

Translation Series No. 2257

Absorption of oxygen by the Ctenophora species
Pleurobractia pileus (O.F. Mueller) as affected by the
temperature and salinity of the environment

by L. P. Lazareva

Original title: O pogloshchenii kisloroda grebnevikami
Pleurobractia pileus (O.F. Mueller) raznykh razmerov
v zavisimosti ot temperatury solionosti okruzhaiushchey
sredy

From: Trudy Karadagskoy biologicheskoy stantsii akademii nauk
Ukrainskoy SSR (Papers of the Kara Dag biological station
of the Academy of Sciences of the Ukrainian S.S.R.),
17 : 85-96, 1961

Translated by the Translation Bureau (HPF)
Foreign Languages Division
Department of the Secretary of State of Canada

Department of the Environment
Fisheries Research Board of Canada
Biological Station
Nanaimo, B. C.

1972

25 pages typescript

DEPARTMENT OF THE SECRETARY OF STATE
TRANSLATION BUREAU
MULTILINGUAL SERVICES
DIVISION



FRB 2257
SECRETARIAT D'ÉTAT
BUREAU DES TRADUCTIONS
DIVISION DES SERVICES
MULTILINGUES

TRANSLATED FROM - TRADUCTION DE RUSSIAN INTO - EN ENGLISH

AUTHOR - AUTEUR LAZAREVA, L.P.

TITLE IN ENGLISH - TITRE ANGLAIS
Absorption of oxygen by the Ctenophora species Pleurobrachia pileus O.F. Mueller as affected by the temperature and salinity of the environment

TITLE IN FOREIGN LANGUAGE (TRANSLITERATE FOREIGN CHARACTERS)
TITRE EN LANGUE ÉTRANGÈRE (TRANSCRIRE EN CARACTÈRES ROMAINS) O pogloshchenii kisloroda grebnevikami Pleurobrachia pileus O.F. Mueller raznykh razmerov v zavisimosti ot temperatury i solionosti okruzhaiushchey sredy

REFERENCE IN FOREIGN LANGUAGE (NAME OF BOOK OR PUBLICATION) IN FULL. TRANSLITERATE FOREIGN CHARACTERS.
RÉFÉRENCE EN LANGUE ÉTRANGÈRE (NOM DU LIVRE OU PUBLICATION), AU COMPLET, TRANSCRIRE EN CARACTÈRES ROMAINS.
Trudy Karadagskoy biologicheskoy stantsii akademii nauk Ukrainsskoy SSR

REFERENCE IN ENGLISH - RÉFÉRENCE EN ANGLAIS Papers of the Kara Dag biological station of the Academy of Sciences of the Ukrainian S.S.R.

PUBLISHER - ÉDITEUR <u>Academy of Sciences of the Ukrainian</u>	DATE OF PUBLICATION DATE DE PUBLICATION <u>S.S.R.</u>			PAGE NUMBERS IN ORIGINAL NUMÉROS DES PAGES DANS L'ORIGINAL <u>85 - 96</u>
	YEAR ANNÉE <u>1961</u>	VOLUME <u>-</u>	ISSUE NO. NUMÉRO <u>17</u>	
PLACE OF PUBLICATION LIEU DE PUBLICATION <u>USSR</u>				NUMBER OF TYPED PAGES NOMBRE DE PAGES DACTYLOGRAPHIÉES <u>25</u>

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MINISTÈRE-CLIENT Environment

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BUREAU NO. N ^o DU BUREAU 183002	LANGUAGE LANGUE Russian	TRANSLATOR (INITIALS) TRADUCTEUR (INITIALES) H.P.F.	AUG 25 1972

ABSORPTION OF OXYGEN BY THE CTENOPHORA SPECIES PLEUROBRACHIA
PILEUS O.F. MUELLER OF DIFFERENT SIZES AS AFFECTED BY THE TEMPERATURE
AND SALINITY OF THE ENVIRONMENT

TRUDY KARADAG BIOL. STATION, NO. 17, Pp. 85-96, 1961

BY

LAZAREVA, L. P.

UNEDITED TRANSLATION

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AUG 25 1972

INTRODUCTION

A study of gas exchange in the Coelenterata is of great interest. On the one hand, the data obtained in the course of such a study would enable one to form a fuller judgement on the evolutionary development of the processes of metabolism in the invertebrates; on the other, one would be able to calculate the daily (24 hour) requirements in food of these animals - on the basis of their oxygen consumption - and thus to ascertain the role played by them in the general economy of the sea.

Yet, the literature on the gas exchange of the Coelenterata contains very few relevant data.

Ledebur (1939), Zeuthen (1947), and other investigators have established that the metabolic rate of the Coelenterata, as calculated on the basis of live weight,

is extremely low in comparison with that of other animals, but it is expressed by the usual values if calculated on the basis of dry weight and nitrogen content.

The influence of environmental factors on the gas exchange in the Coelenterata has not hitherto been studied.

During a period 1959 - 1960 we carried out a number of experiments to ascertain the rate of oxygen absorption by the Ctenophora species Pleurobrachia pileus as affected by the temperature and water salinity, as well as by the size of experimental animals.

Under conditions obtainable at our station, P. pileus were encountered both in the warm and cold months, but the periods of their greatest numerical strength - "population explosions" - alternated with the periods when they were found in small numbers or were entirely absent. This phenomenon may, obviously, be explained by the occurrence of reproductive seasons, as well as by the phenomena of dispersal while forming large aggregates. Young developmental stages of P. pileus were found in the plankton throughout the year, but they were particularly numerous in the period September - December. At this time, only single adult individuals were encountered in our catches among the mass of young P. pileus.

MATERIAL AND METHODS

Experimental P. pileus were collected in the sea almost always in the morning (7 - 9 a.m.), by using a "caviar" strainer. On being brought to the laboratory, the animals were maintained for about one hour at the temperature under which the experiment was to be conducted. To measure their respiration we used cylindrical graduated glass vessels of about 600 c.c. capacity each with tight fitting stoppers. These were filled, using a syphon, with filtered sea water; one of them served as control, while

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the experimental animals were placed in the remaining vessels. In each vessel 8 - 15 (usually 10) individual animals were placed. The exposure time, varying from 4 - 7 hours, was determined according to the temperature of the water. Oxygen content was determined by Winkler's method. On completion of the exposure time, samples were collected (to ascertain oxygen content) both from the experimental and control vessels. Prior to collection of samples the vessels were turned over several times to ensure a uniform distribution of oxygen in the water. To attain this end we occasionally placed in the vessels a metal float which could be set in motion by a magnet outside the vessel. On termination of the experiment, P. pileus were dried on filter paper (till the disappearance of wet spot) and weighed on precision scales. To obtain dry matter, P. pileus were thoroughly dried in the sun to a constant weight and then were placed for a period of several days into an exsiccator. It was established that the weight of P. pileus - after exposure in the exsiccator - usually remained constant. Oxygen absorption by P. pileus was determined by noting the difference of oxygen content in the experimental and control vessels; thereafter, oxygen consumption was calculated per one gram of live and dry weight during one hour, as well as its consumption by a single animal during one hour. Oxygen content in the vessels equalled usually 80 - 90 per cent of saturation. Altogether, we carried out 180 respiration experiments.

CORRELATION BETWEEN GAS EXCHANGE OF CTENOPHORA AND THEIR WEIGHT

The rate of energy exchange (Ivlev, 1959) depends in all instances on the correlation between the active elements of animal body - where the metabolic processes are carried out - and the total mass of the uninvolved elements (bone tissue, body cavity fluids, etc.). The tissues of Ctenophora contain an enormous amount of water (According to our data, dry weight of Ctenophora represents only 2.4 per cent of the live weight). Naturally, the rate of respiration of P. pileus, calculated on live weight, is extremely low. It equals anything between 1/100 to 1/1000 mg of oxygen per one gram of live weight during one hour.

Appropriately enough, a decrease in the rate of gas exchange occurring parallel with an increase in the body weight had been noted by many authors in respect of different animals.

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A parabolic equation $Q = a \cdot W^k$ - reflecting the correlation between the metabolism of an animal and its body weight - was formulated, where Q is the total metabolism, a is the metabolism of an animal the weight of which is a unity, W is the weight of an animal, and k is an abstract number. For many animals (Fishes, insects, crustaceans) the total metabolism is directly proportional to the weight elevated to a power close to .8, and the rate of metabolism is proportional to the weight elevated to a power .2 (Vinberg, 1950, 1956; Ivlev, 1959; Vinberg and Beliatkaya, 1959; Vinberg and Khartova, 1953; and others).

In our studies of the rate of respiration (oxygen absorption per one gram of weight during one hour) of Ctenophora of different sizes we dealt with four size groups (We measured the length of the least diameter).

Group	Size (in mm.)	Average weight of a single animal in grams
I	3 - 6	.06 - .12
II	6 - 8	.13 - .2
III	8 - 10	.21 - .3
IV	10 - 12	.31 - .45

The parabolic equation was found by us to be also suitable for the Ctenophora; in their case a being the metabolism of a Ctenophore the weight of which is .1 gram.

In Fig. 1 is represented - in the logarithmic system of coordinates - the correlation between the rate of oxygen consumption of Ctenophora and their weight at a temperature of 17 - 20° C. The upper straight line was constructed on the basis

O_2 absorption expressed in mg. during one hour per single animal.

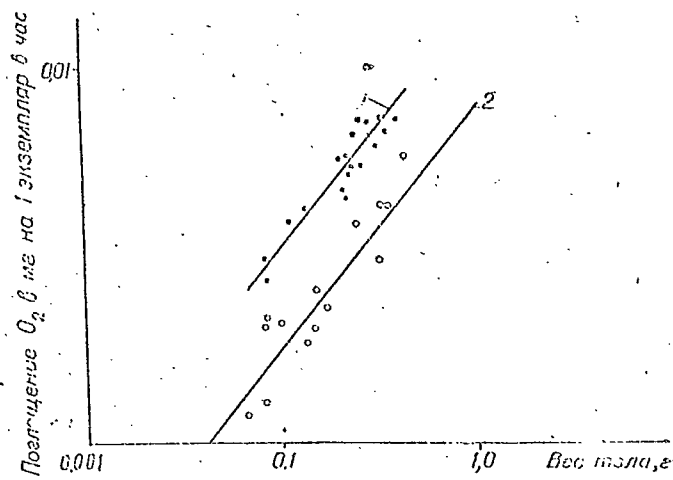


Рис. 1. Зависимость поглощения O_2 от веса тела гребневикув:

1 — данные весенне-летнего периода; 2 — данные летне-осеннего периода.

Body weight in grams

Fig. 1 Correlation between oxygen absorption and the body weight of Pleurobrachia pileus

1. The data obtained during spring-summer period;
2. The data obtained during summer-autumn period.

of 1959 spring - summer data, and the lower one on the basis of summer-autumn data of 1959. It must be noted that the rate of respiration of Ctenophora was greater in spring-summer period (March - June) in comparison with the rate of respiration recorded in other months, though the size of the animals as well as the temperature and salinity remained the same (Fig. 1). Clarification of the causes of seasonal variations in Ctenophora rate of gas exchange would require special observations. Thus, the parabolic equation - in the case of Ctenophora - assumes the following aspect (the parameters of the equation were found graphically) : for the spring-summer period - $Q = .0032 \cdot W^{.625}$; and for the summer-autumn period - $Q = .0017 \cdot W^{.625}$.

INFLUENCE OF TEMPERATURE ON THE RATE OF RESPIRATION OF CTENOPHORA

The majority of investigators who studied the influence of temperature on the processes of respiration in aquatic animals noted a regular increase in the rate of respiration occurring parallel with an increase in the temperature. Krog (1914, 1916) (quoted according to Zernov, 1935) established, empirically, a correlation between the above two factors (the so-called "Krog's normal curve"), which acquired wide acceptance for calculations in respect of poikilothermic animals.

We worked out the values of the temperature coefficient Q_5 for intervals of 5° C. for all four size groups of Ctenophora (Table 1).

Regrettably, we were unable to obtain the low temperature data for the Ctenophora of Group IV, because these animals are absent in cold months of the year.

Q_5 , the temperature coefficient, tends to increase while the temperature

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O₂ absorption expressed in mg/g during one hour.

O₂ absorption expressed in mg/g during one hour.

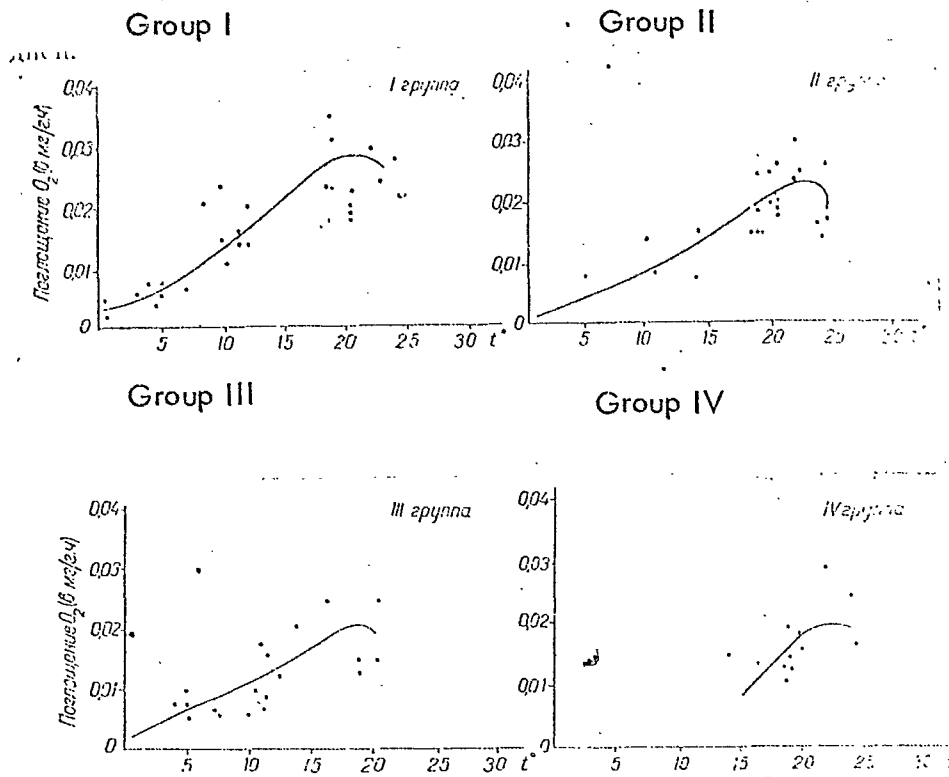


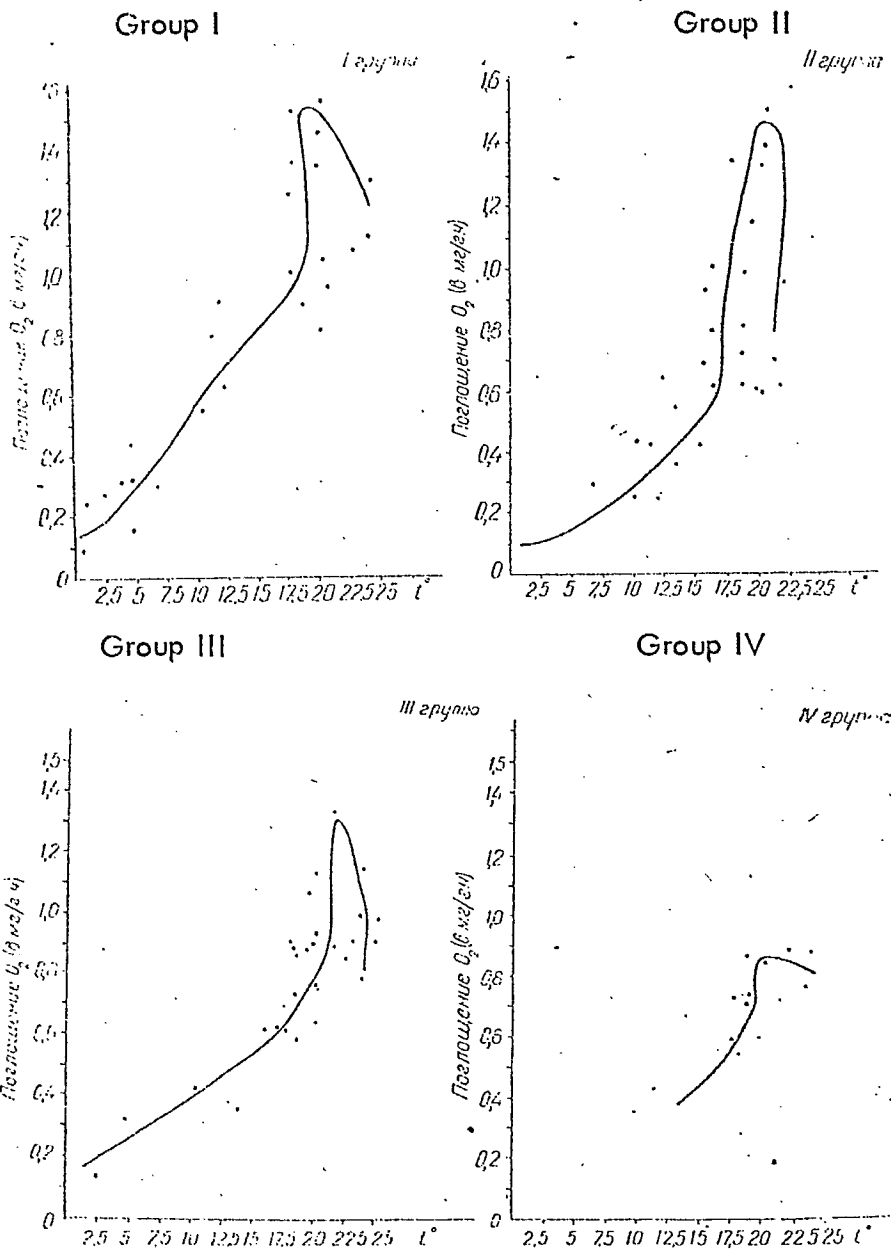
Рис. 2. Влияние температуры на интенсивность дыхания гребневинок *Pleurobrachia pileus* всех четырех размерных групп при расчёте на сырой вес.

raw weight in grams

Fig 2

The influence of temperature on the rate of respiration of *Pleurobrachia pileus* of all four size groups, calculated per live weight.

O_2 absorption expressed in mg/g during one hour.



O_2 absorption expressed in mg/g during one hour.

Рис. 3. Интенсивность дыхания гребневника *Pleurobrachia pileus* в зависимости от температуры при расчете на сухой вес для всех четырех размерных групп.

TEMPERATURE

Fig. 3

The rate of respiration of *Pleurobrachia pileus* as dependent on temperature, calculated per dry weight of all four size groups.

decreases, and, vice versa. When the temperature reaches a certain limit, Q_5 becomes equal to unity, and, then, becomes a negative value, i.e. the rate of respiration not only fails to increase, but, on the contrary, decreases until the animal perishes. This had been already established by Krog (1916, 1941), and also Ege and Krog (1914). As will be seen from Table 1, Q_5 increases in the lower temperature intervals. In the 20 - 25°C. Q_5 is less than unity, a fact which is explained by the repression of respiration of Ctenophora at such temperatures. As may be seen from Fig.2 and Fig.3, the curve representing the correlation between the respiration and temperature falls sharply after 21 - 22° C.

The Ctenophora, being cryophilic animals, became sluggish at temperatures above 18 - 20° C., surviving just a few hours under laboratory conditions. The temperature of 26° C. was lethal, for the animals perished very quickly. At a temperature not greater than 14° C. the animals behaved normally, surviving under laboratory conditions for 2 - 3 days.

In Fig. 2 and Fig. 3 is depicted the change in the rate of oxygen absorption by Ctenophora as influenced by the temperature for all four size groups in a range of .5 - 25° C. The above graphs were constructed on the basis of data obtained in the period from August 1959 to February 1960.

As has already been pointed out, Ctenophora contain in their tissues an enormous quantity of water; and the rate of their respiration calculated on the basis of live weight is quite insignificant. For example, Ctenophora of the size group I absorbed on an average - per one gram of live weight - .004 mg. of O_2 during one hour at .5° C., and .028 mg. of O_2 during one hour at 21° C.;

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Ctenophora of the groups II and III absorbed .003 and .002 mg. of O_2 , respectively, at $.5^\circ C.$, and .023 and .021 mg. of O_2 at $20 - 22^\circ C.$ If calculated on dry weight, one would obtain the maximum figures of O_2 absorption for the animals of groups I and II - 1.55 - 1.65 mg. per hour, and the minimal - .1 - .15 mg. per hour per one gram of dry matter. The animals of group III absorbed between .15 - 1.33 mg. of O_2 per hour per one gram of dry matter; and so on.

In Ledebur's paper (1939) were given data on the rate of respiration of Coelenterata as obtained by Teal, McClendon, Crumbach, and others. In the case of medusas and Ctenophora the following figures were worked out: Aurelia aurita absorbed 1851 - 1259 c.c. of O_2 per one kg. of dry weight during one hour; Rhizostoma pulmo - 1356 - 1560 cc.; Beroe oreneris - 930 c.c.; Cestus veneris - 1562 - 2420 c.c. These figures are somewhat higher than those we obtained in the case of P. pileus.

INFLUENCE OF TEMPERATURE ON OXYGEN THRESHOLD OF CTENOPHORA

We determined the oxygen threshold of Ctenophora at different temperatures. To obtain water with low oxygen content, we placed in vessels containing filtered sea-water some green seaweeds, mainly Cladophora and Enteromorpha. Thereafter, each vessel was wrapped in black cloth and left to stand with its mouth open for 36 - 48 hours. If the animals placed in such a vessel died at once, we added a little fresh sea-water into the vessel, so that P. pileus could remain alive for some time and died only after using up the reserves of oxygen available to them. A sample to test the oxygen content was taken from the experimental vessel at the moment the animals died.

A number of investigators (Ivlev, 1938; Nikiforov, 1953; Lozinov, 1952) showed that the oxygen threshold of animals and critical concentrations of oxygen depended on temperature, increasing parallel with the rise in temperature, and vice versa. As has been shown by our investigations, the oxygen threshold of Ctenophora increased as the result of rise in temperature, but such an increase remained very small. In general, the oxygen threshold of Ctenophora is very low. Even at 21° C. P. pileus perished only when the oxygen content reached .38 mg. per 1 litre which corresponds to 4.6 per cent saturation at that temperature. At 12° C. the animals perished when oxygen concentration was .22 mg. per 1 litre, i.e. 2.2 per cent saturation; yet, they were able to survive for several days at a lowered oxygen content. It must be noted that smaller P. pileus had a somewhat higher oxygen threshold. For example, at 12° C. the oxygen threshold of the Ctenophora of group I is .28 mg. per 1 litre (or 2.8 saturation), whereas the Ctenophora of group III perished - as has been mentioned above - at oxygen content of 2.2 mg. per 1 litre.

ABSORPTION OF OXYGEN BY CTENOPHORA AS INFLUENCED BY THE SALINITY OF THE ENVIRONMENT

According to Belyaev (1951), there are two basic ways of adaptation to salinity:

1. Adaptation of tissues of an organism so as to attain normal functioning under changed (in direct correlation with the environment) concentration (salinity) of body cavity fluid;
2. Development of a capability to maintain a constant osmotic pressure in internal environment independently of changes in the salinity of external environment.

TABLE I

CHANGES IN Q_5 (TEMPERATURE QUOTIENT) AS AFFECTED BY THE TEMPERATURE
AT ITS INTERVALS OF 5° C.

Temperature Intervals	I	II	III	IV
.5 - 5	2	2	2.5	-
5 - 10	2.1	1.8	1.8	-
10 - 15	1.6	1.4	1.5	-
15 - 20	1.3	1.3	1.3	1.9
20 - 25	.85	.81	.87	.84

Таблица 1
Изменения Q_5 в зависимости от температуры при интервалах ее в 5°

Интервалы температур	I	II	III	IV
0,5--5	2	2	2,5	--
5--10	2,1	1,8	1,8	--
10--15	1,6	1,4	1,5	--
15--20	1,3	1,3	1,3	1,9
20--25	0,85	0,81	0,87	0,84

The Coelenterata - as well as other lower invertebrates - followed the path under 1. As distinct from other marine invertebrates, the Coelenterata maintain the state of isotony with the external environment. We studied oxygen absorption by the Ctenophora under conditions of sharp and gradual change of the environmental salinity.

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Water of reduced salinity was obtained by diluting sea water with fresh water; and water of greater salinity was obtained by adding to sea water a concentrate produced by evaporation of sea water in the sun in flat enamelled pans. We carried out seven series of experiments on the influence exerted by a sharp change in salinity on the respiration of Ctenophora at temperatures varying from 3 to 25° C. The animals were placed directly from the water of normal Black Sea salinity (17 - 18 per thousand) into water of variable salinity. The range of degree of salinity varied from 5 - 30 per thousand with intervals of 2.5 per thousand.

Some authors (Zenkevich, 1938; Belyaev, 1954) noted that the invertebrates placed in diluted sea water absorbed water which brought about an appreciable increase in their weight, whereas in water of increased salinity they lost their water content and, thus, lost weight. Therefore, experimental animals in our series were put - after a suitable exposure to diluted water - successively into vessels with progressively increasing salinity until normal Black Sea salinity was reached; and those Ctenophora that were used in increased salinity experiments were placed in water of gradually diminishing salinity. For this reason, we always made our calculations on the basis of the weight of Ctenophora at a normal salinity of Black Sea water.

According to the data of Karpevich (1958), the highest oxygen consumption occurs under optimal salinity conditions. Occasionally, under extremely unfavourable

O₂ absorption expressed in mg/g during one hour

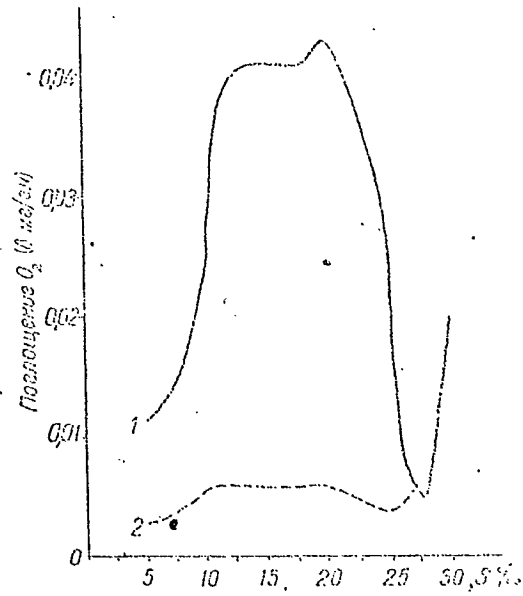


Рис. 4. Влияние солености на поглощение кислорода гребневыми *Pleurobrachia pileus*.
 1 -- при температуре 20°; 2 -- при температуре 3°.

‰ SALINITY

Fig. 4

The influence of salinity on O₂ absorption by Pleurobrachia pileus.

1. At 20° C; 2. at 3° C.

conditions of salinity, oxygen consumption was at first sharply increased, and then decreased with the resultant death of animals. As had to be expected, the range of optimal salinities was much wider in Ctenophora at low temperatures than it was at high temperatures. At low temperatures (3 - 11° C.) and in the cases of a sharp change of environmental salinity in a range of 18 - to 10 per 1000, we observed a low and practically constant rate of gas exchange; only at 7.5 per 1000 salinity and lower was observed a slight decrease in oxygen consumption. In contrast with this, in water of increased salinity at 11° C., the rate of respiration underwent an appreciable increase. At a temperature of 20° C. the level of gas exchange in Ctenophora was much higher than it was at low temperatures at all points of salinity range. Their gas exchange remained practically constant at a range of 12.5 - 20 per 1000; and, thereafter, both with an increase and decrease of salinity, it decreased registering a slight increase at sublethal salinity (30 per 1000). In Fig. 4 is depicted absorption of oxygen by Ctenophora at different degree of salinity at a temperature of 3 and 20° C. Another series of experiments was also carried out at a temperature of 24° C., but the resultant curve was of a chaotic, irregular pattern. At a temperature of 24° C. the greatest unfavourable factor for the Ctenophora was high temperature; a fact which furnishes an explanation of sharp fluctuations in and a sharp decrease of oxygen consumption already at a degree of salinity within the range of 15 - 20 per 1000.

The behaviour of Ctenophora when placed in water of different salinity at different temperatures also varied. At low temperatures the animals - when placed in water of either very low (10 per 1000) or very high (27 - 30 per 1000) salinity - entered the phase of salt "anabiosis"; yet, when placed into water of normal salinity,

TABLE II

ABSORPTION OF OXYGEN BY PLEUROBRACHIA PILEUS IN THE COURSE OF A
SHARP OR GRADUAL CHANGE IN THE SALINITY OF THE ENVIRONMENT

Date	Water Temperature in degrees of C.	Salinity %	Average weight of experimental animals in grams	Absorption of O ₂ per 1 gram of live weight in one hour ml	
				The adapted <u>P. pileus</u>	The non-adapted <u>P. pileus</u>
June 9	17.5	7.5	.23	.01	.012
June 9	17.5	10	.25	.012	.08
June 15	20	27.5	.15	.012	.014
June 17	21	7.5	.16	.016	.018
June 17	21	5	.15	.05	.04
June 23	20.2	20	.27	.011	.013
June 23	20.2	25	.2	.013	.014
Aug 27	22	10	.14-.18	.017	.015
July 28	22	15	.16	.010	.010
July 28	22	25	.09-.13	.016	.018

Таблица 2

Поглощение кислорода гребневиками при резкой и постепенной смене солености среды (данные 1960 г.)

Дата	Температура воды, °C	S, ‰	Средний вес подопытных животных, г	Поглощение O ₂ на 1 г живого веса в час, мл	
				Адаптированные гребневники	Неадаптированные гребневники
9.VI	17,5	7,5	0,23	0,01	0,012
9.VI	17,5	10	0,25	0,012	0,08
15.VI	20	27,5	0,15	0,012	0,014
17.VI	21	7,5	0,16	0,016	0,018
17.VI	21	5	0,15	0,05	0,04
23.VI	20,2	20	0,27	0,011	0,013
23.VI	20,2	25	0,2	0,013	0,014
27.VIII	22	10	0,14-0,18	0,017	0,015
28.VII	22	15	0,16	0,010	0,010
28.VII	22	25	0,09-0,13	0,016	0,018

regained quickly their normal behaviour. At 20° C. the animals developed the state of salt anabiosis already in water with 10 - 25 per 1000 salinity, although their cilia began to move again after approximately one hour. In water of greater or lesser salinity the animals remained in the state of salt anabiosis till the end of the experiment. At 24° C. the Ctenophora developed the state of salt anabiosis already at a degree of salinity equal to 15 - 20 per 1000.

The experiments carried out by Karpevich (1947, 1955, 1958), Zhimunsky and Kiseleva (1957), and others showed that salt adaptation in some species increases salinity tolerance range (which was given the name of "potentially favourable zone" for a given species) or the length of survival in a sublethal salinity environment.

We carried out 10 experiments so as to ascertain the effect of a gradual change of salinity on oxygen consumption by P. pileus. The experiments have been conducted at temperatures 17 - 22° C., because at lower temperatures no sharp fluctuations of O₂ consumption by Ctenophora occur after a change in salinity of the environment. Some of the Ctenophora were placed, prior to the experiment, into water with decreasing (or increasing) salinity until the desired experimental salinity had been reached. The animals were left for up to 30 minutes in each vessel of decreasing or increasing salinity, and, in vessels with experimental salinity, were left for 60 minutes. The remaining animals were placed directly in water with the required experimental salinity.

As will be seen from Table 2, oxygen consumption (absorption) by either group of animals was almost the same.

On the basis of the data obtained by us, we feel inclined to regard P. pileus

species of Ctenophora as euryhaline organisms, and particularly so at low temperatures; this fact being confirmed by the wide area of P. pileus distribution. According to Lindquist (1958) this species inhabits the vicinity of northerly shores of the Baltic Sea in water layers below the depth of 50 meters. Its distribution is limited to the isohaline of 6.3 - 7 per 1000. The species inhabits also the seas with a complete (about 35 per 1000) salinity. One may suppose that the spread of this species into the Sea of Azov is impeded by its temperature, and not by its low salinity.

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CONCLUSIONS

1. During 1959 - 1960 we carried out a number of experiments to ascertain the dependence of oxygen absorption by Ctenophore species P. pileus (O.F. Mueller) on the temperature and salinity of the water, as well as its dependence on the size and condition of experimental animals. All respiration experiments were carried out by using a method of closed vessels. Oxygen content was determined by Winkler's method. Oxygen consumption by the Ctenophora was ascertained by noting the difference of oxygen content in the experimental and control vessels, and, then, its consumption was calculated per one gram of live weight or dry weight, and for each animal during one hour.

2. The correlation between the general energy exchange and weight of the Ctenophora is expressed by a parabolic formula (equation): $Q = .0032 \cdot W^{.625}$ for the spring-summer period, and by the formula $Q = .0017 \cdot W^{.625}$ for the summer-autumn period at a temperature close to 18.5°C .

3. The rate of respiration underwent an increase parallel with the rise in temperature but Q_5 became less than unity in a range of $20 - 25^{\circ} \text{C}$, a fact which is explained by the repression of respiration of Ctenophora. The temperature of $26 - 27^{\circ} \text{C}$. was found to be lethal for that species.

4. We determined the oxygen threshold of Ctenophora at different temperatures. According to our data, their threshold is very low; even at 21°C . it was .38 mg. per 1 litre or 4.6 per cent saturation at that temperature.

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5. We carried out a number of experiments in order to ascertain the effect of both sharp and gradual changes of salinity on the respiration of Ctenophora at different temperatures. At low temperatures the range of optimal salinities became wider.

6. According to our data, preliminary adaptation to a specific salinity environment exerted no influence on the rate of respiration of the Ctenophora.

7. We are inclined to regard P. pileus species of Ctenophora sufficiently euryhaline organism, and particularly so at low temperatures; this fact being confirmed by the wide area of its distribution.

LITERATURE

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AUG 25 1972

GLOSSARY

TRUDY	Papers
UCHIONYEZAPISKI- UZ	Scientific annals
DAN	Doklady - Transactions of the Academy of Sciences of USSR
VNIRO	All-Union Research Institute of Fisheries and Oceanography
IZVESTIA	Bulletin
VNIORKH	All -Union Research Institute of Fisheries
SBS	First "S" indicating location BS - Biological Station