

Modular organisms as objects of population biology

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Summary: The specifics of the organization, functioning, reproductive biology and ontogenesis of modular living organisms determine their fundamental differences in their populational life as opposed to unitary organisms. Populational systems with clones, chimerical and symbiotic organisms, complicated hybrid and agamous complexes gained prevalence in modular plants, animals and fungi. Such biological systems in some ways are similar to their elements in terms of significant specifics of their organization. These specifics differentiate between the modular and unitary types of organization. Some types of modular organisms' populational life show similarities with cenotic-level biosystems.

Keywords: modular organism, ontogenesis, population, biocenosis, biosystems, population biology, ecology, plants, animals, fungi

The realization that modular and unitary organisms are two fundamentally different ways of organizing living organisms became the premise for the creation of the concept of modular organization (HARPER & BELL 1979; TOMLINSON 1982; MARFENIN 1993, 1999; GATSUK 2008b; etc.). These types of organizations are represented in all of the main biota components (NOTOV 2011, 2017). The specifics of modular and unitary organisms are defined by system properties and affect all aspects of biosystems' analysis, including organizational specifics, functioning, individual development, reproduction, evolution and ecology (MARFENIN 1993, 1999, 2008, 2018, 2021; NOTOV 1999, 2005, 2011, 2015, 2016, 2017, 2019, 2020; SIMPSON 2013; BLACKSTONE 2021; etc.). All of these aspects support the importance of the concept of modular organization in various areas of biology and ecology as well as the significance of its further development (NOTOV 2011, 2017). The latter is substantially delayed by the ambiguous interpretations of the terms 'module', 'modularity', (NOTOV 2015; KOSEVICH 2021). However, currently the interest in analyzing the fundamental differences between modular and unitary organisms is beginning to resurge. Testament to that is the organization of special courses on the 'Evolution of Coloniality and Modularity' at the Center for Marine Biology of the University of São Paulo (CEBIMAR-USP) and the increase in the number of new publications (NOTOV 2017, 2018, 2020; MARFENIN 2018, 2021; SIMPSON 2018; BERNARD et al. 2020; BLACKSTONE 2021; BROWN 2021; HIEBERT et al. 2021; KOSEVICH 2021; etc.).

The development of the concept requires a head-on analysis of biodiversity from the point of view of the major biological branches, which will be geared toward understanding the specifics of modular organization (NOTOV 2011). Populational biology holds a special place among them; it is closely related to many disciplines of fundamental and applied biology and ecology. The analysis of specific characteristics of populational life that are common for all modular organisms is equally important for the formation of general and specific 'populational' branches of algology, bryology, mycology and invertebrate zoology. Populational studies of various groups of algae, mosses, ascidians, bryozoans, hydrozoans and corals are currently developing into an independent focus area (OKAMURA & HATTON-ELLIS 1995; RYDIN 2008; ATALLAH & SUBBARAO 2012; SCHIEL &

FOSTER 2015; ROSSI et al. 2017; WESTERMEIER et al. 2017; PATIÑO et al. 2022; etc.). The need to summarize materials and create methodological reviews is increasing. All these developments will generate about a qualitatively new level of the development of populational biology in general.

The goal of this article is to draw attention to the significance of understanding the specifics of populational life of modular organisms.

Materials and methods

Monographies, review papers and educational materials on the subject of populational biology have been critically studied by the authors (HARPER 1977; SOLBRIG & SOLBRIG 1979; YABLOKOV 1987; BEGON et al. 1990; SHORINA 1994; DYAKOV 1998; SHNYREVA 2005; RYDIN 2008; SILVERTOWN & CHARLESWORTH 2009; ZLOBIN 2009; SCHIEL & FOSTER 2015; ROSSI et al. 2017; ATALLAH & SUBBARAO 2012; MARKOV 2012; etc.). Special attention has been paid to publications that discuss the specifics of modular organisms and their populational life (HARPER & BELL 1979; WHITE 1979; TOMLINSON 1982; ZAUGULNOVA et al. 1988; SHORINA 1981, 1994, 2001; ZLOBIN 2000; DYAKOV 2004, 2008; GATSUK 2008a, b; etc.).

Materials on the aspects of populational structure of various groups of modular organisms and examples of the polyvariance of their development have been reviewed (BOLOGOVA et al. 1985; ZHUKOVA & KOMAROV 1990; ZHUKOVA 1995, 2001; NOTOV 2005; MARFENIN 2018, 2021; NOTOV & ZHUKOVA 2019; etc.). Publications about the structure of clones and agamous reproductive complexes, as well as the role of cloning and chimerism in populations of modular organisms have been studied (SENNIKOV 2003; SOMMERFELDT et al. 2003; KAMELIN 2009; KRAHULCOVÁ et al. 2009; DUBINSKY & STAMBLER 2011; RINKEVICH 2011, 2019; TAYLOR et al. 2015; MAJESKÝ et al. 2017; CHKALOV et al. 2018; VANNIER et al. 2019; FRANKLIN et al. 2021; HERBEN & KLIMEŠOVÁ 2020; HIEBERT et al. 2021; KLIMEŠOVÁ et al. 2021; etc.).

Systems analysis based on the functional theory of organization was used when comparing modular and unitary organisms and their populational biosystems (BERTALANFFY 1971; MALINOVSKY 1972; SETROV 1972; VINOGRAY 1989, 2011; NOTOV 2005, 2020). Studies on the relationships between populations in various biocenoses and biomes have been analyzed (BEGON et al. 1990; KARATYGIN 1993; ZHUKOVA 1995; RYDIN 2008; GELASHVILI et al. 2009; DUBINSKY & STAMBLER 2011; SCHIEL & FOSTER 2015; LALAND et al. 2016; ROSSI et al. 2017; CHKALOV et al. 2018; SAVINOV 2018; BRANDL et al. 2019; etc.).

When analyzing different variations of population-level biosystems that are present in modular organisms, we took into account the specifics that are typical for the main groups of modular plants, animals and fungi. The probability of the appearance of the main variants and their characteristics were evaluated. We also evaluated the tendencies and phenomena that are connected with these variants in unitary organization.

Results and discussion

Modular organisms as biosystems

The key attribute of modular organisms is cyclic morphogenesis (open growth). (HARPER & BELL 1979; TOMLINSON 1982; MARFENIN 1993, 1999; GATSUK 2008a, b; NOTOV 2005, 2011; etc.). It is connected to repeated realization of comparatively autonomous morphogenetic programs

and is responsible for the fundamental system properties of modular organization. Due to their capability for open growth, modular systems have an elaborate complex of interconnected and interdependent aspects, which make them different from unitary systems (MARFENIN 1993, 2018; NOTOV 2005, 2011; etc.). Although there is significant diversity among modular and unitary organisms, not all of them are of a qualitative nature (NOTOV 1999, 2005, 2011). However, their connectedness, frequency of occurrence and specifics of appearance in modular organization make it possible to see the latter's distinctness. This distinctness becomes even clearer when analyzing the paradoxical tendencies and phenomena connected with the more peculiar variants of organism-level and population-level modular biosystems. Some of them will be noted below.

Cyclic morphogenesis also shapes the most important system features of modular organisms. These features can be described using the following simplified model. The biosystem constantly replicates an abundance of relatively autonomous elements within itself. Basically, this is the process of 'internal' (within the boundaries of this system) reproduction. This makes the outer boundaries of the system very volatile, 'changeable'. They constantly vary during the growth process. An inner multicomponent network of modules – relatively equal and autonomous elements – is formed. All together they comprise the functional basis of the biological system and its 'reserve' fund. This fund is connected to all aspects of organization: it ensures operational reliability, the possibility of 'external' reproduction (vegetative propagation) and the realization of evolutionary transformation (NOTOV 2015, 2016, 2017). Consequentially, the regulation based "on the redundant organization of the formative system itself" (SCHMALHAUSEN 1961: 111) is carried out. The modular principle of structure and functioning is maintained on all levels of the structural hierarchy of the modular organism. Such an organism is a "system with poorly individualized parts, built in a hierarchical manner and continuously changing in space and time" (SHAFRANOVA 1990: 80). The elements of each level are equal, to a certain extent autonomous and repeatedly reproduced within a given biosystem. This property ensures the organizational unity of the subordinate subsystems and the system as a whole. Combined with other features, it determines the system specifics of modular organisms.

Due to the relative morphological and morphogenetic autonomy of elements of each level and the organizational unity of the subsystems uniting them, some of the common fundamental properties of biosystems have a more distinct outward manifestation in modular objects. Among them are the dynamics, cyclicity, hierarchy and fractality (quasi-fractality). As a result of formation of new modules and the constant growth of the system, all these properties become obvious and are easily detected when analyzing a living object, even on the morphological level (NOTOV 2011, 2016). It is no coincidence that such systems are sometimes called 'superdynamic'. Similar properties of unitary biosystems are revealed only at the anatomical level.

The presence of relatively autonomous equivalent elements in the biosystem and its ability to repeatedly 'reproduce' them within itself define its similarity to biological systems of the next hierarchical (populational) level. The similarities can be seen in all the main aspects of organization: the structure, functioning and development (NOTOV 2011, 2020). Regulation of both a modular organism and a population is decentralized (NOTOV 2005, 2011; MARFENIN 2018; etc.). It is carried out by changing the rate of formation of new elements and their number. Not surprisingly, different modular organisms were repeatedly presented as a colony or a metapopulation by various researchers (WHITE 1979; MARFENIN 1993; etc.). 'Demographic' methods were traditionally used in their morphological analysis. Competitive relationships between different structural elements

of a modular organism also attests to the similarity of such objects and populations (MARFENIN 1993; NOTOV 2005, 2020; etc.). Modular objects that are capable of particulation and formation of clones have even greater similarity with populations. If the physical connection between the body parts is lost, ramets are almost indistinguishable from the genets (HARPER 1977; ZLOBIN 2009; MARKOV 2012; etc.). The wide distribution of complex life cycles with generational change leads to the fact that, at different stages of individual development, the modular organism often serves as different biotypes. They occupy different ecological niches and serve different functions in cenoses. Each of them forms its network of connections, which determines a certain similarity of such living objects with cenotic biosystems. The features mentioned above indicate a lower integrity of modular organisms as compared to unitary organisms.

Ontogenesis, reproduction and environment

The specifics of ontogenesis, reproduction and the characteristics of outside connections with the environment are important to understand the properties of modular organisms' populational life (HARPER & BELL 1979; WHITE 1979; TOMLINSON 1982; ZAUGULNOVA et al. 1988; MARFENIN 1999, 2018; ZLOBIN 2000; GATSUK 2008a, b; NOTOV 2015, 2018, 2020; etc.). They define the organizational distinctness of the individual elements of populations, the variability of their 'behavior' in communities and population-level biological systems' strategies of functioning.

The lower integrity of modular biological systems manifests not only in the nature of relations between the elements or the type of regulation, but also in the features of their developmental program and its informational support, i.e. the specifics of external relations. Cyclic morphogenesis is associated with the blockiness of the developmental program and multiple implementations of various relatively autonomous morphogenetic subprograms. There are several important consequences of regular activity and relatively autonomous developmental subprograms: the indefinite size of modular organism, the total length of ontogenesis (MARFENIN 1999, 2018; SHEFFERSON et al. 2017; MAKRUSHIN 2019) and last but not least, the easy 'separation' of the organism into parts. The latter leads to the disintegration of the ontogenetic process and dissociation into separate fragments (particulation) that continue to live independently. As a result, there are basically insoluble contradictions, when we use the terms 'individual', 'individual development' or 'unit' when talking about modular organisms (see DYAKOV 2008; GATSUK 2008a, b; ZMITROVICH 2010). As opposed to unitary organisms' populations, the elements of which are units (individuals), modular populations are characterized by a broad spectrum of different types of population elements, including different types of clones (ZAUGULNOVA et al. 1988; etc.). Paradoxical situations are frequent, for example when giant clones of plants, fungi or corals spread out over hundreds of hectares and are over tens of thousands of years old (ARNAUD-HAOND et al. 2012; ROGERS & GALE 2017; ANDERSON et al. 2018; etc.).

The strategy of regular activation of morphogenetic subprograms ensures close connection of embryogenesis, growth and reproductive processes and facilitates the emergence of different variants of vegetative propagation (NOTOV 2015). All of this accounts for the significant ontogenesis polyvariance of modular organisms (BOLOGOVA et al. 1985; ZHUKOVA & KOMAROV 1990; ZHUKOVA 1995, 2001; NOTOV 2005, 2020; MARFENIN 2018, 2021; NOTOV & ZHUKOVA 2019; etc.). It can reach incredible levels in modular organisms and leads to multifaceted differentiation of individuals in a population as well as diversity of reproductive pathways (NOTOV 2015, 2011; NOTOV & ZHUKOVA 2019; etc.).

Widespread distribution of dormant developmental stages in the ontogenesis of modular organisms became an important factor in the differentiation of biological systems. They are extremely diverse in many plant, fungi and modular animal groups. Some examples are seeds, plant or fungi spores, diapausing eggs of algae and invertebrates, various kinds of other dormant propagules, cryptic coral recruits, etc. (HAIRSTON & FOX 2009; MARKOV 2012; BATYGINA 2014; SCHIEL & FOSTER 2015; DOROPOULOS et al. 2022; OKADA & MATSUDA 2022; etc.). Diaspore reserves form powerful 'hidden' banks in the soil and other substrates. The quantity of propagules in these banks can be significantly higher than in the 'visible' part of the population. Their role in the populational life of modular organisms is immense, especially under extreme conditions. For example, in the Antarctic bryophyte propagule banks are the main type of populational systems in areas free from vegetation (SMITH 1987). Diaspore (propagule) banks are often seen as subpopulations or 'embryonal populations' (MARKOV 2012; BATYGINA 2014; etc.). In addition to that, in biocenoses they agglomerate to make diaspore (propagule) bank communities, which can have a very complicated structure (OKADA & MATSUDA 2022; etc.).

Complicated ontogenesis with change of the generations and various successive stages of development is often seen in different groups of modular organisms (ZAUGULNOVA et al. 1988; SHORINA 1994, 2001; SHNYREVA 2005; NOTOV 2018; etc.). Such developmental options become an additional factor in populational differentiation. In this case colonies of various generations of one organism form hemipopulations (SHORINA 1994, 2001).

An organic unity of embryogenesis, growth, development and reproduction is characteristic of modular organization. They are closely connected to and in some respects are parts of unified and integrity 'chronic' morphogenesis, which last throughout the organism's lifetime (GATSUK 2008b; NOTOV 2015, 2017; etc.). As a result, the reproductive system of modular organisms is characterized by instability and polyvariance. Reproduction is often done through various pathways, including different types of vegetative (asexual) reproduction (IVANOVA-KAZAS 1977; NOTOV 2011, 2015; BATYGINA 2014; etc.). All forms of polyploidy and apomixis have become widespread. Combined with hybridization they have played a key role in plant evolution (KAMELIN 2009; KASHIN 2009; IGNATOV et al. 2018; HÖRANDL 2022; etc.). However, the significant impact of these processes on the formation of modular organisms, especially corals, is corroborated by varying evidence (VOLLMER & PALUMBI 2002; GREBELNYI et al. 2019; HOBBS et al. 2022; etc.). Polyploidy, apomixis and hybridization can also be found among fungi and algae (DYAKOV 2004, 2008; SOLTIS & SOLTIS 2018; etc.). These characteristics provided for the wide distribution of population systems with colonies of various complexity among modular organisms (DYAKOV 2004, 2008; ATALLAH & SUBBARAO 2012; ANDERSON et al. 2018; HERBEN & KLIMEŠOVÁ 2020; FRANKLIN et al. 2021; etc.). Hybridization combined with apomixis and clonal reproduction make the structure of populational systems significantly more complicated, but also facilitate the formation of agamic (agamo-sexual) complexes (KAMELIN 2009; KASHIN 2009; etc.). Their most paradoxical variants are long-standing complexes of populations of the different species, which interact with each other (even to the point of forming complexes of syngameons that unite species of one genus or even different genera) (GLAZUNOVA 1977; SENNIKOV 2003; KAMELIN 2009; KASHIN 2009; etc.).

Open growth ensures various aspects of instability in the boundaries of a modular organism. Their 'openness' is seen in the specifics of internal and external connections of the biological system. In the former case, the uncertainty of size and level of physical unity of the organism, the duration

and path of its ontogenesis as well as the level of independence of reproduction from growth processes are important for understanding the characteristics of populational life. The specifics of external life may also play a key role. Regular morphogenetic activity combined with low levels of integrity and relative autonomy of different parts of the organism ease fusion (coalescence) in many structures of modular plants, animals and fungi (see NOTOV 2016, 2017; etc.). However, allogeneic fusion (coalescence) is more important for populational life. It manifests in different groups of modular organisms due to their less integral allorecognition system. The instability of immune responsiveness has ensured the wide distribution of chimerism in ascidians, corals as well as in some algae and fungi groups (SOMMERFELDT et al. 2003; SANTELICES & ALVARADO 2008; RINKEVICH 2011, 2019; ROPER et al. 2013; OKUBO et al. 2017; etc.). Chimerism is rare in unitary organisms and occurs only as a result of implantation of alien cells and zygote fusion. In modular organisms it occurs significantly more often and its mechanisms are quite diverse. Allogeneic coalescence of adult individuals and adult colonies is often seen; multi-chimeras are frequently formed. Not only close-kin fusion is possible, but fusion between organisms of various species is also feasible (RINKEVICH 2019). Chimerism plays a big role in populations (SANTELICES & ALVARADO 2008; RINKEVICH 2011, 2019; OKUBO et al. 2017; etc.).

The instability of boundaries of modular organisms is also manifested in the clear tendency to aggregate as well as in the ability to reach high levels of unity of aggregations and symbiotic associations (see NOTOV 2017, 2020; etc.). Consequently, the primary directions of evolution of symbioses of the main groups of modular organisms were huge in terms of the scope of biological diversity. They also played an ecological key role in the evolution of ecosystems. The primary tendency for heterotrophic modular organisms were photosymbioses, while for autotrophic modular organisms – mycorrhiza and nitrogen-fixing symbioses, which improved mineral nutrition. The functioning efficiency of continuously growing modular organisms was improved by the realization of these tendencies. The above mentioned directions are different from the main tendencies of symbiotic evolution in unitary organisms not only in terms of the grandiose scope and the role that the results played in the biosphere. They are also different in the fact that eucaryotes often play the role of associated symbionts, sometimes even multicellular ones, with modular organization (for example, species of the genus *Trentepohlia* Mart., mycorrhizal fungi). The symbiotic associations that are formed often reach an organism level of integrity in terms of many aspects of organization. Among them are not only the correction of ontogenetic programs, metabolic regulation and significant transformations of structure and morphogenesis (see KARATYGIN 1993; ZMITROVICH 2010; NOTOV 2014), but also the formation of super-species genetic systems as well as the formation of functionally integrated complex symbiogenomes (see PROVOROV & VOROBEV 2012; PROVOROV & TIKHONOVICH 2019; ALLEN & LENDEMER 2022; SONG et al. 2022; etc.).

Even though any organism has many symbionts, most often microorganismal, we believe the approach in which an individual is considered an ‘autocenosis’, and its population a ‘democenosis’ is quite appropriate (SAVINOV 2011, 2012). The wide range of autocenoses in terms of various aspects – complexity level, level of integration and integrality as well as the level of auto-regulation (OZERSKY 2013; etc.) – should be noted. This preconditions the tendency for differentiation between symbiotic organisms and free-living organisms (GELASHVILI et al. 2009; ZELEEVEV 2018; etc.). Even though the idea that lichens have an organism level of integrality is quite old, and biocenology classics noted that physical continuity cannot be used as the main criterium of an

organism (BEKLEMISHEV 1928; etc.), lichen population biology started to develop spontaneously by ‘modelling’ other directions in populational ontogenetic research (GLOTOV & SUETINA 2015; SUETINA 2016; etc.). As lichenology develops there are more and more arguments in favor of acknowledging the ‘organism’ level of integrality of lichens (ALLEN & LENDEMER 2022; SONG et al. 2022; etc.) and ‘legalizing’ the existence of lichen population biology. Photosymbioses of modular invertebrates have been less considered from this angle. They have become rather prevalent among modular animals as opposed to unitary animals. Photosymbioses can be found in ascidium (HIROSE & NOZAWA 2020), hydrozoans (STANLEY 2006; GORELOVA et al. 2009; BLACKSTONE 2021), bryozoans and corals (SIMPSON 2013, 2018). However, they played a key role in the evolution of corals and in the formation of an array of different types of modular organization in them (ZAIKA 1991; STANLEY 2006; SIMPSON 2013, 2018; CLAVIJO et al. 2018; BLACKSTONE 2021). Populational biology of corals should develop with consideration for the role of photosymbioses in population life. Photosymbiotic corals have a well-coordinated partnership with algae, cell cycles are synchronized, and the immune system of corals is set up to promote symbiosis (SIMPSON 2018; etc.). The very close connections with cyanobacterial symbionts in some ascidium should also be mentioned: they have formed complex systems of obligatory photosymbiosis. This is the only known example of photosymbiosis among chordates (HIROSE & NOZAWA 2020).

Connections between the modular organism and the environment are ambiguous and often contradictory. On the one hand, its decentralized regulation by means of changing the intensity of growth is associated with the clear determining influence of the external environment. Due to the modular organism’s significant instability, this external regulation is manifested in high polyvariety of ontogenesis and development as well as in corrections to the reproductive processes on the populational and cenotic levels (ZAUGULNOVA et al. 1988; ZHUKOVA & KOMAROV 1990; ZHUKOVA 1995; ZLOBIN 2000; NOTOV & ZHUKOVA 2019; etc.). On the other hand, modular organisms themselves can be very active in influencing the environment. The forms of this influence and the strategies of interaction with the environment are different from those seen in unitary organisms (MARFENIN 1993, 2018; SAVINOV 2015; LALAND et al. 2016; NOTOV 2020; AABY et al. 2021; etc.). Open growth and plasticity of individual development of modular organisms result in their high resistance to environmental effects, ensure their ‘ingrowth’ into the environment, their ability to ‘break down’ and transform it (MARFENIN 1993, 2018; NOTOV 2005, 2020). Unlimited growth, which often ensures a very long lifespan, casting off body parts and metabolic byproducts into the environment together with an attached mode of life – they all promote the environment-forming and cenosis-forming role of modular organisms as well as the execution of the framework-forming function in biocenoses. It is most clearly seen in ecological frames formed by phytocenoses of trees and reef-forming corals. By ‘dividing’ the environment, they significantly increase the amount of ecological niches. Because of lignified and suberificated tissues and skeletal elements, modular plants and animals continue to structure the frameworks of biogeocenoses even after death. Environment-forming (transformative) activity of modular organisms can reach significant levels due to their contribution to the process of generating soil and peat cover as well as coral reef zones (KHOKHRYAKOV 1981; DUBINSKY & STAMBLER 2011; MONSON 2014; BRANDL et al. 2019; etc.). Cenosis-forming engagement is seen in populations (cenopopulations) of modular organisms that are often dominant or edificatory in their communities (SMIRNOVA et al. 2011; SCHIEL & FOSTER 2015; ROSSI et al. 2017; etc.). The key species’ populational dynamics have cenosis-transforming significance: they ensure the

succession of biocenoses (SMIRNOVA et al. 2011; etc.). Large marine modular animals and algae play an important cenosis-forming role in oceanic biomes (SCHIEL & FOSTER 2015; ROSSI et al. 2017; BRANDL et al. 2019; etc.). Mycorrhizal fungi play a significant part in the creation of ecological frameworks of terrestrial communities. They integrate a large portion of phytocenoses into a consolidated geosymbiosis (SAVINOV 2015, 2018; etc.).

Population systems of modular organisms

Population systems of modular organisms are quite diverse. Some important characteristics have already been discussed in publications, but mainly on botanical objects (HARPER 1977; ZAUGULNOVA et al. 1988; YURTSEV 1987; SHORINA 1981, 1994; ZLOBIN 2000, 2009; MARKOV 2012; etc.). It is important to compare the frequency of occurrence of different variants of populational life and the biological phenomena in modular and unitary organisms when analyzing the specifics of populations that have been predicated by modular organization.

For a better understanding of the diversity of modular organisms' populational life, it is useful to compare the similar characteristics between modular organisms and their populations that have been preconditioned by the system specifics of modular organization (Table 1). The significant plasticity of modular organization has created the possibility for a boundless variety of population systems. In terms of their characteristics, they are often different from populations in the traditional sense (Table 1). The term 'population' is used figuratively in some of these systems. Their analysis is of special interest. The use of terms like 'organism', 'individual' is also problematic (see DYAKOV 2008; GATSUK 2008a,b). Populational biology of lichens is evolving (GLOTOV & SUETINA 2015; SUETINA 2016; etc.) and there is a tradition to separate organisms into 'free-living' and 'symbiotic' (GELASHVILI et al. 2009; ZELEEVA 2018; etc.). Taking both these factors into account, we decided that it is possible to use this approach to separate population systems. Such separation concentrates on rather polar variants of 'autocenoses' and 'democenoses' as described by SAVINOV (2011, 2012), which are important when comparing population systems of modular organisms. Whenever possible, the authors attempted to find materials from various groups of modular animals, plants and fungi that correspond to each of the characteristics described (Table 1). Although not all the tendencies described are equally prevalent in all groups, we were almost able to find interesting examples. However, the scope of this article doesn't allow to describe all the sources and materials.

A more detailed analysis of the characteristics described is a matter for future research. Of course, many of the phenomena at hand can be found in unitary organisms: those connected with reproduction, chimerism, complex life cycles and critical species complexes. However, it is in modular organisms that these phenomena became much more widespread, became represented by specific variants and also became linked. All this ensures a greater complexity and originality of such combined variants. When describing the characteristics and variants, we tried to use visual analogies and aphorisms to amplify the contrast in characteristics.

The list of usually interconnected and interdependent common characteristics of modular organisms and their populations can be broadened and added to. However, the characteristics already mentioned above (Table 1) characterize all the main aspects of organization, including structure, functioning, development, regulation, self-replication and connections with the external environment. The rather full organizational self-similarity of modular organisms and their populations is testimony to the clearly manifested fractality of these biological systems. In

certain aspects it can be seen more clearly and obviously, compared to unitary organisms and their populations. This is why modular organization is a rather interesting model object for studying the systemic nature of fractality and the development of methods to reveal fractal 'loci' in biological systems (NOTOV 2011; VINOGRAY 2011; etc.).

The similarity of characteristics of modular organisms and their populations as well as the similar tendencies in the formation of diversity of these objects (Table 1) are preconditioned by the united manifestation of integral system characteristics of hierarchically different biological systems of modular organization. Low levels of integrity, high lability and polyvariance are of crucial importance in this case. They reflect either directly or indirectly in the majority of noted characteristics as well as in the extreme diversity of fundamentally different types of populational life (Table 1). Low integrity, lability and polyvariance are the result of open growth ('fluidity') and decentralization of regulation in modular biological systems.

The specificity of modular organisms and their populations is also notably defined by the different nature of external connections than the one seen in unitary objects. A relatively lower level of separation from the environment, a higher level of openness to different variations of external interactions and other forms of activities, such as taking on the carcass, environment-forming or cenosis-forming role can be found in modular organization (Table 1).

In a simplified 'figurative' understanding, the modular organism and its population are very labile biological systems with low levels of integrity and unlimited growth, decentralized regulation and significant polyvariance of development. Inter-system connections are relatively weak: disintegration in ontogenesis and a lack of mechanisms to ensure integrity of the genome pool in cloning are possible. However, external interactions are quite active (Table 1). Modular biosystems can endure various influencing factors that destabilize their internal structure (apomixis, polyploidy) or lead to the loss of the object's 'identity' (its 'deindividualization', figuratively speaking). The latter can include different forms of inter-system (inter-species) integration, including hybridization, chimerism, creation of complex systems and aggregation. These transformative factors are often combined, which promotes the emergence of peculiar variants of populational life. Among them are complex populational systems of symbiotic organisms, polyploids, agamous reproductive complexes and syngameons, populations with clones and elements of natural chimerism and multi-chimerism. All can be found in representatives from different taxa of modular organisms (DUBINSKY & STAMBLER 2011; SOLTIS & SOLTIS 2018; HOBBS et al. 2022; etc.). Our understanding of multicomponent associations of invertebrates and phototrophic microalgae and cyanobacteria is still obscure (GORELOVA et al. 2009). Of interest is an upfront analysis of all aspects of diversity of populational life of modular organisms, which represent an immense spectrum of objects of varying structural organization and level of integrity (NOTOV 2011, 2019; etc.). The development of approaches to classify the types of developmental polyvariety of populational systems (ZHUKOVA & NOTOV 2018), as well as reproductive mechanisms and modes, needs special attention. Types of pseudo-populations, in which the reasons for the lack of effective self-replication can vary significantly, are of significant research interest (YOUNG 1989; SHORINA 1981, 1994; etc.).

Populations of modular organisms and levels of biosystem organization

The interest in analyzing the main types of biosystem organization and mechanisms of their transformation is currently on the rise (ZELEEV 2010, 2018; RINKEVICH 2019; MEINCKE &

Table 1. Some variants of characteristics common to modular organisms and their populations. The square brackets contain integral system qualities connected to these characteristics (the more important ones are marked bold). *Not high level:* INT – integrity; Se – separation from the environment. *Significant level:* Ac – activity; Au – autonomy of elements (= not high level of integrity); Con – contradictory qualities; Ind – indeterminacy; La – lability; PV – polyvariance; Op – openness. Abbreviations: P – population, PL – population life, VPL – variant of population life.

Characteristics	Manifestation variants	
	Modular organism	Populational biosystems
Diversity of <i>elementary units</i> , often <i>hierarchical</i> system of structural units. [INT La PV]	Different groups of organisms have different <i>elementary modules</i> . Often <i>multi-level hierarchy</i> of modules, multi-component system of structural and biological units (GATSUK 2008a).	Different <i>elementary units</i> P – individuals, various types of genets and ramets, clones and complexes. A system of units can be <i>hierarchical</i> and <i>multi-level</i> .
' <i>Mobility</i> ' and lability of the biosystem <i>boundaries</i> . [INT Se Ac Ind La PV Op]	<i>Open growth</i> and ' <i>ingrowth</i> ' into the environment.	' <i>Spreadability</i> ' (the ability to distribute over mosaic environments), ' <i>fitting</i> ' into a rigid matrix of habitats (YURTSEV 1987: 588).
Ability to <i>disintegrate</i> , Propensity for ' <i>divisibility</i> ' (differentiation, connected to separating the whole into parts). [INT Au Ind La PV]	Various forms of <i>disintegration</i> are common in <i>ontogenesis</i> ; often clone formation. Some modules of multi-level system of semi-autonomous structural and biological units (GATSUK 2008a) can become <i>autonomous</i> . Often various complex life cycles with separate <i>generations</i> (NOTOV 2018).	<i>Disintegration</i> in the process of <i>dispersal</i> of the 'mother' P and its 'splitting'. Often a complex system of autonomous geographical and ecological <i>elementary</i> P is differentiated (ZAUGULNOVA et al. 1988). Separation of ephemeral and dormant stages in the <i>hemiP</i> , <i>subP</i> . <i>Banks</i> of diaspores are often grouped into communities.
Active links with the environment and ' <i>predisposition</i> ' for <i>inter-system integration</i> : - integration of genomes during <i>hybridization</i> ; - inter-organism <i>fusion</i> ; - inter-organism <i>aggregation</i> into high-integrity symbioses. [INT Se Ac Ind La PV Op]	Often <i>hybridization</i> ; polyploidy, <i>apomixis</i> and agamo-sexual complexes; - natural <i>chimerism</i> , <i>multi-chimerism</i> , fusion of adult colonies and individuals; - emergence of ' <i>symbiotic organisms</i> '. The formation of <i>photosymbioses</i> , <i>mycorrhiza</i> and <i>nitrogen-fixing symbioses</i> played a key role in the evolution of the biosphere.	Ability to form of <i>complex interspecies</i> P-systems, that combined <i>syngameon complexes</i> (KAMELIN 2009). The 'splitting' of the 'mother' P can be combined with the ability to <i>reunite</i> and merge with <i>sibling</i> P (YURTSEV 1987). P of lichens often merge into mosaic <i>multi-species complexes</i> , supplemented with lichenicolous fungi.
Diversity of VPL with <i>partial</i> manifestation of <i>main qualities</i> of P-biosystems: - regular reproduction and self-replication of autonomous, relatively equivalent elements, their different ages, competitive relationships; - special mechanisms that ensure the integrity of the P gene pool and genetic polymorphism. [INT Se Ac Au Con Ind La PV Op]	Open growth imitates reproduction and some qualities of P (figurative analogy <i>intra-organism</i> VPL). ' <u>VPL without disintegration</u> ': - self-replication of physically connected <i>semi-autonomous</i> relatively equal modules, their different ages, <i>partial</i> competition. ' <u>VPL with particulation and cloning</u> ': Parts of the organism become <i>autonomous</i> ramets, and competition becomes obvious.	<u>Clonal P</u> – VPL ' <i>single geneta</i> ': - non-recombining reproduction of ramets, their different ages, competitive relationships, but the lack of connections that ensure genetic polymorphism. <u>Pseudo P</u> – VPL <i>without self-replication</i> . <u>P of symbiotic organisms</u> – VPL of the <i>cenotic biosystem</i> with functionally integrated symbiogenomes. <u>P of complexes</u> – VPL <i>agamous complexes</i> , <i>cenospecies</i> and <i>syngameons</i> . <u>P with chimeras</u> – VPL with <i>chimerism</i> .
<i>Polyvariance</i> of development. [INT Au Ind La PV]	Polyvariance of <i>ontogenesis</i> affects all aspects of organization. 11 types have been described in plants (NOTOV & ZHUKOVA 2019).	Polyvariance of <i>development</i> affects all aspects of organization. Approaches to the classification of PV (ZHUKOVA & NOTOV 2018).

<p><i>Decentralized</i> regulation, <i>determining</i> influence of the <i>environment</i>. [INT Se Ind La PV Op]</p>	<p>The important role of the environment is seen in ontogenetic polyvariance.</p>	<p>External corrections to reproductive processes on the cenotic level (ZLOBIN 2000).</p>
<p><i>Environment-</i> and <i>cenoses-</i>forming activity. [Ac PV Op]</p>	<p>Ability to ‘split’ and transform the environment and to fulfill the <i>carcass function</i> in biocenoses.</p>	<p>Cenoses-forming activity of <i>dominates</i> and <i>edificators</i>. The dynamics of <i>key species</i>-P ensures the succession of biocenoses.</p>
<p><i>Contradictory qualities</i> of organization [INT Se Ac Con La Op]</p>	<p>‘<i>Interlevel</i>’ similarities and connections in organization: 1) manifestation of some characteristics and elements of PL on the organismic levels, an ‘<i>organismic</i>’ level of integrity of certain cenotic biosystems; 2) <i>self-replication</i> happens during ‘<i>internal</i>’ and ‘<i>external reproduction</i>’, which doesn’t allow to clearly differentiate between growth and reproduction. The equivalent of ‘<i>internal</i>’ reproduction on the P-level is <i>cloning</i> (‘growth’ of one genet). Low stability of inter-system connections, the predisposition for <i>internal disintegration</i> and tendency for <i>external (intra-system) integration</i>. ‘<i>External</i>’ regulation and <i>environment-forming</i> and <i>cenoses-forming</i> activity.</p>	

DUPRÉ 2020; etc.). Of central importance are several aspects of inter-transitions of biosystems on various integrational and organizational levels such as organisms, populations, ecosystems (ZELEEV 2010, 2018; RINKEVICH 2019; etc.). Populational systems of modular organisms are an important model object in this regard. They clearly contradict the traditional biological theory of three irreducible levels of organization of living organisms – the organism, the population and the ecosystem (ZELEEV 2010, 2018; etc.). Within the huge ‘organism-population’ axis, there are a lot of different transitions in both directions, which lead to the emergence of new organismic and populational biosystems. These transitions happen based on the reproduction and integration of identical elements of the initial structure. The outermost links of these transitions are the result of the changes in the number of ‘elementary organisms’. Due to the increase of integration in both directions, these biosystems are able to gain the characteristics of an integral organism (ZELEEV 2010, 2018; RINKEVICH 2019; etc.).

To develop this area further, it is necessary to reconsider our understanding of the criteria of the organism-level integrity, of our understanding of the periodical nature of integration cycles in living systems of the organismic and supra-organismic levels as well as the criteria of the alternation of opposing organizational principles on various superordinate hierarchical levels (BEKLEMISHEV 1928, 1950; MALINOVSKY 1972; ALEEV 1986; etc.). The existence of their own integrated program of development and regulation is a fundamental characteristic of organismic biosystems (BEKLEMISHEV 1928; ALEEV 1986; etc.). It ensures the internal logic of self-preservation of the organism, even if the physical connection between the biosystem’s components is lost or non-existent (ALEEV 1986). The integrity of the developmental program of a populational system is significantly lower compared to an organism. It represents an integral result of the interaction between the elements of the population with each other and their environment. That is why the formation of such biosystems is very weakly predetermined.

It is possible to separate three organismic levels of functional organization – monobiont, metabiont and cenometabiont. They are connected to the consequent cycles of structural aggregation (integration). They can all be found in modular organisms (ALEEV 1986; NOTOV 2011, 2017). Within each level of structural integration, a significant organizational diversity

of objects of various levels of integrity can be observed. Their numerous variants are difficult to see simultaneously, because to some extent they all imitate some characteristics of populational biosystems. The diversity of populational systems of modular organisms and the modes of transformations within the 'organism–population continuum' is equally as inexhaustible.

This breadth and 'diffusion' of boundaries between the organism and the population are the result of the combination of opposing principles of organization in modular living beings. This combination ensures the addition of certain characteristics of rigid systems to the typical traits of discrete systems (MALINOVSKY 1972). The noted variants of manifestation of integral systemic qualities (Table 1) also testify to the contradictory nature of modular organization. The relatively low rigidity of intra-system connections combined with the tendency for active external interaction and inter-system integration together ease transformations, during which populational biosystems may reach 'organismic' integrity. Certain trends can be seen as major transitions in individuality of a higher level (RINKEVICH 2019; etc.). The role of the cyclic (or pseudo-cyclic) nature of integration processes was important not only in the structural evolution of modular organisms (NOTOV 2016, 2017), but also in the transformation of the variants of their populational life (RINKEVICH 2019; BROWN 2021; etc.). In the latter case there was an increase in the diversity of elementary structural units of populations.

Perspectives of development of populational biology of modular organisms

An frontal analysis of biodiversity based on the modular organization concept is topical for the development of many directions of current complex studies and concepts. Among them are 1) next-generation clonal ecology (FRANKLIN et al. 2021; HERBEN & KLIMEŠOVÁ 2020; KLIMEŠOVÁ et al. 2021; etc.); 2) the concept of ecosystem engineering (ROZENBERG 2022); 3) dormant diaspora banks and propagule banks as well as fundamental problems of bryology (DOROPOULOS et al. 2022; PATIÑO et al. 2022); 4) the concept of biological identity; thinking of biological individuals as ecosystems (MEINCKE & DUPRÉ 2020); 5) macroevolution of colonialism and photosymbiosis (SIMPSON 2013, 2018; BLACKSTONE 2021) and others. Problems of populational biology are connected with many fundamental studies on species and species formation as well as various segments of evolutionary ecology (NIKLAS & COBB 2017; etc.). Populational and ontogenetic research of modular organisms will doubtlessly help form corresponding directions in individual areas of zoology, botany and mycology that are dedicated to specific taxonomical groups. However, the development of general populational biology of modular organisms is of equal importance. Generalization and critical analysis of multifaceted materials will help create the necessary theoretical and methodological basis for populational biology as a whole. Populational biology of modular organisms is also very important for the development of general system studies and research directions dedicated to fractals, developmental cycles and integrity problems.

Conclusion

To conclude, fundamental characteristics of the organization of modular organisms ensure significant differences of their populational life as compared to unitary organisms. A systemic analysis of modular organisms and their populations allowed the authors to see common traits of modular organisms and their populations. They affect all the main aspects of organization, including structure, functioning, development, regulation, self-replication as well as connections with the external environment. The relatively complete organizational self-similarity of modular

organisms and their populations speaks to a clearly manifested fractality of these biosystems. The type of external connections also significantly defines the specifics of modular organisms and their populations. In modular organization there is a relatively lower level of separation of the living system from the environment, a higher openness to different ways of external interactions and other forms of activity, including the carcass, environment-forming and cenosis-forming roles. The boundary between the organism levels and populational levels isn't always clear in modular organization. Some types of populational life of modular organisms demonstrate a likeness to biosystems of the cenotic level. An upfront analysis of all aspects of diversity of modular organisms' populational life is of great interest. It will allow to reach a qualitatively new level of development in many areas of biology and ecology and will promote the positions of system-wide research and the development of approaches to analyze the organizational polymorphism of biosystems.

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Artikel/Article: [Modular organisms as objects of population biology 9-27](#)