ISSN 0096-7807

Vol. 18, No. 3, May-June, 1987

January, 1988

SJECAH 18(3) 123-184 (1987)

THE SOVIET JOURNAL OF

ECOLOGY

ЭКОЛОГИЯ/ÉKOLOGIYA

TRANSLATED FROM RUSSIAN

CONSULTANTS BUREAU, NEW YORK

RELATIONSHIP OF SPECIES DIVERSITY TO ISOLATE TERRITORIAL SIZE

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We studied the effect of the area of an isolate on the species diversity of an animal community with a tendency toward dispersed settlement. The theoretical premises of the work are the equilibrium theory of MacArthur and Wilson (1967) and the results of a study of the effect of spatial organization on population stability in a stochastic environment (Dombrovskii, 1985). Statistical analysis of data from five groups of isolated habitats supported our assumption of a logarithmic relationship between the number of species in a community and the area of the isolate.

One of the pressing problems of conservation biology, which is closely connected to the problems of organizing and maintaining stably functioning biocenoses in reserve zones, is the estimation of reserve areas that are adequate to maintain individual populations and necessary species diversity. In working out the general principles for constructing reserves, an important role belongs to methods of mathematical, particularly simulation, modeling of populations and communities.

The study of the species dynamics of artificial reserves is interrelated with problems of the biogeographical theory of islands (Darlington, 1966; Pianka, 1981*; MacArthur and Wilson, 1967), which are naturally isolated habitats, or ecological isolates. Another example is landlocked or poorly drained lakes.

Consideration of stochastic ecological conditions in a model makes an investigator's problem more complicated, but more realistic. Logofet and Svirezhev (1985) discuss analytical methods for studying community dynamic stability in relationship to habitat range area and suggest a wider use of simulation computer methods for more complex systems.

The problem of analyzing species diversity is obviously connected to the study of population viability. The lifespan of any population in a local habitat with fluctuating environmental conditions is limited. The long-term unfavorable combination of abiotic and biotic conditions must inevitably lead to the extinction of a species at some moment in time. This accords with current ecological ideas and follows from the mathematical theory of stochastic processes (Carlin, 1971).

Dombrovskii and Tyutyunov (1985) propose a method that makes it possible, using a series of statistical experiments with a simulation population model, to estimate the effect of factors of spatial organization (such as size, structure, range heterogeneity, migratory activity, and so forth) on a population's vitality and resistance to stochastic environmental fluctuations.

As a criterion for a population's viability and fitness for a given habitat, we used, following Svirezhev and Logofet (1978), the mean life time T of a population. Simulation modeling provides an effective means for estimating this characteristic. In the simplest stochastic models, this can also be done analytically.

In modeling, we assume a population subdivided into some number of migratorially interrelated subpopulations, each of which inhabits its own spatial locus. The possible configurations of locus spatial orientation are represented in Fig. 1.

Analysis of the results of the statistical experiments indicated that a substantial role in the maintenance of population stability is played by habitat range area, a charac-

*Pianka (1981) not in Literature Cited — Publisher.

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Translated from Ékologiya, No. 3, pp. 3-7, May-June, 1987. Original article submitted December 13, 1985.

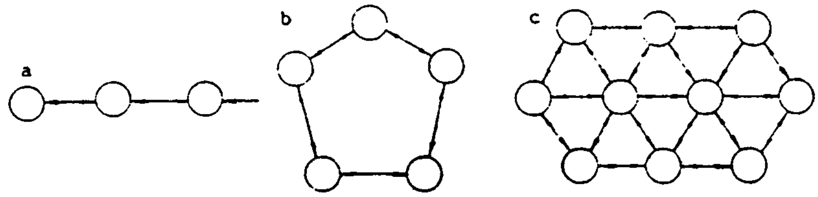

Fig. 1. Configurations of subpopulation spatial distribution. a) linear range; b) circular; c) triangular.

teristic indicator of which is the potential number of habitats M with minimum area S_0 necessary for stable existence. The relatively independent subpopulations, which are a population's structural units, are connected to one another by migratory flows in accordance with a given range's structural configuration.

It was established that for a fixed range structure the dependence of T on the number of loci M is subject to the logarithmic law:

$$T = a \ln M + b, \quad (1)$$

where a and b are constants.

Work-up of a wealth of statistical material in our possession showed that such an approximation is best in the sense of a standard-deviation minimun (even by comparison with a parametrization of the form $T = CM^Z$).

A relationship exists between the mean lifetime T of each population of a community (number of generations) and the number of species inhabiting a given isolate. The number of species N in a community, according to the theory of MacArthur and Wilson (1967), results from a dynamic balance between the processes of immigration of new species to islands and the disappearance of old species. In accordance with this,

$$dN/dt = I(S, N) - D(S, N), \quad (2)$$

where I(S, N) and D(S, N) are, respectively, the species' immigration and extinction rates, which depend on the area of the "island" and the number of species of a given taxon inhabiting it. Of course, these functions also depend on the biogeographical features of the archipelago, but we will concentrate on just the analysis of the effect of habitat size, whose quantitative characteristic is the ratio of the total isolate area S to the minimum area S that ensures the normal existence of a local subpopulation:

$$M = S/S_0.$$

The species extinction rate is directly proportional to the number of species and inversely proportional to the mean lifetime T of a population under the given conditions:

$$D(S, N) = kN/T(M) = kN/T(S/S_0).$$

If, in the simplest case, I(S, N) is a constant, then under equilibrium conditions, we have

$$N = \frac{I}{k} T(S/S_0), \text{ i.e., } N \sim T. \quad (3)$$

Consequently, it can be suggested that the relationship of species number to the area (or the number of habitats of a minimum size) in an isolate (islands, lakes, and so forth) allows an approximation of the function of the form

$$N = \tilde{a} \ln S + \tilde{b}. \quad (4)$$

Theoretically, there is no doubt that the relationship N(S) has properties such as a decrease in species number with a decrease in the habitat size of an isolated community (Darlington, 1966; Pianka, 1967*; Zhakov, 1984), but the specific form of this relationship is still open to question. Darlington (1966) suggests that N decreases by an order of two with each decrease in range area S. MacArthur and Wilson (1967) propose the relationship $N = CS^Z$, where C and Z are constants specific to a given taxon and locality. Zhakov (1984) describes a linear relationship between the number of fish species and reservoir surface area.

*Pianka (1967) not in Literature Cited — Publisher.

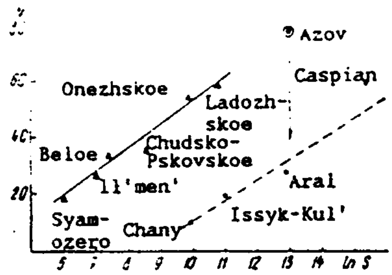

Fig. 2

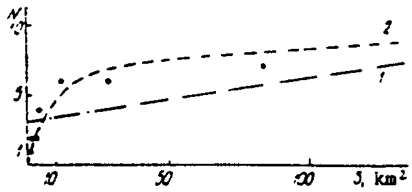

Fig. 3

Fig. 2. Linear relationship of the number of fish species N to the logarithm of surface area S of a body of water for several lakes in the northwestern USSR and saline water bodies in the southern USSR. Arrow indicates direction of possible change in species diversity in the Sea of Azov, given disruption of its migratory connection with the Black Sea.

Fig. 3. Approximation of the relationship N(S) for several lakes in the Pskov Oblast by linear (1) and logarithmic (2) functions.

Presented below, based on specific biological material, are correlations of area S and the number N of amphibian and reptile species on several West Indian islands (based on the data of Darlington (1966), Tables 15-16):

	Saba	Montserrat	Trinidad	Puerto Rico	Jamaica	Haiti	Cuba
S, sq. mi.	5	40	2000	3400	4500	30000	40000
N	3	9	55	40	40	84	76

The least-squares method provides the following estimates for the coefficients in formula (4): $\tilde{a} = 8.5$; $\tilde{b} = -17$. The coefficient of correlation between the calculated and observed values is rather high (0.8).

Examination of analogous data for isolated bodies of water (seas, lakes) makes it possible to describe the correlation of habitat area and species number by a function in the form of (4). Closed lake ecosystems, whose stability greatly depends on their energetic structure, are generally suitable objects for biogeographical study. Study of their organization makes it possible to delineate the basic components of the trophic net of communities, which can, for example, by averaging by trophic levels and substituting a single "pseudo-species" (Logofet and Svirezhev, 1985) for the multitude of species on one trophic level, be "folded" into a trophic chain.

Darlington (1966) notes that it is expedient for zoogeographical purposes to limit oneself to the examination of vertebrates, i.e., species that generally correspond to the upper trophic levels of communities. As applied to lake ecosystems, this means the study of ichthyofauna alone.

We will characterize the size of the potential territory of aquatic communities by the surface area S of a body of water. In our view, this is a more important characteristic of aquacenose productivity than is, for example, volume, since the most highly productive zones of water bodies are their surface layers (Erhard and Sejean, 1984), and it must also be considered in determining minimum adequate territory size for fish-planktophages.

We will present data on five lakes in the northwestern USSR that have approximately the same hydrological characteristics and evolutionary history, but differ in surface area and species diversity (Natural Resources..., 1984):

	Ladozhskoe	Onezhskoe	Chudsko-Pskovskoe	Beloe	Il'men'
Area S, km²	17700	9,690	5570	1284	1200
ln S	9.78	9.18	8.18	7.16	7.09
No. fish species N	4.6	47	37	30	26

There is an obvious connection between the number of fish species N and the logarithm of the surface area of a water body (Fig. 2). In this, the least-squares method gives estimates of 7.5 and −25.1, respectively, for coefficients $\tilde{a}$ and $\tilde{b}$ in formula (4). In this case, the coefficient of correlation between the observed and calculated values of N is 0.97.

TABLE 1. Relationship of Minimum Number of Species in a Community to Relative Area of Lakes in the Pskov Oblast (Zhakov, 1984)

Fishery type of lake	Relative area S	Minimun number of species N
Carp	1.0	1
Tench	1.4	2
Perch-roach	3.6	2
Bream without bleaks	4.4	4
Bream-break	12.0	6
Bream-pike	29	6
Bream-cisco	84	7
Bream-whitefish	290	11

TABLE 2. Number of Fish Species and Area of Saline Water Bodies in the Southern USSR

Body of water	No. of species	Area, thousands, km²
Caspian Sea	75	394
Sea of Aral	24	65.5*
Sea of Azov	80	38
Lake Issyk-Kul'	16	3.6
Lake Chany	8	2.1

*Until lowering of level.

We will find the probability q of fulfilling the null hypothesis that this correlation coefficient (level of significance) is absent. We will construct the statistic $t_q = r\sqrt{n}/(1-r^2) = 0.97\sqrt{5}(1-0.97^2) = 36.7$ and from the correlation $2\Phi_0(t_q) = 1 - q/100$, where Φ_0 is Laplace's function, we obtain $q < 10^{-4}$.

The probability of random coincidence of the data presented above with reality is insignificant. Thus, it is possible to draw certain conclusions about the effect of range area on community species diversity. Of course, for each group of lakes similar in basic biogeographical characteristics, formula (4) has specific limits of applicability, within which it functions satisfactorily.

However, it should not be forgotten that the relationship of species diversity to isolate area is only one of the characteristics that are also substantially affected by other biogeographical features of the range. Thus, the angle of the slope of the line in Fig. 2 must depend on abiotic factors: salinity, mean annual water temperature, pollutant concentrations, and so forth. Table 1 presents data collected by Zharkov (1984) on several lakes in the Pskov Oblast, and Fig. 3 shows approximations of the observed data by linear and logarithmic functions.

We will examine an analogous relationship (Table 2) for several saline water bodies in the southern USSR that are similar in hydrological conditions (see Fig. 2).

It can be suggested that deviation of the point corresponding to the Sea of Azov from some "theoretical" line is connected to the presence of a natural connection (migratory flows) between the ichthyofauna of the Sea of Azov and the Black Sea, due to which the Sea of Azov is not completely isolated from the world ocean. Within the limits of this hypothesis, an almost twofold decrease in the species diversity of the Sea of Azov is quite possible, given a disruption of its migratory connections with the Black Sea. Such a disruption may occur upon completion of a dam construction project in Kerchenskii Strait.

Thus, based on analysis of factual material, a rather convincing correlation between observed and calculated data is obtained for several monotypic groups of water bodies in the USSR. We did not examine such important characteristics as the primary productivity of a biocenose, the structure of trophic relationships, the topographical characteristics, or the evolutionary origin of a community, and we studied only the effect of ecological capacity as estimated by the number of possible habitats of local subpopulations composing a population system. This substantially lowers the generality of our conclusion on the logarithmic relationship of species diversity and area (territory), making it true only for reserves that are similar in other ecological factors.

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INFLUENCE OF TECHNOGENIC EMISSIONS ON PATTERNS OF BEHAVIOR OF COMPOUNDS OF NITROGEN AND PHOSPHORUS IN FOREST BIOGEOCENOSES

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UDC 631.811:502.55(21)

It is shown that the entry of atmospheric emissions of a factory producing mineral fertilizers makes quantitative and qualitative changes in the behavior of the compounds of nitrogen and phosphorus in the system atmospheric precipitation—plant litter—soil—soil solutions—natural waters. An additional quantity of nitrogen and phosphorus compounds is accumulated in the upper part of the soil profile, and the migration of the mineral forms of phosphorus and nitrogen compounds increases with the undesirable accumulation of the latter in soil-group waters.

The production of mineral fertilizers is a source of the atmospheric emission of nitrogen and phosphorous compounds: about 2.2 kg ammonium and up to 16 kg nitrogen- and phosphorus-containing dust per ton of production enters the atmosphere (Awasthi and Pandey, 1979). The total emission of phosphorus into the environment during the production of mineral fertilizers reaches $0.3 \cdot 10^6$ tons per year (Pierrou, 1976).

Industrial emissions enter the surrounding landscapes with the rainfall, settling dust, and during the direct uptake of gaseous compounds by the soil—plant cover. The entry into the biogeocenosis of several compounds of industrial emissions leads to a change in the patterns of migration and accumulation of substances. The fertilization effect upon the entry of biogenic elements into the soil is, as a rule, completely neutralized by the toxicity for plants of gaseous nitrogen compounds, as well as by the presence in the composition of emis-

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0096-7807/87/1803-0127$12.50