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OTNOSHENIYE CHERNOMORSKOGO USONOGOGO RACHKA BALANUS IMPROVISUS DARWIN K USLOVIYAM PONIZHENNOY SOLENOSTI

(The Reaction of the Black Sea B. Improvisus Darwin to Reduced Salinities)

by

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ABSTRACT

Experimental investigations in the tolerance of the Black Sea Balanus improvisus to reduced salinities show that the individuals of the species taken from waters having the salinity of 18 ‰ are capable of enduring an extremely great dilution of water. Observations on the growth, the rate of oxygen consumption, and on spawning of B. improvisus disclose that the salinity range from 18 to 5 ‰ is tolerated by the animals in all stages of development and that they are capable of reproduction. With the reduction in salinity to 3 ‰ and less, the greater part of the barnacles die in a few months and none of them are capable of reproduction. It was further found that barnacles need a certain time for adapting themselves to the new salinity concentrations, the period becoming longer with lower salinity concentrations. The adaptation is most clearly pronounced in the growth of barnacles. At lower salinities the growth rate decreases only for a limited time period; after which it surpasses the usual speed and the barnacles reach a larger size than those living in salinity conditions that are normal to them. As a result, the former become capable of enduring greater salinity reductions for a longer time than other barnacles. Because of the pronounced ability of adaptation, the Black Sea barnacle has spread into the Sea of Azov, where the average salinity concentration is 11 ‰ and, traveling by vessels, is gradually penetrating into the diluted areas of gulfs and estuaries in this sea and infesting the coastal structures.

The Translator

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THE REACTION OF THE BLACK SEA BALANUS IMPROVISUS DARWIN TO REDUCED SALINITIES

The development of industrial construction in the south of the European sector of the country requires, for cooling industrial aggregates, the utilization of sea water, which is taken from the brackish areas of the sea where a considerable fluctuation of salinity occurs. In this connection, the development of organic fouling by marine and brackish water organisms is observed on hydrotechnical structures. In order to prepare forecasts for the settlement of foulers on newly built structures and to combat the existing foulers, it is important to know the lower limit of salinity endured by the animals. This paper is devoted to studying the reaction to reduced salinity of the barnacle Balanus improvisus Darwin. The reaction to salinity of B. improvisus has not yet been studied in detail. The observations made in natural conditions, which are known to us, are limited mainly to the recording of the presence of the barnacle in one or the other biotope, to the counting of its over-all quantity, and to the elucidation of its biomass. The presence of B. improvisus in brackish water basins, gulfs diluted by the influx of large rivers, and in firths (estuaries), demonstrates that this species is capable of enduring a great reduction of salinity.

Technical literature contains indications that B. improvisus has been found in almost completely diluted water. It was mentioned for the first time in 1890 by Andrusov (according to Kudelin, 1913), who had found individual specimens of barnacles in the Ingul River near its confluence with the Bug River, in the Kizil-Shtadskiy liman of the Kuban' River and in a stream of the Kolkhida Plain near its estuary in the Black Sea. Kudelin (1913) had also found several live barnacles in the Bug River near Nikolayev. According to Kudelin, the salinity of river water in the area fluctuates from 0.02 to 3.86 °/oo within a year (Table 1). In his paper, Kudelin also reports the finding of single B. improvisus specimens in the relict Lake Paleostomi. When investigating the fauna of invertebrates inhabiting the lower reaches of Ukrainian rivers, Markovskiy (1953, 1954) found single specimens of B. improvisus several times in the Dnestrovskiy liman, where the salinity fluctuated from 2 to 6 °/oo. Only in the autumn of 1950 did Markovskiy find a more considerable quantity of B. improvisus in the northwestern sector of the Dnepro-Bugskiy liman, where the salinity of water was 3.9 °/oo. The mass of the biocoenose was 69.3 g/m^2, the major portion--62.0 g/m^2--consisting of B. improvisus. In 1951 this biocoenose was not found. Thus, in both of the firths investigated by Markovskiy B. improvisus occurred only sporadically, most frequently in small quantities.

Table 1

THE DISTRIBUTION OF BIOMASS MAXIMUMS AND NUMBER OF BALANUS IMPROVISUS IN CONNECTION WITH THE SALINITY OF WATER (IN AUTUMN SEASONS)

Area investigated and the name of object	Salinity fluctuations, ‰	Number of specimens per 1 m²	Biomass g/m²	Mean Weight of specimen, g	Source
Ingul River, north of Nikolayev; shell	0.1—0.2	Singly		—	Kudelin, 1913
Bug River, near Nikolayev; Dreissena	0.1—2.1	Singly		—	Kudelin, 1913
Sea of Azov, Taganrogskiy zaliv; Monodacna-Tubificidae	0.05-6.4	Singly		—	Mordukhay-Boltovskoy, 1937
Black Sea; Dnepro-Bugskiy liman; Stenogammarus	2.0	Singly		—	Markovskiy, 1954
Black Sea; Dnepro-Bugskiy liman; B. improvisus	3.9	200	62.0	0.31	Markovskiy, 1954
Sea of Azov; Taganrogskiy zaliv; Monodacna	1.8—3.6	15	7.25	0.49	Mordukhay-Boltovskoy, 1937
Sea of Azov; Taganrogskiy zaliv; Hypaniola+Corophium+Tubificida	1.8—3.6	5	1.68	0.33	Mordukhay-Boltovskoy, 1937
Sea of Azov; Taganrogskiy zaliv; Cardium	7.3—9.1	650	39.22	0.06	Mordukhay-Boltovskoy, 1937
Sea of Azov; Taganrogskiy zaliv; Cardium, coastal	7.3—9.1	500	20.40	0.04	Mordukhay-Boltovskoy, 1937
Sea of Azov, combination with Balanus in predominance	9.0	?	134.5	—	Mordukhay-Boltovskoy, 1937
Sea of Azov; Balanus biocoenose	10.0	16140	923.40	0.056	Vorob'yev, 1949

The distribution of B. improvisus in Taganrogskiy zaliv (Gulf) of the Sea of Azov is discussed in detail in a paper by Mordukhay-Boltovskoy (1937). According to his data, the number and biomass of B. improvisus increases steadily from the protected coastal section of the gulf toward the sea. Such an increase in the biomass and number of Balanus improvisus is, according to Mordukhay-Boltovskoy, associated with an increase in salinity, which is also observed in the direction from the protected sector of the gulf toward the Sea of Azov.

Data on the number of B. improvisus in diluted areas, in locations with more or less favorable bottom conditions for the species, and on the salinity of water in the area investigated are presented in Table 1. Because the hydrological regime of the areas discussed in the mentioned papers is determined to a large extent by the influence of large rivers, the salinity of water in the areas varies considerably with the seasons of the year. As emphasized by the mentioned authors, in the spring (April-May) a considerable dilution is observed in these areas, which is associated with spring floods in rivers. In June and July, as a rule, the salinification of the areas begins and in the autumn, i.e. in September and October, the salinity of water in the firths and in Taganrogskiy zaliv is above the average yearly value. In November a limited temporary dilution sets in again. In this connection, Table 1, wherever possible, lists two salinity values: the minimum in the spring and the maximum in the fall. As is seen from Table 1, in locations where the water salinity fluctuates from fresh-water values to slightly brackish concentrations, B. improvisus occurs as single specimens. In locations where the water is constantly brackish and its salinity decreases in the spring, evidently, below 1.5 °/oo, the biomass of B. improvisus is, as a rule, small (of the order of 10 g/m^2); but sometimes it may reach several tens of grams per m^2. In more saline areas, as for /207
instance in the extreme western sector of Taganrogskiy zaliv, where the water salinity fluctuates from 7 to 9 °/oo, the biomass of B. improvisus reaches, as a rule, several tens of grams per m^2. With increase of salinity to 10°/oo and more, the biomass of B. improvisus may increase to several hundreds of grams per m^2 (see Table 1). Thus, with the reduction of water salinity in natural conditions, the biomass of B. improvisus decreases; however, individual specimens of the species can, evidently, live a long time in almost fresh water.

The existing experimental investigations concerning the reaction of the Black Sea B. improvisus to various salinities are limited to a small scope of studies. The survival of individuals of the species in waters with salinities ranging from 0 to 50 °/oo was investigated by Pora and Rosca (1955) with respect to the Black Sea animals assembled in the Babadag area (town in Rumania), where the salinity was 6.6 °/oo. The results of the observations disclosed that B. improvisus can tolerate salinity fluctuations from 3 to 48 ‰. The keeping of barnacles in fresh water for a day did not cause the death of barnacles; the greater part of the barnacles died only after being in fresh water for three days.

The transfer of barnacles to fresh water and to water where the salinity was 50‰ caused abrupt reduction in the activity of their cirri. The effect of various salinities on the rate of oxygen consumption of B. improvisus was investigated by Birshteyn (1936)[1] and Blinov (1936)[1] by utilizing the barnacles taken from the Sea of Azov, where the salinity was 10 ‰ and by Arbuzova (1958) by utilizing the barnacles obtained from the Black Sea, where the salinity was 18 ‰. On the basis of samples obtained by Ya. A. Birshteyn from the Sea of Azov, the oxygen consumption of B. improvisus was normal at salinities ranging from 5 to 25 ‰. An increase by 30 % in the rate of oxygen consumption by barnacles kept in water with a salinity of 18 ‰ should, evidently, be regarded as an exception. However, according to data by L. K. Blinova, the oxygen consumption of B. improvisus reaches its maximum with 10 ‰ and is decreasing with variations in the salinity, whereby the more the salinity deviates from 10 ‰ (normal for the Sea of Azov), the more the rate of oxygen consumption decreases. On the basis of data by Arbuzova, who investigated the rate of oxygen consumption by the Black Sea B. improvisus in the salinity range from 3 to 18 ‰, a gradual variation of salinity from 18 ‰ reduces the rate of oxygen consumption. Further, the speed of oxygen consumption decreases with reduction in salinity. According to tests conducted by Arbuzova with the salinity of 3 ‰, the use of oxygen by barnacles decreased to 25 % of normal consumption.

In all of the mentioned papers, the reaction of B. improvisus to various salinities had been investigated only with respect to one aspect (survival or the rate of oxygen consumption); in addition, the observations on animals after their transfer to experimental environment had been brief. As is seen from the mentioned data, the results of the experimental investigations were far from being uniform. In this connection, experimental investigations on the reaction of the Black Sea B. improvisus to various salinities were carried out at the Black Sea Station of the Institute of Oceanology. The results of the tests are listed below.

SAMPLES AND THE METHOD

The reaction of B. improvisus to various salinities is discussed in this paper with respect to the following aspects: growth, rate of oxygen consumption, maturing of sexual products, and survival in

[1]According to a dissertation by K. S. Arbuzova (1958).

fresh water. The samples for experiments were collected in Gelendzhikskaya bukhta (Bay). The barnacles occupying glass objects placed in the sea were used for the elucidation of the effect of various salinities on the rate of growth. The glass objects with young barnacles were taken to the laboratory where the other foulers were removed from the objects. The barnacles were then counted and their bases were measured in two directions--the longest and the shortest diameters. Assuming that the base of barnacles is an ellipse, its area was calculated. After all of the barnacles had been measured, the glass objects with the animals were placed in glass containers containing water with various salinities. The barnacles were subsequently measured after each ten-day period. The experiments lasted from 40 to 80 days.

In order to determine the rate of oxygen consumption, we used barnacles that had settled on Mytilus shells. For this purpose, the fragments of shells with barnacles were cleaned, removing all the soft threads of Mytilus and other foulers by carefully cutting them off the bases of the barnacles. Such a material enabled us to investigate the speed of oxygen consumption by individual specimens.

The test samples were placed into respiratory containers for six or 16 hours, depending upon the sizes of the animals and containers. The quantity of consumed oxygen was determined by the difference in the oxygen content in the containers at the beginning and the end of the tests. The oxygen concentration in water was determined by the Winkler method. During the experiment, respirometers were placed into a large container with water, most frequently, into the usual bath tub. The experiments were conducted in the August-October period of 1959. During that time the water temperature varied from 17 to 23°C. In certain tests the variation of water temperature did not exceed 1°C. All the data on the rate of oxygen consumption obtained by us were then reduced to 20°C with the aid of cofactor tables (Vinberg, 1956).

The observations on the rate of oxygen consumption by barnacles were carried out by us for a period of one to one and one-half months. For this purpose, selected barnacle groups (consisting of three to four specimens) or single barnacles were kept for eight to 10 days in water having a salinity of 18 °/oo. Further, the tests aimed at determining the rate of oxygen consumption were of equal duration; and they were conducted daily at the same time. The mean value of data (eight to 10 cases) obtained by this method was considered as a normal amount of oxygen consumption for each group or each barnacle. Afterwards, the barnacles were transferred to the experimental salinity, where the rate of oxygen consumption was determined almost daily for 10 to 12 days. The results were compared with the established standard value.

For observations on the maturing of sexual products at various salinity concentrations, young barnacles with undeveloped gonads (their carina-rostral diameter being less than 1.5 mm) were used. They had been kept for at least two months in containers with reduced salinity. In order to determine the state of the sexual products, the barnacles were dissected and examined by microscope. The presence of mature eggs in the mantle of barnacles and live sperm in the sexual canals was considered as a sign of sexual maturity. In addition, observations on the spawning of barnacles were carried out; for this purpose, the water in con- /209 tainers with sexually mature animals was regularly examined.

The transfer of animals from salinities equalling that of the Black Sea (17.5 °/oo) to water with a reduced salinity was made in all of the experiments by gradual variation of salinity. First, the barnacles were placed in water having a salinity of 14 °/oo, then in water with 12°/oo, 10 °/oo, and so on, the intervals being 2 to 3 °/oo; further, the animals were kept at least two days in each salinity.

The barnacles were kept in containers with and without running water; in the latter case, the water in the containers was changed two or three times a day, depending upon its temperature. All the experiments carried out with a view to elucidating the effect of various salinity concentrations on growth were made in containers with running water. The rate of oxygen consumption was determined in animals which, in intervals between the tests, had been kept in containers with and without running water. Observations on spawning were also carried out in containers without running water.

All of the test animals were regularly fed twice a day. As a food, we used planktonic algae Prorocentrum (micans) mykans and Exuviella marina, whose cultures were kept in a laboratory. In addition, we utilized for this purpose the epiphytic algae and detritus washed off of the stolons of Cystoseira, as well as the eggs of bivalve mollusks, mainly Mytilus. It need be noted that food plays an extremely important role in barnacles subjected to lengthy tests. By changing the type and quantity of food, it is evidently possible to change the intensity of metabolism in laboratory conditions. Such variations cause, first of all, changes in oxygen consumption.

An example of such an increased oxygen consumption as a result of changes in food for B. improvisus is listed in Table 2. The first three days the animals were fed on tiny algae washed off Cystoseira and on detritus; afterwards they were fed on Mytilus eggs for two days, but in the subsequent two days they were fed again on detritus. When fed on Mytilus eggs, the rate of oxygen consumption in barnacles increased considerably (2 to 2.5 times) whereas during the two subsequent days, when fed on detritus, the rate decreased (approximately 1.5 times).

Table 2

VARIATIONS IN THE RATE OF OXYGEN CONSUMPTION BY DAYS DEPENDING UPON THE FOOD CONTENT (ML/HOUR; REDUCED TO 20°C)

Aug. 31	Sept. 1	Sept. 2	Sept. 3	Sept. 4	Sept. 7	Sept. 8
Detritus	Detritus	Detritus	Mytilus eggs	Mytilus eggs	Detritus	Detritus
0,00205	0,00263	0,00304	0,00532	0,00600	0,00328	0,00366
0,00107	0,00176	0,00174	0,00157	0,00497	0,00322	0,00353
0,00113	0,00176	0,00233	0 00174	0,00740	0,00325	0,00343
0,00088	0,00120	—	0,00286	0,00500	0,00236	0,00256
0,00144	0,00227	0,00146	0,00378	0,00646	0,00378	0,00564
0,00128	0,00139	0,00172	0,00203	0,00398	0,00158	0,00164
—	0,00147	0,00080	0,00216	0,00410	0,00238	0,00179
0,00112	0,00176	0,00199	0,00257	0,00320	0,00121	0,00317
0,00078	0,00183	0,00298	0,00500	0,00454	0,00264	—
Mean						
0,00122	0,00178	0,00201	0,00334	0,00506	0,00263	0,00318

Accounting for the possibility of such fluctuations in the rate of oxygen consumption from test to test, we endeavored to sustain the most uniform conditions in containers with barnacles. However, we did not succeed in eliminating entirely the irregularities in growth rate and considerable fluctuations in oxygen consumption in the same animals.

OBSERVATIONAL RESULTS

Growth. Observations on the growth of the Black Sea B. improvisus in water having reduced salinity were carried out in the summer of 1956 and 1957. The tests consisted of four series. During the tests it appeared that the barnacles kept in the laboratory were very sensitive to the conditions they were in. Temperature fluctuations, irregular feeding, or deficient water exchange resulting in a decrease in oxygen content caused a considerable irregularity in the growth rate of barnacles. Because of this, only the results of two series of the experiments are discussed in this paper. In these series the growth rate of barnacles was rather uniform.

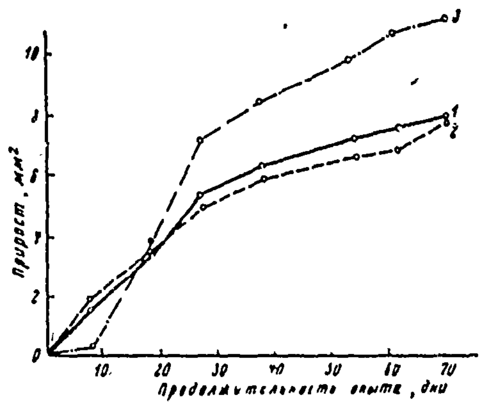

Fig. 1. Increment of B. improvisus in reduced salinity conditions. 1—18 °/oo; 2—12 °/oo; 3—8 °/oo.

Key. Abscissa: duration of experiment; days.
Ordinate: increment, mm^2.

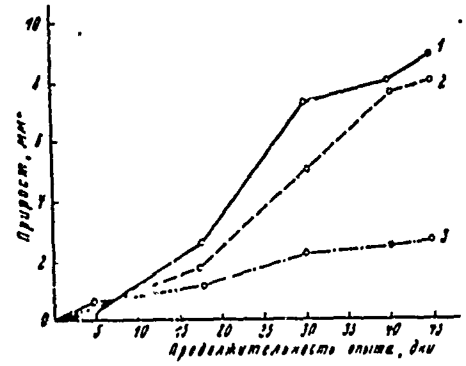

Fig. 2. Increment of B. improvisus in reduced salinity conditions. 1—8 °/oo; 2—5 °/oo; 3—3 °/oo

Key. The same as in Fig. 1.

Series I (Fig. 1) was initiated on July 10, 1957. The experiments in this series lasted 75 days and were carried out at 18 °/oo (control), 12, and 8 °/oo. For this series of tests we used barnacles with the mean basal area not exceeding 2 mm^2. Twenty-five to 30 specimens were used in each experiment. The results disclosed that within the salinity range of 18 to 12 °/oo the intensity of growth of B. improvisus was similar. With the salinity of 8 °/oo, a considerable retardation in the growth rate was observed during the first 10 days; afterwards the rate increased considerably. This increase resulted in an increased increment by the end of the month, in comparison with salinities of 18 and 12 °/oo. Further, as seen from the diagrams, the growth rate of barnacles at 8 °/oo continued to remain more intense than at 18 °/oo, and by the end of the observations the value of increment at 8 °/oo exceeded the value at 18 °/oo by almost one-fourth.

Series II (Fig. 2) was initiated on August 10, 1957, as a supplement to Series I. Observations lasted for 45 days and they were carried out at 8 °/oo (control), 5, and 3 °/oo. For this series we selected barnacles just after their settling, if their basal area did not exceed 0.5 mm^2. As seen from the diagram, the intensity of growth at 5 °/oo, during the first month, was considerably below that at 8 °/oo, but afterward it increase and by the end of the observations the increment at 5 °/oo was almost the same as at 8 °/oo. In water having a salinity of 3 °/oo the growth rate of barnacles remained small throughout the test and by the end of the experiment the increment was only one-fourth of the value reached in water with a salinity of 8 °/oo.

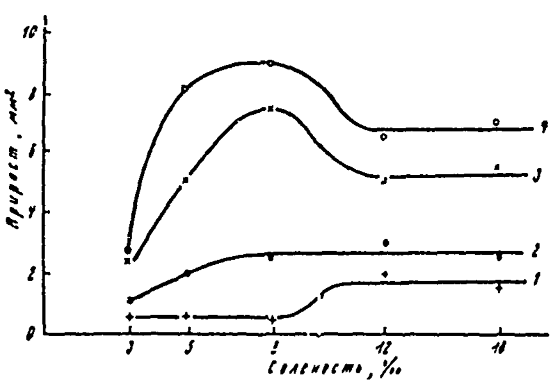

Fig. 3. Variations in the growth value in B. improvisus at various salinities.

1—8 days; 2—15 days; 3—30 days; 4—45 days.

Key. Abscissa: salinity, °/oo.
Ordinate: increment, mm^2.

Variations in the growth value in B. improvisus with time depending upon the salinity is presented in Fig. 3, showing the averaged result of all the data that were at our disposal. It is seen from the diagram that during the first eight days of the experiment, growth was observed only within the salinity range of 18 to 12 °/oo. With the salinity of 8 °/oo and less, growth was not observed. After 15 days of experiment, the growth value at 8 °/oo was comparable with that at 18 °/oo(control); at 5 °/oo it increased considerably, remaining, however, below the control rate; but at 3 °/oo the rate increased very little. After 30 days of experiment, the form of the growth curve assumes a substantially different character. Within the range of 18 to 12 °/oo the growth value remains the same, but at 8 °/oo it increases abruptly (almost twice in comparison with the control salinity). At 5 °/oo the magnitude of increment also increases considerably and is comparable to that at control salinity, and only with 3 °/oo the increment remains small as before. After 45 days of experiment, the form of the growth curve preserves the same character; only with the salinity of 5 °/oo the value of increment increases and, being almost the same as with 8 °/oo, exceeds the value of the control salinity by 14 °/o.

Thus it is possible, evidently, to assume that the growth rate of the Black Sea B. improvisus, taken from water with the salinity of 18 °/oo, is almost unchanged within the salinity range from 18 to 12 °/oo. With a further decrease in salinity to 8 and 5 °/oo, the growth rate is retarded at the beginning, but later on it surpasses the growth rate observed at 18 °/oo. During 70 days of observation (Series I), the increment of barnacles kept in water having the salinity of 8°/oo appeared to be by 26 °/o greater than the increment at 18 °/oo. A reduction of salinity to 3 °/oo retarded the growth of the Black Sea barnacles during the entire period of observations.

Table 3

RELATIONSHIP BETWEEN THE BODY WEIGHT OF B. IMPROVISUS OF THE SEA OF AZOV AND THE BLACK SEA

Area	No. of sample	Mean diameter mm	Number of specimens	Dry weight, mg		Relationship of body weight to shell weight, °/o
				Shell	Body	
Sea of Azov, Kazantip	1	6,04	50	2,9595	0,0576	1,95
	2	6,01	50	2,5711	0,0428	1,66
	3	5,92	70	2,9701	0,0522	1,76
	4	5,82	50	3,3898	0,0445	1,81
Black Sea, Tuapse	5	6,05	50	1,3214	0,0795	6,00
	6	5,98	50	0,9803	0,0662	6,75
	7	6,02	40	0,7327	0,0448	6,1[illegible]
	8	5,75	50	0,9919	0,0662	6,66
	9	5,75	50	0,8673	0,0415	4,78

Endeavoring to find an explanation for such an increased growth of B. improvisus at 8 and 5 °/oo, we investigated the relationship between the weight of body and shell in uniform groups of individuals of the species that live in waters having different salinities. For this purpose, we collected animals from two environments: from the Sea of Azov (Mys Kazantip (Cape K.) area), where the salinity of water was about 11 ‰, and from the Black Sea (Tuapse), where the water had a normal salinity--18 ‰--for the sea. The obtained data are presented in Table 3. As is seen in it, the dry body weight of barnacles taken from the Sea of Azov constitutes 1.5 to 2 % of shell weight in barnacles having the size of 6 mm; whereas the shell weight of barnacles taken from the Black Sea is somewhat smaller in barnacles having the same size. In this case the dry body weight makes up 5 to 7 % of the shell weight. A more intense accumulation of calcium in the shell of B. improvisus inhabiting the Sea of Azov cannot be attributed, as it was assumed at the beginning, to a greater quantity of calcium in the water. The measurements of calcium content in the Black Sea water, diluted with fresh water, and in the water of the Sea of Azov (Table 3) demonstrated that the calcium content decreases with a reduction of salinity. Obviously, such an increase in the growth rate with a reduction of salinity to 8-5 ‰ in aquariums, as well as a more intense accumulation of calcium in natural conditions in the Sea of Azov, is explained not by the quantity of dissolved calcium but by some other causes.

The rate of oxygen consumption. In order to investigate the effect of reduced salinity on the rate of oxygen consumption in B. improvisus, two series of tests were set up. It need be noted that the rate of oxygen consumption by barnacles during the observation period, evidently, increased considerably (especially in Series I) at the expense of the growth of barnacles. For the sake of comparison, we calculated the average rate of oxygen consumption during the last three days of the experiment, i.e. the rate of oxygen consumption which was determined seven to 10 days after the barnacles had been transferred to new salinity conditions.

Series I (Table 4). The observations were carried out at salinities of 18.5 and 3 ‰ on groups of barnacles containing three to four individuals. We selected such groups that contained possibly more uniform /213 animals. After the observations, the animals were weighed, the weight equalling from 0.12 to 0.27 g. The over-all duration of observations in this series was 43 days.

As is seen in Table 5, the rate of oxygen consumption by the groups of barnacles, used as controls (18 ‰), increased on the average 2.5 times by the end of the observation period. A similar increase in the rate of oxygen consumption is also observed at 5 ‰. With this salinity, only in one group of barnacles (No. 9) was the increase in oxygen consumption smaller than in the remaining groups subjected to the same salinity and in control animals. With a salinity of 3 ‰, on the contrary, only in two groups (Nos. 5 and 13) out of five was the increase in oxygen consumption the same as with 18 and 5 °/oo; in the remaining groups the rate of oxygen consumption increased to a somewhat smaller degree.

Table 4

THE QUANTITY OF DISSOLVED CALCIUM IN WATER HAVING VARIOUS SALINITIES

No. of sample	Location of sample obtained	Salinity, determined by the areometer, °/oo	Quantity of dissolved calcium, g/l
1	Black Sea water from the sea water supply line of the Black Sea Experimental Station	18	0.244
2	Same	12	0.180
3	"	8	0.147
4	Fresh Water	0.2	0.094
5	Water from the Sea of Azov	12	0.169

Series II. The experiments designed for the investigation of oxygen consumption by barnacles treated, in this series each animal individually, at 18.5 and 3 °/oo. The total duration of observations was two days. The weight of animals subjected to the tests ranged from 0.12 to 0.03 grams (Table 6).

The rate of oxygen consumption by control animals increased on the average 1.3 times during the observations. Only in one individual, with the smallest weight, the rate of oxygen consumption increased twice. In the barnacles kept at a salinity of 5 °/oo an increase in oxygen consumption was observed by the end of the observations, the value being on the average near that at the salinity of 18 °/oo. However, in two specimens of barnacles (Nos. 4 and 6) kept at 5 °/oo, the rate of oxygen consumption at the end of the experiment was somewhat smaller than at the beginning (at 18 °/oo).

Table 5

OXYGEN CONSUMPTION BY BALANUS IMPROVISUS

Series I.

Salinity, °/oo	Number of groups	Duration of observations, days	Frequency of occurrence: At 18 °/oo	Frequency of occurrence: At the salinity of experiment	Weight of one animal by the end of observations, g	Average O_2 consumption by one animal, ml/hour (M): At 18 °/oo, (M_1)	Average O_2 consumption by one animal, ml/hour (M): At the salinity of experiment (during the 3 last days) (M_2)	Relation $\frac{M_2}{M_1}$, %: For each group	Relation $\frac{M_2}{M_1}$, %: Mean for the salinity
18	1	43	9	13	0.256	0.00412	0.00917	222	250
	4	43	9	13	0.270	0.00319	0.00777	244	
	11	43	8	13	0.208	0.00264	0.00790	299	
5	6	43	6	10	0.161	0.00228	0.00650	285	305
	7	43	7	10	0.129	0.00311	0.0105	461	
	8	43	8	13	0.213	0.00293	0.00842	287	
	9	43	9	13	0.134	0.00268	0.00573	214	
	10	43	9	13	0.232	0.00194	0.00826	424	
3	2	43	9	10	0.204	0.00386	0.00800	207	238
	3	43	9	10	0.121	0.00325	0.00677	208	
	5	43	9	10	0.190	0.00364	0.00890	244	
	12	43	7	13	0.188	0.00328	0.00676	206	
	13	43	9	13	0.167	0.00247	0.00795	322	

Table 6

OXYGEN CONSUMPTION BY BALANUS IMPROVISUS

Series II

Salinity, ‰	Number of groups	Duration of observations, days	Frequency of occurrence: At 18 ‰	Frequency of occurrence: At the salinity of experiment	Weight of animal: Initial	Weight of animal: Final	Average O_2 consumption by one animal, ml/hour (M): At 18 ‰, (M_1)	Average O_2 consumption by one animal, ml/hour (M): At the salinity of experiment (during the 3 last days) (M_2)	Relation $\frac{M_2}{M_1}$, %: For each group	Relation $\frac{M_2}{M_1}$, %: Mean for the salinity
81	1	22	11	11	0,068	0,068	0,00457	0,00585	128	132
	9	22	11	11	0,025	0,041	0,00360	0,00313	87	
	16	22	8	11	0,014	0,031	0,00167	0,00342	204	
	21	22	9	11	0,089	0,110	0,00468	0,00509	108	
	22	22	9	10	0,080	0,087	0,00323	0,00372	115	
	23	22	9	11	0,117	0,120	0,00372	0,00710	191	
5	3	22	9	9	0,064	0,092	0,00391	0,00440	112	115
	4	22	9	8	0,040	0,051	0,00344	0,00258	755	
	5	22	7	11	0,056	0,056	0,00333	0,00523	157	
	6	22	9	11	0,057	0,066	0,00525	0,00420	80	
	7	22	8	11	0,038	0,039	0,00438	0,00517	125	
	8	22	7	11	0,042	0,045	0,00263	0,00411	156	
	10	22	8	11	0,035	0,043	0,00330	0,00338	102	
	11	22	9	11	0,042	0,044	0,00304	0,00450	148	
3	12	22	8	10	0,030	0,030	0,00251	0,00187	74	96
	13	22	8	10	0,032	0,032	0,00298	0,00238	80	
	14	22	8	10	0,017	0,023	0,00216	0,00200	93	
	15	22	8	11	0,021	0,031	0,00287	0,00160	56	
	17	22	6	10	0,034	0,036	0,00245	0,00326	133	
	18	22	6	10	0,090	0,093	0,00144	0,00110	92	
	19	22	6	11	0,049	0,054	0,00535	0,00427	80	
	20	22	6	10	0,095	0,098	0,00276	0,00507	183	

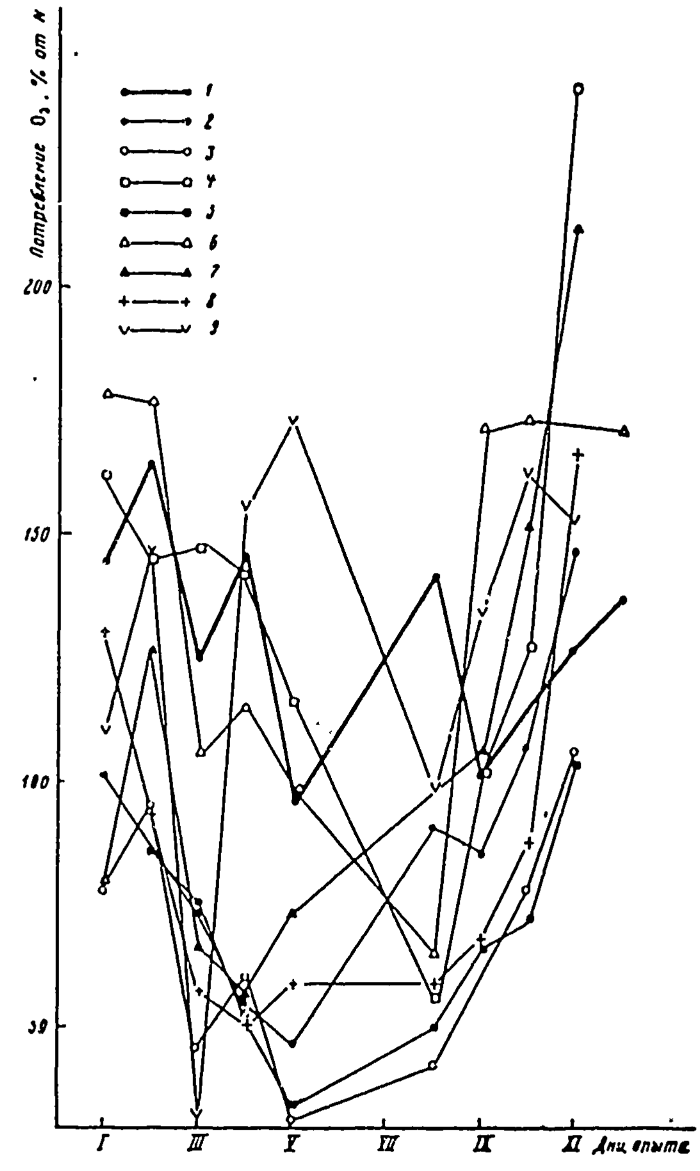

Fig. 4. Variations in the rate of oxygen consumption by B. improvisus in water having a salinity of 5‰.

1—mean oxygen consumption at 18 ‰. Barnacles in water having a salinity of 5‰; 2—No. 3; 3—No. 4; 4—No. 5; 5—No. 6; 6—No. 7; 7—No. 8; 8—No.10; 9—No.11.

Key. Abscissa: days of tests
Ordinate: use of O_2, % of N.

A small decrease in the rate of oxygen consumption, in comparison with 18 °/oo, generally was observed in barnacles kept at a salinity of 3 °/oo. In one specimen (No. 15) it decreased almost by 45 °/o, but in five others (Nos. 12, 13, 14, 18, and 19) the decrease ranged from 10 to 25 °/o. However, in two barnacles (Nos. 17 and 20), we observed an increase in the rate of oxygen consumption at 3 °/oo, as in the case of the control animals.

The mean values of the oxygen consumption at reduced salinities which /216 are listed above, present only a general idea of the reaction of *B. improvisus* specimens to variations in the salinity of water. A more detailed idea can be obtained when examining the graphs presenting variations in the rate of oxygen consumption in individual animals by days (Figs. 4 and 5).

Because the results of both series of tests, carried out by us, are very similar, and the variations in the rate of oxygen consumption by barnacles are more clearly manifest in the results of Series II, we shall /217 discuss in this paper the data based on Series II. The variation in the rate of oxygen consumption by barnacles when they are transferred to water having a salinity of 5 °/oo is presented in Fig. 4. After the transfer, the rate of oxygen consumption was reduced in all of the specimens; the status lasted three to four days. In certain individuals the rate of oxygen consumption during the period was reduced to 30°/o of the normal value. In three to four days the rate of oxygen consumption began to increase so that in some animals, the rate by the end of the observations exceeded the standard value. It is seen from the presented graph, that the restoration in the rate of oxygen consumption occurs at various times in various individuals. Thus, for instance, in the case of barnacle No. 11 the change occurred as follows: on the 4th day after its transfer to water with a salinity of 5 °/oo, the use of oxygen increased to 150 °/o; later on, the decrease was not smaller than 100 °/o. In the case of barnacles Nos. 5 and 7, an increase in the use of oxygen to 100 °/o was observed on the 9th day after their transfer to water having a salinity of 5 °/oo; whereas in the case of barnacles Nos. 3 and 6, the use of oxygen was normalized only on the 11th day. As was mentioned in connection with Table 6, in the two latter barnacles the rate of oxygen consumption was below the normal value by the end of the observations (mean during the last three days).

Also, with the transfer of barnacles to water having a salinity of 3 °/oo (Fig. 5), a considerable reduction (to 30 °/o of normal value) in the rate of oxygen consumption was observed during the first three to four days. However, in contrast to the reaction of barnacles at 5 °/oo, the restoration of the normal rate of oxygen consumption at 3 °/oo was observed only in two barnacles (Nos. 17 and 20), in which the reduction in oxygen consumption was not significant during the

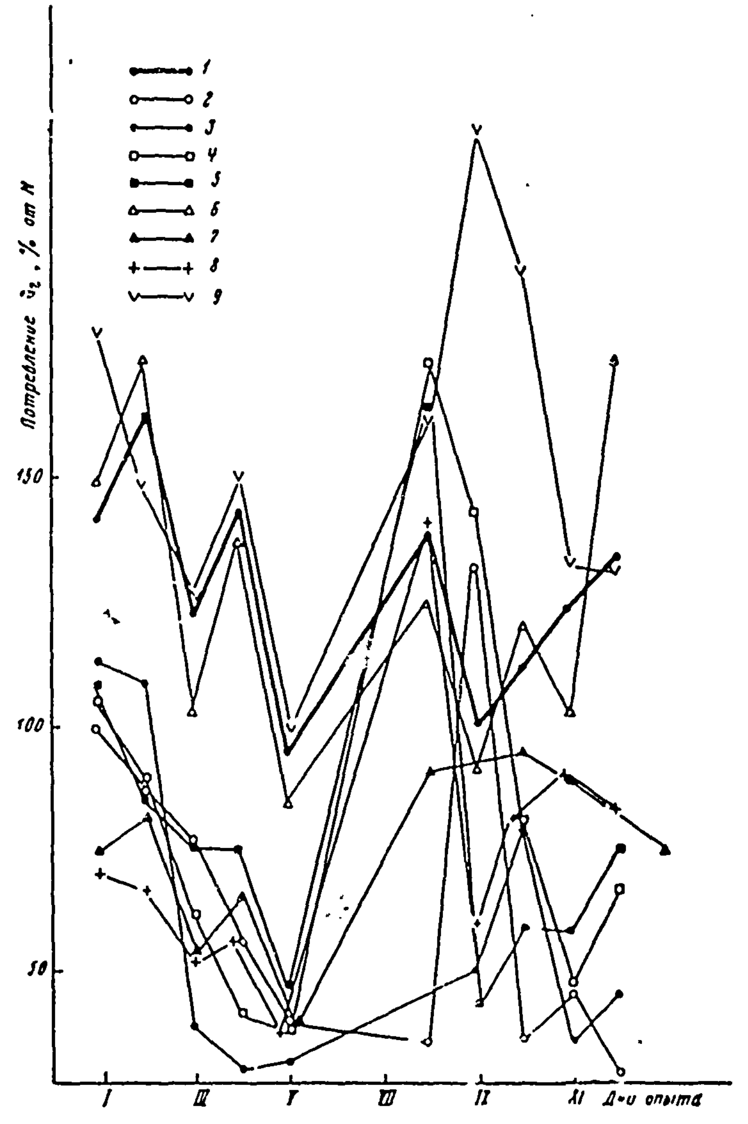

Fig. 5. Variations in the rate of oxygen consumption by B. improvisus in water having a salinity of 3‰. 1—mean oxygen consumption at 18 ‰. Barnacles in water having a salinity of 5‰; 2—No.3; 3—No.4; 4—No.5; 5—No.6; 6—No.7; 7—No.8; 8—No.10; 9—No.11.

Key. Abscissa: days of tests
Ordinate: use of O_2, % of N.

Table 7

VARIATIONS IN THE RATE OF OXYGEN CONSUMPTION BY BALANUS IMPROVISUS DURING EXPERIMENTS (ML/HOUR PER ANIMAL)

Series II

Salinity, °/oo	Number of animals	Mean rate of O_2 consumption at 18 °/oo	Rate of oxygen consumption at the salinity of a given test		
			1st day	4th day	10th day
18	1	0,00457	0,00710	0,00520	0,00540
	9	0,00360	0,00510	0,00440	0,00260
	16	0,00467	0,00386	0,00352	0,00273
	21	0,00468	0,00523	0,00730	0,00591
	22	0,00323	0,00386	0,00464	0,00323
	23	0,00372	0,00575	0,00616	0,00727
5	3	0,00391	0,00394	0,00216	0,00570
	4	0,00344	0,00266	0,00208	0,00364
	5	0,00333	0,00540	0,00472	0,00807
	6	0,00525	0,00150	0,00272	0,00543
	7	0,00438	0,00557	0,00360	0,00533
	8	0,00263	0,00204	0,00144	0,00559
	10	0,00330	0,00429	0,00168	0,00514
	11	0,00304	0,00334	0,00465	0,00459
3	12	0,00254	0,00257	0,00144	0,00123
	13	0,00298	0,00343	0,00096	0,00112
	14	0,00216	0,00231	0,00112	0,00109
	15	0,00287	0,00205	0,00224	0,00173
	17	0,00245	0,00369	0,00336	0,00255
	18	0,00441	0,00334	0,00296	0,00395
	19	0,00535	0,00386	0,00312	0,00495
	20	0,00276	0,00196	0,00416	0,00372

entire test period. In the case of all the other barnacles, the rate of oxygen consumption during the second half of the test (6th and 11th days) fluctuated considerably, increasing in certain animals (Nos. 14 and 15) well above the normal rate, but remaining, on the whole, well below the normal rate set at the salinity of 18 °/oo. The values of oxygen consumption by barnacles during the 1st, 4th, and 10th days of experiments of Series II are listed in Table 7. The data listed in the table illustrate the reduction in the use of oxygen during the first days after the transfer of barnacles to new salinity conditions, as well as the subsequent increase in its use at 5 ‰ and the absence of increase in the greater part of the animals at 3 ‰. Analagous data based on Series I are listed in Table 8.

Table 8

VARIATIONS IN THE RATE OF OXYGEN CONSUMPTION BY *BALANUS IMPROVISUS* DURING THE EXPERIMENT (ML/HOUR PER ANIMAL).

Series I

Salinity, ‰	Number of animals	Mean rate of O_2 consumption at 18 ‰	Rate of oxygen consumption at the salinity of a given test		
			1st day	5th day	10th day
18	1	0,00412	0,00600	0,00575	0,01055
	4	0,00319	0,00495	0,00658	0,00870
	11	0,00264	0,00378	0,00579	0,00695
5	6	0,00228	0.00355	0,00454	0,00709
	7	0,00311	0,00570	0,00500	0,01060
	8	0,00293	0,00264	0,01005	0,00413
	9	0,00268	0,00358	0,00755	0,00427
	10	0,00194	0,00272	0,00764	0,00441
3	2	0,00386	0,00609	0,00403	0,00880
	3	0,00325	0,00650	0,00315	0,00490
	5	0,00364	0,00553	0,00348	0,00812
	12	0,00328	0,00438	0,00790	0,00427
	13	0,00247	0,00440	0,00573	0,00440

In this series we observed a relatively pronounced reduction and subsequent increase in the rate of oxygen consumption only at a salinity of 3 ‰. At 5 ‰ we did not observe such a reduction. Such a difference between the results in Series II and I of the tests was obviously determined by a longer period of observation and by greater sizes of animals used in Series I of the tests. In the case of large barnacles that were subjected to experiments for one and one-half months, the adaptation to new conditions relative to the rate of oxygen consumption was almost unnoticed.

Maturing of sexual products and spawning. In order to elucidate the problem of the effect of reduced salinity of water on the maturing of sexual products in B. improvisus, we dissected about 70 barnacles of various sizes. As was pointed out above, these barnacles were preliminarily kept in water having the salinity of 18 °/oo and in water having reduced salinity. When the barnacles were dissected, it appeared that the development of gonads begins at an early age when the basal diameter is about 2 mm. With the growth of barnacles, a further development of gonads takes place. In animals that have reached 4 mm is basal length, the spermatozoans usually are active, and the eggs assume a roundish oval form and lie at a certain distance from one another, not in a compact mass. Individual eggs of such barnacles penetrate oviducts. When examining larger specimens, we did not succeed in finding substantial differences in the status of gonads. Evidently, the individuals of the species become sexually mature when their basal diameter reaches 4 mm (the carinal-rostral diameter of the base).

When examining the status of sexual products in mature barnacles that had been kept in various salinities, we discovered that the sexual products of the animals mature within the salinity range of 18 to 5 °/oo. In barnacles with a basal diameter of 4 mm and more, which had been kept in water having the salinity of 5 °/oo, as well as in barnacles kept at higher salinities, we found completely mature active spermatozoans, oval eggs, and developing embryos in mantles. In barnacles that are kept in water having a salinity of 3 °/oo, the sexual products evidently do not mature. We examined 20 specimens having a basal diameter of 4 to 6 mm. The gonads of all of the barnacles were small and compact. We did not find any mature eggs or sperm in them.

As the B. improvisus was kept in water with various salinities, we repeatedly observed the presence of early nauplii in containers with mature barnacles. This was observed in water having salinities of 18, 12, and 5 °/oo. In water with a salinity of 3 °/oo, the presence of young larvae was never observed. Evidently, the salinity limit for the maturing of sexual products and the development of young larvae in B. improvisus lies at a level of 4 °/oo.

Survival in fresh water. On September 20, 1954, a large scale experiment designed to examine the survival of B. improvisus in fresh water was set up. The experiment involved 400 specimens, which were transferred gradually, within two weeks, from water with a normal Black Sea salinity to fresh water. A group of barnacles consisting of 200 specimens was kept in water having the salinity of 18 °/oo to be used for control purposes. The results of the experiment are presented in Table 9.

Table 9

SURVIVAL OF B. IMPROVISUS IN FRESH WATER

Data	Days of Experiment									
	1	2	3	4	5	6	7	8	9	10
Number of dead barnacles	40	77	86	24	87	34	37	—	5	1
Mean area of base of the dead barnacles, mm^2	0.57	1.37	1.75	2.90	3.25	5.80	4.50	—	6.54	4.70

As can be seen from Table 9, the main mass of tested barnacles (391 specimens) died during the first 10 days, the youngest barnacles dying first. The mean size of dead barnacles increased gradually from the first to the sixth day, beginning from 0.57 and ending with 5.80 mm^2. The sexually mature barnacles endured fresh water about five days, after which they began to die. From the fifth to the ninth day, the basic mass of sexually mature barnacles died. Of the remaining nine specimens, seven died gradually during the subsequent 30 days of the experiment, but two barnacles, whose carinal-rostral diameter of base was 6.50 and 7.25 mm respectively, endured the entire test period, lasting for one and one-half months. /220

DISCUSSION OF RESULTS

During recent years, papers dealing with ecology mention more and more frequently that the intensity of metabolism of marine and brackish water animals, which have been transferred to new salinities and have become acclimatized to the conditions, remains on the normal level. With respect to marine invertebrates, it was first mentioned by Karpevich in connection with the Caspian Dreissena (1947, 1953) and a number of species of fodder benthos inhabiting the Sea of Azov (Karpevich, 1955). Karpevich succeeded in proving that the individuals of the investigated species are capable of sustaining the intensity of metabolism at normal level within a wide salinity range, which may coincide with

the natural salinity range of the species. The ability to maintain the functions of life at a normal level within a wide salinity range, which exceeds by far the fluctuations of salinity in natural environment, was disclosed also with respect to the bivalve mollusk Teredo navalis L. (Soldatova, 1961), the polychaete worm Mercierella enigmatica Fauvel (Turpayeva, 1961) and the bryozoan Lepralia pallasiana Moll. (Simkina and Turpayeva, 1961). Experimental investigations of the reaction of the Black Sea B. improvisus to reduced salinities demonstrated that the individuals of the species taken from water having a salinity of 18 °/oo are capable of enduring very great dilution. Observations on the growth, the rate of oxygen consumption, and on spawning of B. improvisus make it possible to arrive at a conclusion that the salinity range from 18 to 5 °/oo is entirely favorable for the Black Sea representatives of the species. With 5 °/oo, as was already mentioned, the growth of barnacles is even more intense than at 18 °/oo, but the rate of oxygen consumption is normal (Tables 5 and 6). At this salinity, as well as at 18 °/oo, the sexual products mature, eggs develop, and spawning takes place. In water having a salinity of 3 °/oo, the growth of the Black Sea barnacles during the period of our observations was considerably retarded. The oxygen consumption was on the average below the normal rate, but the maturing of sexual products and spawning were not observed. However, the data on the rate of oxygen consumption in water having a salinity of 3 °/oo demonstrate that at this salinity, which is unfavorable for the larger portion of representatives of the Black Sea B. improvisus, some individuals (four out of 13 in our experiments, about 30 °/o) appeared to be capable of preserving the rate of oxygen consumption at the normal level. It is possible that, by lengthy observations involving many specimens, certain individuals may be found that would grow normally and develop sexual products at the salinity of 3 °/oo. In fresh water, as was already mentioned, by far the greatest portion of barnacles died with- /221
in a month; however, two large specimens (0.5 °/o of the total number of tested animals) endured the entire period of observations (1.5 months).

Thus, the experimental investigations concerning the reaction of B. improvisus to reduced salinities demonstrated that the representatives of the Black Sea populations of the species, inhabiting waters having the salinity of 18 °/oo, are capable of enduring the same range of dilution (from 18 °/oo almost to 0 °/oo), within which the individuals of the species are found in natural circumstances (see Table 1). If, however, the salinity decreases to less than 5 °/oo, only part of the individuals appeared to be capable of sustaining a normal intensity of metabolism, whereas in the greater part of the animals the metabolism remained below the normal rate throughout the length of the experiment. In these circumstances, the nonuniformity in the reaction of barnacles to dilution of water begins to become clearly manifest. The cause for such a nonuniformity is, evidently, explained by the fact that various individuals of the Black Sea populations of barnacles are endowed with different tolerance to dilution. It is interesting to note that our data are basically analogous to data obtained by Ya. A. Birshteyn (cited by Arbuzova, 1958). As was already mentioned, he found that the oxygen consumption by B. improvisus was normal within the range of salinity from 5 to 25 °/oo, and that it decreased if salinity surpassed these limits. Differences between his and our data were detected only with salinities below 5 °/oo. Also, it is possible that in Birshteyn's tests the mentioned nonuniformity in the reaction of barnacles to dilution was apparent in these circumstances. The decreased value of oxygen consumption by barnacles in water having a salinity of 3 °/oo, which is listed in a diagram by Birshteyn, is in all probability the result of averaging nonuniform data. Undoubtedly, the variations in the tolerance of Black Sea barnacles to dilution also should occur with smaller reductions in salinity. With more data at our disposal, this will probably be true of salinities 8, 10, and even 12 °/oo. It can be assumed that the nearer the value of salinity to 18 °/oo, the smaller the percentage of individuals not tolerating the given salinity. In conditions forming the limit of tolerance of the species, such nonuniformity must be very clearly pronounced.

The same differences in the tolerance of various individuals to dilution were disclosed for the bivalve mollusk Teredo navalis (Soldatova, 1961) and for the hydroid Cordylophora caspia Pallas (Kinne, 1956).

Possibly, it is this difference in tolerance to dilution in various individuals of B. improvisus that is also manifest in natural circumstances by the decrease in numbers and biomass of the given species in diluted sectors of Taganrogskiy zaliv and firths (see Table 1). This decrease in numbers and biomass of barnacles with dilution may be the reason for the elimination of barnacles not tolerant to dilution. The barnacles that are tolerant to dilution make up, in all probability, the smallest portion of the species. It is they that constitute the small colonies of B. improvisus, which were found in diluted areas.

Regrettably, we do not have at the present time the data that would enable us to draw conclusions concerning the ecological status of individual barnacles in such populations. We know only that these barnacles are, as a rule, larger in size than those inhabiting waters of higher salinities. Thus, when investigating the benthos of Taganrogskiy zaliv, Mordukhay-Boltovskoy (1937) paid attention to the fact that individual B. improvisus increase in size in waters where the concentration of salinity is near the limit of their tolerance. An analogous phenomenon is also noticeable for all the populations, on which the data are presented in Table 1. In biocoenoses where the barnacles have developed /222
at salinities below 7 to 9 °/oo, the mean weight of one barnacle

fluctuates from 300 to 500 mg in the fall, whereas in biocoenoses where they have developed at salinities ranging from 7 to 9 °/oo and more, the corresponding weight varies from 40 to 60 mg.

It is possible that the increase in the size of barnacles with dilution of water in natural circumstances and increase in the growth rate of barnacles with salinities of 8 to 5 °/oo, disclosed in experiments, are brought about by the same causes that are not yet known. Nevertheless, the large sizes of barnacles that are observed in diluted water attest to the fact that barnacles are not in a depressed state in such environments. Evidently, even such a great dilution of water appears to be favorable for certain individuals of B. improvisus. This all confirms once more the suggestion that the value of salinity does not affect adversely B. improvisus within the salinity range from 18 to 3 °/oo once the specimens have adapted themselves to the given salinity.

Considerable dislocations in the intensity of metabolism are observed in the process of adaptation to new salinity conditions; however, later on the dislocations are equalized and the rate of metabolism returns to its normal level. When examining these experimental data, it is readily seen that a retardation of metabolism is observed in B. improvisus with variations in the concentration of salinity. Thus, in barnacles kept at the salinity of 5 °/oo, a decrease in the rate of oxygen consumption was observed during the first two or three days, and a slow return to the normal rate was observed two or three days later (Fig. 4). The entire process of decrease and restoration in the rate of oxygen consumption at 5 °/oo lasted nine to 11 days in the greater part of barnacles tested by us. A considerable retardation is also observed in the growth of barnacles. As was already mentioned, no growth was observed in the animals during the first days in water having a salinity of 8 °/oo and less (Fig. 3). Only after 15 days of being in water with a salinity of 8 °/oo was the growth rate of barnacles comparable to that of the animals kept at 18 °/oo. Only in a month's time is the growth rate of barnacles kept at 5 °/oo, comparable to the growth rate of barnacles kept at 18 °/oo.

The difference in the time needed for the restoration of the normal rate in the two processes is noteworthy. While the oxygen consumption at 5 °/oo is restored to its normal rate in about 10 days after the animals have been put into new salinity conditions, the growth is retarded, evidently, for a longer period so that it approaches the normal value only in a month's time. Similar displacements in the intensity of metabolism with variations in salinities were observed by us (Soldatova and Turpayeva, 1960) in the polychaete worm Mercierella enigmatica, where, in contrast to B. improvisus, an increase in oxygen consumption was observed at the beginning, which later on decreased, reaching the normal rate.

The study of intensity in the respiration and growth of B. improvisus kept in various salinities enabled us to determine variations in metabolism, the primary, as well as the secondary, variations occurring in organisms with variations in the salinity of water. The primary variations denote at the present time the intensity of respiration and osmoregulation, but the secondary variations denote changes in the growth and reproduction (Skadovskiy, 1939, 1956). The investigations carried out by us disclosed once more the need for lengthy observations on investigated objects. If experiments are of short duration, ending 3 to four days after the animals have been put in new salinities, the elucidation of the effect of salinity on the intensity of respiration is incomplete, because the animals cannot adapt themselves to the new conditions, even if the change of salinity is gradual. The results of such /223 experiments reflect only a part of the process of acclimation of barnacles to new salinities, but they do not give a correct idea on the actual reaction of B. improvisus to the given salinity of water. It is this fact that explains, evidently, the gradual reduction in the rate of oxygen consumption by B. improvisus when the salinity of the environment is changed gradually, as it was done by Blinov (1936) and Arbuzova (1958). Observations on the intensity of respiration after the animals had been transferred to water having a different salinity were carried out by Arbuzova in three days.

The duration of adaptation to new salinities and a different tolerance of individual B. improvisus to dilution, call for a need to conduct lengthy observations dealing with individual animals. Such investigations enabled us to determine the tolerance of certain representatives of the Black Sea population of B. improvisus to greatly diluted waters, and to disclose an almost complete coincidence of the lower salinity limit for the existence of the Black Sea B. improvisus with the lower salinity limit for the propagation of the species in the Azov-Black Sea basin.

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