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ON THE RELATION BETWEEN METABOLISM AND TEMPERA-TURE IN SOME MARINE LAMELLIBRAN-CHES, AND ITS ZOOGEOGRAPHICAL SIGNIFICANCE

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INTRODUCTION

ur knowledge of the metabolism of the marine Invertebrata is rather poor. In the course of time a few species have been investigated; as regards the older literature I can reter to the book by KROGH (1915) and the paper by KESTNER (1922) in Winterstein's Handbuch. In recent years some other investigations on the metabolism of marine Invertebrata have been published as for instance the papers by BERKELEY (1921), BRUCE (1926), COLLIP (1921), FISHER, DUVAL & RAFFY (1933), MARSHALL, NICHOLS & ORR (1935), and the two papers by RAFFY from 1933, one containing a bibliography of the subject. But in spite of these publications investigations have hitherto not been made from the point of view of elucidating the relation of metabolism to the geographical distribution of the species investigated and to the normal condition of temperature of the same species. In the last few years the present author has made determinations of the consumption of oxygen of a series of common Lamellibranches. These investigations have been made partly in the Zoophysiological Laboratory of the University of Copenhagen, partly during a stay at the Zoological Station at Naples in 1930. Further, determinations by using the same method have been made by THAMDRUP (1935) in Danish waters, and by THORSON (1936) in arctic waters.

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Summarizing these different investigations I think we have now the possibility of examining the hypothesis set forth by the present author (1926) to the effect that the relation between metabolism and temperature is one of the factors playing an important part in the competition among the species in nature, thus being of no small consequence to the regulation of the distribution of the animals.

I am much indebted to the Director of the Zoophysiological Laboratory of the Copenhagen University, Prof. Aug. KROGH, for laboratory facilities and kind advice during these investigations. Further I wish to acknowledge financial assistance received from the Carlsberg Foundation.

Method and Material.

The oxygen consumption has been determined by the method of WINKLER as described by BJERRUM (1903) and transformed in the Laboratory of Zoophysiology to a micro method by using a microburette. In most cases a number of animals, about 10, have been used in each single experiment for the purpose of checking out individual variations. The animals are placed into a glass bottle of a size varying from 100 to 2000 cc. according to the size of the animals of the experiment. The bottle is provided with a ground glass stopper. The bottle with the animals is put into an aquarium with sea-water of the temperature at which the determination is to be made. The content of oxygen of the water in the aquarium is determined. Then the plug is placed in the bottle, the latter is laid on the bottom of the aquarium so that the animals can be evenly distributed in the water which is now enclosed in the bottle. After a suitable time which depends on the relation between the oxygen

consumption of the animals and the water volume available, the bottle is taken out of the water and shaken. The plug is carefully taken out, and by means of a siphon a sample of water of 12 to 15 cc. is taken from the bottom of the bottle into the special sampling flasks, and the oxygen content is now determined again. The difference between the content of oxygen in the water of the aquarium at the beginning of the experiment and that of the water in the bottle at the end of the experiment is due to the consumption of the animals.

One or two of the special sampling flasks of 12 to 15 cc. capacity are filled from the bottom of bottle. To these 0.1 cc. of each of the WINKLER reagents is added, and after a suitable interval HCl is added and 5 or 2 cc. samples pipetted off for titration.

The duration of the single experiment has been varying, and for each species been determined by preliminary experiments with a view to the consumption of oxygen and the size of the animals. In most cases the duration of the single experiment has been a few hours. At very high temperatures only 1 or 1/2 hour. Care has been taken that the content of oxygen in the bottles was never below 20 to 30 per cent. at the end of the experiment. Before the animals were taken into the experiments they have lived 24 to 48 hours in sea water of the same salinity and temperature as in the water of the experiment. As will be demonstrated later the consumption of oxygen at a certain temperature is not the same in cases when the animals have suddenly been transferred to water of that temperature, and in cases when they have lived for some time at that temperature. When each experiment has been finished the animals have been transferred to an aquarium with the same temperature and salinity as that of the experiment. In most cases several experiments have been made with the same individuals of each species at different temperatures.

The consumption of oxygen is given in cubic cms. per kilo per hour. The animals of each experiment were weighed at the beginning of each series of experiments and again when it was finished. Then the animals were killed and all organic material was taken out of the shells, dried by means of filter paper and then weighed again. In the determination of the consumption of oxygen per hour and kilo these last weights of the animals without shells and the water between the shells have been used.

As far as can be seen the animals do not move in the experimental bottles. Moreover the animals have been narcotized in some cases by means of ethyl-uretane and hereby it has been proved that it is of no importance if the animals in these experiments are narcotized or not.

The material used in the experiments in Copenhagen has been procured partly in the Sound, partly in the Great Belt by the courtesy of the Danish Biological Station, which also has taken some material in other parts of the Danish waters. The material of the experiments in Naples has been procured through the fishermen of the Zoological Station at Naples. The following species have been investigated: In the Mediterranean Pecten varius, P. flexuosus, Lima hians, L. inflata, Venus verrucosa, V. gallina, Loripes lacteus, Dosinia exoleta, Tapes decussatus, Tellina planata, Cardium edule, Mytilus edulis, Psammobia vespertina and Cardita trapezia. In Danish waters Ostrea edulis, Mytilus edulis, Cardium edule, Macoma baltica, Saxicava arctica, Astarte borealis, A. montagui, A. elliptica and Scrobicularia plana. Further some Ostrea edulis and Gryphaea angulata from West France have been investigated. THAMDRUP (1935) determined the oxygen consumption of a few of the above-mentioned species and further that of

Mya arenaria. At last 380 should be mentioned the determinations 360 by THORSON (1936) 340 of the oxygen consumption of a series 320 of arctic species. 300

The oxygen consumption at different temperatures.

The results of the 2 experiments mentioned above are shown 2 in the graphs figs. 2 1-16. In these graphs the temperatures are 4 set off on the abscissa 2 and the consumption in cc. per hour and 4 kilo on the ordinate. 4 The intention of the 4 experiments was not 4

Fig. 1. Oxygen consumption of *Pectinidæ* and *Limidæ* in cc. per kilo and hour. *P. groenlandicus* the fully drawn line, *P. varius* the thick dotted, *P. flexuosus* the thick crossed, *L. inflata* the fine dotted, *L. hians* the fine crossed.



Nr. 5. R. Spärck:

to determine the metabolism from a physiological point of view, but to find out the consumption at different tempe-



Fig. 2. Cardita (the fine crosses) and Dosinia exoleta (thick crosses). The broken line shows the consumption by suddenly transferring to high temperature.



Fig. 3. Tapes decussatus (thick crosses) and Loripes lacteus (fine crosses). Broken line as above.

ratures under otherwise normal conditions to get an idea of the actual requirements of oxygen of the different species in nature. I admit that these results are obtained under experimental conditions, which are not altogether natural, so that they can only give an approximate idea of the amount of the consumption. But I am of the opinion

that nevertheless these approximate results are sufficient for the purpose of the present investigation.

From the graphs it is obvious that the Lamellibranches investigated have a rather different con-

sumption and further

a considerably different relation between temperature and this consumption. The differences are very marked and more-

over they coincide with other features so that they cannot be due to chance or experimental errors. The Lamellibranches



Fig. 4. Venus gallina (dotted) and V. verrucosa (crosses). Broken line as fig. 2.

can as regards their consumption of oxygen be divided into 3 groups. One group comprising the investigated species

of the families *Pec-100 tinidæ* and *Limidæ* (fig. 1) has a fairly ⁸⁰ high consumption, and the increase of ⁶⁰ the consumption of oxygen at rising temperatures is very considerable. The arctic¹ species, *Pecten groenlandicus*, which lives at temperatures



Fig. 5. Tellina planata, young (small crosses) and bigger (thick crosses) specimens.

¹ In all the graphs the arctic species is shown by fully drawn lines, that of boreal species by dotted lines, and that of mediterranean by crossed lines. The two larger crosses on the graphs show the limits of the "normal" temperature of the species.

constantly below zero or at least only a few degrees centigrade above zero, has a consumption at $\div 1^{\circ}$ C. of about



Fig. 6. Astarte borealis at Greenland (fully drawn) and Denmark.



Fig. 7 Astarte elliptica at Greenland (fully drawn) and Denmark.

25 cc. per kilo and hour, and already at a few degrees above zero the consumption is about 50 to 60 cc. And it has not been possible to keep this species alive in experiments at

temperatures above 8 to 10° C. Turning to the boreal-mediterranean species *Pecten varius* it will be seen that this species



Fig. 8. Astarte montagui at Greenland (fully drawn) and Denmark.



Fig. 9. Mya truncata at Greenland (fully drawn) and M. arenaria at Denmark (dotted).

has a consumption of about 25 cc. at 5° C. increasing to about 250 cc. at a little above 20° C. and to about 300 cc. at 30° C.

This species lives normally at temperatures between 10 to 20° and at these temperatures may be regarded when at rest as having an oxygen consumption of about 120 to 150 cc. Finally the mediterranean species *Pecten flexuosus* at 5° has an oxygen consumption of about 10 cc. increasing to about 200 cc. between 20 and 25°, and the two *Lima* species *L. inflata* and *L. hians* show quite the same type of consump-



Fig. 10. Ostrea edulis (dotted) and Gryphaea angulata (crosses).

tion and temperature relation using about 20 cc. at 5° and increasing very steeply to 2-300 at 20° .

Quite different is the oxygen consumption in another much larger group comprising species of *Tellinidæ*, *Astartidæ*, *Veneridæ* and further *Cardita*. As will be seen from the graphs figs. 2—9 all these Lamellibranches at temperatures about zero have a very low consumption. In the mediterranean species only some few cc. per kilo and hour, in the arctic about 10 cc. And further the increase is very slow at rising temperatures. In most species of this group, especially the mediterranean ones, the consumption does not reach

more than 20 to 60 cc. even at temperatures of 20 to 30° C.

Between these two groups, one with a consumption steeply increasing with the temperature and attaining very



Fig. 11. Macoma baltica (dotted, the upper in spawning time) and M. calcaria (fully drawn).

high values before fatal temperatures are reached and the other with a very low consumption slowly increasing with the temperature we have an intermediate group consisting of the *Mytilidæ* and *Cardiidæ*, and also *Saxicava* which have a medium consumption of oxygen increasing rather steeply with the temperature but not so markedly increasing as in the Pectinidae and Limidae.



It is obvious that these differences in the type of oxygen consumption in the three groups may be related with the different ecology of the species of the families in these

groups. The first group (the *Pectinidæ* and *Limidæ*) consists of species which among the Lamellibranches are the only



Fig. 13. Saxicava arctica at Greenland (fully drawn lines) and Denmark (dotted).



ones which are able to move rapidly, it being well known that they can swim fairly well. In contradistinction to the

families of the first group are the members of the second group practically without the possibility of moving over a greater distance. The species of the second group are all living buried into the bottom material, and they are practically sedentary. If food is lacking or scarce a *Pecten* or



Fig. 15. Modiolaria laevigata at Greenland (fully drawn), Mytilus edulis at Denmark (dotted) and in the Mediterranean (crosses).

Lima specimen is able to move to other places in search of it. But a Mya, Tellina, Venus etc. must in such a case remain on the place where it lives, it can only move some few metres, and try to get through the period of scarcity by reducing its consumption. It is a well known fact that it is rather difficult to keep *Pecten* alive for a longer time in aquaria and specially above the water, whereas the most Lamellibranches of the group with a low oxygen consumption can be kept



for months in aquaria and for hours and days in moist air. The intermediate group consists of species of the epifauna,



or of species with a certain possibility of moving as *Cardium* and *Psammobia*. The species of the epifauna as for Vidensk. Selsk. Biol. Medd., XIII, 5. 2

instance the *Mytilidæ* and *Saxicava* do not live buried down into the bottom material in calm waters, they are sitting on rocks, stones, vegetation etc. more or less above the bottom material, and their possibility of obtaining food must be regarded as much better than that of most *Tellinidæ*, *Veneridæ* etc.

As it is obvious from the above mentioned facts there seems to be a marked relation between the type of oxygen consumption especially its relation to temperature and the ecology of the species. Species with a high consumption in which there is a steep increase with the temperature are also by moving and swimming able to get the sufficient food for this high metabolism, and only species with a low oxygen consumption and a slow increase with temperature have been able to live buried down in the bottom material, whereas they cannot compete in localities where the food conditions are good enough to allow the species of the epifauna with a higher metabolism and higher food requirements to live. I am therefore of the opinion that it is justifiable to say that the relation between oxygen consumption and temperature characteristic of each species is an important factor in the competition among the species in nature.

Even if considered more in detail this result seems to be correct. If we are looking at *Scrobicularia plana* (fig. 12) it appears that this Lamellibranch has a peculiarly steep increase of the oxygen consumption with the rising temperature in spite of the biology of the species. *Scrobicularia* is allied to the *Tellinidæ*, but nevertheless the oxygen consumption at a temperature of 25 to 30° C. is about 200 cc., and still the species lives quite as the other *Tellinidæ*, *Veneridæ* etc. with their low consumption of oxygen. As pointed out some years ago by the present author (1926 p. 282) *S. plana* has a re-

markable distribution indicating that the food problem may be of special importance to this species. It occurs near the mouth of rivers, in the innermost parts of some shallow water inlets and fjords, where there is a considerable production, and finally S. plana is characteristic of tidal coasts with the great renewal of water. All these three types of localities are of such a nature that they may be considered to offer exceptionally good food conditions for a sedentary Lamellibranch buried down in the bottom. And a glance at the graph fig. 12 corroborates this view in that the oxygen consumption of *Scrobicularia plana* is of quite another type than that of most other Lamellibranches buried down in the bottom. This explains the peculiar distribution of this species. Also Macoma baltica and Macoma calcaria seem to differ to a certain degree from the normal type of the Tellinidæ (fig. 11), at least at the spawning time during which the consumption of oxygen is rather high. And Macoma calcaria has a comparatively high oxygen consumption compared with several other arctic bottom Lamellibranches. In this connection it should be pointed out that just these two species are characteristic of the shallow water of the boreal and arctic waters, and especially Macoma baltica is restricted in most waters to a belt of a few meters' depth, only in the Baltic where the majority of their competitors are lacking is it found at greather depths. C. G. JOH. PETERSEN (1918) has explained this phenomenon in the way that the cause of the greater bathymetrical distribution of *M. baltica* in the Baltic is the lack of enemies, especially Asterias rubens, and this may perhaps also be partly responsible for this distribution. I think however that the relatively high oxygen consumption of M. baltica, at least in periods, presumably accounts for the explanation that it is the lack of competitors which

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is the cause of the greater bathymetrical distribution of this species in the Baltic. In some waters, for instance in the Greenland and the North Atlantic fjords, *Macoma calcaria* has a more restricted bathymetrical distribution than in the North Russian seas and the Spitsbergen waters, and this difference may perhaps also be due to the same cause.

Also among the epifaunistic Lamellibranches there is an exception, the oysters *O. edulis* and *G. angulata* (fig. 10). They have a comparatively low oxygen consumption of the same category as that of the Lamellibranches which live buried down in the bottom. This may certainly be explained in the way that the oysters are absolutely sedentary and cannot move at all for which reason it must be considered of importance to these species in the competition to have an oxygen consumption which rises slowly with temperature.

It should be pointed out that differences in the consumption of oxygen may be expected according to age of the investigated animals and according to the season of the year. BRUCE (1926) has shown that there is a remarkable increase in the oxygen consumption at the time of spawning. This has also proved to be the case in several of the Lamellibranches investigated here, for instance in Macoma baltica and Cardium edule, which have a higher consumption of oxygen in spring and summer than in the autumn, whereas Astarte borealis which is an autumn spawner has a higher oxygen consumption in the autumn. When the consumptions of oxygen are compared care must be taken that animals from the spawning season are not compared with animals from another season, and further that the animals are of the same size category, since small individuals have a somewhat higher consumption calculated per unit weight.

As mentioned above there is a difference in the relation

between temperature and oxygen consumption in cases where the animals are suddenly transferred to a higher or lower temperature and in cases where the consumption has been determined after a period of acclimatization. If the animals are suddenly transferred from a higher to a lower temperature, the oxygen consumption will decrease considerably at the beginning and then rise a little (figs 2, 3, 16). When they are transferred suddenly to a much higher temperature the consumption will also decrease in some cases, but in most cases the consumption will increase again after a period of acclimatization so that we will get a normally rising curve.

In some cases however an acclimatization to the high temperature is of no effect (fig. 2, 4, 5 and 9), and it is remarkable that three species in the Mediterranean, *Tellina planata, Venus gallina, Dosinia exoleta*, have a decrease of oxygen consumption at temperatures about 20° C, i. e. temperatures which in summer time occur in the waters in which they live. I think that this peculiar phenomenon can be explained in the way that these species live buried down in the bottom so that they are able to avoid to a certain degree the high temperatures of the water.

The zoogeographical importance of the relation between temperature and oxygen consumption.

If the view set forth in the above, namely that the said relation is an important factor in the competition among the species, is correct, it seems likely that a certain geographical relation of the different types of oxygen consumption can be demonstrated. If we look on the graphs figs. 1—16 it is obvious that there is such a relation. Some years ago the present author put forth the hypothesis that species of the Arctic could be expected to have a relatively high oxygen consumption, whereas species of waters with a high temperature could be expected to have a relatively low consumption of oxygen. If we are looking at the graphs it will be seen that the consumption of oxygen of the arctic species (the fully drawn lines) is relatively high. The arctic Pecten groenlandicus has a considerably higher oxygen consumption at about 0° C. than that of the boreal-mediterranean Pecten varius and the mediterranean Pecten flexuosus, and the latter has the lowest consumption of oxygen. If we look at the graph fig. 15 it will be seen that the consumption of oxygen of the boreal Mytilus edulis is higher than that of the mediterranean M. edulis f. galloprovincialis, and the arctic Modiolaria laevigata has a still higher consumption. The borealmediterranean Venus gallina has a higher consumption of oxygen than the more southerly distributed Venus vertucosa (graph fig. 4). Further Mya truncata has a greater consumption than the southerly Mua arenaria, Macoma calcaria a greater consumption than Macoma baltica and the common European oyster, O. edulis, consumes more oxygen than Gryphaea angulata of which it is shown that it is able to supplant O. edulis in several localities.

All this seems to show that there exists a relation between the type of oxygen consumption and the geographical distribution of the species to the effect that among allied species that species which has the most northerly distribution also has the relatively highest oxygen consumption when compared at the same temperature. In this connection we touch upon the problem of the influence of temperature on the distribution of the species. It is a well known fact that there is a correlation between temperature and

the geographical occurrence of the different species. This correlation is to a large extent due to the influence of the temperature on the reproduction and the larval development as it is has been shown in a series of cases. But the present investigations seem to me to indicate that the effect of the temperature also may to a certain degree be due to its influence on the oxygen consumption. If an animal with a relatively high oxygen consumption (arctic type) is transferred to a water with a temperature of about 20°C, the metabolism will rise rapidly so that the need for food will increase in such a degree that the animal will run the risk of dying from starvation. Whereas the influence of temperature on the reproduction and larval development in most cases limits the species towards the north, it is not unlikely that it is the effect of temperature on the metabolism which limits the distribution of the arctic animals towards the south. So-called sthenothermic animals may, at least in some cases, be regarded as animals with an arctic type of oxygen consumption.

If we regard the oxygen consumption of the same species at different localities within its area of geographical distribution there are indications of a certain difference, geographically related, of the type of oxygen consumption within the same species. As appears from graph fig. 15 it may be seen that *Mytilus edulis* of Danish waters has a distinctly higher oxygen consumption than that of *Mytilus edulis* from the Mediterranean. The different *Astarte* species seem in Greenland to have a higher oxygen consumption than that of the same species in Danish waters. It must be considered probable that also regarding the type of oxygen consumption we may find within the species geographically located physiological races. RUNNSTRÖM (1927, 1930 and 1936) has demonstrated that races of a similar character may be found regarding the reproduction and breeding time of several marine invertebrates.

On all the graphs the minimum and maximum temperatures to which the particular species are exposed in the locality where they live are marked with a cross. It will be seen that the arctic species at the low temperatures at which they normally live have an oxygen consumption of about 20 to 30 cc. in most cases, which is somewhat but not essentially lower than the consumption of most of the boreal and mediterranean species at the temperatures at which they live. And there are several mediterranean species which have an oxygen consumption at their "normal" temperature which is even lower than that of the arctic species. They may perhaps be explained by the poor food conditions in the Mediterranean. If the oxygen consumption found in marine invertebrates by other investigators is compared with the consumption found in this investigation it seems that the oxygen consumption of the Lamellibranches is comparatively low. Only the Pectinidæ and Limidæ have a consumption of the same size category as has been found by the same method by the present author in some pelagic fishes and Crustacea and in the Oyster larvae. This is perhaps due to the fact that most Lamellibranches are to be regarded as almost sedentary.

Summary of results.

1. It has been shown that among marine Lamellibranches several types of relation between oxygen consumption and temperature exist.

2. There is a marked correlation between the type of oxygen consumption and the ecology of the species, so that species which can move or are living above the bottom have a relatively higher consumption than that of the species living more or less sedentary in the bottom.

3. Further, differences within the above mentioned ecological types of oxygen consumption can be stated. These last named differences are related to the geographical distribution of the species, a relatively high consumption being characteristic of the arctic species, a relatively low one of the mediterranean species.

4. It is likely that an important influence of the temperature on the distribution of marine animals is due to the effect of temperature on the metabolism, and thereby on the food problem and competition among the species.

5. Even within the same species locally different races n this respect seem to exist.

(From the Laboratory of Zoophysiology, University of Copenhagen & the Zoological Station, Naples.)

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