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6. This work was supported by grant No. 15890 from the National Science Foundation. The technical assistance of Virginia Findeisen is gratefully acknowledged.

28 June 1962

Metabolic Requirements for the Swimming Activity of Three Antarctic Fishes

Abstract. The logarithm of the amount of oxygen consumed per unit swimming velocity in meters per minute for steadily swimming antarctic fishes at freezing temperatures is of the same order as the rate for temperate species at their lower temperature ranges. In contrast to temperate fishes, the antarctic fishes have their greatest swimming activity around −1.8°C and a level of no excess activity at about +2°C.

Field and laboratory observations of the swimming behavior of several fishes in McMurdo Sound have indicated that species of the genus *Trematomus* (family Nototheniidae) are generally sluggish. Demersal *Trematomus bernacchii* (*1*) and *T. centronotus* could not be induced to swim in a rotating, annular metabolism chamber which had been successfully utilized for arctic fish (*2*) and temperate fish (*3*). Demersal *T. hansoni* and *T. loennbergi* occasionally could be induced to swim slowly; pelagic, plankton-feeding *T. borchgrevinki* would swim steadily in the chamber. These species live in waters that are continuously at the freezing temperatures of −1.9° to −1.8°C. However, none of them would swim consistently at temperatures much higher than the natural temperatures, and at the highest laboratory temperatures to which they would become acclimated—about +2°C—they tended to cease swimming. Because this type of behavior contrasts sharply with temperate fishes for which similar data are available, metabolic requirements per unit swimming activity of the three swimming species were investigated.

The multiple regression technique (*2–4*) of relating oxygen consumption rates (Y = log milligrams of O_2 consumed per hour) as a measure of metabolism to the body weight (X_w = log grams), to the temperature (X_t = °C) at which the fish have been acclimated, and to the swimming velocity (X_s = m/min) has proved useful in the form:

$$Y_e = a + b_w X_w + b_t X_t + b_s X_s$$

In this form Y_e is the estimated logarithm of the number of milligrams of O_2 consumed per hour, b_w is the partial regression coefficient of increase in Y_e (usually about 0.8) for constant X_t and X_s, b_t is the increase in Y_e per degree increase in temperature (usually about 0.02 to 0.06) for constant X_w and X_s, and b_s (the respiration-swimming coefficient) is the increase in Y_e per unit swimming velocity in meters per minute for a constant X_w and X_t, and a is a constant whose value depends in part upon the degree of "cold adaptation" (*1, 2, 4, 5*).

In Table 1 are b_s values calculated over various experimental temperature and swimming velocity ranges as indicated for the three antarctic species. The usefulness of the b_s log milligrams of O_2 consumed per hour per unit swimming velocity in meters per minute is that energy expenditures are expressed in units independent of weight and absolute swimming velocity. The 1960–61 data are for fish acclimated at −1.8°C for a period of 48 hours before O_2 consumption rates were measured; 1961–62 data are for 5-day acclimation periods. Temperatures were raised at the rate of no more than 1.0°C per 24-hour interval, with 2- or 5-day acclimation periods at each of the successively higher temperatures before the respective O_2 consumption rate determinations. Among the fish that would swim in the chamber, pelagic *Trematomus borchgrevinki* would swim consistently for determinations over at least 10 minutes while the more sedentary *T. hansoni* and *T. loennbergi* would swim fairly steadily for 45-minute determinations.

From published data as indicated in Table 1, respiration-swimming coefficients can be calculated for a few diverse temperate and arctic fishes by taking the difference between the logs of the O_2 consumption rates at resting and at active conditions and dividing the difference by the swimming rate in meters per minute.

The maximum swimming activity for temperate species appears to be at temperatures somewhat below the seasonal maxima to which the species would normally be subjected (*6*). For the antarctic species the maximum tends to be at freezing temperatures.

For the 1960–61 *T. borchgrevinki*: 44 of 46 fish (−1.8° to −1.7°C) swam at an average velocity of 6.1 m/min; 17 of 22 (−0.8°C), at 6.1 m/min; 19 of 24 (+0.8° to +0.9°C), at 5.9 m/min; and 1 of 20 (+1.8°C), at

Table 1. Respiration-swimming coefficients with swimming velocity and temperature ranges for three antarctic species and for various temperate and arctic species.

Species	Temperature (°C)	Swimming rate (m/min)	Respiration-swimming coefficient	Source of data
Antarctic *Trematomus* spp:				
T. borchgrevinki; N = 112; all fish	−1.8 to +1.8	0–13.5	0.0307	Dec. 1960–Jan. 1961
T. borchgrevinki; N = 92; active swimming range	−1.8 to +0.8	0–13.5	.0345	Dec. 1960–Jan. 1961
T. borchgrevinki; N = 46; "natural" temp. range	−1.8 to −1.7	0–13.5	.0243	Dec. 1960–Jan. 1961
T. borchgrevinki; N = 63; "natural" temp. range	−1.8 to −1.7	0–11.4	.0406	Nov. 1961
T. loennbergi; N = 30	−1.8 to +2.4	0– 4.4	.1124	Jan. 1962
T. hansoni; N = 35	−1.8 to +2.2	0– 2.8	.0660	Jan.–Feb. 1962
Other species:				
Coregonus sardinella	8.3 to 10.8	1.0–10.0	.0243	Arctic Summer (*2*)
Oncorhyncus keta; males; Amur R. migration	12	80	.0111	(*9*)
O. keta; females; Amur R. migration	12	80	.0113	(*9*)
Salvelinus naymacush; 1-yr stock	16	31.4	.0227	(*10*)
S. naymacush; 2-yr stock	16	38.7	.0202	(*10*)
S. naymacush; 1-yr stock	9	21.3	.0402	(*10*)
S. naymacush; 2-yr stock	9	28.3	.0368	(*10*)
S. fontinalis	15	44.2	.0143	(*11*)
S. fontinalis	5	23.2	.0320	(*11*)
Lepomis macrochirus	22.0 to 26.5	1.0–14.4	.0138	Summer (*3*)
L. macrochirus	11.0 to 22.4	0–14.3	.0142	Autumn (*3*)
L. macochirus	8.2 to 12.0	0– 9.0	.0427	Winter (*3*)
L. macrochirus	14.0 to 23.0	0–12.5	.0250	Spring (*3*)
Trachurus trachurus	20	0–60	.0125	(*9*)
Carassius auratus	25	30.5	.0088	(*7*)
C. auratus	5	14.6	.0291	(*7*)

0.5 m/min. For the November 1961 *T. borchgrevinki*, all 63 fish swam at −1.8° to −1.7°C at an average of 7.3 m/min. The difference between the −1.8° to −1.7°C Table 1 data for the two seasons is only partly explained by the differences in acclimation times.

For *T. hansoni*: 3 of 8 (−1.8° to −1.7°C) swam at an average of 2.1 m/min; 1 of 8 (−0.8°C), at 2.4 m/min; none of 7 (+0.2° to +0.4°C) swam; 1 of 6 (+1.2°C) swam at 1.4 m/min; and none of 5 (+2.1° to +2.2°C) swam.

For *T. loennbergi*: 3 of 11 (−1.8° to −1.7°C) swam at an average of 3.5 m/min; 3 of 8 (−0.9° to −0.6°C), at 3.3 m/min; 3 of 4 (+0.2° to +0.3°C), at 3.2 m/min; 2 of 5 (+1.1° to +1.3°C), at 3.1 m/min; and the single fish at +2.4°C did not swim. The high b_s of 0.1124 appears to be a consequence of "labored" swimming activity.

Thus both the propensity to swim and the average swimming rate tend to decline with temperature over a very narrow temperature range. The "level of no excess activity" (*7*) with O_2 at near-saturation appears to be at about +2°C for the three antarctic species. By contrast, the tabulated data for the more eurythermal temperate species indicate that these fishes have lower swimming rates at lower temperatures. Possibly because the water viscosity increases greatly with decreasing temperature, the respiration-swimming coefficients tend to be larger at the lower temperatures and of the same order for both temperate and antarctic species (*8*).

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5 June 1962

Alveolar Pathways during 90-Foot, Breath-Hold Dives

Abstract. The gas tensions of mixed expired and alveolar air were measured at various depths during descent and ascent. A reversed carbon dioxide gradient from the lungs into the blood was demonstrated at the 50-foot depth. At 90 feet, 45 percent of the pre-dive carbon dioxide content of the lungs had disappeared. There was no indication of a reversed oxygen gradient during ascent.

During the training of submarine crews in submarine escape procedures, such as "free or buoyant ascent," instructors at the escape training tank frequently hold their breath under water and perform "skin" dives to depths as great as 90 feet. The ascent is carried out by climbing up a line. (These diving maneuvers are similar to those practiced by sponge and pearl divers.) The escape tank at the New London Submarine Base afforded us an opportunity to study the pulmonary gas exchange during this type of diving.

In previous investigations (*1*, *2*) alveolar gas samples were obtained from divers at the surface, at 90-foot depth, and after their return to the surface of the escape training tank. Results showed that a considerable amount of the predive CO_2 content in the lungs had disappeared during descent to 90 feet, thus indicating a transfer of CO_2 from the lungs to the blood. On the basis of theoretical equations, DuBois (*3*) had predicted such changes in pulmonary gas exchange during diving. They were subsequently confirmed in simulated breath-hold dives in dogs (*4*) and recently in men (*5*). Our report presents, for the first time, detailed data on alveolar pathways during breath-hold dives and gives direct evidence of the existence of a reversed CO_2 gradient during descent.

The experiments were carried out with an experienced diver who was well trained as a subject in respiratory experiments and whose lung volumes had been determined repeatedly. Prior to the descent the diver exhaled to residual volume and then inhaled 4 liters from a spirometer. After reaching a predetermined stopping point, he exhaled the major part of his expiratory volume through a mouth-piece into the first bag used for the collection of mixed expired air; he exhaled the remainder into a second bag used to collect "alveolar air." (The latter usually contained 10 to 20 percent of the total expiratory volume.) The bags were brought to the surface. Gas samples from the bags were collected in mercury tonometers and the volumes of the bags were measured. Gas analysis was carried out in duplicate with a Scholander 0.5 gas analysis apparatus. The CO_2 and O_2 content (STPD) in the lungs at various depths was calculated from the measured gas tensions and volumes of mixed expired and alveolar air, the known volume of residual air, and the total dry gas pressure in the lungs.

Results plotted in the O_2–CO_2 diagram show the alveolar pathways during natural breath-hold dives to a 90-foot depth (Fig. 1). The resting alveolar pCO_2 of 40 mm-Hg was lowered to 29.5 mm-Hg by the inhalation of 4 liters of air. The alveolar pO_2 increased correspondingly. During descent, the rising ambient pressure compresses the lungs and the alveolar gas tensions are quickly elevated. At 25 feet, alveolar pCO_2 reached 46 mm-Hg. The normal "virtual" venous (oxygenated venous blood) pCO_2 is 48 to 50 mm-Hg, which corresponds to the crossover point between CO_2 elimination and reabsorption (Fig. 1). At this point, CO_2 is already transferred from the lung alveoli into the pulmonary capillary blood, a condition which is indicated by the disappearance of the normal gradient between CO_2 tensions in mixed expired and alveolar air. At 50 feet, pCO_2 in mixed expired air is 6 mm-Hg higher than the alveolar pCO_2. At 90 feet, only mixed expired samples could be obtained because of the small lung volume. However, it can be assumed that under these conditions mixed expired air and alveolar gas tensions have reached an equilibrium. In spite of the large ambient pressure increase, there is little change in the measured alveolar

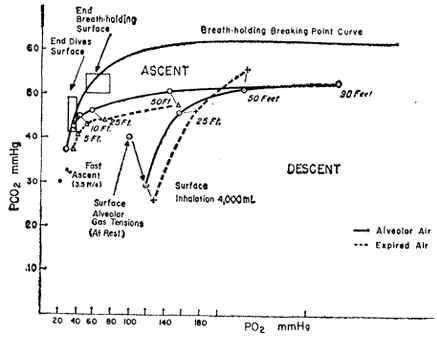

Fig. 1. Alveolar pathways during breath-holding dives to 90 feet showing reversed CO_2 gradient. At 50 feet pCO_2 mixed expired air is 6 mm-Hg higher than pCO_2 "alveolar air." Surface breath-holding breaking point curve drawn for comparison with diving breath-holding curve. End dive alveolar pCO_2 decreased with increasing rate of ascent reaching 30 mm-Hg at 3.5 ft/sec.