such tubular body is only 20 to 30 m. It is known that generally the surface of a unitary organism increases twofold when its volume increases three fold [61]. In colonial hydroids, both the surface and the volume of their bodies correspond exactly to their linear dimensions, so by measuring the length of stolons and shoots one can estimate the weight of the colony by multiplying its total body length by a certain constant obtained empirically or by calculations. Upon some allowances, this statement is also true for all other types of modular organisms: fungi, plants, other colonial invertebrates [8, 112]. Thus, the modular structure provides for not only variation of body size within a wide range, but also for rapid grow under permissive environmental conditions.

Motility of the Modular Organisms

The vast majority of the modular organisms are sessile, except for syphonophores (the order Syphonophorae of the class Hydrozoa), salps and pyrosomes (the class Thaliacea of the subtype Tunicata), which slowly sail in water mass due to pulsations of their bell-shaped modules or whole bodies. This is sufficient for syphonophores to trap their prey better and for salps and pyrosomes to filter phytoplankton better. Other sessile modular organisms cannot travel in space by moving their bodies. However, they can travel from one place to another due to the growth of their stolons, which enables them to settle down at new places at the expense of leaving their died out old parts behind.

Such subtle and slow displacement along the substrate can actually lead to significant changes in the conditions of existence. Many colonial hydroids grow on algae. For example, *D. pumila*, *G. loveni*, and *L. flexuosa* live on rockweed thallomes. Dwelling conditions and especially nutrition often differ significantly on the opposite planes of the same thallome. On the inner plane, which faces the neighboring rockweeds, the probability of contact with a prey is much lower than on the opposite plane, where water flow in algae thickets is decreased.

Rockweed thallome width does not usually exceed 2 to 3 cm. As a colonial hydroid grows, its stolons reach the edges of its substrate (in this case, rockweed thallome) and pass to its opposite side. If hunting conditions are better on that side, the rates of stolon and shoots growth and branching increase, thus increasing the number of zooids and the amount of food received by the colonial organism.

Discussion: extrapolation of conclusions

Studying the decentralized organization as it is exemplified by the colonial hydroids allows presenting this phenomenon in its “pure form”, that is, in the absence of the hierarchically ordered regulation of the vital activity of an organism and, at the same time, upon multiple duplications of all processes in it. The parallelisms of processes and their essential independence from each other distinguish fundamentally the decentralized organization from the centralized one. In addition, a system featuring the decentralized self-regulation is easily represented as a set of certain processes and simple measurable indicators.

As shown above, the decentralized organization of the colonial hydroids may be characterized with the following general features:

– *Multiplication* (*or*, according to Zamorsky, *polymerization* [15]) within the limits of a multicellular organism, which is usually regarded as incomplete vegetative reproduction;

– *The absence of regulatory organs*, which are characteristic of the unitary multicellular animals;

– A *considerable independence of components,* i.e. modules and their aggregates (shoots, colony rays), which is expressed in their independent behavior, growth, and morphogenesis;

– A *high resistance* of a colonial organism to impacts on its individual parts;

– The *plasticity of the shapes* and a wide variability of the sizes of adult organisms;

– *"Ingrowing" into the surrounding space, that is* the conformance of the shape of a colonial organism to the surrounding space, which may be anisotropic with regard to the distribution of environmental factors;

– *A network body shape* adapted to capture food and to be fixed on places suitable for life;

– *Cyclic morphogenesis*, i.e. a repetitive algorithm of the formation of the modules of a colonial organism;

– *Overcoming of age restrictions due to* the renewal of modules by their orderly resorption and substitution with new ones.

The above characteristics of decentralization are featured not only by colonial organisms, but also by supra-organismal biological and social systems, i.e. populations, ecosystems, and different social groups.

Multiplication

Whereas a colonial organism is formed by incomplete vegetative proliferation, the *populations* of any species exist due to the completed reproduction of organisms, both sexual and asexual. In both cases, the repeated reproduction of stereotyped components is indispensable for maintaining a complex system. It is not much important how to term this process, i.e. reproduction, multiplication, transcription or polymerization. The result is anyway a set of similar elements, which are equivalent and therefore are not co-subordinated hierarchically in terms of their interactions. An individual is the module of a population. A cenopopulation of different species and their groups is the module of an ecosystem. Humans and their groups are the modules of a social system.

As the components of a system undergo differentiation, i.e., as their diversity increases and their functions become divided between them [13, 50], and as the number and varieties of interactions grow, the degree of integration of the whole, which consists of numerous elements (modules), increases. Integration manifests itself in the ordering of structure (morphological integration) and in the enhancement of self-regulation processes (functional integration).

A colony of independent individuals, such as bees or ants, is a specialized variant of a part of a population where relationships between the members of a family are structured, and individuals are specialized in their specific functions or even are different morphologically (polymorphism).

A society is a particular case of population featured by the species *Homo sapiens*. A diversity of variants of centralization is possible within it, and multiplication manifests itself not only in population size, but also in the sizes of the groups comprising the population.

Within the multiplication context, an ecosystem is the community of species. This approach makes it possible to consider integration processes not only between separate individuals, but also between the cenopopulations of different species making up a biogenocenosis. The number of species is determined by the specifics of the habitat and by the duration of the stable existence of an ecosystem [130, 161]. Interaction between species in an ecosystem is generally represented by mutually complementary trophic levels, i.e. producers, consumers and decomposers, which provide for the turnover of substances, that is, for the renewal of resources.

Essential Independence of Components, i.e. Modules and Their Assemblages

This is a distinguishing feature of all non-centralized systems. At the same time, connectivity between the parts and the whole is still quite evident in animal colonies, in populations, and in ecosystems. Population density is important for every member of a population. On the other hand, the condition of each individual can affect the entire population, e.g. in the case of the spread of infectious diseases. At the ecosystem level, the stability of the entire ecosystem is an important factor for each of the species in it. The stability of an ecosystem depends on its size and on the degree of species duplication at its trophic levels [63, 100, 101, 114, 115]. This also reflects the reciprocal dependence of an ecosystem upon its species. Hence, non-centralized systems are characterized by both the essentialin dependence of their components and their high integrity. The latter is different from the integrity of an organism, yet is still indispensable for invertebrate colonies, for populations, and for ecosystems.

The Absence of Regulatory Structures

All non-centralized systems exist without control structures. Nevertheless, they are characterized by varying degrees of integrity. The highest integrity is featured by organisms. Even a decentralized organism is not disunited but is an integral body. Each individual parts of such an organism is connected with its other parts by receiving food or nutrients from them and by at their disposal completely; that is, for example, zooids of colonial hydroids may decrease in size (resolve) locally because of a number of causes making their cell mass to compensate for the lack of food in the other locations of a colony.

Colonial insects also lack control structures, although the activities of an entire anthill or hive community seem to be ordered and coordinated. This is caused by a high interactivity between the members of a colony, which implies that in their activities every member of the colony affect the others in one way or another. With all irregularity and stochasticity of their interactions, instincts inherent in them predetermine the overbalance of the positive results of activities vs. the negative one.

The lack of managing structures is even more characteristic for populations and ecosystems. The combination of the habitat proper and the genetically determined responses to the environmental factors provides for a certain degree of integrity of both the populations and the ecosystems. For example, the existence of a forest biogeocenosis is possible only under certain climatic conditions depending on the relief and soil. Ponds and lakes are possible only in the hollows of a relief. That is how the environment determines the boundaries of an ecosystem. However, the ecosystem itself changes its habitat and makes the conditions that contribute to its self-maintenance. For example, luminance is lower under forest canopy, and this affects meadow plants growth negatively and forest plants growth positively.

High Resistance to Impacts on Individual Parts

This is a typical feature of the non-centralized systems. The higher system integration is, the greater is the effect of every system component on the rest of the system, and, therefore, the stronger are the consequences of an impact on one of the components of the system for the rest of it [102, 126]. Vice versa, the lower system integration is, the weaker are the consequences of an impact on one its component for the rest of them and for the whole system. All non-centralized systems, be it a modular organism, an animal colony, a population, or an ecosystem, easily survive the damage or even the loss of any of their parts [49, 116, 134, 157].

By contrast, the centralized systems are very vulnerable to damage. It is easy to kill a unitary organism and much more difficult to kill a modular organism. High centralization becomes possible in nature because numerous genetically identical organisms are reproduced in a population. The loss of individual organisms is compensated for by the reproduction of other identical organisms. Population is a typical non-centralized system featuring low vulnerability to local impacts.

It is only due to the existence of the non-centralized organization that centralization becomes possible in the individuals reproduced in a population. In other words, high centralization at the organismal level has become possible only due to the non-centralized self-regulation and low integration at the population level.

The very existence of the centralized organization of a system is possible only if there is a well-developed non-centralized system of which the centralized one is a part. Thus, centralized and non-centralized self-regulation are the two sides of the same coin, i.e. one is impossible without the other.

The Plasticity of the Shape and the High Variability of the Dimensions of an Object

These properties are expressed in non-centralized systems much more strongly than in centralized ones, e.g. in unitary organisms. Actually both, the plastic form and the indefinite size, are important advantages of the non-centralized systems compared with the centralized ones. Any population can provide for the preservation of its species, regardless of the shape and size of the population, if death rate does not exceed birth rate.

"Ingrowth" into the Surrounding Space

This ability is featured not only by modular organisms, such as colonial invertebrates, plants, and fungi, but also by supra-organismal systems, i.e. populations, ecosystems, and social groups. All of them produce excessive numbers of individuals that settle down "randomly" at all possible locations. Those that found themselves in favorable habitats survive, and the rest die. This "trial and error" method makes it possible to use the available space effectively and to spot places that are difficult to detect even by sophisticated targeted searching. This is analogous to speciation by natural selection, as well as to free (i.e., non-centralized) market economy. At the first glance, "ingrowth into the environment" is accompanied in all cases by significant expenditures in terms of both materials and time. Many individuals die, and many social initiatives are doomed to fail in the course of the non-centralized expansion of a population, ecosystem or market. However, the positive effects cover the costs by allowing a population to accommodate to a new place, and, in the case of a successful company, to a new free market niche to gain more profit. The idea of costs thus proves to be erroneous, since material losses must be proportioned not only to the capacity of a system in the present, but also to its capacity in the future, i.e. as it will develop.

The Network Shape of a Non-Centralized System

In colonial organisms, their non-compacted bodies with varying degrees of branching are usually well adapted to capture prey from water stream. This has been established by using hydroids and corals as examples [45]. In the true colonies of invertebrates, family members control a large area around the nest in order to collect prey and protect the space occupied by them.

In both of the above variants, the net-like harvesting of food benefits the system as a whole. In a colonial organism, food obtained by one zooid is transferred to the other parts of the body [20, 29-31, 109, 110, 154]. In bryozoans and ascidians, this occurs despite the absence of a developed distribution system. This is also true of the hymenoptera colonies, where all collected food is available to the whole family and can be used by not only the pickers but by the other individuals as well.

The shapes of populations are also network-like, but the integration effect of this coverage of space is much lower. Populations of all species usually spread over territories rather than concentrate in single places, which obviously corresponds to a network and provides for covering space with such a network. However, populations usually are not characterized by trophic integrations and food redistribution. The main advantage of the network arrangement of a population is the increased probability of getting food, at least by some of its members. This may be enough to save the population itself and thus to preserve the respective species.

For a unitary organism, that is a centralized system, such logic is unacceptable because usually it is not enough for the survival of a unitary organism to provide food to only a part of it since its survival fully depends on the normal functioning of all its parts.

Cyclic Morphogenesis

In general terms, this means a regular succession of developmental states, which ends with the transition to the initial state. According to such generalized understanding, cyclic morphogenesis is not limited to the organismal level alone, but is a particular case of the universal law of cyclicity of natural processes, which is manifested at all systemic levels [21, 64, 69]. As it is known, not only biological processes in bodies, populations and ecosystem, but many physical (e.g. thermodynamics) and chemical processes (e.g. the Belousov-Zhabotinsky reaction) are cyclic too[7]. Social processes also show clear signs of cyclicity, e.g. Kondratyev's cycles in economy [22, 46]. In recent decades, cyclic processes in economics, business, history, politics, psychology, etc. were addressed in many publications.

The succession of generations in a population and wave propagation in an ecosystem are the closest analogues of cyclic morphogenesis among a large number of other analogues [140]. Under the conditions of overt seasonal cyclicity in the environment, reproduction in populations and ecosystems may be possible during certain periods of the year.

However, the cyclic development does not mean that all "modules" of a system undergo developmental stages simultaneously. In a modular organism, the phases of cyclic morphogenesis of its component systems may be shifted. In colonial hydroids, the internodes of shoots and stolons develop independently, whereas bryozoans are characterized by independently developing zooids, and corals, by independent budding of new zooids within growth zones.

In populations, the individual developmental cycles, which usually culminate in reaching the adulthood and in reproduction, also occur independently of each other. In ecosystems, the incoherence of species reproduction may be even more pronounced. However, cyclicity in a habitat common to all may facilitate the synchronization of the processes that are essentially independent from each other.

Cyclicity may be of exogenous or endogenous origin. Exogenous cyclicity depends mainly on external changes. Thus, the seasonal cyclicity is determined by the position of the Earth in its orbit and the location of a given site on the Earth.

The endogenous cyclicity is mainly determined by internal processes in a system. For example, the states of wakefulness and sleep regularly alternate in many organisms, one of the states naturally exhausting itself after some time and making prerequisites for transition to the other state. Such endogenous cyclicity does not change the whole system, i.e. does not drive its development.

In another scenario, endogenous cyclicity is accompanied by certain unidirectional changes in the state of a system after the completion of each regular cycle. An example is the ecological succession, which is a process of unidirectional annual changes in the proportions of species in a biogeocenosis [78, 117, 146][5].

Another example of cyclicity associated with the succession of an ecosystem is its periodic rejuvenation, that is, returning to the initial or an intermediate state of ecosystem development. Being the result of some disturbances of the mature state of the ecosystem because of fires, tempests, or storms, this is usually followed by another cycle of secondary succession [128].

Cyclicity means that development leads to repetition. Only when repetition (multiplication, polymerization) becomes a means for forming multiple stereotyped components of the whole, conditions are created for decentralized reciprocal interactions of equivalent parts. Thus, the endogenous cyclicity of development accompanied by multiplication is the basis of non-centralized self-organization. Such cyclicity is manifested not only in the formation of a colonial organism, but also in cell divisions at the previous level of organization, i.e. in the course of the formation of the multicellular unit organism of a colony, and at the subsequent levels of organization, i.e., at the population and ecosystem levels. The social variants of "cyclic morphogenesis", which have their own specific features, may be considered by analogy with processes at the levels of organisms, populations and ecosystems.

Overcoming Age Limitations

Comparison of unicellular and multicellular organisms offers insights into their age-related features. In unicellular compared with multicellular organisms, lifespans are usually shorter by orders or magnitude (if the existence

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[5] There are various types of successions, but mostly they are driven by internal factors.

of the encysted forms of unicellular organisms is not taken into account). It is difficult to determine the lifespan of individual cells in a multicellular organism. Nevertheless, preliminary data about the lifespans of individual types of human cells suggest that epithelial cells live for 5 days, epidermal cells for 2 weeks, erythrocytes for 150 days, and muscular cells in adults, for 15 years on average [150].

In hydras, all cells are renewed during 20 to 30 days [152], whereas an individual hydra can live for many years [145]. According to our data, the lifespan of a hydranth of the colonial hydroid *Gonothyraea loveni* ranges from two to fourteen days, whereas the entire colonial organism can live for several years [42].

Age limitations in the organismal systems are much more stringent than in the supra-organismal ones. Adaptation to the environment proceeds better at the levels of ecosystems and populations and worse at the level of individual organisms, being limited by their lifespans.

The lifespans of species, which are typical non-centralized systems[6], exceed many times the lifespans of individuals that constitute them. The maximum lifespan of a multicellular animals rarely exceeds 100 years, and in many species is limited to several years [66], whereas the average duration of species existence, according to paleontological data derived from various sources, varies from 10,000 to 5 million years [94, 113, 114, 131]. At the same time, it should be emphasized that at the species level, there is a regular sequence of stages of the historical development of a species, including its formation, youth, primetime, and decrement [90].

At the ecosystem level, adaptation is reflected in varying species composition of a community depending on the conditions of its existence. The tundra, the taiga, the steppe and the desert are vivid examples of responses of respective biotas to their environments, as manifested not only in different species composition, but also in the balanced mutual adjustment of different species to each other, which is expressed in stable turnovers of biogenic substances. Considering ecosystems in their development with due regard to their successions makes it obvious that their lifespans are indeterminate, although they depend on the stability of living conditions.

Populations are able to adapt to the specific features of their habitats due to their genetic variability. The duration of the existence of a population is difficult to define. A success of adaptation of ecosystems and populations to their environments depends not on the duration of their existence, but on the life expectancy of organisms. A shorter life expectancy is associated with a higher probability of rapid adaptation of a species or community to changes in conditions, even though the speed of evolution depends on the duration of life cycle not exclusively, but is determined by a number of other factors [74].

The nodular organisms represent a variant of partial removal of age limitations inherent in unitary organisms, because the modular organization provides for the non-centralized regulation, which provides for a higher stability of a system due to an increase in its morphological and functional plasticity.

Within the above context, age limitations of unitary organisms are necessary because they increase the probability of species survival due to adaptation to environmental conditions.

Combination of the Centralized and Non-centralized Forms of Self-regulation and the Emergence of Centralized Regulation at the Level of the Biosphere

The centralized form of self-regulation has emerged in the course of evolution two times, and, perhaps, the third time is underway nowadays.

Unicellular organisms were the first centralized organisms. The function of a regulatory organ was performed by DNA in them [141, 142]. The emergence of multicellularity was associated with decentralization, i.e. the transformation of the unitary organisms was into the modular ones [18, 123, 124]. The present-time sponges and trichoplaxes prompt an idea about the arrangement and functioning of multicellular organisms without central regulation.

Progressive differentiation of cells [88, 91, 96], body parts and organ systems enhanced the morphological and physiological integration in multicellular organisms, whereas the development of the nervous system was associated with the consolidation and subsequent strengthening of the centralized form of self-regulation [1, 96, 144].

Simultaneously, another decentralization took place at the multicellular level through incomplete vegetative reproduction. As a result, the modular multicellular organisms developed [33]. However, progressing centralization of multicellular organisms remained to be the leading vector of evolution to result in the development of species having a sophisticated brain and higher nervous activity.

Homo sapiens, which is one of such species, has become a monopolist. This species has no competitors, and this has led not only to its prosperity and rapid intellectual development, but also to increasing pressure on the nature. Human race has become a powerful factor affecting the biosphere. Concerns about possible catastrophic consequences of imbalances in the turnover cycles in the biosphere made incentives to revise nature management procedures in the 20th century [37]. However, the imperfection of social processes hampers the practical implementation of the recognized principles and methods

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[6] Species relate to systems with unclear boundaries and insufficiently defined integrity, because there may have been transitional forms between species. Nevertheless, a species is a vivid example of a non-centralized system from the viewpoint of internal relations, i.e. the interaction of individuals.

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of rational and sustainable management of nature that provide for the opportunity to maintain the equilibrium of the biosphere long enough (by our standards), despite the anthropogenic impact, which is increasing significantly.

If the Mankind overcomes social contradictions, then, hopefully, *H. sapiens* would be able to manage not only its relationships with nature but also the natural processes themselves, which would mean the consolidation of the potentialities of the initially decentralized self-regulation with the centralized control and with adequate corrections of deviations from the normal biospheric processes. Actually, this is what V.I. Vernadsky believed in when he envisioned the possibility that the biosphere may enter a qualitatively new state, called the ***noosphere*** by him [38].

However, it should be born in mind, no matter how perfect the centralized organization is, that the highest reliability is, nevertheless, ensured by the decentralized self-regulation [9, 85, 86], which thus requires much more attention than it has received so far.

CONCLUSION

Colonial invertebrates are a vivid example of decentralized organization. It is believed that coloniality emerged as a result of the vegetative reproduction, which was not brought to its completion, that is, because many of the daughter individuals remained connected to the maternal one. Plants have a similar structure, except for that their bodies consist not of individuals, but of multiple parts referred to several varieties. Both, colonial invertebrates and multicellular plants, are similar in that they are characterized by the formation of multiple body parts, none of which becomes dominant or controlling. This process, which is universal in nature, is called polymerization. Parts combined to form an integrated whole can undergo specialization and integration. If both of the two processes are not expressed, then such a system (an organism in the present case) remains non-centralized yet integral, because, although all its parts (modules) are equal to each other, their interaction is sufficient to provide for systemic processes. The non-centralized organization has several advantages over the centralized one. Thanks to polymerization, that is multiple duplication, decentralized organisms are resistant to external impacts and easily overcome damage or disintegration into fragments. Under favorable conditions, they can increase their size more quickly and significantly than their unitary "relatives" can. The forms of modular organisms vary widely; and due to that, they can better fit the space occupied by them. The lifespans of modular compared with unitary organisms are less limited because the former undergo constant renewal associated with that younger body parts develop to replace the older ones, which die or dissolve. Such features make modular (non-centralized) organisms well suited for having network-like structures and functioning modes. Colonial hydroids are a convenient model to study and simulate such principles of self-organization, which are featured by other systems, such as populations, ecosystems, social associations of various levels, and ultimately the biosphere at large.

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REFERENCES

1. Beklemishev VN. Osnovy Sravnitelnoy Anatomii Bespozvonochnyh. T.1 Promorfologiya. Moscow: Nauka; 1964. (In Russ. English version: Principles of Comparative Anatomy of Invertebrates: Volume 1. Promorphology. Univ Chicago Press, 1970)
2. Burykin YuB. [The relationship in the growth of different parts of the colony Dynamena pumila (L.) (Hydrozoa, Sertulariidae) with different amounts of food]. Zhurn Obshch Biol 1993;54(6):722-38. (In Russ.)
3. Burykin YuB. [The dependence of the growth and structure of the colony Dynamena pumila (L.) (Hydrozoa, Sertulariidae) of pathways in a food]. Vestnik MGU Ser16 Biol. 1986;(3):44-52. (In Russ.)
4. Burykin YuB. [Interconnection of processes between growth and sexual reproduction in the colony Dynamena pumila (L.) (Hydrozoa, Sertulariidae) at different levels of food intake]. Izvestiya RAN Ser Biol. 1995;2:240-8. (In Russ.)
5. Burykin YuB. [The relationship of growth and resorption processes at starving colony Dynamena pumila (Hydrozoa, Sertulariidae)]. Zool Zhurn. 1995;74(6):12-22. (In Russ.)
6. Burykin YuB, Marfenin NN. [Growth and the structure of the colony hydroids Campanularia

platycarpa Bale (Hydrozoa, Campanulariidae)]. Zool Zhurn. 1983;62(9):1417-9. (In Russ.)

7. Vavilin VA. [Self-oscillations in liquid-phase chemical systems]. Priroda. 2000;(5):19-24. (In Russ.)
8. Volkov IV. [Spatial Strategy of the plants]. Vestnik Tverskogo Gosudarstvennogo Pedagogicheskogo Universiteta. 2006;6(57):166-7. (In Russ.)
9. Gorshkov VG. Fizicheskiye i Biologicheskiye Osnovy Stabilnosti Zhizni. [Physical and Biological Bases of Life Stability]. Moscow: VINITI; 1995.
10. Grebelnyj SD. [Are there many clonal species in the world. Part One. The difference from the conventional forms of clonal bisexual species]. Zhurn Zool Bespozvonochnykh. 2005;2(1):79-102. (In Russ.)
11. Darvin Ch. Puteshestviye Vokrug Sveta na Korable Bigl. Tom 1. Pervoye Izdaniye s Portretom Ch. Darvina. Saint ptesburg: Izdaniye Knyazya Golitsyna; 1865.
12. Dogel VA. [The phenomena of polymerization and oligomerization of homologous organs in the animal kingdom and their evolutionary significance]. Izvestiya Akademii Nauk SSSR Ser Biol. 1947;4(4):71-86. (In Russ.)
13. Dogel VA. Oligomerizatsiya Gomologichnykh Organov Rfr Odin iz Glavnykh Putey Evoliutsii Zhivotnykh. [Oligomerization of Homologous Organs as One of the Main Ways of Animal Evolution]. Leningrad: Izdatelstvo LGU;1954. (In Russ.)
14. Zamorskiy AD. [Supercellular structures]. Zhurn Obshch Biol 1969;30(6):664-71. (In Russ.)
15. Zamorskiy AD. [Polymerization of organism]. Zhurn Obshch Biol. 1971;32(3):332-40. (In Russ.)
16. Zamorskiy AD. [Structural levels of biological systems]. In: Razvitiye Kontsepsii Strukturnykh Urovney v Biologii [Development of the Concept of Structural Levels in Biology]. Moscow: Nauka; 1972. p. 332-41. (In Russ.)
17. Zamorskiy AD. [About a concept of polymerization and oligomerization in morphology]. Arkhiv Anatomii Gistologii Embriologii. 1980;78(6):5-18. (In Russ.)
18. Ivanov AV. Proiskhozhdeniye Mnogokletochnykh Zhivotnykh. [The Origin of the Multicellular Animals]. Leningrad: Nauka; 1968. (In Russ.)
19. Ivanova-Kazas OM. Bespoloye Razmnozheniye u Zhivotnykh. [Asexual Reproduction in Animals]. Leningrad: Izdatelstvo LGU; 1977. (In Russ.)
20. Karlsen AG, Marfenin NN. Hydroplasm movements in the colony of hydroids, Dynamena pumila (L.) and some other species. Zhurn Obshch Biol. 1984;45(5):670-80. (In Russ.)
21. Kolesnik YuA. Tsyklichnost Biologicheskikh Protsessov i Rol; Porozhdayuschiky Ikh Faktorov Okruzhayuschey Sredy. [The Cyclic Nature of Biological Processes and the Role of the Environmental Factors That Generating Them]. Vladivostok: Izd-vo Dalnevostochnogo Universiteta; 1997. (In Russ.)
22. Kondratyev ND, Oparin DI. Bolshiye Tsykly Konyunktury: Doklady i Ikh Obsuzhdeniye v Institute Ekonomiki. [Long Cycles of Conjuncture. Presentations and Discussions thereof at the Institute of Economics]. Moscow; 1928. (In Russ.)
23. Kosevich IA, Marfenin NN. [Colonial morphology of the hydroid Obelia longissima (Pallas, 1766) (Campanulariidae)]. Vestnik MGU Ser 16 Biol. 1986;(3):44-52. (In Russ.)
24. Letunov VN. [Digestive-distribution apparatus of hydroids genus Obelia (Hydrozoa, Thecaphora, Campanulariidae)]. Zhurn Obshch Biol. 1987;48(5):651-7. (In Russ.)
25. Lodkina MM. [Features of morphological evolution of plants, due to the specifics of their ontogenesis]. Zhurn Obshch Biol. 1983;44(2):239-53. (In Russ.)
26. Marfenin NN. [Studying of Dynamena pumila colonial integration using quantitative morphological criteria]. Zhurn Obshch Biol. 1977;38(3):409-22. (In Russ.)
27. Marfenin NN. A morpho-functional analysis of a temporary hydroid colony, Moerisia maeotica (Ostr., 1896) (Leptolida, Limnomedusae) taken as an example. Zhurn Obshch Biol. 1984;45(5):660-69. (In Russ.)
28. Marfenin NN. [On the spatial relationship of the skeleton and soft tissues in Hexacorallia]. Nauchn Dokl Vysshey Shkoly Biol Sci. 1984;4:36-9. (In Russ.)
29. Marfenin NN. [A morpho-functional analysis of creeping colonies organization in the hydroids, Cordylophora inkermanica Marfenin (Athecata, Clavidae) taken as an example]. Zhurn Obshch Biol. 1985;46(4):541-55. (In Russ.)
30. Marfenin NN. [The formation of the compact stolonal colonies in hydroids, Clava multicornis (Leptolida, Athecata) taken as an example]. Zool Zhurn. 1985;64(7):975-81. (In Russ.)
31. Marfenin NN. [The functioning of the pulsatory-peristaltic type of a transport system in the colonial hydroids]. Zhurn Obshch Biol. 1985;46(2):153-64. (In Russ.)
32. Marfenin NN. [Colonial structure evolution in Leptolida]. In: Morfogenez i Puti Razvitiya Kolonialnosti Mshanok i Kishechnopolostnykh. [Morphogenesis and Colonial Development of Bryozoans and Coelenterates]. Moscow: Nauka; 1987. p. 4-19. (In Russ.)

33. Marfenin NN. Fenomen Kolonialnosti. [The Phenomenon of Coloniality]. Moscow: Izdatelstvo MGU; 1993. (In Russ.)
34. Marfenin NN. Funktsionalnaya Morfologiya Kolonialnykh Gidroidov. [Functional morphology of the colonial hydroids]. Saint Petersburg: ZIN RAN; 1993. (In Russ.)
35. Marfenin NN. [The essence of the modular organization]. Zhurn Obshch Biol. 1999;60(1):5. (In Russ.)
36. Marfenin NN. [Development of the concept of modular organization]. Zhurn Obshch Biol. 1999;60(1):6-17. (In Russ.)
37. Marfenin NN. Development of biosphere and humankind in the last 100 years. In: Rossiya v Okruzhayuschem Mire (Analiticheskiy Yezhegodnik) [Russia in the Surrounding World (Analytic Yearbook)]. Moscow: Izdatylstvo MNEPU; 2001. p. 12-51. (In Russ.)
38. Marfenin NN. [The imperative of noospherogenesis]. In: Noosfera: Realnost’ Ili Krasivyi Mif. [The Noosphere: A Reality or Fancy Myth?]. Moscow: Novyj Vek; 2003. p. 43-8. (In Russ.)
39. Marfenin NN. [Fundamental laws of modular organization in biology]. Vestnik Tverskogo Gosudarstvennogo Universiteta Ser Biol Ekol. 2008;9(1):47-61. (In Russ.)
40. Marfenin NN, Burykin YuB, Ostroumova TV. [Organismic regulation balanced growth cnidarian colony Gonothyraea loveni (Allm.)]. Zhurn Obshch Biol. 1999;60(1):80-90. (In Russ.)
41. Marfenin NN, Burykin YuB. The growth of the hydroid colonies Dynamena pumila (L.) as the function of the quantity of food. Vestnik MGU Ser Biol. 1979;1:61-8. (In Russ.)
42. Marfenin NN, Kosevich IA. Biology of the hydroid Obelia loveni (Allm.): colony formation, behaviour and life cycle of hydrants, reproduction. Vestnik Moskovskogo Universiteta Ser 16 Biol. 1984;(3):16-24. (In Russ.)
43. Marfenin NN, Kosevich IA. [Morphogenetic evolution of hydroid colony pattern]. In: Materialy X Nauchnoy Konferentsii Belomorskoy Biostantsii MGU. Moskow: Grif i K; 2006. p. 118-24. (In Russ.)
44. Marfenin NN, Kosevich IA., Kraus YuA. [Cyclic morphogenesis in modular organisms]. In: Materialy Nauchnoy Konferentsii Posvyashchennoy 70-letiyu Belomorskoy Biologicheskoy Stantsii MGU. Moscow: Grif i K; 2008. p. 177-81. (In Russ.)
45. Marfenin NN, Malyutin OI. [Water flow influence on the solitary stems of different hydroid species]. Zhurn Obshch Biol. 1994; 55:119-27. (In Russ.)
46. Menshikov SM, Klimenko LA. Dlinnye Volny v Ekonomike: Kogda Obchestvo Meniayet Kozhu. [Long Waves in Economy: When Society Changes Its Skin]. Moscow: LENAND. 2014. (In Russ.)
47. Naumov DV. Gidroidy i Gidromeduzy Morskikh Solonovatovodnykh i Presnovodnykh Basseynov SSSR. Mocow-Leningrad: Izdatelstvo AN SSSR; 1960. (In Russ. English version: Naumov DV. Hydroids and Hydromedusae of the USSR. Israel Program for Scientific Translations (January 1, 1969)).
48. Notov AA. [On specificity of functional organization and individual development of modular objects]. Zhurn Obshch Biol. 1999;60(1):60-79. (In Russ.)
49. Notov AA. [Reproductive systems of modular organisms: modus and ways of rise of reliability]. Vestnik Tverskogo Gosudarstvennogo Pedagogicheskogo Universiteta Ser Biol Ekol. 2010;19(27):83-128. (In Russ.)
50. Notov AA. [Homeosis and the reliability of the reproductive system of modular organisms]. Izvestiya RAN, Ser Biol. 2015;3:248-57. (In Russ.)
51. Notov AA. [Pseudocyclical similarities and structural evolution of modular organisms]. Izvestiya RAN Ser Biol. 2016(3):276-85. (In Russ.)
52. Oleskin AV. [Network Structures of the Society in Terms of Biopolicytic]. POLIS. 1998;1:68-86. (In Russ.)
53. Oleskin AV, Kirovskaya TA. [The issue of network identity]. In: Logos Zhivogo i Germenevtika Telesnosti. Postizheniye Kultury. (The Logos of Life and the Hermeneutics of Physicality. Comprehension of Culture). Moscow: Rossijskiy Institut Kulturologii Akademicheskij Proyekt; 2005. p. 600-22. (In Russ.)
54. Polilov AA. [The consequences of miniaturization in insect morphology]. Vestnik MGU Ser 16 Biol. 2015; (3):37-43. (In Russ.)
55. Spenser G. Osnovaniya Biologii T. 2 [Principles of Biology. Vol. 2]. Saint Petersburg; 1870.
56. Tramble A. Memuary k Istorii Odnogo Roda Presnovodnyh Polipov s Rukami v Forme Rogov (Memoirs on History of a Genus of Freshwater Horn-Shaped Polyps). Moscow-Leningrad: Biomedgiz. 1937. (In Russ.)
57. Khokhryakov AP. [Shapes and polymerization steps in the evolution of plants]. Zhurn Obshch Biol. 1974; 35(3):331-45. (In Russ.)
58. Shafranova LM. [On metamericity and metameres in plants]. Zhurn Obshch Biol.1980; 41(3):437-47 (In Russian with English Summary).
59. Shafranova LM. [The plant as a life form (on the question about the content of «plant»)]. Zhurn Obshch Biol. 1990;51(1):72-89. (In Russ.)
60. Shafranova LM, Gatcuk LE. [The plant is a spatiotemporal metameric (modular) system]. In: Us-

pekhi Ekologicheskoy Morfologii Rastenij I Yeyo Vliyaniye na Smezhnye Nauki. Moscow: Izdatelstvo Prometey MPGU imeni V.I. Lenina; 1994. p. 6-8. (In Russ.)

61. Schmidt-Nielsen K. Razmery Zhivotnyh: Pochemu Oni Tak Vazhny. Moscow: Mir; 1987. (In Russ. English version: Schmidt-Nielsen K. Scaling: Why Is Animal Size So Important? Cambridge & New York: Cambridge University Press; 1984).
62. Shulman SS. [The problem of the origin of multicellularity]. Trudy ZIN. 1974;53:47-82. (In Russ.)
63. Ehlton Ch. Ekologiya Nashestviy Zhivotnykh i Rasteniy. Moscow: Izdatelstvo Inostrannoy Literatury; 1960. (In Russ. English version: Ehlton Ch. The Ecology of Invasions by Animals and Plants. London: Methuen; 1958)
64. Yakunin VI, Bagdasaryan VE, Kulikov VI, Sulakshin SS. Variativnost' i Tsyklichnost' Globalnogo Sotsualnogo Razvitiya Chelovechestva. [Variability and cyclicity of global social development of mankind]. Moscow: Nauchnyj Ekspert; 2009. (In Russ.)
65. Adil AM, Ko Y. Socio-technical evolution of decentralized energy systems: A critical review and implications for urban planning and policy. Renewable Sustainable Energy Rev. 2016;57:1025-37.
66. AnAge Database of Animal Ageing and Longevity. URL: http://genomics.senescence.info/species/query.php
67. Andersson AE, Zhang W-B. Decision centralization and decentralization in a dynamic economic system. J Comput Appl Mathems. 1988;22:319-37.
68. Ayre DJ, Grosberg RK. Aggression, habitation, and clonal coexistence in the sea anemone Anthopleura elegantissima. Amer Nat. 1995;146(3):427-53.
69. Babaev E, Hefferlin R. The concepts of periodicity and hyper-periodicity: from atoms to molecules. In: Rouvray D. (ed.) Concepts in Chemistry: a Contemporary Challenge. London: Research Studies Press; 1996. p. 24-81.
70. Berking S. Hydrozoa metamorphosis and pattern formation. Curr Top Develop Biol. 1998;38:81-131.
71. Beutel RG, Pohl H, Hunefeld F. Strepsipteran brain and effect of miniaturization (Insecta). Arthropod Struct Dev. 2005;34(3):301-13.
72. Bradshaw AD. Evolutionary significance of phenotypic plasticity in plants. Adv Genet. 1965;13:115-55.
73. Braverman MH. The cellular basis of hydroid morphogenesis. Publ Set Marine Biol Lab. 1973;20:221-56.
74. Bromham L. Why do species vary in their rate of molecular evolution? Biol Letts. 2009;5:401-4.
75. Buddemeier RW, Kinzie RA III. Coral growth. Oceanogr Marine Biol Annu Rev. 1976;14:183-225.
76. Chapman G, Stebbing ARD. The modular habit – a recurring strategy. In: Tardent P, Tardent R (eds). Developmental and cellular biology of coelenterates. Amsterdam; 1980. p. 157-62.
77. Chindapol N, Kaandorp JA, Cronemberger C, Mass T, Genin A. Modelling growth and form of the scleractinian coral Pocillopora verrucosa and the influence of hydrodynamics. PLoS Comput Biol. 2013;9(1):e1002849.
78. Clements FE. Plant Succession and Indicators. New York; 1928.
79. Crabbe MJC, Smith DJ. Sediment impacts on growth rates of Acropora and Porites corals from fringing reefs of Sulawesi, Indonesia. Coral Reefs. 2005;24:437-41.
80. Crowell S. The regression-replacement cycle of hydranths of Obelia and Campanularia. Physiol Zool. 1953;26(4):319-27.
81. Dreher A, Fischer JAV. Decentralization as a Disincentive for Transnational Terror? System Stability Versus Government Efficiency: An Empirical Test. Research Paper Series #41. Switzerland: Thurgau Institute of Economics and Department of Economics at the University of Konstanz; 2008. URL: http://www.twi-kreuzlingen.ch/uploads/tx_cal/media/TWI-RPS-041-Dreher-Fischer-2008-11.pdf
82. Gierer A, Meinhardt H. A theory of biological pattern formation. Kybernetik. 1972;12:30-39.
83. Gili JM, Coma R. Benthic suspension feeders: their paramount role in littoral marine food webs. Trends Ecol Evol. 1998;13:316-21.
84. Girvan M, Newman MEJ. Community structure in social and biological networks. Proc Natl Acad Sci USA. 2002;99(12):7821-6.
85. Gorshkov VG. Physical and Biological Bases of Life Stability. Man, Biota, Environment. Berlin: Springer-Verlag; 1995.
86. Gorshkov VG, Gorshkov VV, Makarieva AM. Biotic Regulation of the Environment: Key Issue of Global Change. London: Springer Verlag; 2000.
87. Grigg RW. Orientation and growth form of Sea fans. Limnol Oceanograph. 1972;17(2):185-92.
88. Grosberg RK, Strathmann RR. The evolution of multicellularity: A minor major transition? Annu Rev Ecol Evol Syst. 2007;38:621-54.
89. Foote M, Crampton JS, Beu AG, Marshall BA, Cooper RA, Maxwell PA, Matcham I. Rise and fall of species occupancy in Cenozoic fossil mollusks. Science. 2007;318:1131-4.

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90. Francis L. Cloning and Aggression among Sea Anemones. Biol Bull. 1988;174:241-53.
91. Furusawa C, Kaneko K. Origin of complexity in multicellular organisms. Phys Rev Lett. 2000;84(26):6130-33.
92. Hamilton NB, Gray DH. Decentralized terrorism: Ramifications for a centralized international system. Global Security Studies. 2012;3(2):24-42.
93. Halle F. Modular growth in seed plants. Phil Transact Roy Soc L Ser B Biol Sci. 1986;313:77-87.
94. Harnik PG, Lotze HK, Anderson SC, Finkel ZV, Finnegan S, Lindberg DR, Liow LH, Lockwood R, McClain CR, McGuire JL, O'Dea A, Pandolfi JM, Simpson C, Tittensor DP. Extinctions in ancient and modern seas. Trends Ecol Evol. 2012;27(11):608-17.
95. Highsmith RC. Reproduction by Fragmentation in Corals. Marine Ecol Progr Ser. 1982;7:207-26.
96. Heylighen F. The growth of structural and functional complexity during evolution. In: Heylighen F, Bollen J, Riegler A. (eds.). The Evolution of Complexity. Dordrecht: Kluwer Academic; 1999. p. 17-44.
97. Hugoson M. Centralized versus decentralized information systems: A historical flashback. In: Impagliazzo J, Järvi T & Paju P (eds.), History of Nordic Computing. Berlin-Heidelberg: Springer; 2009. p. 106-115.
98. Huxley JS, de Beer GR. Studies in dedifferentiation. IV. Resorption and differential inhibition in Obelia and Campanularia. Quart J Microsc Sci. 1923;67:473-95.
99. Josephson RK. Colonial responses of hydroid polyps. J Exper Biol. 1961;38:559-77
100. Kang S, Ma W, Li FY, Zhang Q, Niu J, Ding Y. Functional redundancy instead of species redundancy determines community stability in a typical steppe of Inner Mongolia. PLoS ONE. 2015;10(12):e0145605
101. Kerr SR, Dickie LM. The Biomass Spectrum: A Predator-Prey Theory of Aquatic Production. New York- Chichester: Columbia University Press; 2001.
102. Klingenberg CP. Morphological integration and developmental modularity. Annu Rev Ecol Evol Syst. 2008;39:115-32.
103. Kosevich IA. Branching in colonial hydroids. In: Davis J. (ed.) Branching Morphogenesis. Boston, MA: Springer US; 2006. p. 91-112.
104. Kosevich I. Morphogenetic foundations for increased evolutionary complexity in the organization of thecate hydroids shoots (Cnidaria, Hydroidomedusa, Leptomedusae). Biol Bull. 2012;39(2):172-85.
105. Leversee GJ. Flow and feeding in fan-shaped colonies of the gorgonian coral, Leptogorgia. Biol Bulletin. 1976;151(2):344-56.
106. Leys SP, Eerkes-Medrano DI. Feeding in a Calcareous Sponge: Particle uptake by pseudopodia. Biol Bull. 2006;211(2):157-71.
107. MacArthur R. Fluctuations of animal populations and a measure of community stability. Ecology. 1955;36(3):533-6.
108. Marfenin NN. Functional morphological differences in the hydroids Obelia longissima, O.geniculata, Gonothyraea loveni, and Laomedea flexuosa (Obelia, Cnidaria, Hydrozoa), inhabiting a communal biotop in the White Sea. Phenomenon. Aspects of investigations. Perspectives of employment. Zoosystematica Rossica, Suppl. 1. 1999:101-8.
109. Marfenin NN. Non-radial symmetry of the transport system of Acropora corals. Invertebrate Zool. 2015;12(1):53-9.
110. Marfenin NN. A new method for studying the transport system in colonial hydroids. Hydrobiologia, 2015;759(1):133-46.
111. Marfenin NN, Kossevitch IA. Morphogenetic evolution of hydroid colony pattern. In: Fautin DG, Westfall JA, Cartwight P, Daly M, Wyttenbach CR. (eds) Coelenterate Biology 2003: Trends in research on Cnidaria and Ctenophora. Hydrobiologia. 2004; 530/531. p. 319-27.
112. Mauseth JD. Theoretical aspects of surface-to-volume ratios and water-storage capacities of succulent shoots. Am J Bot. 2000;87(8):1107-15.
113. May RM, Lawton JH, Stork NE. Assessing extinction rates. In: Lawton JH, May RM. (eds) Extinction rates, Oxford: Oxford University Press, 1995. p. 1-24.
114. May R. The future of biological diversity in a crowded world. Curr Science. 2002;82(11):1325-31.
115. McCann KS. The diversity–stability debate. Nature. 2000;405:228-33.
116. Meesters EH, Pauchli W, Bak RPM. Predicting regeneration of physical damage on a reef-building coral by regeneration capacity and lesion. Marine Ecol Progr Ser. 1997;146:91-9.
117. Meyer KM, Wiegand K, Ward D, Moustakas A. The rhythm of savanna patch dynamics. J Ecol. 2007;95:1306-15.
118. Mitton JB, Grant MC. Genetic variation and the natural history of quaking aspen. BioScience. 1996;46(1):25-31.
119. Modular organisms: case studies. Papers relating to a discussion meeting (London, June 1985) on growth and form in modular organisms. Proc Roy Soc Lond Ser B. 1986;288:109-224.

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120. Muko S, Kawasaki K, Sakai K, Takasu F, Shigesada N. Morphological plasticityin the coral Porites sillimanianiand its adaptive significance. Bull Marine Science. 2000;66:225-39.
121. Newman MEJ. The structure and function of complex networks. SIAM Rev. 2003;45:167-256.
122. Newman MEJ. Modularity and community structure in networks. Proc Natl Acad Sci USA. 2006;103:8577-82.
123. Niklas KJ, Newman SA. The origins of multicellular organisms. Evol Develop. 2013;15:41-52 .
124. Niklas KJ. The evolutionary-developmental origins of multicellularity. Amer J Bot. 2014;101(1):6-25.
125. Notov AA. Modular organization – a model for biological research. Wulfenia, 2011;18:113-31.
126. Olson EC, Miller RL. Morphological Integration. Chicago: Univ. Chicago Press; 1958.
127. Pearcy RW. Responses of plants to heterogeneous light environments. In: Pugnaire F, Valladares F. (eds.). Functional Plant Ecology. 2nd Edition. Boca Raton: CRC press; 2007. p. 213-58.
128. Pearson RG. Recovery and recolonization of coral reefs. Marine Ecol Progr Ser. 1981;4:105-22.
129. Potts DC, Done TJ, Isedale PJ, Fisk DA. Dominance of a coral community by the genus Porites (Scleractinia). Marine Ecol Progr Ser. 1985;23:79-84.
130. Primack RB. Essentials of conservation biology (6th Edition). Sunderland: Sinauer Associates, Inc. Publishers; 2014.
131. Raup DM. A kill curve for phanerozoic marine species. Paleobiology. 1991;17(1):37-48.
132. Rensch B. Histological changes correlated with evolutionary changes in body size. Evolution. 1948;2(3):218-30.
133. Riedl R. Water movement: Animals. Marine Ecol. 1971;1(2):1123-49.
134. Rinkevich B. Do reproduction and regeneration in damaged corals compete for energy allocation? Marine Ecol Progr Ser. 1996;143:297-302.
135. Rinkevich B, Loya Y. Intraspecific competition in a reef coral: effects on growth and reproduction. Oecologia. 1985;66(1):100-5.
136. Riisgård HU, Manríquez P. Filter-feeding in fifteen marine ectoprocts (Bryozoa): particle capture and water pumping. Marine Ecol Progr Ser. 1997;154:223-39.
137. Roark EB, Guilderson TP, Dunbar RB, Fallon SJ, Mucciarone DA. Extreme longevity in proteinaceous deep-sea corals. Proc Natl AcadSci USA. 2009;106(13):5204-08.
138. Rockart JF, Leventer JS. Centralization vs decentralization of information systems: a critical survey of current literature. URL: http://dspace.mit.edu/bitstream/handle/1721.1/1906/swp-0845-02293677-cisr-023.pdf?sequence=1.
139. Rosen BR. Modules, members and communes: a postscript introduction to social organisms. In: Larwood G, Rosen BR. (eds.) Biology and Systematics of Colonial Organisms. New York, London: Academic Press; 1979. p. 13-25.
140. Row JR, Wilson PJ, Murray DL. Anatomy of a population cycle: the role of density dependence and demographic variability on numerical instability and periodicity. J Anim Ecol. 2014;83(4):800-12.
141. Ruiz-Trillo I, Nedelcu AM. (Eds.) Evolutionary Transitions to Multicellular Life. Principles and Mechanisms. Dordrecht: Springer; 2015.
142. Ruiz-Trillo I, Burger G, Holland PW, King N, Lang BF, Roger AJ, Gray MW. The origins of multicellularity: a multi-taxon genome initiative. Trends Genet. 2007;23(3):113-8.
143. Sagarin R. Learning From The Octopus: How Secrets From Nature Can Help Us Fight Terrorist Attacks, Natural Disasters, And Disease. Perseus Books; 2012.
144. Satterlie RA. The search for ancestral nervous systems: an integrative and comparative approach. J Exper Biol. 2015;218:612-7.
145. Schaible R, Scheuerlein A, Dańko MJ, Gampe J, Martínez DE, Vaupel JW. Constant mortality and fertility over age in Hydra. Proc Natl Acad Sci USA 2015;112(51):15701-6.
146. Schieber B. Changes in the seasonal rhythm of two forest communities during secondary succession. Biologia, 2007;62(4):416-23.
147. Schoonmaker AL, Lieffers VJ, Landhäusser SM. Uniform versus asymmetric shading mediates crown recession in Conifers. PLoS ONE. 2014;9(8):e104187.
148. Seeley TD. When is self-organization used in biological systems? Biol Bull. 2002;202(3):314-18.
149. Southwood TRE. 1977 Habitat, the template for ecological strategies? Presidential address to the British Ecological Society, 5 January 1977. J Animal Ecol, 1977;46:337-65
150. Spalding KL, Bhardwaj RD, Buchholz BA, Druid H, Frisen J. Retrospective birth dating of cells in humans. Cell. 2005;122:133-43.
151. Sponaugle JS, LaBarbera M. Drag-induced deformation: a functional feeding strategy in two species of gorgonians. Exper Marine Biol Ecol. 1991;148:121-34.
152. Steele RE. Developmental signaling in Hydra: what does it take to build a «simple» animal? Dev Biol. 2002;248:199-219.

153. Sueur C, Deneubourg J-L, Petit O. From social network (centralized vs. decentralized) to collective decision-making (unshared vs. shared consensus). PLoS One. 2012;7(2):e32566.
154. Taylor DL. Intra-colonial transport of organic compounds and calcium in some Atlantic reef corals. Proc Third Internat Coral Reef Symp. 1977;1:431-6.
155. Todd PA. Morphological plasticity in scleractinian corals. Biol Rev. 2008;83:315-37.
156. Velimirov B. Orientation in the sea fan Eunicella cavolinii related to water movement. Helgolander Wiss Meeresunters. 1973;24:163-73.
157. Wahle CM. Regeneration of injuries among Jamaican gorgonians – the roles of colony physiology and environment. Biol Bull. 1983;165:778-90.
158. Wijgerde T. Feature Article: Coral Feeding: An Overview. Advanced Aquarist. 2013. URL: http://www.advancedaquarist.com/2013/12/aafeature
159. Wolpert L. Positional information and the spatial pattern of cellular differentiation. J Theor Biol. 1969;25:1-47.
160. Wyttenbach CR, Crowell S, Suddith RL. Variations in the mode of stolon growth among different genera of colonial hydroids, and their evolutionary implications. J Morphol. 1973;139(3):363-75.
161. Yadav SK, Mishra GC. Biodiversity measurement determines stability of ecosystems. Int J Environ Science. 2013;4(3):68-72.
162. Zabojnik J. Centralized and decentralized decision making in organizations. J Labor Econ. 2002;20(1):1-22.

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