Oxygen consumption of the lobster, *Homarus americanus* Milne-Edwards

DONALD W. MCLEESE

Biological Station, St. Andrews, New Brunswick, Canada

KURZFASSUNG: **Sauerstoffverbrauch des Hummers *Homarus americanus* Milne-Edwards.** Bei einer Gruppe von 25 Hummern wurde der Sauerstoffverbrauch in Dauerfluß-Respirometern gemessen. Bei 10° C erwies er sich als im wesentlichen konstant über einen Bereich der Sauerstoffkonzentration im umgebenden Wasser von 1,0 bis 8,5 mg/l. Bei Gruppen von 35 und 50 Hummern, welche bei 15° C getestet wurden, nahm der Sauerstoffverbrauch jedoch mit fallender Sauerstoffkonzentration etwas ab. Anstieg der Individuenzahl pro Raumeinheit ("crowding") führte zu steigender Bewegungsaktivität und zu erhöhtem Sauerstoffverbrauch. Nahrungsaufnahme verursachte fast eine Verdoppelung des Sauerstoffverbrauchs. Kleine Individuen verbrauchen pro Gewichtseinheit mehr Sauerstoff als große. In manometrischen Respirometern stieg der Sauerstoffverbrauch bei hohen Sauerstoffkonzentrationen im umgebenden Wasser mit der Temperatur. Bei 6° bis 25° C war der Sauerstoffverbrauch in der Luft wesentlich geringer als im Wasser.

INTRODUCTION

Considerable information on oxygen consumption has been reported for the European lobster *(Homarus vulgaris)* by THOMAS (1954) and by BRAMSNAES & BOËTIUS (1953). Information for the American lobster *(Homarus americanus)* is scarce. AMBERSON et al. (1924) showed total oxygen consumption for only one lobster of unstated weight at one temperature. BOSWORTH et al. (1936) gave a few figures for one lobster at 15° C and for two others at 22° C. To provide additional information for the American lobster, oxygen consumption was measured in relation to various ambient oxygen concentrations and in relation to size and temperature. Oxygen consumption in air was measured in relation to temperature.

MATERIALS AND METHODS

Test animals

A total of 244 vigorous, hard-shelled lobsters of both sexes, ranging in weight from 0.9 to 12,300 grams (g), were used in this study. Of this total, 226 within the limited size range of 380 to 520 g were used in most of the experiments. Fifteen

smaller (0.9 to 305 g) and 3 larger lobsters (1,764 to 12,300 g) were used only in a size effect test. All were maintained in the laboratory in tanks supplied with flowing, aerated sea water.

Thermal acclimation

The lobsters were acclimated as described by McLeese (1956). They were kept at a constant temperature for three or more weeks preceding a test at the same temperature. Temperatures of 6°, 10°, 12°, 15°, 20° and 25° C were usually maintained within ± 0.3° C with occasional fluctuations of ± 1° C. The lobsters were not fed during the acclimation period. This treatment seems reasonable since Thomas (1954) found that starvation over a 4-week period had no noticeable effect on the rate of oxygen consumption of the European lobster.

Routine oxygen consumption

The animals were acclimated at the test temperature to eliminate effects of temperature change. There was a delay after the animals were placed in the respirometers before measurements were made, to overcome effects of handling. The respirometers were darkened either with black covers (continuous-flow respirometers) or by keeping them in subdued light (manometric respirometers).

By reducing or eliminating these stimuli, the individual lobsters were routinely active, a level of activity which includes spontaneous activity. The rate of oxygen consumption of these lobsters was the routine rate.

Oxygen consumption at various oxygen concentrations

Continuous-flow respirometer for groups. A continuous-flow respirometer described by Saunders (1963) was used to measure oxygen consumption of groups of lobsters at various oxygen concentrations. In brief, the animal chamber was a cylindrical fibreglass tank (91.5 cm diameter and 61.0 cm high) sealed from the atmosphere with a floating plywood cover. Mixing within the chamber was accomplished with a submersible pump.

Lobsters were placed in the respirometer, and measurements were begun 7 days later. During the pre-experimental period the water flow was adjusted to maintain ambient oxygen levels above 80% air saturation. Thereafter, flows were adjusted to give a variety of ambient oxygen concentrations. After the flow was adjusted, a minimum period of 8 hours was allowed for equilibration before the dissolved oxygen concentrations of the inflow and of the outflow water were determined. Then the difference in the readings over a period of one hour or more during which the readings remained nearly constant was used in calculating oxygen consumption in mg/kg body weight/hour.

A group of 25 lobsters (11.4 kg) was kept in the respirometer at 10° C for a

total of 31 days. During this period, 1 weak and 1 dead lobster were replaced with healthy ones. Another group of 50 (22.7 kg) was kept in the respirometer at 15° C for a total of 32 days during which time 7 dead, 4 weak and 2 others that had laid eggs while in the respirometer were replaced. Thirty-five (15.9 kg) from the group of 50 were retained in the respirometer for an additional 21 days during which 5 dead were replaced. To determine the effect of feeding on oxygen consumption, the group of 35 was fed 35 herring (605 g) on the 50th day in the respirometer. Oxygen consumption was determined at intervals over the following 3 days.

Continuous-flow respirometer for individuals. A small respirometer of the continuous-flow type described by SAUNDERS (1962) was used to measure routine O_2 consumption of individual lobsters at various oxygen concentrations. Observations were begun one day after the lobster was placed in the respirometer, and a minimum period of 4 to 5 hours was allowed for equilibration after a change in the rate of water flow before observations were made. Lobsters were kept in the respirometer for 5 to 15 days.

To extend the size range tested, 14 lobsters within the weight range 16 g to 305 g and 2 weighing about 1,800 g were used. These were held in the individual respirometer for 1 day before determining oxygen consumption at a high ambient oxygen concentration. The group respirometer was used for the 12.3 kg lobster. Mrs. D. H. STEELE measured the oxygen consumption of the 0.9 g lobster in a volumetric microrespirometer similar to one described by SCHOLANDER (1942). All dissolved oxygen determinations were made by the ALSTERBERG modification of the WINKLER method (American Public Health Association 1960).

Oxygen consumption at various temperatures

Manometric respirometer. Manometric apparatus similar to that depicted by FRY (1957) was used to determine oxygen consumption of individual lobsters at various temperatures. The apparatus was immersed in a constant temperature bath of sea water to maintain the desired temperature. A wide form porcelain crucible, size 00, was filled with a CO_2 absorbent ("Ascarite" 8 to 20 mesh, A. H. Thomas Co., Philadelphia, Pa.) and suspended in the air space during some tests at each temperature. Apparently CO_2 was effectively buffered by the sea water in the respirometer because no colour change was detected in the CO_2 absorbent. Checks at each temperature showed no appreciable change in pH during experiments in the absence of the CO_2 absorber. The ambient oxygen concentration remained high during the tests. Water samples taken from the animal chamber before and after experiments at each temperature showed that dissolved oxygen content averaged 96% of air saturation at the start and 85% at the finish of the tests.

A lobster was placed in the respirometer at least 12 hours before the animal chamber was closed. The total amount of oxygen injected into the closed system over a 3- or 6-hour period was used to calculate oxygen consumption.

Oxygen consumption in air

A simplified manometric apparatus was used to determine oxygen consumption in air in relation to temperature. Filter paper saturated with sea water was placed in the bottom of the plexiglass animal chamber and a CO_2 absorber was suspended from the cover. Blank runs at each temperature showed no oxygen consumption. Relative humidity was 100 % at 6°, 10°, 15° and 20° C and 85 % at 25° C. Within an hour, air temperature in the apparatus equilibrated with that of the water bath after which the chamber was closed and measurements were begun. The total amount of oxygen injected into the closed system over a $3^1/_2$- to 4-hour period was used to calculate oxygen uptake.

RESULTS AND DISCUSSION

Oxygen concentration

The results for 2 individuals and for the group of 25 lobsters at 10° C are shown in Figure 1. The rate of consumption by the two individuals increased over the range of concentrations from 2.3 to 9.0 mg O_2/l (Fig. 1A). The rate of consumption by the group was practically constant at an average of 28.3 mg/kg/hr at concentrations of 1.0 to 8.6 mg O_2/l (Fig. 1B).

The results for 4 individuals and for groups of 35 and 50 lobsters at 15° C are shown in Figure 2. The rate of oxygen consumption by the individuals increased as

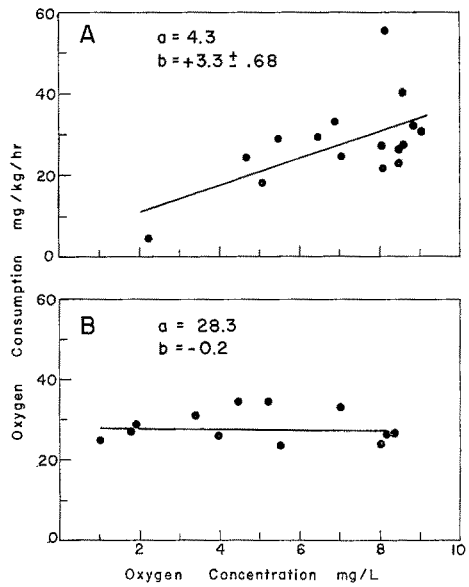

Fig. 1: Routine oxygen consumption at various ambient oxygen concentrations at 10° C. A: Two individuals, 478 g and 457 g; *a* is intercept, *b* is slope with 95 % confidence limits. B: A group of 25 lobsters ranging in weight from 380 to 520 g (total weight 11.4 kg)

the ambient oxygen concentration increased (Fig. 2A). Similarly the rates of consumption by the groups of 35 and 50 lobsters were proportional to ambient oxygen concentration (Fig. 2B and 2C). The slopes of the regression lines for the two groups were not significant.

When the activity of lobsters was increased by crowding, the general rate of oxygen consumption was higher. The rates of consumption read from the regression lines of Figure 2 at 5 mg/l for individuals and groups of 35 and 50 are 29, 38 and 55 mg/kg/hr respectively.

The rate of oxygen consumption for individual European lobsters at 5 mg O_2/l is about 65 mg/kg/hr (derived from Fig. 4 of THOMAS 1954), which is appreciably higher than that found for the group of 50. The slope of his line relating consumption

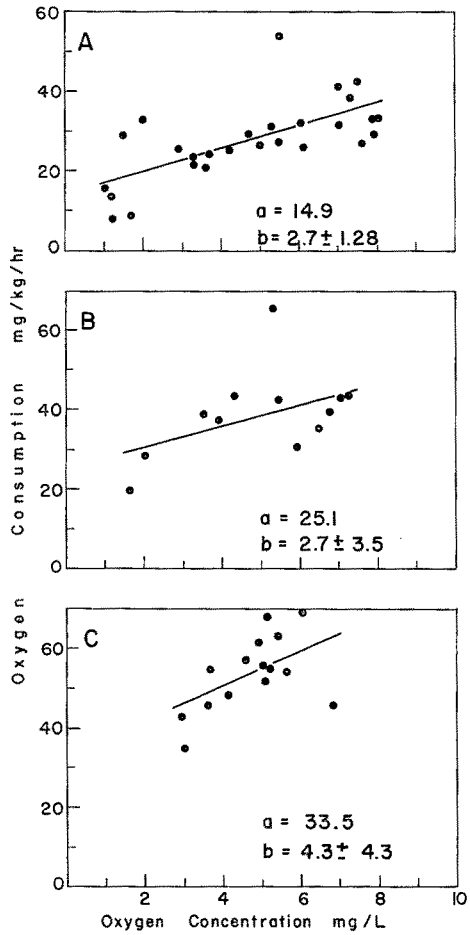

Fig. 2: Routine oxygen consumption at various ambient oxygen concentrations at 15° C. A: Four individuals, 520 g; 468 g; 489 g and 448 g; *a* is intercept of regression line, *b* is slope with 95 % confidence limits. B: A group of 35 lobsters (total weight 15.9 kg). C: A group of 50 lobsters ranging in weight from 380 to 520 g (total weight 22.7 kg)

and concentration (cf. Fig. 4, THOMAS 1954) was about 12.2 or about 4.5 times greater than the slope of 2.7 found in the present study (Fig. 2A). The main difference between the two sets of data may be related to different levels of activity of the animals. It appears likely that THOMAS' measurements were made with lobsters that were more active. Most of his experiments were done while the oxygen concentration was decreasing and soon after a temperature change. For some tests temperature was changed daily; for the others, a 10-minute adjustment period was allowed between temperature changes. In some tests, the lobsters were held by a rubber disk around the first abdominal segment, and in some others a cowl was placed over the anterior half of the cephalothorax. It is possible that the rate of oxygen consumption determined by THOMAS approached the maximum (active) rate "... the level which will permit the highest continued level of activity" (FRY 1957). According to FRY (1947), respiratory dependence is well expressed over a wide range of concentrations only when animals are respiring at their active rate.

FRY (1957) points out that the restriction imposed on the active rate by a decrease in concentration means a restriction of activity. Assuming that Figure 4 of THOMAS (1954) represents active oxygen consumption, the lines for individuals and groups from Figure 2 should intersect the active line where activity is limited by

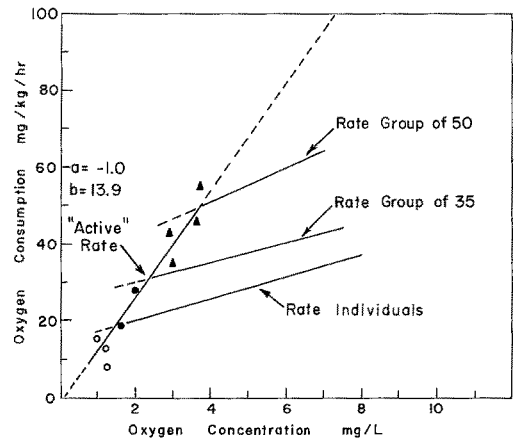

Fig. 3: "Active" oxygen consumption by groups and individual lobsters at 15° C at oxygen concentrations where consumption is probably restricted (dependent). The data are for concentrations below 3.6 mg/l for 50 lobsters ▲; below 2.2 mg/l for 25 ●; below 1.2 mg/l for individuals o, taken from Figure 2. *a* is intercept and *b* is slope of regression line. The lines for routine consumption from Figure 2 are superimposed on the figure

concentration. In the present case they should intersect at about 1.2 mg O_2/l for individuals and at 2.2 and 3.6 mg O_2/l for groups of 35 and 50 respectively.

Values for oxygen consumption from Figure 2 at and below these concentrations are plotted together in Figure 3 to represent active oxygen consumption at concentrations that may be limiting the rate. The regression line through the data approximates the position and slope of the line from Figure 4 of THOMAS (1954). The lines from Figure 2 are superimposed on Figure 3. The effects of different levels of crowding

suggested by this figure are similar to differences found between active and resting fish (SHEPARD 1953, FRY 1957).

McLEESE (1956) found the lethal level of oxygen (50 % mortality in 48 hours) for lobsters acclimated and tested at 15° C to be 0.83 mg O_2/l. The consumption of 10 mg/kg/hr read off the "active" curve of Figure 3 at the asphyxial concentration (0.83 mg O_2/l) is an estimate of the basal metabolic rate for lobsters at 15° C. This study provides the first clear indication that the oxygen requirements of lobsters differ depending on the level of crowding and the activity resulting from this crowding.

Feeding

The rates of oxygen consumption by the group of 35 lobsters before and after feeding are presented in Table 1. The rate just prior to feeding was 41.7 mg/kg/hr. This rate was determined after the group of lobsters had been in the respirometer without food for 50 days. By one hour after they were fed, the rate had increased to 72.5 mg/kg/hr, and this increased rate was maintained over the following 3 days. BRAMSNAES & BOËTIUS (1953) report similar results for European lobsters.

Table 1

Rates of oxygen consumption for a group of 35 lobsters before and after being fed at 15° C

Time before and after feeding hr	Ambient O_2 mg/l	Oxygen consumption mg/kg/hr
1 before	5.4	41.7
1 after	4.4	72.5
3 „	4.3	78.0
6 „	4.2	76.0
10 „	4.3	73.5
26 „	4.3	74.2
53 „	4.4	71.2
73 „	4.2	76.0

Weight

The oxygen consumption of lobsters ranging in size from 0.9 g to 12,300 g is presented in Table 2 and illustrated in Figure 4. The regression line was fitted to the data by the method of least squares. The slope is 0.88, indicating that small lobsters use more oxygen per unit weight than large ones. The slope of this relationship is within the general range for fish (FRY 1957, WINBERG 1956).

Temperature

Oxygen consumption by individual lobsters at high ambient oxygen concentrations was determined for individual lobsters (380–520 g) at temperatures of 12°, 15°, 20° and 25° C using the manometric respirometer. The results are summarized in

Table 2

Oxygen consumption (mg/lob/hr) and rate of oxygen consumption (mg/kg/hr) at 15° C for lobsters ranging in weight from 0.9 g to 12,300 g

Weight lobster g	Ambient O_2 conc. mg/l	Oxygen consumption mg/lobster/hr	Rate of O_2 consumption mg/kg/hr
.9	–	0.054	60.0
16	4.2	1.2	75.0
45	7.4	3.2	71.1
47	8.2	2.4	51.1
48	7.0	4.4	91.5
50	7.5	4.7	94.0
145	7.4	12.6	87.0
157	6.9	9.9	63.0
160	6.4	13.0	81.4
162	7.2	7.9	48.7
169	7.1	11.7	69.2
175	5.9	15.0	85.7
203	7.2	8.3	40.9
208	6.6	10.2	49.0
302	6.9	14.0	46.5
448	7.0	14.7	32.8
468	7.0	16.4	35.0
489	7.0	16.0	32.7
520	7.0	16.5	31.7
1,764	6.0	87.0	49.2
1,898	6.0	98.5	51.9
12,300	7.4	260.0	21.1

Table 3 and presented in Figure 5. The regression line was fitted by least squares. Average oxygen consumption increases with temperature at a constant rate between 12° and 25° C.

The rate of 39.5 mg/kg/hr at 15° C from this series of tests agrees closely with the rate of 35–37 mg/kg/hr for similar-sized individuals at corresponding oxygen concentrations in the continuous flow apparatus (cf. Fig. 2A at 6.9–7.7 mg/l).

Table 3

Average oxygen consumption of lobsters (mg/kg/hr) at various temperatures at high concentrations of oxygen

Acclimation and test temperature °C	Average O_2 consumption mg/kg/hr	Standard deviation	No. lobsters tested
12	30.6	*9.8*	14
15	39.5	*11.3*	26
20	56.0	*19.1*	21
25	61.7	*25.0*	21

Thomas (1954) found a similar relationship between rate of oxygen consumption and temperature for the European lobster. However, his values which range from about 35 to 110 mg/kg/hr at 6° to 18° C respectively (derived from Fig. 7 of Thomas

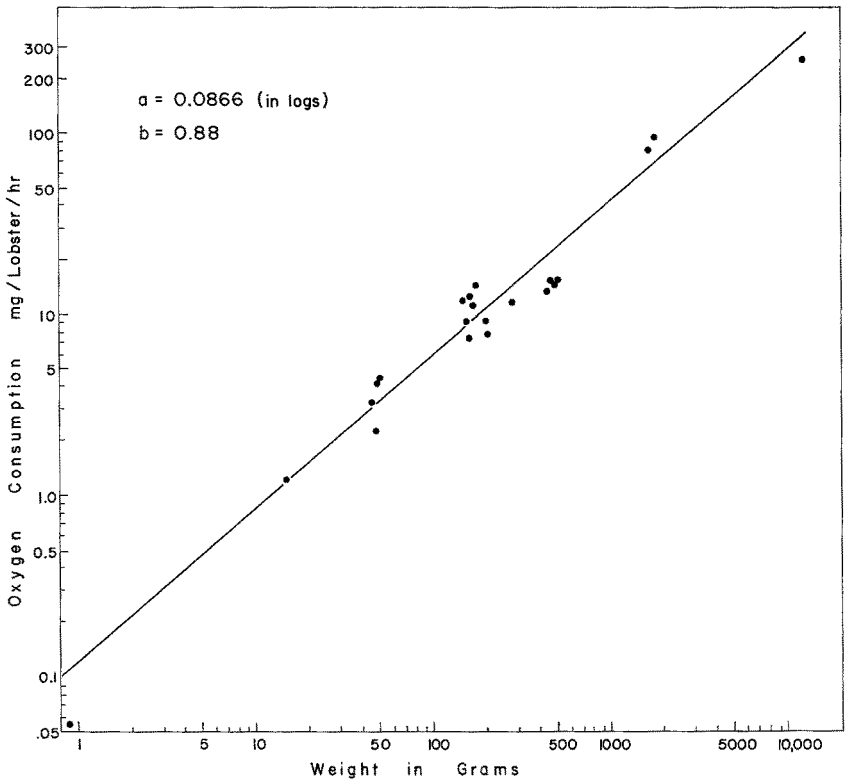

Fig. 4: Relationship between size and routine oxygen consumption plotted on logarithmic scales

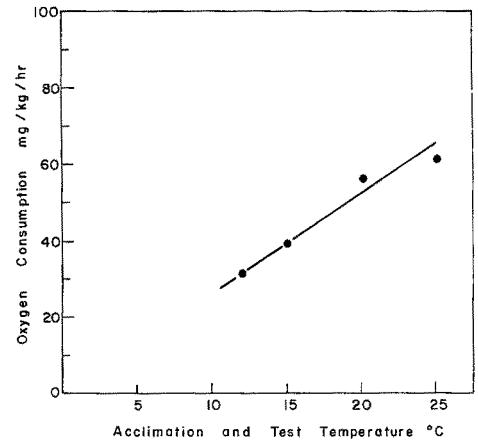

Fig. 5: Average routine oxygen consumption of lobsters at high oxygen concentrations in relation to temperature

at 5 ml O_2/l) are approximately double those for the American lobster. As argued previously, it is likely that different levels of activity account for the major difference in the results.

Oxygen consumption in air

Rates of oxygen consumption by individual lobsters in air are summarized in Table 4 and illustrated in Figure 6. The curve was drawn by eye. Oxygen consumption in air is considerably less than in water as comparison of Figure 5 and 6 clearly shows.

Table 4

Average oxygen consumption of lobsters (mg/kg/hr) in air at various temperatures

Acclimation and test temperature °C	Average O_2 consumption mg/kg/hr	Standard deviation	No. lobsters tested
6	12.0	*1.9*	8
10	17.2	*2.0*	7
15	14.9	*11.3*	8
20	11.4	*4.6*	12
25	1.6	*3.0*	8

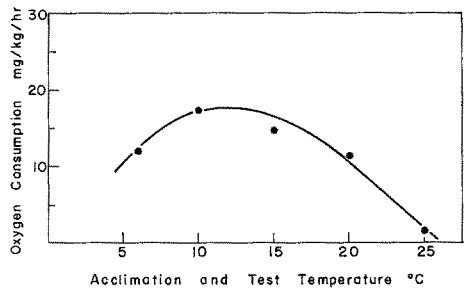

Fig. 6: Average oxygen consumption of lobsters in air in relation to temperature

The low rates in air probably result from inefficiency of the respiratory mechanism in air. Even though the gills remain moist, they are not supported effectively in air, and the respiratory area is probably reduced. In addition, ventilation by the action of the scaphognathites is probably inefficient in air. THOMAS (1954) reported similar low rates of oxygen consumption for the European lobster in air.

SUMMARY

1. Oxygen consumption by a group of 25 lobsters was essentially constant over a range of ambient oxygen concentrations from 1.0 to 8.5 mg/l. Consumption by groups of 35 and 50 lobsters at 15° C decreased as the concentration decreased.
2. Oxygen consumption by individuals at 10° and 15° C increased as the oxygen concentration increased.
3. Oxygen consumption increased as activity increased with crowding.
4. Oxygen consumption almost doubled after feeding.

5. Oxygen consumption per unit weight decreased with increasing size.
6. The average rate of oxygen consumption by individuals doubled over the temperature range 12° to 25° C.
7. Oxygen consumption in air at 6° to 25° C was much less than in water.

ACKNOWLEDGMENTS

The valuable assistance of R. D. Lisk and Elizabeth Quance, who carried out the experiments, is gratefully acknowledged. Appreciation is expressed to Dr. R. L. Saunders for making his continuous-flow respirometers available. Appreciation is expressed also to Dr. D. G. Wilder for advice and helpful criticism.

LITERATURE CITED

Amberson, W. R., Mayerson, H. S. & Scott, W. J., 1924. The influence of oxygen tension upon metabolic rate in invertebrates. *J. gen. Physiol.* **7**, 171–176.

American Public Health Association, 1960. Standard method for the examination of water and waste water including bottom sediments and sludges. 11th ed. *Am. Publ. Health Ass., Inc., New York*, 626 pp.

Bosworth, M. W., O'Brien, H. & Amberson, W. R., 1936. Determination of the respiratory quotient in marine animals. *J. cell. comp. Physiol.* **9**, 77–88.

Bramsnaes, F. & Boëtius, J., 1953. Storage of live lobsters. *Medd. Fisk. Minist. Forsøgslab.*, November 16 pp. [*Fish. Res. Bd Can. Transl. Ser.*, No. 63.]

Fry, F. E. J., 1947. Effects of the environment on animal activity. *Univ. Toronto biol. Ser.*, No. 55 (Publ. Ontario Fish. Res. Lab., No. 68), 62 pp.

— 1957. The aquatic respiration of fish. *In:* The Physiology of Fishes, edited by M. E. Brown. Acad. Press Inc., New York, Vol. 1, 1–63.

McLeese, D. W., 1956. Effects of temperature, salinity and oxygen on the survival of the American lobster. *J. Fish. Res. Bd Can.* **13**, 247–272.

Saunders, R. L., 1962. The irrigation of the gills in fishes. II. Efficiency of oxygen uptake in relation to respiratory flow activity and carbon dioxide concentration. *Canad. J. Zool.* **40**, 817–862.

— 1963. Respiration of the Atlantic cod. *J. Fish. Res. Bd Can.* **20**, 373–386.

Scholander, P. F., 1942. Volumetric microrespirometers. *Rev. Sci. Instrum.* **13**, 32–33.

Shepard, M. P., 1955. Resistance and tolerance of young speckled trout *(Salvelinus fontinalis)* to oxygen lack, with special reference to low oxygen acclimation. *J. Fish. Res. Bd Can.* **12**, 387–446.

Thomas, H. J., 1954. The oxygen uptake of the lobster (*Homarus vulgaris* Edw.). *J. exp. Biol.* **31**, 228–251.

Winberg, G. G., 1956. Rate of metabolism and food requirements of fishes. *Nauchnye Trudy Belorusskovo Gosudarstvennovo Universiteta imeni V. I. Lenina Minsk*, 253 pp. [*Fish. Res. Bd Can. Transl. Ser.*, No. 194.]

Discussion following the paper by McLeese

Schlieper: Have you tried to adapt *Homarus* for longer periods to low oxygen tensions?

McLeese: Experiments were done with low oxygen concentrations; after reaching equilibrium, these were maintained for at least one hour, but sometimes for as long as 18 hours. The animals were not, however, acclimated to low O_2 prior to this.

WELLS: Did you find any effect of the moulting cycle on oxygen consumption?

McLEESE: No. These experiments were done with non-moulting, hardshelled lobsters.

OHLE: Can you please give us more information about the technique you have used in estimating oxygen tension in air?

McLEESE: I have used methods somewhat similar to the SCHOLANDER type of apparatus – a very large respirometer kept moist on the inside and connected by a manometer to an O_2 syringe – and as the lobster used some oxygen, additional oxygen was injected to keep the equipment in balance, and the amount of oxygen that they had used was measured from the syringe. The lobsters themselves were kept in moist air with the CO_2 absorber within the chamber.

PROSSER: Can you indicate in more detail how you separated active and standard metabolism?

McLEESE: In all experiments the animals were given time to settle and to acclimate to the temperature; they were not fed and kept in darkness. Rate called routine would change with changes in activity. Therefore routine is always somewhat higher than basal rate.