

Primary and Secondary Succession Modelling in Marine Bottom Biotopes (Black Sea)

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International Journal of Marine Science, 2019, Vol.9, No.8 doi: [10.5376/ijms.2019.09.0008](https://doi.org/10.5376/ijms.2019.09.0008)

Received: 14 Sep., 2019

Accepted: 28 Oct., 2019

Published: 07 Dec., 2019

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Preferred citation for this article:

Mazlumyan S.A., 2019, Primary and secondary succession modelling in marine bottom biotopes (Black Sea), International Journal of Marine Science, 9(8): 66-76 (doi: [10.5376/ijms.2019.09.0008](https://doi.org/10.5376/ijms.2019.09.0008))

Abstract This paper discusses the ecological succession principle and shows interrelations of this concept with many approaches of biodiversity analysis and general systems theory. After a description of succession process, system model is introduced as emergent community properties, their characteristics are explained, and different stage types are distinguished in primary and secondary succession. Systems modelling, lognormal analysis, diversity indices and relevant methods of investigation provided an opportunity of details quantified description of succession process. The results defined time-span of colonization (primary) and recovery (after hypoxic event) community structure (secondary), community structure. Thereafter, while observing succession development, structure changes are related to particular stage, and the roles of disturbances are discussed. Possible adverse impacts caused by succession drivers are identified. The study provides a step towards a more understanding of the link between marine benthic fauna and ecosystem functioning.

Keywords Time-span of colonization, NW of Black Sea, Hypoxic event, Ecosystem modelling, Quantified description of succession, Diversity indices, Lognormal analysis

1 Introduction

The ecological impact of humans on marine ecosystems requires a deep understanding of their interactions with these ecosystems. In particular, the consequences of human actions on sand bottom environment need to be understood. Succession occurs in essentially lifeless bottom areas as a result of hypoxia events, sand exploitation, dredging. Succession creates a continually changing mix of benthos species within sand communities as disturbances of different intensities, sizes, and frequencies. This situation imposes a partially unpredictable sequence of change in the species composition in sand biotopes during succession. The ever-varying community is an objective of our study. We mean the process by which the structure of a biological community evolves over time. If we observe the structure in successive time intervals even within a single biotope, we'll never find the community with the same structure. In certain cases, these changes are immediately noticeable, when the community formed using the resources of newly liberated locality. Over time the community changes its composition, structure and the "face of biotope." If community is destroyed under the external influences, its restoration will act, as a sufficiently slow process. Species, initially adapted to habitat destruction, are gradually replaced by original members of the association until the community will reach its inherent structure. The sequence of such changes is called succession. As the newly opened ecological process the succession was first observed by plant community researchers (Dureau, 1825; Cowles, 1899; Clements, 1916).

In succession studies for marine environment, there has been a considerable delay. The continuous research process to a large extent was impeded by the unavailability of essential visual observation due to the location of marine habitats. Adolphe Dureau de la Malle was the first to make use of the word "succession" concerning the vegetation development after forest clear-cutting (Dureau, 1825). Henry Chandler Cowles (Cowles, 1899) was adhered to the concept of deterministic and climatically conditioned succession. In 1916 Frederic E. Clements (Clements, 1916) preconceived the basic stages of succession. An important contribution of named field ecologists was that "succession is viewed as an occupation of an area by organisms involved in incessant process of action and reaction which in time results in changes in both environment and the community, both undergoing continuous reciprocal influence and adjustment" (Margalef, 1969). According to Clements, succession is a process involving several

phases. Clements (Clements, 1916) proposed to recognize only one true climax whose characteristics are determined solely by climate of each particular area (climatic climax). Clements ideas stimulated botanists to create a hierarchy of modified or discontinued series which they named sub-climax, pre-climax and post-climax. Using gradient analysis Robert Whittaker (Whittaker, 1953) created a theory of the mosaic climax: there was a mosaic of open regional climax communities. In a given area community composition depends only on conditions of specific environment, which fully proves to be true for zonality of benthic communities (Thorson 1946, 1950, 1955, 1957, 1958). The climax pattern theory recognizes a variety of climaxes governed by responses of species populations to biotic and abiotic conditions. According to this theory the total ecosystem environment determines regional species composition and community structure. The universal nature and flexibility of Whittaker theory allows its application to the climax communities with different initial conditions and drivers causing succession. H.T. Odum and R.C. Pinkerton (Odum and Pinkerton, 1955) based on Lotka's law of maximum power principle (Lotka, 1925) in biological systems pointed that the succession is linked with a fundamental shift in the energy flux. As a result, system is maintained by accumulated organic matter and biomass with increase amount of energy. Later R. Margalef (Margalef, 1962; 1969) has bolstered the concept of bioenergetics succession grounds with actual data including marine communities (Margalef, 1962). Quantitative treatment of the succession process became possible thanks to the involvement of data on the organic matter change, the primary production, and diversity changes in different process steps. Quantitative changes occurring during succession specified by R. Margalef (Margalef, 1969):

- the biomass increases during succession;
- the ratio of primary production to total biomass drops;
- diversity increases to a certain value and then decreases again in the final stage of succession;
- the increase in diversity is related to the constancy of achieved abundance;
- populations are not forced to reconstruct themselves rapidly after drastic and extensive destruction;
- on the final stage of a succession, when the ecosystem is in equilibrium with the existing supply of species and the properties of the local environment detected an asymptotic process.

The central point in the succession studies is the duration of colonization process: "Ecosystems are composed of replicable prefabricated pieces – individuals of different species. The supply of species is limited; thus, succession cannot go on forever. Succession is an asymptotic process. Only evolution in the framework of the ecosystem can improve things a bit and allow further progress" (Margalef, 1969). Change of dominance in succession is closely related to the life strategy of species, i.e. methods of the territory development, survival and maintenance of species abundance (Whittaker, 1953). Under certain conditions species, which are adapted to a large number of dimensions of a multidimensional ecological niche, can dominate, therefore they are less likely to face limiting dimensionality. In other conditions, species that are adapted to one dimension can dominate (McNaughton and Wolf, 1970). An objective of the study is the ecological succession principle and setting of quantitative interrelations of this concept with mane approaches of biodiversity analysis and general systems theory for marine bottom community during natural colonization and recovery after hypoxic event.

2 Materials and Methods

2.1 Model of succession

Succession can build its history only when the environment is stable. The only limit set to this is progressive change is interference from the physical environment. In unsteady environment selected ecosystem will be composed of species with a high reproductive rate and lower special requirements. Such an ecosystem is less diverse and less complex. Modelling the succession process energy flow per unit biomass remains relatively high. The conclusion is that in any estimation of maturity, not only diversity, but also predictability of changes with time has to be considered. Ordinarily both characters are correlated. Less mature ecosystems not only have a lower diversity, but in them transition between successive stages includes a higher amount of uncertainty. And more diverse ecosystems have, in general, more predictable future states. In other words: in more mature ecosystems the future situation is more dependent on the present than it is on inputs coming from outside. Homeostasis is higher in mature ecosystems. On the other hand, future states in less mature ecosystems are heavily influenced by external inputs, by changes in the physical environment.

The definition given below may be applied only to the structure kinetics of succession and excluded functional aspects. This is due to the fact that the above-mentioned functional characteristics regardless of studied phenomenon characterize any time slice in any community (with inherent features).

Def. Ecological succession is the process of change in the species structure of community over time.

Let us discuss the succession model applied to marine ecosystems. The marine ecosystem system will be considered as a non-empty factor sets ratio:

$S \subset \times \{F_i : i \in I\} - (1)$, where, F_i is the biotic and abiotic factors, which composed marine ecosystem.

The set $\{F_i\}$ represents the finite set of system objects as: $S \subset F_1 \times F_2 \times \dots \times F_n - (2)$. Then $I^b \subset I$ and $I^e \subset I$ provide for the set partition into biotic and abiotic constituents $I^b \cap I^e = \emptyset$, $I^b \cup I^e = I - (3)$

Let succession is caused by a change in the ecosystem parameters. Since the organisms are adapted to survive and reproduce in a specific environment, they must interact with environment. Consequence of environment deterioration is discarded organisms beyond the norm. During succession ambient parameters are deviate from accepted norm. "If therefore an organism be really high adapted to the place it fills in its environment, this adaptation will be constantly menaced by any undirected agencies liable to cause changes to ether party in adaptation" (Fisher, 1930). Adaptation may be defined as the correspondence between the organism and the environment. Adaptation is characterized by many dimensions, since most organisms must correspond to variety of different aspects of habitat. Namely, adaptation includes adaptation in the physical environment and interaction with competitors and predators. Organisms can relatively easily adapt to well predictable environmental conditions, not the extremes (Pianka, 1978).

R.A. Fisher (Fisher, 1930) in the model of non-directional changes (climate, random events) proceeded from the fact that none of organisms is absolutely adapted, and to varying degrees manifests its misfit to environment space of many dimensions). Specialized forms have inherent limitations of homeostatic capabilities, so they cannot tolerate major changes in the environment "Adaptation in the sense of conformity in many particulars between two complex entities, may be shown, by making geometrical properties of space of many dimensions, to imply a statistical situation in which the probability of a change of given magnitude effecting an improvement decreases from its limiting value of one half as the magnitude of change is increased" (Fisher, 1930).

The global ecosystem response already occurs in a specific area of normal functioning under external disturbance: $\{P_u \subset L : u \in U\} - (4)$.

Adaptation mechanism can be assumed as the driver of buffering capacity of the ecosystem: $R: (P \times X) \rightarrow Y$, such as $(x,y) \in S \Leftrightarrow (\exists p) [R(p, x) = y] - (5)$.

Under conditional ecological norm the ecosystem would be in equilibrium and exists in the multidimensional area of a set: $X_n = \times \{F_i : i \in I_x\} - (6)$. The set $\{X_n\}$ includes in a broad sense all components of the ecosystem. Let's call them the resources, meaning their utilitarian value. The utilitarian value of resources consists in the mutual use of species of vital habitat for habitats. In real ecosystems the resources are always limited.

In the case when there is a disturbing effect: oil spills and pollutants of all kinds, siltation, a drop in the level of oxygen, etc. The process, as a rule, is directed by the "violating" driver and causes the ecosystem parameters to deviate from the state of ecological equilibrium. Under this mechanism, everything that takes the ecosystem out of the state of ecological equilibrium is implied. By disturbance driver for some resource-dependent species resource accessibility is deregulated, while for certain species carrying capacity would multiply (Mazlumyan, 2015). In modified environment "not prosperous" species set $\{N_{i+1}\}$ are able to realize its potential carrying capacity, due to available resources, which were used by previous series of set species $\{N_i\}$. It should be mentioned, that species position in series is determined by its colonization rate and environmental alterations during succession time. Under the influence of stress factor, opportunistic populations give rapid random bursts of numbers in the early stages of succession. At late, climax stages of succession, equilibrium states with their resources are reached by species whose

densities are stable, provided that the amount of resources in the biotope does not change. The r - type of selection varies by the K - type of selection (MacArthur, Wilson, 1967). In the broadest sense, the balance between resources and organisms refers to the relationship between species and environment, regardless of whether they are r-strategists or K-strategists. Large K-strategists are slowly colonized or slowly growing after colonization and therefore become dominant in community on the later stages of succession. Small r-strategists are contented with modest capabilities of disturbed environment and have the advantages on early succession stages. Though, r-strategists set $\{N_{i+1}\}$ will provide trophic benefits for slowly developed, but more competitive K-strategists. Development cycle of each species in full or in part defines its role in succession (Ricklefs, 1980). Continuous environment changes facilitated species substitution. Succession continues until new species incorporation and expulsion of earlier settled species leaves unaltered environment of emerging community. For each species from set $\{N_i\}$ corresponds set $S \subset \times \{F_i; i \in I\} - (7)$ of environmental conditions under which these species grow and reproduce. Species $\{N\}$ are adapted and flourish until set $\{S\}$ is conditionally stable.

Each species in the ecosystem has set of environmental conditions under which these species generate its own environment: $S \subset F_1 \times F_2 \times \dots \times F_n - (1)$. The set $\{F_i\}$ is optimal for the first series species $\{N_i\}$. In altered conditions $\{F_{i+1}\}$ will be optimal for other set species $\{N_{i+1}\}$ series. Under altered conditions the first set of species $\{N_i\}$ may fail to flourish and the second set $\{N_{i+1}\}$ species may flourish. Potential population growth rate of r-strategists set is realized to a certain extent (less than the intrinsic rate of population growth). Species reputed as r-strategists will occupy the vacated ecological niche. The potential capacity is formed on S - an altered vector space, with the set of conditions $\{F_{i+1}\}$ created to achieve T_D^P - potential carrying capacity for set $\{N_{i+1}\}$

Transition from the real capacity T_D^R to the potential T_D^P formally expressed by:

$$\max_{x_n} D\{X\} = T_D^R \rightarrow \max_{x_n} D\{X\} = T_D^P - (7)$$

Mechanism of action is carried out by buffering capacity of the preserve's ecosystem structural properties through activation of the mechanism of potential capacity for the species becoming main participants of another succession series.

2.1 Analysis of structural changes in a succession series

Def. A serial community is an intermediate stage found in an ecosystem advancing towards its climax (Figure 1). In many cases more than one serial stage evolves until climax conditions are attained (Margalef, 1969; Clements, 1916).

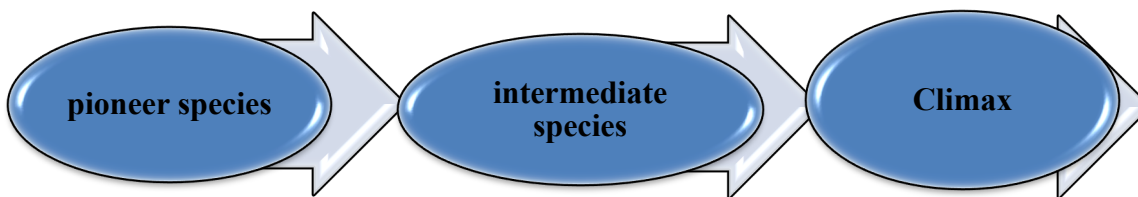


Figure 1 Serial community in succession

The sequence of species in the series depends on changes in the physical environment derived under the effect of species colonization. It is believed that succession conducts to the ultimate expression of the development, called the climax community. Our study of successions found that many series, developing under special conditions established in the local environment, transformed in the same climax communities. This can be seen in the structure of the mature community of violations unaffected biotope. Natural conditions in habitat are continuously changing. In response the communities themselves change. For a relatively long time, a true sustainable community is rarely found. In our studies we observe constant mutual fluctuations of the community and the environment, which cause permanent series, with deviations from the stable state

Unless, as a measure of stability we accept the level of biodiversity and the balance between the dominant K-strategists, at each selected biotope we will observe the constant change of structures, resulting in only a short period to a state of stable equilibrium. Practical studies (Pearson and Rosenberg, 1978) involved evaluation of the temporal diversity development (Shannon and Weaver, 1949), species dominance (Simpson, 1949) and evenness (Pielou, 1966) in experimental and bottom communities.

Lognormal model to some extent is a measure of community structural stability (Preston 1948, 1960, 1962). In state of relative environmental balance lognormal curve is given by a straight line. Numerous studies of structurally unstable communities under disturbing effects showed the form of a deviation from the lognormal model (Gray and Mirza, 1979; Ugland and Gray, 1982; Gray, 1983; Mazlumyan, 1989; Mazlumyan et al., 2008). The process of lifeless area colonization or secondary succession graphically looks like the change of transition states. In certain cases, it may be a relative balance model. Supposed climax moment is a straight-line curve. Structure that is the most appropriate to canonical model structure will be considered as a state of ecological equilibrium (Preston, 1948; 1960; 1962). Thus, succession process on lognormal curves looks like the change of the transition states run up to equilibrium states.

The renewal process or secondary succession is well described by change of the lognormal model parameters. In this case, the effect of hypoxia on the structure can be compared with disturbance, which intensity decreases over time. Correspondingly lognormal model parameters should be changed gradually, becoming similar to the model parameters in a state of ecological balance.

2.2 Succession drivers in marine ecosystems

Climate changes, namely temperature, can shift the biotic connection in an ecosystem that often occurs in the plankton community, bringing with warm water mass thermophile species, and to modify the effects of the prevailing regional climate. “Whilst climate change is unlikely to affect the physical habitat part of a biotope, it may affect the biotic element, the community. Effects on biotopes will therefore be ‘driven’ by effects on component species. If those species are key structural, key functional or are characteristic species that help to identify a particular biotope, then the biotope may cease to exist and will change to a different biotope at affected locations” (Hiscock 2004 et al.).

3 Results and Discussion

3.1 Primary succession on soft substratum

Succession studies were performed at experimental and nature conditions in coastal waters of the Western Crimea (Black Sea) (Prosvirov, 1990; Mazlumyan and Prosvirov, 2002; Mazlumyan and Prosvirov, 2016). Experimental work on observation the colonization of sandy habitats was carried out in the sea. At a depth of 13 meters 4 container with a layer of lifeless sand were installed.

Simultaneously with experiments were collected benthic samples directly from a natural sand biotope. Up species were determined polychaeta's and mollusks. The rest of the group was determined to class. It was conducted three series of experiments. The first series took place from February to August. Experimental community structure becomes stable in the fourth month of colonization, which coincides with the development of meroplankton and settlement of larvae on a substrate (Figure 3).

The second series took place from August to September. The third series took place from September to November (Figure 4). Community structure was shaped at first month of exposure. Season of mass meroplankton development (July and September) would actually favor more stable structure.

On initial succession series sustainability of bottom community depends on colonization season (due to planktonic larvae that settle and metamorphose into sessile benthic adults or migration of adult individuals). Structure of first month communities were stable due to a mass settlement of plankton larvae. The environmental conditions get modified by the action of species occupying the habitat: diversity increased (Figure 5). High species density provides barrier for possible invasion of any other species in the structure of new community (Prosvirov, 1990).

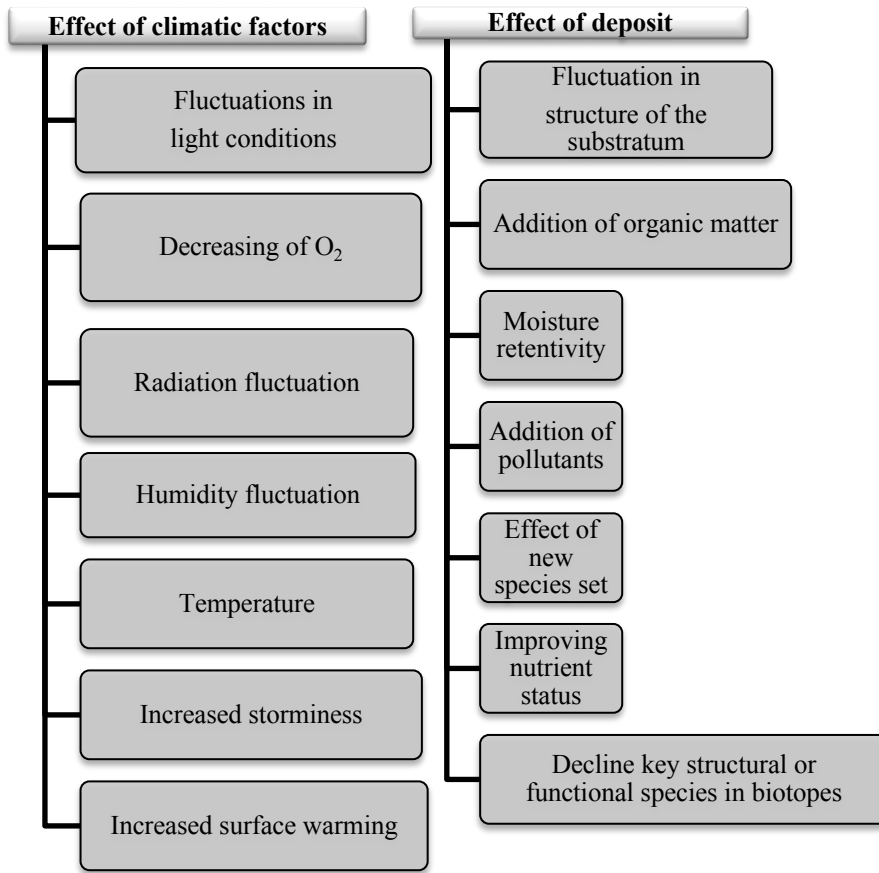


Figure 2 Abiotic effect of succession drivers

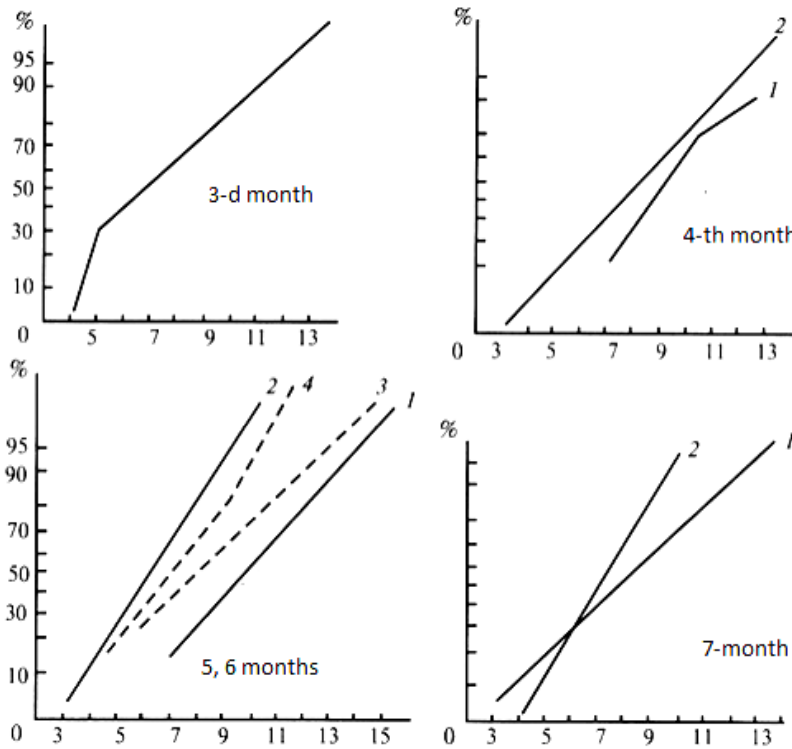


Figure 3 Lognormal plots of succession (1, 3) — in sand bottom and (2, 4) —experimental communities: exposure period (February-August) —190 days

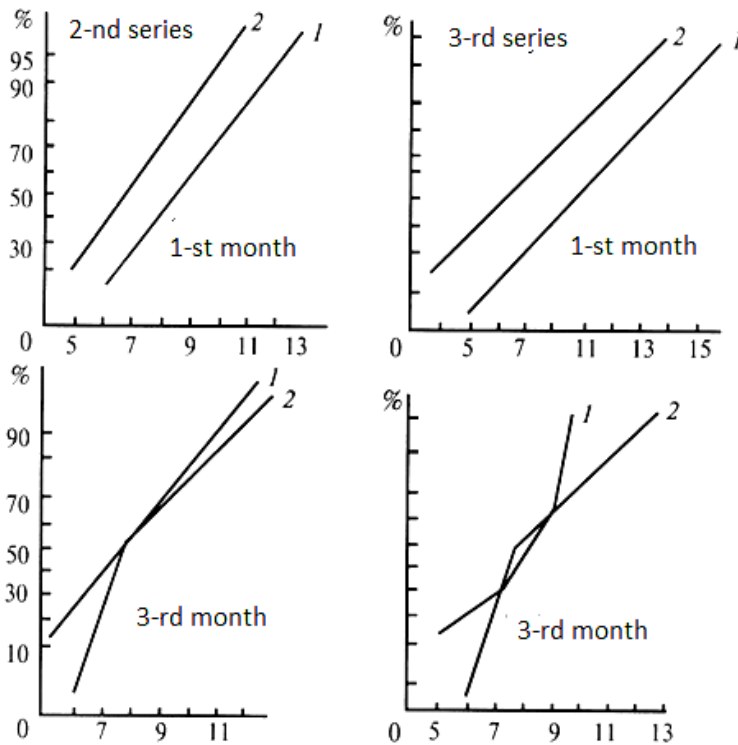


Figure 4 Lognormal plots of succession in (1) – sand bottom; (2) – experimental communities. Exposure period (2-nd series: August – October 95 days; 3-rd series: September –November – 63 days).

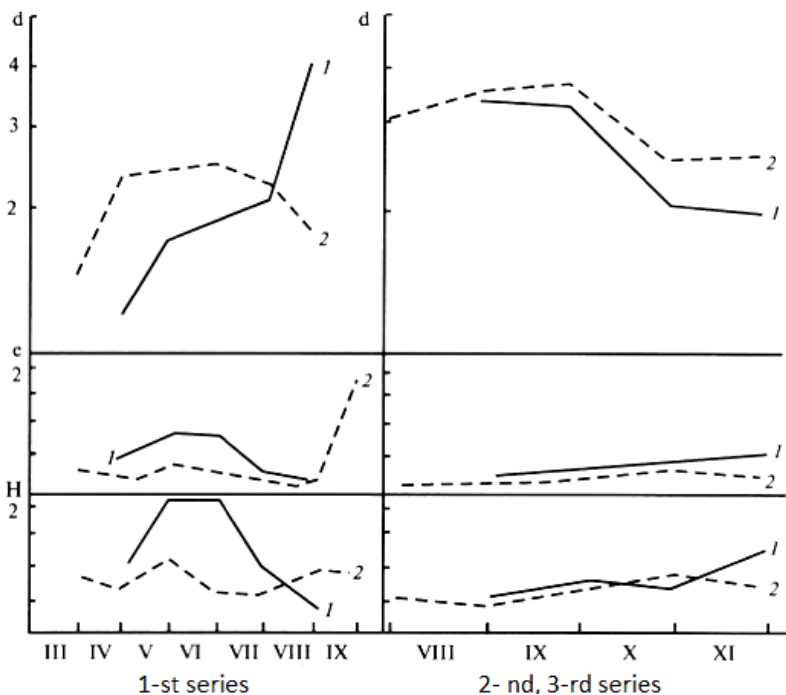


Figure 5 Changes in the H – Shannon-Wiener diversity index; e- evenness by Pielou; d- species dominance Simpson for succession in (1) – experimental and (2) – sand bottom communities

On lifeless bottom areas the rate of fauna recovery covered 4-5 months during meroplankton development period. At the primary and secondary stages in experimental succession process physical stress was reduced by micro-environment. Communities colonized by the adult r - strategies had a relatively low density and low diversity. Structure in r - colonized community was open for invasion or migration for any other species, thereby becoming

unsteady. The phase of the initial dominance of small and short-lived r - colonialists, which is characteristic for the colonization of loose soil in this case, was absent. It dominates the settled juveniles of large K - colonizers: *Pitar rudis* (Poli, 1795), *Prionospio cirrifera* Wirén, 1883, *Parvicardium exiguum* (Gmelin, 1791) (WoRMS Editorial Board, 2019). The absolute number of r - colonial societies in the experiment bath was equal to or even superior to the absolute number of r - colonial communities in baths of the first experiment. An index of diversity and evenness above for the experimental community in the first four months of formation, as compared to the bottom biocenosis and species diversity index is higher in the bottom biocoenose. With the end of July, the value of this index is higher in the experimental community. The observed changes in the dynamics of species richness index values can be explained by the fact that in bottom biocoenose abundant species make up a small percentage compared to the experimental community. Consequently, the number of species that come to the logarithm of the number of individuals is higher than that of the bath communities where significant percentage of abundant species.

3.2 Secondary faunal succession. Renewal after hypoxia event

In 1978, in the western part of the Karkinitzky Gulf acute hypoxia events occurred, which killed mussel bank. Community of *Mytilus galloprovincialis* Lamarck, 1819 (WoRMS Editorial Board, 2019) was found again in 1979 in that area. The increasing abundance was observed for most species of community. Over a period 1978 – 1982 after the hypoxic event community was in gradual recovery process.

For comparative method of inquiry secondary succession, we need to select *M. galloprovincialis* community, located in the “area of environmental standard”. The structure of such a community will serve us a natural model. This is necessary because in investigating community structure at different stages of renewal process we need a pattern community, with set of $\{X_n\}$ belonging to the “area of environmental norm”. Comparing the model for community of *M. galloprovincialis* in area of environmental standards with pattern community outside of this area, we can draw conclusions about the progress of secondary succession. The pattern community selected community from area of environmental standards situated at the Tarhankut peninsula.

Lognormal models of the mussel community c 1979 to 1982 describe the process of structural change during secondary succession (Figure 6).

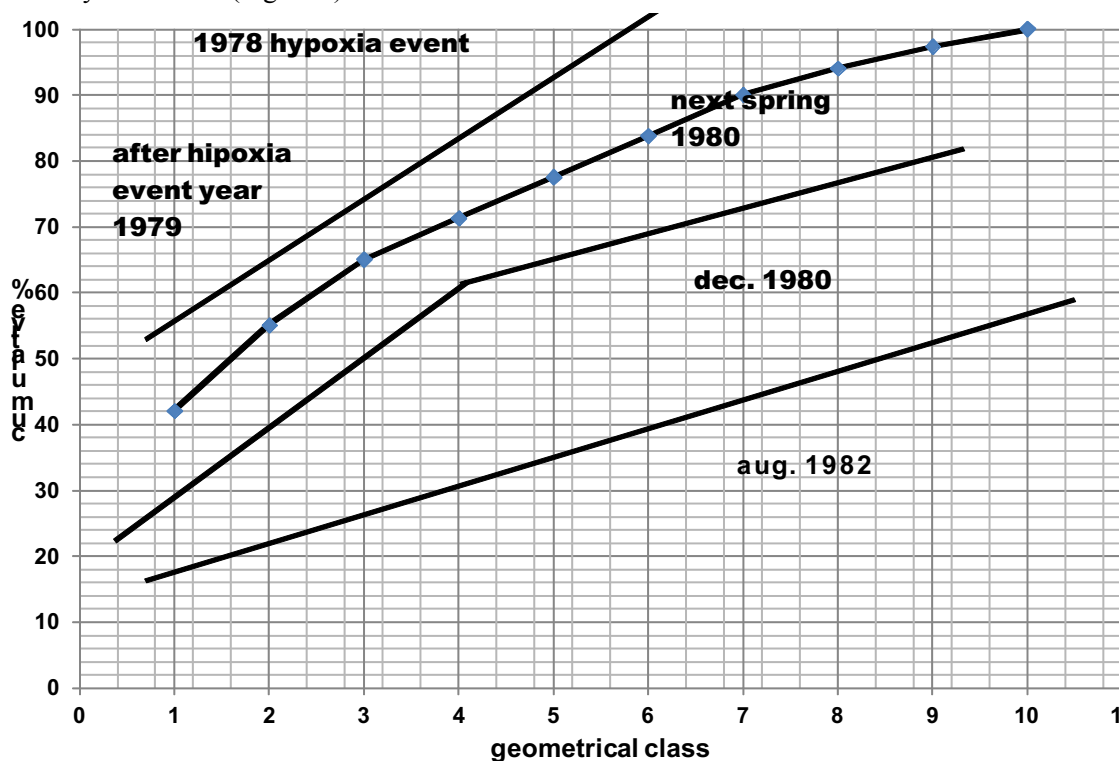


Figure 6 Lognormal models of the mussel community c 1979 to 1982 (The area of Schmidt rising, NW Black Sea)

Constantly changing species composition on the lognormal models is expressed in the change in the number of geometric classes and increasing the number of species of log-normal angle of the line. This means in mussel community during recovery represents a change in a series of successive structures. Each of the following structures is more stable than the previous one, which is explained by the fact that the species composition changes in the direction of increasing diversity.

According to the results of the constructed lognormal models the area at the Tarkhankut Peninsula can be characterized as area of environmental standard. Evidence is provided by the species composition of the community (Figure 7). In the area of the Schmidt rising, a slightly different picture is observed: the structure of the mussel community constantly changing from 1979 to 1982.

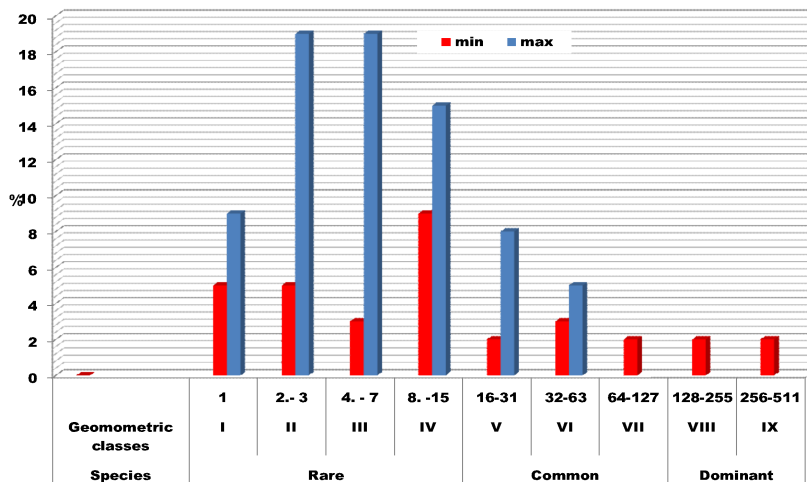


Figure 7 *M. galloprovincialis* community structure recovery after hypoxia event (the area of Schmidt rising, NW Black Sea).

The determination of the time required for restoration of a community after acute hypoxia events is similar to the study of changes in its state under the influence of damping intensity (Mazlumyan, 1989). Comparing the parameters of the lognormal models in the post-summer period, with the parameters of the stationary community models, it can be seen that the community structure is closest to the state of ecological equilibrium only by September 1980. Seasonal and inter-annual fluctuations in numbers do not significantly affect the form of the lognormal graph in the state of ecological equilibrium is a straight line (Preston, 1948; 1960). The characteristic of the composition in stationary community is different from the structure of the recovering community. This is expressed in the fact that the number of species in all geometric classes defined by the lognormal model is higher for the community located – “area of environmental standard.” Structure after hypoxia event essentially differed from ecologically equilibrium: for rare species - 3 times, for characteristic species - 2 times, for mass - 2 - 7 times (Figure 7; Figure 8).

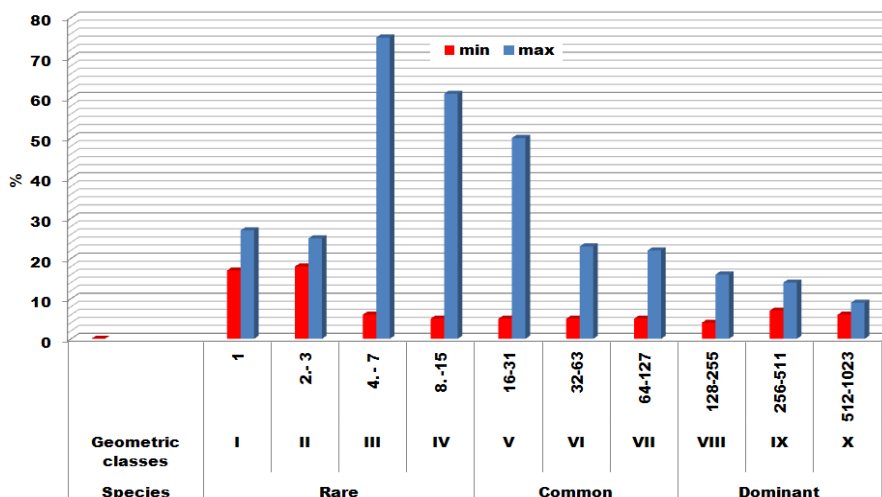


Figure 8 *M. galloprovincialis* community structure at the area of environmental standard (the Tarkhankut peninsula, Black Sea)

According to a model developed for a heterogeneous community (Ugland and Gray, 1982) the sum abundance in it is distributed lognormal. Rare species make up 65% of the total number of species, characteristic - 25%, dominant - 10%. This is also true for the mussel community, which has a mosaic structure in the study area, while the distribution of the number of species in different samples collected both in the mussel spot and outside it is lognormal. In pattern community the relationships between the three structural groups (rare, characteristic, dominant) species are somewhat biased (Figure 7; Figure 8). However, this is natural, since empirical numbers are always characterized by fluctuations caused by a number of environmental factors (Preston, 1948; 1960). The complexity of the analysis of the structure of the community recovering after acute hypoxia event was that the proportion of the abundance of different groups of species in this community is less pronounced than in the environmentally stable community. This can be explained by fluctuations in the abundance of individual species in the process of community restoration.

Acknowledgements

I am grateful to my colleagues Yuri Prosvirov and Alexander Povchun. The observation of lifeless substrate colonization, conducted by Yu. Prosvirov, made materials on primary succession truly unique. It inspired my model interpretation. The inquisitive expeditionary studies by A. Povchun, who craved for understanding the internal environmental mechanisms, had an invaluable impact and influenced my further research.

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