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COMPARATIVE RATES OF OXYGEN CONSUMPTION IN MARINE FORMS[1]

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The present paper presents data gathered by the writer in a study made on the rate of oxygen consumption in some of the marine fishes and invertebrates, and gives additional weight to a report by Professor Scott before the Society of Experimental Biology, XII, pp. 146-147.

That different animals show very marked variability in their respiratory interchange has been known since the science of chemistry first contributed to our knowledge of physiological oxidations. Furthermore, in animals of the same species, it is a well known fact that various physical and bio-climatic conditions contribute to modify the amount of metabolic interchange in any given unit of time. Thus temperature, size, sex, exposure to light, kind of food, state of activity, storage capacity, oxygen tension, altitude and other factors (to mention but a few), are all to be reckoned with in quantitative studies. Bearing upon the general problems of respiration is a background of such workers as Boyle (1666), Mayow (1673), Hooke (1667), Black (1757), Priestly (1775), Lavoisier (1790), Liebig (1855), Pfluger (1872), Herring (1868) Rosenthal (1882), Rubner (1883), Geppert (1888), Zuntz (1888), and contemporaneously, Henderson (1910-23) and Haldane and Smith[2], and many others.

On the quantitative side, data on oxygen consumption and carbon dioxide liberation of air breathing forms were obtained by technical developments in the calorimeter, which in its crude form in the hands of the early workers (Priestly, Black, Lavoisier and others) consisted of an inverted bell jar in which an animal could be confined. Various improvements in details have been devised until under the guiding genius of Haldane in England, and Benedict in America, this method has yielded very accurate and valuable data. For animals that derive their oxygen through the med-

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[1] Published by permission of the commissioner of Fisheries; from the U. S. Bureau of Fisheries Station, Woods Hole, Mass, and the department of Zoology, Iowa State College. In collaboration with Professor G. G. Scott, College of the City of New York.

[2] For a complete historical review of the general problems in respiration, see Haldane's recent book "Respiration" Yale University Press, 1922.

ium of water, however, a different method must be employed. Although such early workers as Spallanzani, Treviranus, Edwards, Müller and others were able to observe the now well established fact, that the cold-blooded animals could subsist on a much less respiratory exchange than the warm-blooded types, it remained for Humboldt and Provencal in 1807,[3] to describe methods which could be employed and quantitative data obtained on marine forms. The fishes were placed in a flask of water, the gaseous content of which had been previously analyzed, and after an interval of time, a sample of water was analyzed and the alteration in its gases was determined. The quantity of water was measured and thus it was possible to estimate the gases absorbed and liberated by the fish. A similar method was employed by Vernon [4] in 1896 to determine the respiratory exchange in marine invertebrates. Jolyet and Reynard [5] in 1877 bubbled a stream of air slowly through the water in which the animal was placed; this air was analyzed for carbon dioxide, and the oxygen absorbed by the animal was replaced by a corresponding amount supplied from a gasometer. Improvements in titration methods have made it possible to devise fairly accurate procedures in working with marine forms. In experiments about to be described, the so-called Winkler method of analysis was used. To a known volume of water is added by pipette successively 2 cc. each of manganous sulphate, sodium hydrate and sulphuric acid and the mixture is shaken. This then is titrated with known sodium thyosulphate using starch as an indicator. By simple computation the number of cubic centimeters of oxygen can be derived expressed in terms of cc. per liter of sea water.

EXPERIMENTAL

Animals to be subjected to experimental conditions were brought to the fisheries laboratory, weighed and placed in containers of known capacity, a sample of water was analyzed and recorded as normal for the specific case. The temperature of the water was taken at intervals, and at definite times previously determined, successive samples for analysis were drawn. From the samples and the capacity of the container, the amount of oxygen per Liter, the total oxygen available, and the oxygen consumed were each tabulated, and from these computations in conjunction with the observed weight of the animal, the gram-hour rate of metabolism was derived. Because it was desired to get an index as to the widest possible range of conditions affecting consumption, numer-

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[3] Humboldt and Provencal, Journal f. Chem. u. Phys. Nürnberg, Bd. 1, s. 86.

[4] Vernon, Journ. Physiol., vol XIX, p. 18, 1895-96.

[5] Jolyet and Reynard, Arch. de physiol. norm. et path., Tome IV,, p. 44, *Paris*, 1877.

ous individual experiments were performed which departed from the general procedure, although in practically all cases the rate in cc. per gram-hour was computed, and is a fairly accurate basis for comparisons throughout this paper.

Oxygen Consumption in Fish.—A large number of experiments were performed with fish but because of lack of space only striking and typical comparisons from the data can be given here. For comparative purposes abbreviated data from mackerel, experiments on butterfish, scup, dogfish, skate, tautog, sea-bass and flounder have been assembled into table I. It will be noted from this compilation that active fish like the mackerel and butterfish head the list in gram-hour oxygen consumption with an average of 0.725 and 0.301, respectively, and that the comparatively slow moving

TABLE I

Mackerel. July 20. Seven Specimens. 32 Liters Water. Wt. 138 gm.				
MINUTES TIME	O_2 PER L.	TOTAL O_2	O_2 CONSUMED	GM. HR. RATE
0	N 5.22	167.0		
30	3.21	101.6	65.4	0.945
60	2.16	68.7	33.8	.526 Av. .726
Butterfish. July 13. Ten Liters. Wts. 223, 195, 135				
0	N 5.80	58.0		
A 20	2.40	24.0	34.0	0.450
B 40	2.60	26.0	32.0	.246
C 60	2.36	23.6	34.4	.306 Av. 301
Scup. July 12. Seven Liters Water. Wt. 123 gms.				
0	N 5.85	41.0		
60	2.78	19.6	21.4	0.174
Dogfish. July 14. Thirty-two Liters Water. Wt. 425 gms.				
0	N 5.22	167.0		
60	3.80	125.5	46.5	0.109
Skate. July 14. Eight Liters Water. Wt. 227 gms.				
0	N 5.37	43.0		
60	3.02	23.3	19.7	0.087
Tautog. July 30. Sixty-two Liters Water. Wt. 120 gms.				
0	N 5.40	335.0		
7 hours	0.35	22.2	312.8	0.062
Sea Bass. July 30. Eight Liters Water. Wt. 500 gms.				
0	N 5.37	43.0		
60	1.00	8.0	35.0	0.070
Flounder. July 28. Thirty-two Liters Water. Wt. 630 gms.				
0	N 5.50	176.0		
60	4.30	132.2	39.8	0.063

This table shows comparative rate consumption of oxygen in different fishes.

or sluggish fish like the sea-bass and flounder have the lowest gram-hour consumption, being 0.07 and 0.06 respectively.

Although these figures show wide variance at first sight they apparently are well within reasonable limits when compared with limits found to hold for other animals, especially the birds. For example, Schafer[6] in his textbook cites a table (p. 706) where Reiset[7] found the oxygen consumption of the goose to be 0.677 cc. per gram-hour and Regnault and Reiset found in the crossbill a consumption of 10.974.

Some fish show more tolerance to low oxygen tension than others. Among the typical records bearing out this point are selected the two records shown in table II. On July 14, for example, a comparatively small sea-bass weighing 400 grams was placed in eight liters of water, and samples were drawn at definite intervals, the volume being maintained by adding an equal amount at each withdrawal. Under the same conditions a Scup weighing 174 grams was placed in an equal volume and samples were taken at the same intervals. The Scup survived the conditions only two hours, the sea-bass was alive after three hours. During the first thirty minute intervals, the Scup consumed oxygen at the rate of 0.313 gram hours, as against the sea bass' consumption of 0.192, which is about one-third as great.

TABLE II

Scup. July 14. In Eight Liters Water. Wt. 174 gms.				
MINUTES TIME	O_2 PER L.	TOTAL O_2	O_2 CONSUMED	GM. HR. RATE
0	N 5.87	47.0		
30	2.49	19.8	27.2	0.313
60				
90	0.78	0.23	14.73	.089
120	0.91	7.25	0.51	.0058
Dead at the end of 120 minutes				
Sea Bass. July 14. In Eight Liters Water. Wt. 400 gms.				
0	N 5.37	43.0		
30	2.18	17.4	25.6	0.192
75	0.54	18.4	14.1	.047
120	0.63	5.05	1.71	.002
175	0.68	5.44	1.02	.0025
Still alive				

This table shows comparative tolerance of low oxygen content of the two forms.

These data are suggestive in connection with the often observed

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[6] Schafer, Text book of Physiology, vol. 1, p. 706.

[7] Reiset, Ann. de chim. et Phys., Ser. 3, Tome LXIX, p. 129, Paris, 1863.

fact that it is almost impossible to keep mackerel alive in containers in which the water is not frequently replenished, while the sea-bass, tautog, and more especially the flounder, are able to maintain life in water surprizingly low in oxygen content.

To find the influence of light and temperature, three specimens of Scup were placed in 7 liters of water. Specimen "E" was placed in direct sunlight. "A" was placed in the dark room, and "B" was placed in the refrigerator, the temperature of which was 12 ° C. Table III shows the comparative rates of metabolism under the three conditions. It appears that under experimental conditions the oxygen consumption is greatest in the light, is somewhat reduced in the dark, and is considerably reduced in the refrigerator. In this case the reduction in temperature reduced metabolism about 20 per cent. In another series of experiments the temperature was carried to 4° C, and under those conditions the reduction was about 40 per cent. Although under experimental conditions just cited, a noticeable reduction of oxygen consumption was apparent, no diminution of this nature was noticed in night and day rates.

TABLE III

Scup. July 12. In Seven Liters Water. Wt. E, 208 grams. A, 185 grams. B, 122 grams

Minutes Time	O_2 per L.	Total O_2	O_2 Consumed	Gm. Hr. Rate
E 0	N 5.85	41.0		
60	1.27	8.5	32.5	0.156
A 0	N 5.35	42.8		
105	0.66	5.3	37.5	0.115
B 0	N 5.35	42.8		
180	0.92	7.4	35.4	0.091

E. in sunlight. A. in the dark. B. in refrigerator 12°C.
This table shows rate of oxygen consumption in light, dark and cold.

That animals consume oxygen more rapidly in round narrow necked vessels or in tall vessels than in the shallow ones, is indicated by the following typical experiment: On August 4, three series of mackerel of about equal total weight were placed each in 6.3 L. of water; one in a tall McDonald hatching jar; one in an oblong white dish of shallow capacity; and one in a round glass bowl fourteen inches in diameter at the neck surface. After one hour, samples of water were drawn from the three containers and analyzed. In the round necked bowl the fish had reduced the total oxygen content to 1.24 cc. per L., in the tall jar the reduction was to 1.73 cc. per L., while in the shallow dish it had been reduced only to 2.62 cc. per L. By moving about in the shallow dish the fish tend to aërate the water and thus conserve the oxygen content to a considerable degree.

Invertebrates.—Type forms of the various phyla were studied. In the Mollusks were such forms as *Yoldia, Pecten* and *Squid*; among the Arthropods were Hermit and Green and Lady crabs, *Limulus, Crangon,* etc.; in the Echinoderms the Starfish; in the worms were *Rhyncobolus, Nereis, Phascolosoma, Amphitrite* and *Cerebratula*; in the Coelenterates, *Gonionemus* and *Dactylometra, Sagartia* and others. Among the mollusks worked with, the Squid show a comparatively high consumption rate. Two typical records showed that specimen "A" weighing 148 grams, in 8 L. of water

TABLE IV

INVERTEBRATES

Squid. July 16. A in 8 Liters Water. Wt. 148 gms. B. wt. 27 gms.				
MINUTES TIME	O_2 PER L.	TOTAL O_2	O_2 CONSUMED	GM. HR. RATE
0	N 5.80	46.5		
30	1.52	12.3	34.2	0.462
B. 30	3.89	19.4	9.6	0.685
Green Crab. July 9, in Seven Liters Water. Wt. 40 gms.				
0	N 5.96	41.8		
30	5.78	38.8	3.0	0.150
Limulus. July 7, in Eight Liters Water. Wt. 240 gms.				
0	N 5.63	45.2		
20	4.34	33.5	11.7	0.147
45	2.91	21.6	11.9	0.198
65	2.20	15.6	6.0	.060
85	1.62	11.0	4.6	057
Starfish.				
0	C 5.04			
5 hrs.	N 2.04	2.59	4.63	0.020
5 hrs.	D 3.40	4.48	3.03	.018
Worms. July 13, Five Specimens in fingerbowls. Normal 5.80 per L.				
Rhyncobolus 5½ hrs.	N 5.80			
Nereis 5½ hrs.	3.75	2.03	1.16	0.291
Phascolosoma 5½ hrs.	2.04	1.12	2.01	.367
Amphitrite 5½ hrs.	4.46	2.41	0.72	.131
Cerebratula 5½ hrs.	4.22	2.30	0.86	.156
	3.90	2.11	1.02	.187
Jellyfish. *Dactylometra* 750 gms. in Eight Liters Water				
0	N 5.55	44 4		
60	3.60	28.8	15.6	0.020
Sagartia. 4.5 gms. in 545 cc. Water				
0	N 5.69	3.08		
5½ hrs.	1.97	1.08	2.00	0.026

This table shows abbreviated records taken on various type forms of invetebrates showing comparative gram hour oxygen consumption.

consumed 0.462 cc. gram hour, and specimen "B" weighing 27 grams, consumed 0.685 cc. gram hour. Since these forms are very active, such a rate might be expected. The data for *Yoldia* and *Pecten* when they are averaged yield figures of consumption rates in these forms very closely comparable to each other, being 0.224 and 0.265 cc. gram hour, respectively. Five small hermit crabs (*Longicarpus*) weighing 0.6 grams (av.) showed an average consumption of 0.61 cc. gram hour, while an equal number of larger specimens averaging 6.9 grams, gave an average consumption over a five hour period of 0.059 cc. No such marked variability was noted in the case of the green crabs, two typical records showing an average hourly consumption of 0.135 cc. The horseshoe crabs (*Limulus*) showed an average consumption of 0.08 cc. gram hour.

Typical records from starfish show an average consumption rate of 0.019 cc. gram per hour over a five hour period.

Among the Coelenterates studied, the Jelly Fish (*Dactylometra*) seems to maintain a fairly constant rate of oxygen consumption. A typical individual placed in 8 L. of water consumed 0.020 cc. gram hour, for the first hour, 0.019 cc. during the second and 0.016 cc. during the third hour. Specimens of *Sagartia* collectively weighing 4.5 grams, showed an average consumption of 0.026 cc. during a five hour period, while three specimens of *Goneionemus* showed an average hourly consumption of 0.21 cc.

Worms show some variations in rate of consumption. In three series of experiments running five, seventeen and eighteen hours respectively, *Nereis* heads the list with an average consumption of 0.23 cc. gram hour; *Rhyncobolus* with 0.18 cc. and *Phascolosoma* with 0.13 cc.

Table IV brings together a few typical records of various invertebrates for comparative purposes.

SUMMARY

1. Using the Winkler method it is possible to quantitatively determine with fair accuracy, the oxygen consumed by marine forms in given time and under given conditions.

2. Oxygen consumption in different species of fish when reduced to the cc. gram hour basis shows fluctuations within comparatively wide limits. Mackerel (0.726) and Scup (0.301) have a higher metabolic rate than the more sluggish fish, flounder (0.063), tautog (0.062) or sea-bass (0.070). These limits of fluctuations in the fish, however, are not any greater than those reported for the birds (Goose, 0.677) (Crossbill, 10.974).

3. In a test case, lowering the temperature (scup) to 12 ° C,

reduced oxygen consumption 21 per cent, further cooling to 4 ° C. reduced consumption about 40 per cent.

4. When it was in the light (scup) a test animal showed average hourly consumption of 0.156 cc. gram hour, when it was in the dark this was reduced to 0.115, showing a slowing of metabolism in the dark.

5. Resistance to low oxygen is marked in some forms; dogfish, tautog, flounder, etc., live in water the oxygen content of which will not sustain life in mcakerel, butterfish and scup.

6. Fish confined in containers of constricted surface area but of equal capacity show more complete utilization of the oxygen than those in wide shallow dishes, probably due to aëration of the water in the latter by movement of the animals.

7. Among the invertebrates, the squid (mollusk) (0.685-0.516) shows a comparatively high rate of consumption, the echinoderms (starfish, 0.019) and the coelenterates (*Dactylometra*) (0.020-0.016) show a low rate; the worms are between these extremes (0.23-0.14) in their rate consumption.

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