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On biocoenoses

by A.A. Shorygin

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- - - ON BIOCOENOSES.

By A. A. Shorygin.

In order to understand the nature and laws governing a biocoenosis, it is essential to analyse at least schematically the following three cardinal problems:

1. What is responsible for the characteristic structure of a biocoenosis and what is its purpose, in particular what determines the correlation between the numbers (more correctly, the biomasses) of species forming biocoenoses.

2. What are the predominant interrelations between different species within the biocoenoses.

3. What are the correlations of these species with the biotope which they inhabit.

THE STRUCTURE OF BIOCOENOSIS AND ITS BIOLOGICAL SIGNIFICANCE.

If we analyse the numerical correlation or, still more important, the correlation between biomasses of species found within a biocoenosis, we find that whatever the number of species forming the given biocoenosis, its main bulk usually consists of a few, though abundantly represented, species, the biomass of which prevails to a greater or lesser degree over that of other species. This fact was observed long time ago and described by a number of authors. V. A. Brotskaya and L. A. Zenkevich (1939) termed such prevalent species "the leading species of first order". In different biocoenoses the

degree of prevalence of leading species is variable. Thus, in the catches of fish obtained in sea basins, the main bulk of catches (from 70 to 98%, on an average 83.8%) is formed by 5 (!) species only whatever the overall number of species found in the catches (from 10 to 118). Even in the Northern zone of the Atlantic Ocean, where the catches consist of as many as 118 different species, 5 species constituted 78.6% of the overall catch. The above figures result from analysis of 22 catches in different sea basins⁽²⁾ and show that a clearly pronounced predominance of a limited number of species within a society is a rule. However, the relative degree of prevalence varies considerably.

Further analysis has shown that the few, though abundantly represented, species forming the main bulk of the biocoenosis are not all equally important. Usually there is one species whose biomass strongly predominates over the remaining "characteristic species of the 1st order". Consequently, the law governing the biocoenosis as a whole is equally valid_λ for this particular group of species. In the above-mentioned catches obtained in sea basins the most numerous species constituted on the whole from a quarter to up to three quarters of the catch, i.e. on an average somewhat less than half the catch

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(1) This posthumous article by A. A. Shorygin deals with the important problem of the nature of a biocoenosis, which the author studied during the last few years of his life and intended to develop more thoroughly. The publication of this article has been delayed due to a number of circumstances beyond the control of the editor. The article is published with insignificant abbreviations. (Editor's note).

(2) 1) Aral; 2) Caspian - the mean data for a number of years; 3) Caspian in 1936 - prevalence of benthophagi; 4) Caspian in 1917 - prevalence of planktophagi; 5) Caspian in 1939 - prevalence of predators; 6) Azov sea; 7) Black Sea; 8) Northern Sea; 9) Barents Sea - the year of cod; 10) Barents sea - the year of herring; 11) Baltic Sea; 12) White Sea; 13) Northern Atlantic Ocean; 14) Northern Atlantic-Northern series; 15) Northern Atlantic-Northern series, European zone; 16) Northern Atlantic, Northern series, American zone; 17) Northern Atlantic-Southern series, American zone; 19) Bering sea; 20) Sea of Okhotsk; 21) Sea of Japan; 22) Northern Pacific. References to the bibliographic sources containing complete statistical data have been quoted in the work by T. S. Rass (1948).

(28-78% M = 44.5%). This shows the truth of the theory of prevalence of one species over another set forth above. We observed more considerable fluctuations (almost threefold) in the case of individual prevalence of one species over another than in the case of the relative predominance of the entire group of "characteristic species of the 1st order".

Thus, although the laws determining the composition of biocoenosis remain unchanged, the degree to which these laws manifest themselves in different individual cases may vary. Alongside with the biocoenoses, where a few or even one species is overwhelmingly predominant (78%), we encountered biocoenoses where this prevalence was considerably more moderate (22%).

We shall first of all endeavour to clarify the factors accounting for these divergences and the differences in the position of species forming a biocoenosis in the two cases discussed above. For this purpose we shall analyse two abstract cases simplified to the maximum. Let us consider two biocoenoses consisting of three species each (A, B, C) the overall biomass which equals 100 in both cases. In the first biocoenosis (type I) species A is prevalent over all the remaining species. In the second biocoenosis (type II) this prevalence is considerably less pronounced.

The interrelations between the species with regard to feeding and other needs is identical in both cases.

Type I.

Biomass of the species A = 70

" " " " B = 20

" " " " C = 10

Overall biomass 100

The intraspecies competition under otherwise identical conditions will be, as we mentioned before, (A. A. Shorygin, 1939a) directly proportionate to the biological volume of the species in question, i.e.:

Intraspecies competition of the species A equals 70
 " " " " " B " 20
 " " " " " C " 10

The overall intensity of the intraspecies competition is proportionate to 100.

The interspecies competition under otherwise identical conditions will be directly proportionate to the sum of the biomasses of competing species:

The interspecies competition between the species A and C is proportionate to 70 plus 20 = 90

The interspecies competition between the species B and C is proportionate to 20 plus 10 = 30

The interspecies competition between the species C and A is proportionate to 10 plus 70 = 80

The total intensity of the interspecies competition equals 200.

Consequently, the total intensity of both the intraspecies and interspecies competition per species will be proportionate to the following figures:

The total intensity
 of the species A - 70 plus 80 plus 90 = 240 or 48%
 of the species B - 20 plus 90 plus 30 = 140 or 28%
 of the species C - 10 plus 80 plus 30 = 120 or 24%

Type II.

Biomass of the species A = 40
 " " " " B = 30
 " " " " C = 30

Total biomass = 100

On the basis of considerations presented in the former case:

The intraspecies competition of the species A is proportionate to 40

The intraspecies competition of the species B is proportionate to 30

The intraspecies competition of the species C is proportionate to 30

The total intensity of the intraspecies competition is proportionate to 100

The interspecies competition between the species A and B is proportionate to
40 plus 30 = 70

The interspecies competition between the species B and C is proportionate to
30 plus 30 = 60

The interspecies competition between the species C and A is proportionate to
30 plus 40 = 70

Total intensity of the interspecies competition is proportionate to 200.

Total intensity of the inter and intraspecies competitions per
species A - 40 plus 70 plus 70 = 180 or 36%
species B - 30 plus 70 plus 60 = 160 or 32%
species C - 30 plus 70 plus 60 = 160 or 32%

Let us juxtapose the results obtained in the two cases (table 1).

Table I.

The relative position of individual species in different types of the biocoenoses.

Species	Types of biocoenoses	Biomass	Total intensity	Relative intensity	Competition		Char acte of comptit-ion
					(1) Inter-species	Intra-species	
A	I	70	48	0.7	70	170	2.4
	II	40	36	0.9	40	140	3.5
B	I	20	28	1.4	20	120	6.0
	II	30	32	1.1	30	130	4.3
C	I	10	24	2.4	10	110	11.0
	II	30	32	1.1	30	130	4.3

(1) By the relative intensity the author means the relation of the total intensity to the biomass (Editor's note).

(2) By the character of the intensity of competition the author means the relation of the interspecies competition to the intraspecies competition (Editor's note).

We may draw the following conclusions from the above presented juxtaposition:

In type I, species A occupies the most favourable position: 1) it has the lowest relative intensity of competition (0.7), i.e. the lowest intensity of the summary competition at unchanged quantity or, which means the same, the highest number of representatives at unchanged overall intensity of competition; 2) in the overall intensity of competition of this species the intraspecies competition is the highest, while the index of the interspecies competition is the lowest (2.4). The relation between the interspecies and intraspecies competition varies considerable in different species (from 2.4 to 11.0, i.e. more than four times).

The figures used in our examples are incorrect, since the case discussed has been simplified to the extreme and the intensity of interspecies competition as compared with such of the intraspecies competition has been strongly exaggerated due to the fact that we ignored the biological divergences between different species, which decreased the intensity of intraspecies competition accordingly. Nevertheless, the character of fluctuations has been expressed correctly. The remaining species are in the less favourable position, the lesser their number: with the drop in the number of population their relative intensity of competition increases (1.4 and 2.4), the relative value of the intraspecies competition decreases and the interspecies competition becomes intensified (6.0 and 11.0).

In type II, in its extreme expression, the position of all the species is equal. The total intensity of the interspecies and intraspecies competition at otherwise identical conditions is equal in both types (100 and 200). Their

proportions are also equal (1:2). Thus, the types differ only in the relative position of different species. This difference may be characterized as follows: 1) in type II in its extreme expression all the species are in an identical position; 2) in type I the most numerous species is affected by the highest intraspecies competition at the relatively lowest effect of restraining outer pressure (i.e. the interspecies competition). This circumstance probably accounts to a considerable extent for the fact that the species is more numerous than could be expected judging from the total intensity of the interspecies and intraspecies competition or that of the former only. In other words, it probably suffices to achieve a slight biological advantage in order to attain a considerable prevalence in number within a uniform biotope. Furthermore, the greater the quantitative prevalence, the higher the degree of relative advantage of the most numerous species.

If this is correct, then an ideal biotope unchangeable in time should be populated by one single species. On the other hand, only a biotope deviating to the maximum degree from the standard towards the conditions to which that particular species has become adapted, may be populated by a single species.

Type II in its extreme expression is possible only on condition that it be populated by several ideally equivalent species. We may also observe type II, though not in its extreme expression, under conditions of a highly varied biotope changeable in time.

Since there exist no perfectly uniform biotopes, nor perfectly equivalent species, types I and II cannot be observed in practice in their extreme expressions (monocoenoses may be encountered only within biotopes deviating from the standard maximum). The more uniform in time and space a biotope is the closer the biocoenosis populating it should approach the

extreme position of type I (monocoenosis). The more multiform the biotope the closer the biocoenosis populating it approaches the extreme position of type II (heterocenosis).

If the aforesaid is correct, the degree of approximation of a biocoenosis to one or the other type is the derivative and may serve as a measure for determining the degree of uniformity or multiformity of a biotope.

This theory may be verified on factual material: the narrower and the more uniform the biotope under investigation, the more closely the biocoenosis populating it resembles type I and the lesser is the number of species comprising the biocoenosis. We believe that the latter characteristic is of secondary importance as compared with the former. The above theory has been confirmed by the catches of fish (table 2). Indeed, proceeding from our theory, the composition of the overall catch of the entire water basin (which is a mixture of numerous and most varied biotopes) should be the farthest removed from type I. The composition of catches of the planktophagi should be the closest to type I, since they populate the most uniform biotope, and comprise the smallest number of species. The catches of benthophagi and predators populating more varied biotopes than those inhabited by planktophagi, should be intermediate in character, somewhat remote from type I and more varied in the composition of species than planktophagi. The catches of benthic and pelagian predators, considered separately, should be closer to type I than the summary catches of predators, since in the former case the biotope of predators is divided into two more uniform parts. We believe that the catches of benthic predators are several times closer to type I than those of benthophagi, since the latter inhabit a considerably more multiform biotope.

Table 3 has been drawn on the basis of analyses of the above-

mentioned 22 catches obtained in sea basins, and shows the comparative values of the five most numerous species and the number of species recorded in the said catches. The relative importance of the 1st species confirms with absolute precision the alternation of magnitudes forecast in our theoretical estimates.

TABLE 2.

Mean value (in%) of the most numerous and five most numerous species and the number of species found in the catches obtained in sea basins.

Catch	1st species	1+V species	Number of species
Entire water basin	44.5	88.3	33.9
Consumers of benthos	51.3	93.4	17.6
Consumers of plankton	67.6	96.5	14.0
Predators	51.65	88.5	21.7
Predatory consumers of benthic fish	62.1	92.4	14.3
Predatory consumers of pelagic fish	56.2	92.9	14.6

The figures expressing the relative importance of the five leading species, constituting over 4/5 of the entire catch also correspond on the whole to the data of our theoretic estimates, although with less precision. The alternation of the number of registered species (a magnitude that should be handled very carefully) also coincides with our assumptions. Our theory may be also confirmed on the basis of ecological, as well as geographic division of the biotope. Thus, when we divide the catches from the North Atlantic Ocean into sections, the importance of the 1st species changes (table 3). Consequently, the narrower geographically a biocoenosis is, the closer it

approaches type I. The American zone of the Northern series (27.8%) is the only exception, probably due to insufficient commercial exploitation of that area.

Our assumptions have been also confirmed in part by the experimental research. Thus, G. F. Gause (1934a) arrived at the following conclusion: "This problem has been already investigated from the theoretical point of view by Haldane, Volterra and Lotka. It appears that the qualities of the above presented equations showing the struggle for existence are such that a species possessing advantages over another species will inevitably force out the latter completely. We wish to point out that it is extremely difficult to verify this supposition under natural conditions. Nature provides a great number of "niches" of varying conditions and while in one of the niches a competing species possessing advantages over another form forces out the latter, in a different niche and under different conditions of competition the second competing species is in a favourable position and consequently, forces out the former. As a result, two affinitive species continue coexisting in relative equilibrium, though occupying somewhat different niches". Subsequent research of H. F. Hause fully confirmed the theory maintaining that within a uniform medium one species inevitably forces out another species. The degree of superiority of the conquering species does not enter into question at all, since the degree could have merely affected the duration of the process of forcing out, but would never alter its final outcome. The aforesaid deductions fully coincide with our theories, theories reached through a different process, and based on wholly different data.

TABLE 3.

Percentage of the most numerous species in the North Atlantic Ocean.

North Atlantic Ocean

Mean value for the Northern Atlantic.	Northern series.		Southern series.		
	Mean value for the Northern series.	Europe	America	Europe	America
33.0	38.0	39.0	27.8	42.8	58.2

In his later work H. F. Haue (1934b) showed that in a uniform biotope a lengthy coexistence of a predator and a victim is impossible and inevitably results in the disappearance of both. Their coexistence may be observed only under conditions of a non-uniform medium or immigration. The periodic fluctuations in the quantities of predators and victims, which Lotka and Volterr regarded as inevitable, occurred only in the latter case. In this work H. F. Haue emphasizes the importance of the immigration factor in predator-victim relations. He omitted this factor in the work quoted above then discussing the problem of two competing species, although it may serve as an example of the possible permanent coexistence of two competing species, which in this case are biologically unequal even under the conditions of a perfectly uniform medium unchangeable in time. In the natural medium the effect of the immigration factor must be ubiquitous and considerable. It would seem that under such conditions the number of representatives of a species, the continuous presence of which within the given biotope is supported by immigration only, should as a rule, be smaller than population of the species successfully inhabiting the given biotope and constantly forcing out the immigrating species. The effect of immigration will be stronger, of course, during the period of rapid changes in the biotope, when the processes of succession will depend to a considerable degree on the phenomenon of immigration. Thus, as it may be seen from the aforesaid, immigration should remove the biocoenosis still further from type I. All

this leads us to conclude that the most typical biocoenoses of type I exists in the most monotonous biotopes during the periods of their maximum stability. The "transitory" zones, characterized by a great variety of conditions, should be populated by biocoenoses further removed from type I, i.e. by what we may consider as "transitory" biocoenoses. The same should occur during the period of rapid changes in biotopes, i.e. during the periods of accelerated successions. Biocenoses closely approaching type I characterise uniform and stable biotopes. Remoteness of biocoenoses from type I is a sign of "transitory" character of the biotopes in space and time.

We have analyzed the factors responsible for the phenomenon of the prevalence in a biocoenosis of one or several species and the nature of the said phenomenon. We shall now proceed to investigate the nature of two classes of phenomena: 1) the relations existing between the species forming a biocoenosis and 2) the relations existing between these species and the biotope.

INTERRELATIONS OF DIFFERENT ORGANISMS WITHIN A BIOCOENOSIS.

Biocoenosis is the group of organisms populating a biotope and selected in a manner enabling them to utilize to the maximum degree all the possibilities provided by the given biotope on minimum struggle with each other. Thus the interrelations between different species within a biocoenosis should have in the majority of cases a negative, centrifugal character. This theory is not new in itself and has been expressed before, although in a somewhat less sharply defined manner, by V. P. Vorobyev (1949), Ya. A. Birstein (1947), and G. V. Nikolsky (1947 a,b). These negative interrelations between different species in a biocoenosis arise as a result of the struggle between different species for the space, food etc. With the increase in the density of population in a biotope the competition

between different species inevitably increases until it reaches the level, at which certain species begin forcing out the remaining forms. The process of forcing out leads to the territorial separation of competing species (i.e. to the negative dependences in their distribution), which, in turn, reduces the intensity of interspecies competition.

This, however, does not mean that there exist no positive relations between the different species inhabiting a biocoenosis. The relations observed in symbiosis, when an organism serves as substratum for another organism (hermit-crab and sea-anemone, gastropoda mollusks and sea-anemone or hydrozoa etc.) are positive. It would be erroneous to believe that negative relations (competition, extermination) will always lead to negative interdependences in the distribution of organisms. Thus, even the distribution of a predator and its victim should to some extent be positively correlated.

For the 22 aforesaid examples of catches in sea basins the coefficient of correlation between the composition of sea fish (benthophagi and planktophagi) and predators (benthophagophagi and planktophagophagi) may be expressed as follows:

$$r = +0.82 \pm 0.005 (!!).$$

Thus, we deal here with a truly direct interdependence in distribution of certain organisms (predator-victim) according to different biocoenoses, if we may regard a sea basin as a biocoenosis. In the water basins, where there are more benthic than pelagian fish, the former are consumed by predators in great numbers and vice versa. Should we determine the relation between the aforementioned composition of sea fish and composition (plankton and benthos) of their food base we would have probably also revealed a direct dependence. Moreover, we believe that a direct dependence exist in the distribution of predator and victim within a biocoenosis.

However, in accordance with the results of experiments set up by H. F. Hause, the latter dependence cannot be considerable. H. F. Hause emphasized that should the distribution of the two fully coincide and the victim be unable to evade predators at least temporarily, the latter would inevitably exterminate the victim. (In nature, this phenomenon in its pure expression may occur only in the case of monophagy, i.e. when the predator is unable to feed on some other victim. In the contrary case, the predator changes to feeding on other organisms as soon as the number of his favourite victim drops beneath a certain level, thus enabling the said victim to avoid extermination and restore its numbers (A. A. Shorygin, 1952). This transition from feeding on one organism to feeding on other organisms may be frequently observed in nature.

However, if such positive interdependences in the distribution of organisms within a biocoenosis do exist, they should constitute, as a rule, a definite minority, considerably lagging behind the negative interdependences. This is true to an even greater extent of relations. In our opinion the two conceptions (i.e. relation and dependence in distribution) must be clearly differentiated.

If the positive relations (of the type of symbiosis) produce in a biocoenosis a positive interdependence in distribution of corresponding organisms, then negative relations (competition of different genera, mutual extermination as a result of feeding etc.) will result in some cases (competition) in negative dependences in the distribution of organisms, in other cases (feeding of certain organisms on other organisms) the negative relations will result in positive interdependences in the distribution of organisms according to different biocoenoses and within the biocoenoses proper.

It may seem that the negative relations and interdependences

in the distribution of organisms should be most clearly pronounced between the organisms of affinitive biological groups (for example, benthophagi or planktophagi, between the swallowing or collecting organisms) and considerably less clearly defined between the organisms belonging to different biological groups.

RELATIONS BETWEEN SPECIES AND BIOTOPE.

As we already mentioned above, the species forming a biocenosis are selected in a manner enabling them to utilize to the fullest extent the variety of conditions available in the biotope.

The data on the catches of fish in sea basins, which we discussed above, confirm this theory (table 4). All the industrial fishes have been divided into 3 large biological groups: benthophagi, planktophagi and predators (moreover, the latter group has been divided into benthopelagic and pelagic predators or, more precisely, benthopagophagi and planktophagophagi). We may see from the data that out of 22 examined, the Aral sea alone provided catches of fish consisting of the representatives of two groups only (the planktophagi were missing), whereas in the remaining 21 cases all the three groups were represented in the catches. Furthermore, we discovered that the 5 prevalent species, which we also mentioned above, included in the majority of cases (16 cases or 73%) the representatives of all three groups. Only in a quarter of the cases (6 cases or 27%) one of the group had no representatives among the dominant species. We observed no catches at all where all the five dominant species belonged to the same biological group. It is interesting to note that the first five place were distributed as a rule among the five most powerful groups. Thus, the first two places (as we may see from table 4) were occupied most frequently (in half the cases) by planktophagi (i.e. representatives of the most numerous group occupying the most powerful "ecological niche"). In comparison with planktophagi the predators, and

particularly the benthophagi, played a subordinate role in the two first places. The third place was shared by representatives of all the three groups. The last two places (fourth and fifth) were most frequently occupied (in half the cases) by predators. Planktophagi were only rarely found. Not only does the entire population of the biocoenosis as a whole, but even the slight portion which is important (from the viewpoint of the number of representatives) consists of biologically multiform components, a factor enabling the biocoenosis to fully utilize the variety of conditions existing in a biotope.

It is interesting to note that the biological multiformity seems to be expressed even more markedly among the few leading species of a biocoenosis than in the biocoenosis as a whole. We succeeded in estimating the degree of affinity⁽¹⁾ between the feeding habits of industrial fishes in the Caspian and Barents seas (table 5). We drew the said estimates for the Caspian sea on the basis of the scan data on the composition of summary catches for 32 years, and for three years considered separately. The data showed strongly varying catches: 1936 - showed the prevalence of benthophagi, 1917 - of planktophagi and 1939 - maximum prevalence of predators. We collected identical data for the Barents sea for 1937 and 1934. We determined the prevalence in the catches of predators (mainly cod) during the former and of planktophagi (herring) during the latter. Thus, in a well exploited water basin, (such as Caspian sea) where the composition of catches corresponds to some extent to the composition of the ichthyofauna of the water basin, the degree of affinity of feeding habits of the five most numerous species is lower than the mean degree of affinity in the character of feeding of 11 species registered. The degree of similarity between the two most numerous species is the lowest. The

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(1) The method of estimation of the feeding affinity of fishes has been explained in the works by A. A. Storygi (1939a,b) and M. V. Zheltenkova (1939).

catches obtained in 1936 were the only exception, due no doubt to the fact that the character of feeding of *Rutilus rutilus caspicus* and bream is relatively similar and that we have not considered the degree of divergence of these species in space. The aforesaid regularity was most clearly expressed in 1933. In the Barents sea it is much less clearly pronounced due to the fact that the said sea is subjected to little industrial fishing.

We may see from the aforesaid, that the species composition of catches expresses but little the true correlation between the quantities of the species in question in the given water basin. This is particularly apparent during the years, when predators are especially abundant in catches. Predators are usually caught in relatively great numbers as compared with representatives of other biological groups, in the water basins that are little exploited.

TABLE 4.

Classification of the 5 species pretoleux in the catches obtained in sea basins, according to different biological groups (number of cases).

The place occupied by each individual species.	Benthophagi	Planktophgi	Predators
I	5	10	7
II	4	12	6
III	7	8	7
IV	6	4	12
V	8	3	11

This may be seen, for example, from the fact that predators occupy the first place in a series of sea basins, whereas it is equally

obvious that they cannot be the most numerous species of the biocoenosis (i.e. the given water basin). In 1937, 3 out of 5 first places in the catches of Barents sea (I,III and IV) were occupied by predators, which during the given year constituted 58% i.e. more than half, of the overall catches obtained in that water basin.

TABLE 5.

Degree of affinity of the character of feeding (in%) of industrial species of fish. (1)

Considering the number of species.	Caspian sea.		Barents sea.			
	Mean index for several years.	1936	1917	1939	1937	1934
2	5.0	27.0	5.0	2.0	35.0	15.0
3	14.3	11.3	14.3	5.7	40.3	20.7
4	12.2	16.3	10.5	12.7	46.0	28.8
5	16.6	18.8	13.6	13.4	38.0	34.5
6	16.3	24.1	14.7	15.3	27.7	30.0
7	15.2	21.7	18.7	16.2	29.5	23.1
8	18.2	19.3	18.2	18.0	24.7	22.1
9	19.3	18.1	19.3	18.8	26.4	24.6
10	18.0	19.9	22.2	21.1	25.3	25.3
11	20.3	22.0	23.9	22.0	24.1	24.1

In 1934, when planktophagi constituted a relatively large portion of catches obtained in the Barents sea, and when the degree of divergence

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(1) The author determined the can degree of similarity between the feeding habits of two, three, for etc. most numerous fish species found in the catches. (Editor's note).

between the composition of catches and that of ichthyofauna became reduced, the aforeindicated regularity was also observed to a certain extent in the Barents sea: i.e. the degree of affinity in feeding habits of the three fish species most numerous in the catches of that year was lower than of all the registered species.

The aforementioned regularity leads to very serious consequences.

1) The population of different parts of the biotope (we avoid the term "ecological niche" thus far) is subject to the same regularity, as is the remaining population of the biotope, namely - here too, one species prevails over the remaining species and several species constitute the main bulk of the population of the part of the biotope examined by us. Moreover, as we already observed above, the population of such parts is as a rule, closer to type I than the population of the biotope as a whole, i.e. the prevalence of one or several species over the remaining species is more clearly pronounced.

2) The great biological multiformity of the leading species should most considerably reduce the struggle for existence existing among these species. This is a most important factor, since without it the struggle for existence between the leading species would be, in view of their great quantities, considerably more marked than that occurring between less numerous species. Thus, the biological multiformity of species forming a biocoenosis, which penetrates the entire population of the biocoenosis, from the most numerous to the most important species, and is most strongly pronounced among the most numerous species, enables the population of the biocoenosis to utilize most thoroughly the variety of conditions available in the biotope, yet reduces most considerably the negative relations between individual species characteristic of the biocoenosis.

The two aspects of the problem, which we have thus far considered

separately, fuse, as we mentioned before, forming a unit, as a result of which the biocoenosis proper appears to us as an integral whole, where relations of species with the biotope and with each other form a unit.

BIOTOPE AND ECOLOGICAL NICHES.

In connection with the aforesaid, we now face the following problem: thus far, we have discussed the biotope the multiple conditions forming it, its separate parts, without defining with precision the very conception of the biotope and separate components into which it may be divided. We wish to point out that in further discussions we shall proceed not from the knowledge of corresponding bibliographic data, which are rather abundant, but from our own conceptions of the biology of water basins, which have been already exposed in the present article.

First of all, what is a biotope (i.e. the place of existence).

The entire earth may be regarded as a biotope and the life it contains as its biocoenosis. On the other hand, a water basin (regardless of whether it is a small pond or the entire Atlantic Ocean) is also a biotope. The benthopelagic layers of water and the surface strata of ocean floor may be also considered as a biotope and their population - as a biocoenosis, and so on.

Large biotopes can be, of course, divided into smaller biotopes, the latter into still smaller units and so forth. It is equally obvious that such a division may be made proceeding from most varying principles, that the biotopes may be divided into any number of smaller units and that no universal system for such a division can be established. In view of the aforesaid, we may regard any part of a biotope, whatever its size, as an individual biotope and its population as a biocoenosis. Then what is an ecological niche?

As we may see from the term, it covers something more or less ecologically uniform. If this is the case, we may define the main

difference between a biotope and an ecological niche as follows: a biotope is characterized (as a rule) by variety in living conditions, an ecological niche - by uniformity in living conditions. In order to verify this theory, let us consider a few concrete examples. V. A. Brotskaya and L. A. Zenkevich (1939) understand by biocoenosis the combination of organisms that are obtained by an ocean-floor scoop. The biotope populated by such biocoenosis consists of the upper layers of soil on the ocean-floor and surface of the ocean-floor, or, to the more precise, the transition zone between the soil and benthopelagic layers of water. The principle of multiformity characteristic of a biotope is, as we may see, very well expressed in this case. On the other hand, the three aforementioned parts of such a biotope are considerably more uniform ecologically and may be considered as ecological niches.

If this is true, then the benthopelagic biotope consists of at least three ecological niches: the soil, the surface of the soil (or the transition zone between the soil and water) and benthopelagic layers of water. Each of these ecological, more or less uniform, niches is populated by its biologically more or less uniform group of organisms: the soil - by the swallowing, the surface of the soil - by the gathering (or sedimentators?), the benthopelagic layers of water - by the active filtrators (Turpaeva, 1948). Thus, everything corresponds to the scheme suggested above. What happens if we regard a water basin as a biotope and its population as a biocoenosis? It is quite obvious that such biotope will contain a great variety of conditions and may be divided into ecologically more uniform parts, such as, first of all, the surface of the water, the water, the surface of the ocean-floor and the layer of soil populated by living organisms. We may thus regard them as ecological niches of the large biotope considered in the given case. Each of these

niches, though rather uniform ecologically, may be divided anew into ecologically more affinitive units. Moreover, this division may be also carried out proceeding from different principles. Thus, the zone of water may be divided into the layer situated under the layer of temperature discontinuity, we may isolate the layers of salt content discontinuity (if such exists and the depth layer showing oxygen deficiency. The latter layer may be divided into a few more units differing from each other in degree of oxygen deficiency, etc. We may also approach the division from a different angle: we may separate the water volumes forming a arm or, on the contrary, a cold current, water of halistatic zones, fresh water of the areas situated near the river mouths, littoral waters etc. These would be smaller and more uniform fragments of the large ecological niche, which we may name "the zone of water". Each such fragment will be characterized by its specific selection of species.

We may similarly consider the soil. Depending on the degree of saturation of oxygen and biogenic elements, we may regard its different layers a small, individual and more uniform ecologically niches forming in their sum a larger and less uniform niche - i.e. "the populated layer of soil". The large ecological niche, i.e. the "surface of the ground", may be likewise divided into a very great number of smaller sub-divisions depending on the character of the soil, its angle of inclination and depth. This division may be carried very far. Thus, a stone lying on oozy ground is, of course, an ecological niche, which cannot be amalgamated within the same group with the surface of the ooze proper. Moreover, if the stone is within the zone affected by a current, its surface oriented towards the current and its opposite surface may be regarded as separate ecological niches.

As in the case of the biotope, the division of an ecological niche may be carried out on the basis of most varying principles and go very far. All the stages of such a division, from the large to the smallest units, will be fully justified. They will depend on the organisms with which we deal. If we take the small, immobile or only slightly mobile species, belonging to the group highly sensitive to the effect of external conditions, then it is quite obvious that we shall deal with tiniest subdivisions of ecological niches, since even the smallest subdivisions will differ from each other in the composition of species. The larger and more mobile the forms examined by us, the larger the ecological niches we shall deal with. The scale on which we shall divide the ecological niches will, consequently, depend upon the character of the biological material the living conditions of which will be subjected to analysis in each individual case. From this point of view the researchers analyzing the scarcely mobile benthic forms are justified in regarding the populated layers of soil (sub-divided according to the mechanical composition of the soil), surface of the soil (with identical sub-divisions plus the stones) and the benthopelagic layers of water (sub-divided according to the divergences in depth, conditions of aeration, sedimentation etc.) as ecological niches. However, when such tiny niches are considered, the mobile forms (omnivora), the propagation of which cannot be classified under any specific small sub-division must be disregarded. We are equally justified in regarding the fish populating a water basin (be it even a large sea basin) as a part of a biocoenosis. In this case our ecological niches will be as follows: the zone of water (coenosis consisting in the main of phyto- and zooplankton, peaceful pelagian fish and pelagic predators) and the benthopelagic zone (coenosis and phyto- and zoobenthos, benthic sea fish and benthic predators). In the majority of cases we encountered no difficulties in regarding the

entire population of a water basin as a biocoenosis (at least from the viewpoint of the propagation of the most mobile species). In certain cases, however, it is almost impossible. This occurred, for example, when we examined very large water basins (such as the North Atlantic ocean), which naturally breaks down into a series of zoogeographic zones. The same may also occur within relatively small water basins if the latter consist of two (or more) more or less equivalent zones with sharply differing conditions (such as the depth and the surface zones in Baykal). In these cases the water basin can hardly be regarded as a single biotope and its population as a biocoenosis even from the viewpoint of the propagation of the largest and most mobile representatives of fauna.

Should we endeavour to summarize the aforesaid, we would see that the conceptions of biotope and ecological niche may be defined only approximately: by a biotope we understand a part of a biosphere consisting of several multiform ecological niches and differing by the characteristic (i.e. frequently observed) combination of these niches and, consequently, by the characteristic (i.e. frequently observed) combination of the organisms populating the niches. Then an ecological niche is the part of a biotope characterized by the uniformity of conditions which it provides for the living organisms populating it and differing by these conditions from the rest of the biotope.

Thus, the only difference which we succeeded in establishing between a biotope and an ecological niche resides in the multiformity of living conditions in the former and the uniform character of the latter. However, even this difference is not absolutely clear. The very concepts of uniformity or multiformity are relative and depend upon the scale of division applied in each case. What seems multiform in one case and is, therefore, defined as a biotope, may appear uniform in a different case and be regarded

as an ecological niche. Indeed, should we consider the entire population of the earth as a biocoenosis (and no one can prevent us from doing so) and the earth itself as a biotope, then the firm land on one hand, and the water basins, on the other, will have to be regarded as ecological niches. The prevalence of water, which is the habitat of water basins, and that of air on the firm land renders each of these two zones ecologically uniform, as a result of which our conceptions would be fully appropriate in both cases. Should we, however, consider the distribution of marine organisms alone, the water basin becomes immediately transformed from a relatively uniform ecological niche into a most versatile biotope. The transformation will occur due to the fact that in this particular case we shall be concerned with divergences of a very different order than those considered in the previous case. Should we operate with the largest and most mobile representatives of sea populations, fish for example, then the entire water basin will appear as a single biotope. In this case (as we already mentioned above) the benthopelagic zones, i.e. the benthopelagic layers of water, the surface of soil and the populated layer of the soil proper will serve as ecological niches characterized by a certain degree of uniformity and differing from the other ecological niche - i.e. "the zone of water". As we already said before, the coenosis populating such an ecological niche will consist of the phyto- and zoobenthos, peaceful benthic fish and benthic predators. The necessity of including in our analysis the mobile benthopelagic fishes will prevent us in this case from breaking up this ecological niche into zones and compel us to consider it as something ecologically more or less uniform, i.e. as an ecological niche. If further division should prove inevitable, we would only deal with a small number of large units. Should we proceed from fishes to less mobile animals, however, then the benthopelagic zone will change anew from an ecological niche into a most varied biotope. Thus, even the above defined difference

enabling us to distinguish between a "biotope" and an "ecological niche" is of a purely relative character.

In view of the aforesaid there arises one more problem: if the population of a biotope that consists of a characteristic (i.e. frequently encountered) combination of species is considered as a biocoenosis, what term shall we apply to the population of an ecological niche? It is obvious that the name "ecocoenosis" would be most appropriate. The term proper indicates that in distinction from the biocoenosis, the population of a more or less ecologically uniform niche shows features of a certain ecological uniformity. Here, however, we are compelled to repeat what has been already mentioned above: since we failed in establishing a clearly defined difference between the biotope and ecological niche, the difference between a biotope and ecocoenosis will be also of a purely relative character. Depending on the biological material with which we shall operate and with the scale on which the subdivision of such material can be conducted, the group of organisms regarded as a biocoenosis in one case will appear as an ecocoenosis in another case and vice versa.

As we have already seen, the division of a biotope, as well as of an ecological niche, may be conducted on a highly varying scale. This division may be carried out proceeding from different principles. We could endeavour to analyse this problem more thoroughly, and establish some hierarchy in such subdivisions, having found a unit of measurement in the form of the smallest possible subdivision of biotope and ecological niche, beyond which no division can be conducted. For this purpose we must determine the tiniest subdivision that can be naturally considered as the elementary ecological niche and elementary biotope.

It is obvious from the aforesaid that the elementary ecological

niche must show the maximum degree of ecological uniformity. The experiments of H. F. Hause (1934a and b) and our reasoning have shown that such an ecological niche should be populated by a single species that is most adapted to the conditions existing in it. Consequently, we may give the following definition: an elementary ecological niche is the part of a biotope populated by the representatives of a species, belonging to one of the smallest subdivisions into which we may divide this species. These representatives must be a similar age and in an identical physiological state. We were compelled to add the three last factors since it is clear that representatives of different sub-species of the same species may inhabit different ecological niches (particularly if they belong to different ecological subspecies). The same may be said of the representatives of the same race and of the same species if they are of a different age and in a varying physiological state. In order to show the extent of possible divergences, let us consider the following example: the spawning *caspiatosa kessleri kessleri* in Volga and the feeding *caspiatosa kessleri kessleri* in the Central zone of the Caspian sea. By accepting the definition suggested above we shall understand under the elementary biotope a part of the biosphere consisting of several elementary ecological niches. Such a biotope will be populated by the elementary biocoenosis consisting of several species belonging to different ecological groups; moreover, the number of species forming the elementary biocoenosis will correspond to the number of elementary ecological niches forming the given biotope. Proceeding from these principles we may assume that the elementary biocoenosis will consist of one single species (observing the three aforesaid conditions).

At first sight everything seems consistent, simple and clear, which it would be but for the most variable ecological flexibility of organisms is its direct result, their most variable eurytopicality will

account for the fundamental divergences in different ecological niches, which will vary depending on the species, from which we proceed in each individual case. The elementary ecological niche occupied by calamus would be very large covering a considerable portion of the water zone of Barents sea. On the other hand, the niche occupied in the same sea by some stenotopous? plankter would be considerably smaller. We could quote a great number of similar examples. In the meantime the definition of an elementary ecological niche has already lost some of its clarity. To all this we should add one more complicating factor - namely, immigration. In confirmity with the experiments of H. F. Hause, even a perfectly uniform niche may be populated simultaneously and permanently by several species. The species which became most thoroughly adapted to the living conditions available in the given niche, will prosper in it and endeavour to force out the remaining species; nevertheless, the latter will be able to exist in the given niche by constantly migrating into it from vicinal niches, where they in their turn prosper. It matters little whether we deal with competing species or predators. We may see to what degree the phenomenon of immigration is ubiquitous in nature if we realize that it is hardly possible to find a place in the biosphere that would be populated by one single species.

In view of the aforesaid, our definitions of the elementary ecological niche and elementary biotope lose their practical value. We have thus failed in establishing the smallest unit of measurement by means of which we would be able to establish the above discussed system of classification for biological niches and biotopes. Consequently, we are compelled to accept the definitions of biotope and ecological niche, which have been provided thus far and reconciled to the vague and relative character of the definitions.

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