Journal of Vasyl Stefanyk Precarpathian National University
http://journals.pnu.edu.ua
Vol. 8, No. 4 (2021), 34-44

UDC 574.2
doi: 10.15330/jpnu.8.4.34-44

ECOLOGICAL CONSORTIUM AS AN ELEMENTARY ECOSYSTEM

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Abstract. Each of the large autotrophic or heterotrophic organisms reproduces an environment for many organisms, living in, on and around it. This central organism and all other organisms, living in the sphere of its influence, constitute together an elementary community or ecosystem if to take into the consideration soil, air and other elements, which are included into the sphere. In East European ecological tradition such the elementary ecosystems are named individual consortia. Population and species consortia integrate individual consortia of population and species representatives correspondingly. Each central organism has unique genotype, and, thus, reproduces unique environment for its inhabitants. In this reason, the result of interaction between consorters and their host depend both from the genotype of central organism from one side and from genetic structures of the consorters from another side. Thus, autotrophic or heterotrophic individual consortium is a spatially limited unity of different organisms, zone of life concentration, in which specific composition of living and non-living components with peculiar energetic and informative exchange is forming arround the determinant, anough large central organism.
Keywords: Consortium, genoplast, extended phenotype, “gene-to-gene” relations.

1. INTRODUCTION

Each organism reproduces an environment for many other organisms, living in, on or around it. This central organism and all other organisms, living in the sphere of its influence, constitute together an elementary community or ecosystem if to take into the consideration soil, air and other elements, which are included into the sphere. In East European tradition such the elementary ecosystems are named individual consortia [1]. Population and species consortia integrate individual consortia of population and species representatives correspondingly.

The term Consortium in its ecological sense was independently and practically simultaneously introduced in the East European ecological practice by zoologist V.M. Becklemishev and botanist L.G. Ramensky. Becklemishev [1] pointed that each organism is no included in an ecosystem as a single unit, but as a part of some consortium, which consists of representative of the edificatory species and those specimens, epibionts and endobionts, what inhabit outer or inner spaces of the edificatory body. As an example, he described a pine consortium with inhabiting it arthropods, mycorrhizal and parasitic fungi, epiphytic bryophytess and cladinas. He represented a vole with its ecto- and endoparasites as another example of a consortium. According to his view, no population, but distinct relatively big autotrophic or heterotrophic organism may be an edificatory specimen of a consortium. He considered that any consortium may be determined using topical relations (local inhabitation) as a criterion.

L.G. Ramensky [2] determined the consortium as joining of different organisms, which are closely related each with other in their vital functions and common future. In his imagination, consortia may form only on the base of trees (pine, oak, birch, linden-tree etc) with their parasites, saprophytes, epiphytes, symbionts, pests, pollinators etc. Hence, in spite of Becklemishev, he considers that only autotrophic and, at the same time, not epiphytic plant may serve as an edificator of a consortium. Thus, he understood consortium wider than Becklemishev, counting pollinators and other organisms (for example, dispersing seeds), which contact with the central organism for short periods, and which are not topically relate with it, as members of a consortium. Both the authors similarly considered that any consortium includes those species only, which are directly related with a central species or a consortium determinant. After V.M. Becklemishev, consortium may be autotrophic or heterotrophic, depending on that, what organism, autotrophic or heterotrophic, correspondingly, plays a role of its determinant.

2. DISCUSSION

2.1. To the history

V.V. Mazing [3] developed the concept of consortium, including in it both the specimens, directly related with the center, and those indirectly related with it through the firsts. Apart from V.N. Becklemishev, describing a consortium, V.V. Mazing used both the topical relations and those trophic as well. After him, consortium consists of a couple of organisms, living functions of which are related to some autotrophic, non-epiphytic higher plant. V.V. Mazing represented his understanding of a consortium graphically as central organism with related to it consorters, which forms a range of con-centers (figure 1). First con-center of the autotrophic consortium consists of organisms directly related to the consortium determinant trophically only (phytophagans), topically only (epiphytes, lianas, birds), or both trophically and topically (symbionts, parasites etc.). These organisms obtain their energy from the consortium determinant.

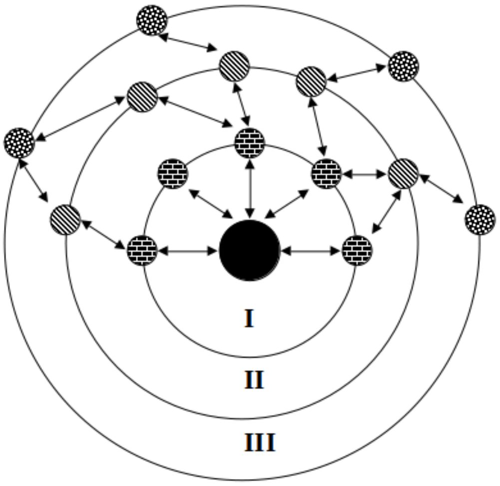


Fig. 1. Consortium structure after V.V. Mazing [3]:

▦ *– Consortium determinant (central organism);*

● *– Consorters of the 1-st con-center;*

▨ *– Consorters of the 2-nd con-center;*

▩ *– Consorters of the 3-st con-center;*
I, II, III – Con-centers

Three groups of organisms may be recognized among the consorters of the first con-center; they are: biophages, exploiting energy of living organs of the autotrophies, saprophages, depending from dead parts of the plants, and excretophages, collecting energy from excretions of living central organism.

Organisms, trophically related to the consorters of first con-center, belong to the second con-center of the consortium. Under the same principle organisms may be distributed to the third and following con-centers. Consorters of the second and following con-centers exploit no energy of autotrophic determinant, but influence it throughout the phytophagans and phytoparasites, regulating their densities. Distribution of the organisms abroad the con-centers is frequently conditional because some consorters may belong to two or more con-centers simultaneously. For instance, blue titmouse may be a second con-center consorter, when feeding by moth larvae, which eat the tree leaves, or a third con-center consorter, when feeding by their pupal parasitoids, and, at last, if the bird has winded a nest on the tree branches, then it may be considered as a first con-center consorter, topically related to the determinant.

Thus, consortional relations should not be reduced to trophic chains, because besides trophic relations there are topical, fabric and other relation in a consortium. Central relatively large organism, supplies all the consorters with the energy and transforms the environment specifically, adding to it fourth organism's component besides air, water and soil.

Two approaches, individualistic and populational, to recognition of a consortium developed from the very beginning, based on single large specimen or couple of specimens correspondingly as the edificators. Discussion between their supporters led to the synthesis, which joined the approaches, extending the conception for three levels: individual, population and species.

Individual consortium is a unit of ecosystem, which consist of a couple of organisms, related to the individual of the determinant species [1]. Populational consortium is a couple of organisms, related to a population of higher plant [4]. Species consortium is a couple of species, related to the edificatory species. Hence, all the consortium types originate from elementary and indivisible individual consortium. Thus, population consortium is a couple of individual consortia of the determinant in the territory of its population. Species consortium integrates population consortia in the species areal of the determinant.

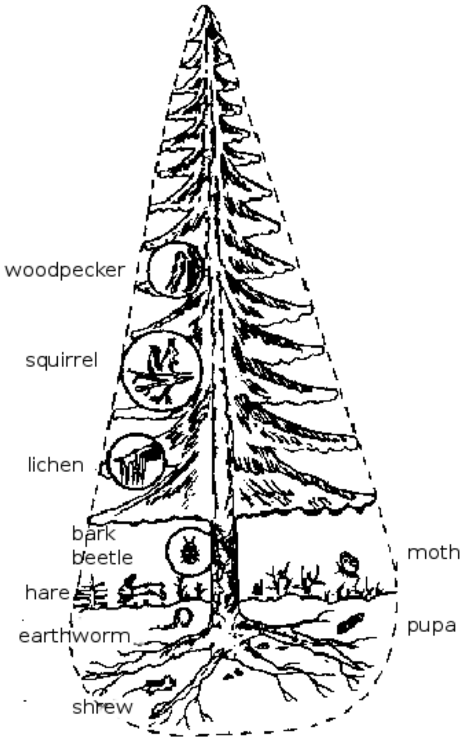


Fig. 2. Structure of ecological consortium after M.A. Holubets ([8] p. 43)
(the consortium includes all of the obligate consorters and their environment)

Famous Ukrainian ecologist M.A. Holubets made great theoretical insights in the consortium concept. In his fundamental work "Actual questions of ecology" [5] and in other works [6] he studied individual consortium and considered it as an elementary ecosystem, which may be described with features peculiar to the ecosystem level of Life Organization. M.A. Holubets and Yu.M. Chornobay, analyzing many literature sources and developing their own theoretical generalizations, gave following its definition: "As a consortium it should be considered such the couple of representatives of different species, which is determined by any autotrophic or heterotrophic organism in its centre, components of which are related with the centre by trophic, topic, fabric and phoric ties, and which forms specific micro-environment" (Holubets and Chornobay [7] p. 25). Their concept is represented in the fig. 2. Introducing the micro-environment, they added a sufficient supplement to the Mazing's scheme (fig. 1). In its last presentation the individual autotrophic consortium may be considered as an elementary structural-functional unit of ecosystem or elementary ecosystem. However, it should be understood that only autotrophic individual consortium may form an elementary ecosystem. Even so powerful animals as elephant or whale with all the small organisms inhabit them are no elementary ecosystems because the matter cycles are not complete in limits of the consortia.

In aquatic ecosystems, when autotrophic organisms are mostly small and are not able ensuring the existence of many other organisms inside them or on their surfaces, we may speak only about trophic chains, which begin from them. With that large aquatic animals, as concentrators of the matter and energy, create conditions favorable for other small organisms. And as L.G. Ramensky has pointed, they are joining among themselves by "… their definitely common fate". If the large organism dies, then its consorters also die or lose their environment.

2.2. Modern state

Sufficient success in the development of the consortium concept last time was reached due to investigations of Ukrainian ecologists. Their numerous works add to the modern understanding of the concept.

Study of consortia in the Lvov's ecological school of thought is represented in works by M.A. Holubets, M.P. Kozlovsky, K.A. Malinovsky, M.P. Rudishin, Yo.V. Tsarik, I.I. Tsarik and Yu.M. Chornobay. In particular, the great cycle of works was dedicated to the theoretical generalization in this area, as well as to the complex research of mountain pine (*Pinus mugo*) and alpine sorrel (*Rumex alpinus*) meroconsortia and individual consortia.

Dnipropetrovsk's consortium school of thought was founded and developed due to works by A.P. Travleev, V.L. Bulakhov, V.S. Gavrilenko, A.L. Ponomarenko, S.I. Scherbakova and other researches. A range of the works are devoted to detailed description of the intra-consortium relations of different edificators, their comparisons, their dynamics, to understanding of the ratio between consortium structure and biodiversity level in the ecosystems of Near-Dnipro steppes.

The third, Crimean ecological school of thought (A.V. Ivashov, A.P. Simchuk, G.E. Boyko, L.A. Demidenko, I.G. Savushkina), studying consortia, devotes main attention to the interaction between the consortium determinant and its consorters on the examples of pubescent (*Quercus pubescens* Willd.) and sessile (*Quercus petraea* Mattuschka/Liebl.) oaks and their consorters, with special attention to biochemistry and genetics of the interactions. Fundamental investigation by L.A. Demidenko was focussed on heterotrophic consortia of Caspian seals.

2.3. Individual consortium as an elementary ecosystem and all-biological phenomenon

Individual consortium with autotrophic core has the same functional components as any ecosystem. Its living part (biocenosis) includes organisms from three functional blocks: 1) producents, 2) consuments, 3) decomposers. Lifeless part (ecotope) includes inorganic and organic substances. Processes of substance cycles and energy transformation, peculiar to any ecosystem, also take place here. As well as any ecosystem, individual consortium consists of sub-structures, for instance, of central organism's organs with many consorters related to them. The consorters aggregated with certain organ or part of the consortium determinant are together named mero-consortium. For instance, fillophagous insects inhabiting an oak tree belong to the mero-consortium of its leaves, while the oak trunk inhabitants belong to the trunk mero-consortium. Also we may in the same manner describe mero-consortia of branches and roots.

The concept of individual consortium integrates organism, population and ecosystem levels of life organization, because there is an individual in its center, populations of consorters are represented in the consortium by their micro-populations inhabiting it, and the micro-community including the determinant in its base with environmental organic and inorganic substances form an elementary ecosystem (figure 3).

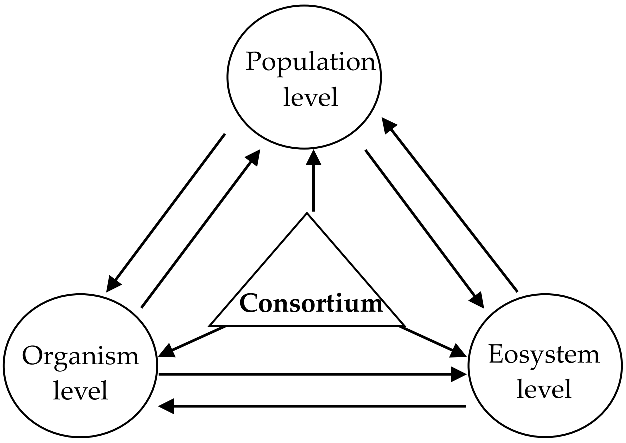


Fig. 3. Position of individual consortium in relation to different levels of life organization [9]

T. Rabotnov [10] has pointed that ecological consortium is a result of long-term evolutionary process. Ecological consortium was formed during conjugate evolution of the determinant and consorter species. Adaptive interaction among the determinant and its consorters takes place at the level of individual consortium. Central organism determines many properties of the consorters habitat. The consortium core influence the consorters from different concenters directly and indirectly lays a role of selective factor for them. With that, individual consortia, as over-organismic systems, have stochastic, i.e. probabilistic nature.

2.3. Genetic aspects of intra-consortium relations

Sources of the question come directly from the theoretic works of Ukrainian scientist, member of Ukrainian Academy of Sciences M.A. Holubets [6, 7, 8], who develops the concept of *genoplast*. In accordance to the concept, each ecosystem contains the controlling subsystem, genoplast, which may be described as a system including gene pools of all the populations of the community. The Crimean ecological school of thought determined genoplast as a couple of probabilistically interacting genotypes of all the individuals included into the ecosystem [11, 12]. From the gene-centristic point of view, its structure may be described as all the "gene-gene" interactions including those intra-species and inter-species, that occur into the ecosystem. As individual consortium is an elementary ecosystem, it also has the controlling subsystem, which includes genotypes of the determinant and all its consorters. It is obvious that all the matter-energetic processes occurring there should be strongly influenced by genetic information controlling futures of the organisms included.

During last decades there were collected many data, not always full but sufficient, on interplay between central core of consortium and its consorters. Among others, it was found that there is some correspondence between the consortium core and genotypes of consorters. For example, G.F. Edmunds [13] studying interaction between Douglas fir (*Pseudotsuga menziesii*) and its pest black pine-leaf scale insect (*Nuculaspis californica*) has found that each tree has its own deme of the insects, which are most adapted to the tree. Genetically similar firs were inhabited by similar demes of the insect. Close relations were found in the gray larch tortrix (*Zeiraphera griseana*) and its different host species: four forms of the insect inhabit correspondingly four coniferous host species [14]. Genetic relations between host plant and its phytophagous consorters are relatively stable and may be expressed in successive generations. For example, beetles *Phratova vitellinae* prefer feeding in those cottonwood trees, in which their ancestry have fed [15].

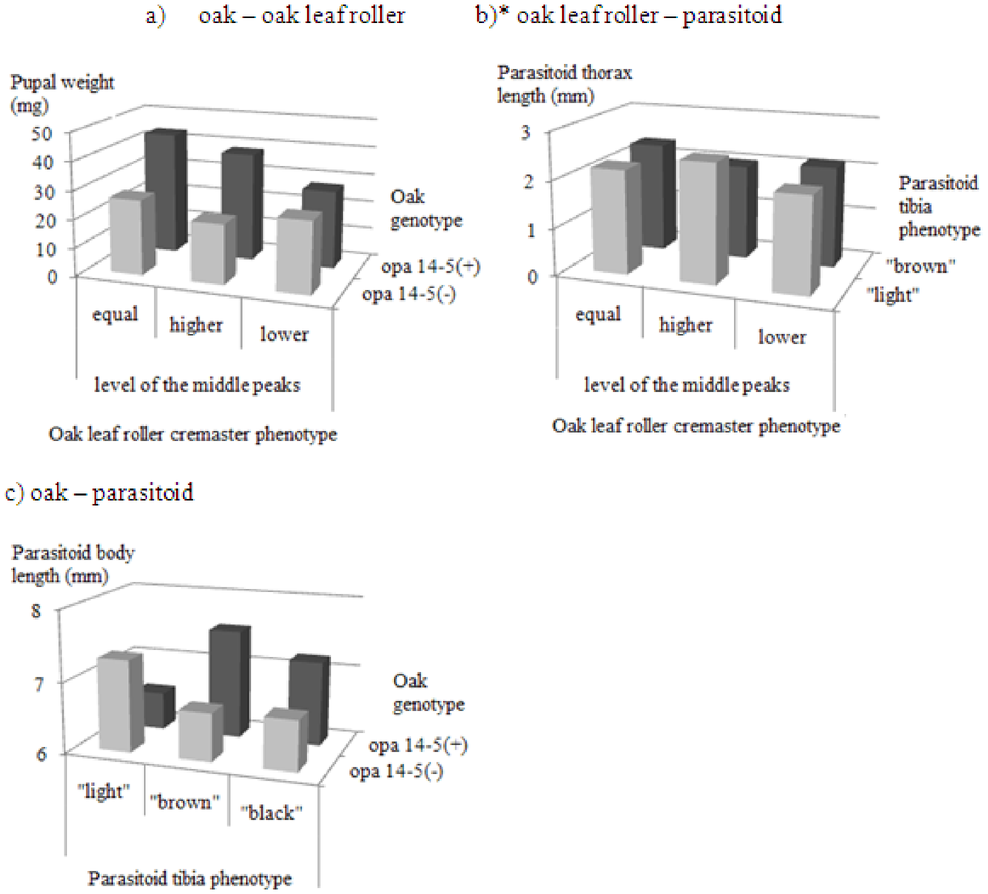
Recent investigations concerning interplay between genetics and ecology raised a question on foundation of a new field of enquiry "community genetics" [16, 17, 18], usefulness of which was discussed in the Special Feature (Ecology, 2003, vol. 84, no. 3). Community genetics, by our opinion, should address its attention to the gene pools of the populations, which interact in a community, discovering the situation when alteration in gene pool of one population evokes corresponding alterations in another one. Such the situation may arise only in that case when the fitness of a specimen depends on the kind of another species representative, with which it interacts in a community.

Studying individual consortia of pubescent oak (*Quercus pubescens*) in Crimea, we have found that genetic variation in host tree influences variation in pest densities and thus may affect structures of the micro-communities inhabiting them [12]. These data show that oak genes have effects on the levels higher than population. Such the effects were named "extended phenotype" [17]. Among others, extended phenotype (*sensu* Whitham and others [17]) may cause predictable composition of arthropod community in eucalypt hybrids [19], willow [20], evening primrose [21] *etc*. At the same time, we find no any author, pointing that extended phenotype depend on genotypes of all the interacting representatives. Herbivore composition depends not only from genetic variation in host plant, but also from genetic futures of the herbivores, because they choose the host plants due to their specific genetic constitution, including genes, which determinate this choice and its variation. In this relation, the question arises what organism expresses the extended phenotype? It obviously should be peculiar to the whole community, including both the host plant and the herbivores. In this case the term "phenotype" is not correct, because it should belong to an organism. Misuse of the term is a first step to further incorrect conclusions. As classic phenotype is heritable, this was incorrectly transferred also to "extended phenotype", and, hence, to community level.

We also studied a question what role inter-population genetic heterogeneity plays in tri-trophic interaction among oaks, their herbivores and parasitoids, infesting these herbivores. According to our results, entire picture of the niche partitioning in the *T. viridana* parasitoids as well as in herbivores, damaging oaks, has hierarchic construction. Parasitoids attack preferably unfit hosts and divide them among themselves with each species having its own niche, which then divided among intra-species groups such as genotype classes or phenotypes [12].

When two individuals of different species interact, their genotypes, coding for their futures and requirements, should influence result of this interaction. Thus, fitness of an individual depends, among others, on the genotypes of individuals, with which it interacts in a community. Direct estimation of specimen fitness is a difficult task if possible at all. One of useful ways lies in measurement of quantitative signs related with average fitness, such as body sizes in insects [22, 23]. Studying variation of fitness-related signs in dependence on genetic variation in interacting species we may find inter-level genetic ties.

The data obtained show that variation in the *T. viridana* pupal weights depends not only from their phenotypes, but also from genotypes of the oaks, which they inhabit (Figure 4a). Variation in parasitoid sizes depends from their phenotypes, phenotypes of their hosts (Figure 4b) and genotypes of the oaks (Figure 4c). Moreover, the relations have some common regularity. 'Light' phenotype parasitoids reach maximum sizes when developing in the oak leaf roller pupae with the 'high' cremaster phenotype (Figure 4b). Thus, the parasitoid phenotype is most adapted to the host phenotype. At the same time, these hosts are unfit on oaks without OPA 14-5 DNA fragment in their genotypes (Figure 4a). As the result, the parasitoids, attacking small, unfit hosts, obtain advantage on these oaks and, thus, reach maximum sizes (Figure 4c). Analogous causal chain may be created for 'brown' parasite and 'lower' oak leaf roller phenotypes on oaks with the DNA fragment. Thus, genotypes of representatives of the three trophic levels are related. This means that alterations in genetic structure at one of the levels should influence genetic structures at other dependent levels. This example reflects the role, which inter-species genetic variation plays in ecological interactions among the species in a community.


a) oak – oak leaf roller

b)* oak leaf roller – parasitoid

c) oak – parasitoid

Fig. 4. PositionGenetic aspects of interaction among oaks (Quercus pubescens Willd.) (fig. 1a), oak leaf roller (T. viridana L.) and its parasitoid (Itoplectis maculator F.); oak leaf roller pupal weights in relation to the pupae phenotypes and the genotypes of the oaks which they inhabit [12]

Found associations represent ties among the gene pools of populations, interacting in a community. As we have elements, gene pools, and ties among them, we once more may say about some system, “genetic” system of a community. M.A. Holubets [5, 7] heuristically described this system as ecosystem “memory”, regulatory, informative subsystem driving ecosystem functioning, and called it genoplast.

As genoplast arises on the base of selective processes within each of the interacting populations, its explanation requires no introduction of such the categories as “ecosystem selection” or “ecosystem heritability” [17, 18]. Of course, as heritability is peculiar to each of the individuals included in a community, there should be some succession among the past, present and future states of the community. This ecosystem succession is equivalent to the heritability at the level of individuals, and may mimicry for it in the case, when species participants of a community strongly differ in their life cycle durations. Genoplast is the next hierarchy level after population gene pools. It arises from interactions among the representatives of different species, and its succession integrates individual heritabilities in the same manner as pressure of a gas integrates velocities of the molecules it consists of.

2.5. Heterotrophic consortia

It must be pointed that data on heterotrophic consortia rarely happened in the World-wide literature than those on autotrophic consortia. L.A. Demidenko has presented very interesting data on consortive ties of Caspian seal [24].

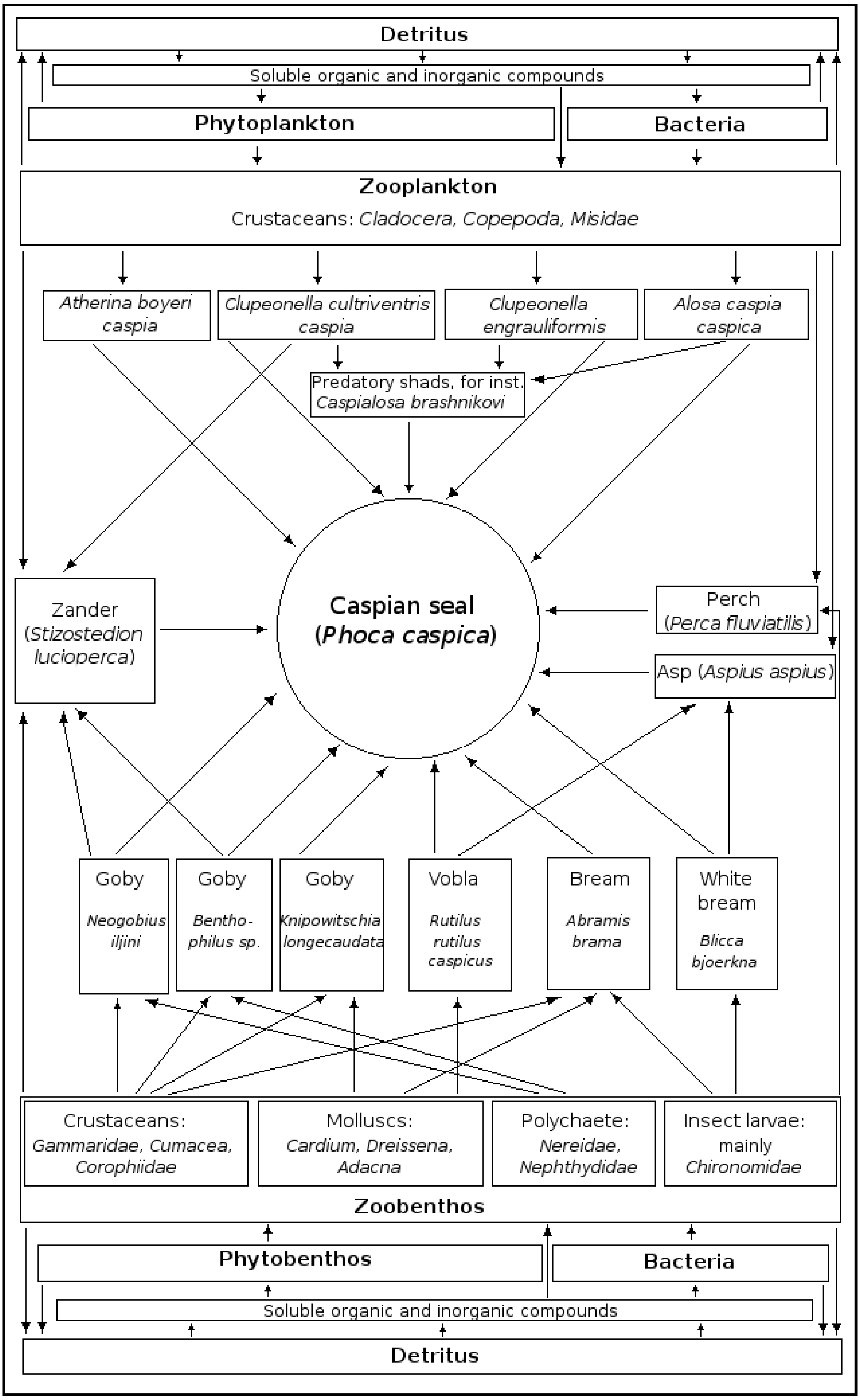


Fig. 5. Trophic relations of Caspian Seal (Phoca caspica Gmelin, 1788) [24]

Caspian seal (Phoca caspica Gmelin, 1788) is a marine mammal with weight 50-85 kg and 130-140 cm in length. Its location in trophic chain is reflected in figure 5. Caspian seal consuming there different fishes as third, fourth and even fifth link covers many food chains. At the same time many helminths, its consorters are feeding in it or on it. The helminths are wide spread and many of them have a set of hosts both residual and intermediate. For example, helminths Eustrongylides excisus join the consortia, which are determined by the seals, voblas, zanders, oligochaetes and cormorants (figure 6). The parasites, thus, join cores of many consortia of vertebrate animals from ecosystem of Caspian sea. Doing that they integrate Caspian sea communities into the whole unity. Furthermore, life cycles of many Caspian seal helminths include birds and terrestrial animals as alternative hosts, and these helminths, thus, participate in inter-ecosystem relations.

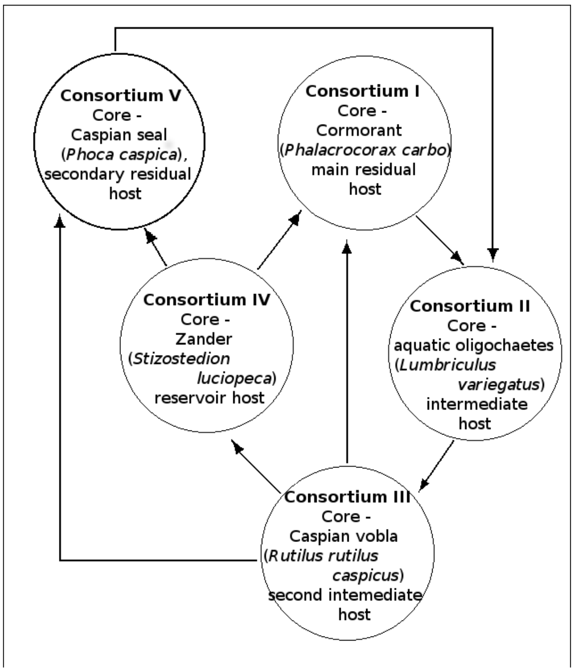


Fig. 6. Relations among the consortia with different cores when Eustrongylides excisus is a consorter

On the whole, Caspian seal consortia include 23 helminth species as there consorters. No any from fifty studied seals have been found free of helmints. Each of them was inhabited by a couple of helminths including representatives of 3 to 7 species [24]. It was found that only one helminth species, Pseudamphistomum truncatua, inhabited mero-consortia of liver, gall bladder and pancreas in Caspian seal. Small intestine of the seal was the most attractive for helminths. It is inhabited by ten helminth species from different classes, with trematodes Ciureana badamschini and Mesorchis advena dominating among them.

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Received: 8 October 2021; **revised:** 20 November 2021.

Івашов Анатолій, Сімчук Андрій. Екологічна консорція як елементарна екосистема. *Журнал Прикарпатського університету імені Василя Стефаника*, **8** (4) (2021), 34–44.

Кожен з великих автотрофних або гетеротрофних організмів створює середовище для багатьох організмів, які живуть у ньому, на ньому та навколо нього. Цей центральний організм і всі інші організми, що живуть у сфері його впливу, складають разом елементарне угруповання або екосистему, якщо брати до уваги грунт, повітря та інші елементи, які входять до цієї сфери. У східноєвропейській екологічній традиції такі елементарні екосистеми називаються індивідуальними консорціумами. Популяційно-видові консорції, у свою чергу, об'єднують окремі консорції популяцій і представників видів відповідно. Кожен центральний організм має унікальний генотип, і, таким чином, створює унікальне середовище для своїх мешканців. У зв'язку з цим результат взаємодії консортів та їх хазяїна залежить як від генотипу центрального організму, з одного боку, так і від генетичних структур консортів з іншого. Таким чином, автотрофна або гетеротрофна індивідуальна консорція – це просторово обмежена єдність різних організмів, зона концентрації життя, в якій навколо детермінантного досить великого центрального організму формується специфічний склад живих і неживих компонентів зі своєрідним енергетично-інформаційним обміном.

Ключові слова: крнсорція, генопласт, розширений фенотип, взаємодія типу “ген-ген”.