some absolute Dio. ex. 5 mm - at higher tem. - nearer saturation. - may explain any de well at 20-25" Scope for Activity & Temp. Dickson & Kramer: Big. 1 adult R.B. (need) · use more oxygen for sotius metabolism at 15° Than 20° toble 2 Active metabolism -5 10 15 20 250 02 used by Hztdury RB 384. 468 576 570 478 366 492 552 592 wild kn 588 1718F Jan. 1 max = 19 21.10 standard hatch 36 42 786 \$4(7) 138 wild 42 54 66 94 120. Scope for setuit - quer - 20°C -AJS bedlook _ 25 food increased to excers temp. for max growth in ruesor -Socieen

Factors Influencing Scope for Activity and Active and Standard Metabolism of Rainbow Trout (Salmo gairdneri)¹

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Scope for activity was similar for hatchery and wild rainbow trout (*Salmo gairdneri*), except at 25 C where values for wild trout were significantly higher than those for hatchery trout. In hatchery and wild rainbow trout, respectively, scope for activity was highest at 15 and 20 C. Active metabolism increased with temperature to 570 and 592 mg O_2/kg per hr at 15 and 20 C, respectively. At 25 C, active metabolic rates of wild trout were higher than those for hatchery trout. In hatchery and wild trout, respectively, standard metabolism increased from 36 and 42 mg O_2/kg per hr at 5 C to 138 and 120 mg O_2/kg per hr at 25 C.

Scope for activity of hatchery trout was highest after 6 days starvation. Starvation had no effect on active metabolism of hatchery trout, but decreased their standard metabolism after 2 days.

Scope for activity and active and standard metabolism of wild trout were similar during forenoon to those during afternoon when light simulated natural day and night and also when lighting was constant for 24 hr.

Active metabolism of hatchery trout was higher during the spawning period than other periods of the year and was consistently the higher for males throughout the year.

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This study was undertaken to (1) determine and compare scope for activity of catchable-size hatchery and wild rainbow trout throughout their temperature tolerance range and (2) at the temperature for which scope for activity was highest, to describe the effects of starvation, time of day, sex, and season on rainbow trout metabolism. Numerous factors may influence standard or active metabolic rates, or both, and can therefore affect scope for activity (Fry 1957). These terms have recently been defined by Fry (1967). Scope for activity has been considered as a means to assess environmental stress on fishes (Brett 1958), as an index of the energy available for swimming fish (Brett 1964), and, more recently, as an index to total energy expenditure by fish (Beamish and Dickie 1967). It was used in our study primarily to compare the effect of temperature on the respiratory metabolism of hatchery and wild trout and to show the effect of other factors on rainbow trout metabolism.

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Little has been done to describe scope for activity and standard and active metabolic rates throughout the temperature tolerance range for a particular species of fish, a notable exception being the study of sockeye salmon (*Oncorhynchus nerka*) by Brett (1964). Even less attention has been given to respiratory studies of particular fish strains though differences in growth and survival of domestic and wild trout reported by Flick and Webster (1964), Vincent (1960), and others indicate that physiological differences may exist.

Materials and Methods

The study was based on 422 active and 196 standard metabolism measurements from October 1966 to December 1967. Hatchery (Hull-Erickson) and wild (De Smet) trout were raised in hatcheries of the Utah State Division of Fish and Game at Logan and Glenwood, respectively. At the hatcheries, fish were held outdoors and exposed to natural photoperiods. Fish were fed a commercial pellet fish food. They weighed approximately 100–400 g and were 10–14 months old. Fish were acclimated to 5, 10, 15, 20, and 25 C. They survived well at the lower temperatures, but at 25 C they refused to feed and were generally smaller than others.

One fish was used in each measurement of metabolism. Fish were starved for 24 hr before transfer to the respirometers to avoid undue deposition of feces in the chambers. After each experiment, fish were killed, dried with ab-

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sorbent paper, weighed, measured (fork length), and sexed.

Unless otherwise indicated, all experiments were conducted under continuous laboratory illumination (2-12 ft-c). Water analyses except those for temperature and dissolved oxygen were done by the Utah Water Research Laboratory (Table 1). The Alsterberg azide modification of the Winkler method (American Public Health Association 1960) was used to determine dissolved oxygen concentration. The difference in dissolved oxygen concentration in water samples collected from the respirometers at the beginning and end of each test period, multiplied by the respirometer volume, was taken as the amount of oxygen consumed by a fish. On the few occasions that two oxygen determinations on a water sample differed by more than 0.1 ml sodium thiosulphate (0.01 N), a third titration was done and the three measurements averaged.

"Air saturation" in this study was taken as dissolved oxygen concentrations in excess of 90% air saturation. The duration of the test periods was varied according to the water temperature to maintain relatively high dissolved oxygen concentrations, those at the end of tests being seldom less than 6 ppm and rarely as low as 5 ppm. The decline in concentration during the test period due to fish respiration was usually about 1.0 ppm and seldom exceeded 2.0 ppm.

TABLE 1. Physical and chemical properties of water from fish acclimation tanks, Utah State University Fisheries Laboratory, Logan, Utah, 1967. Expressed as parts per million unless stated otherwise.

Item	Mean	Range
Color (units)	<5	_
Turbidity (JTU) ^a	<25	_
Dissolved oxygen	8.6	6.7-10.0
Temp (C)	-	5-25
Total hardness as CaCO ₃	187	160-210
Alkalinity total	216.2	212.2-218.3
Bicarbonate	216.2	212.2-218.3
Carbonate	0	-
Chloride as Cl	5.6	3.5-7.5
Calcium as Ca	18.0	5.3-35.2
Magnesium as Mg	33.9	23.6-41.8
Sodium as Na	1.4	1.2-1.8
Potassium as K	0.4	0.3-0.6
Sulphate as SO ₄	8.36	6.70-9.60
Ammonia as NH ₃	0.44	0-0.78
Phosphate as PO ₄	0.189	0.005-0.340
Nitrate as NO ₃	0.40	0-1.00
Silica as SiO ₂	3.4	2.9-3.8
Electrical conductivity		
(µmhos/cm)	311	290-325
Total dissolved solids	180	158-207
pH	8.2	7.4-8.8

^aJackson Turbidity Units.

RESPIROMETERS

Respirometers were submerged in 400-liter constanttemperature water baths. Water temperatures in the baths were controlled by buffering thermoregulatorcontrolled heaters against a Min-O-Cool³ refrigeration unit, in the active respirometer bath within ± 0.3 C, and in the standard respirometer bath within ± 0.1 C.

Active metabolic rates were determined using a 27.5liter respirometer slightly modified from apparatus described by Smit (1965) and Blazka et al. (1960). It consisted of two clear acrylic plastic chambers in which water was drawn through the inner cylinder by a propeller, and returned between the outer and inner cylinders. Fish were forced to swim against the current in the inner cylinder. A stainless-steel grid in front of the propeller, electrified with approximately 8–10 v a-c, stimulated the fish to continue swimming. Fish were inserted and and removed through a lid in the top.

Standard metabolism measurements were made with apparatus resembling that described by Beamish and Mookherjii (1964). A 12.6-liter, thin-walled, stainlesssteel sauce pot fitted with a flowmeter was used for the respiration chamber. The flowmeter operated on a heat-loss principle and was used to estimate the activity of a fish in the chamber. This respirometer differed from that employed by Beamish and Mookherjii (1964) in several aspects: this chamber increased conductance of heat to the outside bath; time of heater operation was measured in seconds by a manual reset electrical timer; variation in baseline settings was reduced by adjusting the heater circuit closure time to 50% ($\pm 3\%$) of the experimental period; water samples were collected manually; the thermoregulator was installed directly into a simple heater relay-coil circuit; and the respirometer was flushed at a rate of approximately 1.5 liters/min by an electric pump. Fish in the darkened chamber appeared indifferent to the introduction, presence, or removal of the pump-flushing tube.

ACCLIMATION

Procedures described by Beamish and Mookherjii (1964) were followed for acclimating fish to 5, 10, 15, 20, or 25 C. For each temperature, 25 fish were placed in an insulated 400-liter tank. The water exchange was maintained at 115 liters/hr. Water temperatures in the tanks were increased or decreased 1 degree C per day until the desired temperature was obtained. Fish were held at the test temperatures for at least 2 weeks before they were used in experiments. Acclimation temperatures were controlled to within ± 0.5 degree C.

ACTIVE METABOLISM

Immediately before active metabolism measurements, each fish was allowed a 15–20-min adjustment period in the respirometer while it was flushed to allow dissolved oxygen concentrations to reach air saturation. During this time, water was circulated slowly in the

³A refrigeration unit and fiberglass reservoir.

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respirometer to allow each new fish to orient itself. Fish were usually exercised for 15–20 min at a velocity of about 91 cm/sec (3.0–4.7 lengths/sec) depending on the temperature. Temperatures of 5 and 25 C reduced swimming ability of some trout and these fish were exercised at lower velocities (67 cm/sec) at these temperatures.

Preliminary tests were conducted to determine the approximate velocities required to cause fish of different sizes acclimated to different temperatures to respire at their active metabolic rate. Seventy small (60-147 g) and 55 large (135-241 g) hatchery trout were acclimated to 5, 10, 15, 20, and 25 C and exercised at velocities from 43 to 107 cm/sec (1.5-5.1 lengths/sec). Where possible, at least two measurements of oxygen consumption were made for small and large fish at each velocity and temperature. Results indicated that the active metabolic rate was not significantly increased at velocities higher than 67 cm/sec (Fig. 1). These tests indicated that in some instances, fish may respire at active metabolic rates when forced to swim at speeds as low as 1.5 lengths/sec (41 cm/sec). This is not remarkable because fish stimulated by handling immediately before experiments (Keys 1930; Wells 1932; Black et al. 1939) or by an electric field (Basu 1959) may respire at the active rate at low water velocities. However, the mere handling of fish is not always sufficient to induce maximum oxygen consumption, and fish must be forced to swim and exert themselves to obtain this value (Job 1955). It was concluded, therefore, that handling of fish, the electrical stimulus, and forced exercise at relative high swimming speeds were sufficient for full expression of the active metabolic rate in these experiments.

STANDARD METABOLISM

Before standard metabolism experiments, a baseline reading for the flowmeter heater was obtained immediately before placing a fish in the respirometer. Each fish was allowed an overnight period of adjustment to the respirometer. A black plastic cover was fitted over the transparent lid of the chamber and precautions were taken (Fry 1957) to suppress external stimuli that might stimulate the fish. Fresh water was pumped through the chamber (1.5 liters/min) continuously before each experiment. Oxygen consumption and activity determinations lasted 40 min at 5 C; 30 min at 10, 15, and 20 C; and 15 min at 25 C. At the end of each test period,

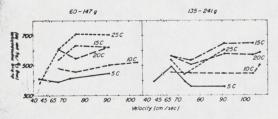


FIG. 1. Active metabolism of hatchery rainbow trout in two size ranges at various water velocities and temperatures.

activity was recorded, and the chamber flushed for 20 min to restore the original concentration of dissolved oxygen.

Each experiment lasted 5–7 hr to allow at least six simultaneous determinations of oxygen consumption and spontaneous activity. Results were discarded when baseline determinations before and after each experiment differed by more than 60 sec (6.7% of the shortest test period). The six determinations of oxygen consumption and activity were plotted on a semilogarithmic grid. A straight-line relation was obtained by plotting the logarithm of oxygen consumption against activity. Standard metabolism was estimated by extrapolation of this line to zero activity.

The semilogarithmic relation between oxygen consumption and activity presumably resulted from the high degree of swimming activity permitted in the large respirometers used in this study. Using the same type of flowmeter and relatively smaller respirometers, Mc-Kenzie (MS 1960), Beamish and Mookherjii (1964), and Mather and Shrivastava (MS 1967) found a linear arithmetic relation between oxygen consumption and spontaneous activity. Beamish and Dickie (1967) attribute the comparatively high rates of oxygen consumption of fish spontaneously active at low levels of activity to the high cost of intermittent swimming, which becomes more efficient at faster, more continuously maintained speeds.

Unlike measurements of active metabolic rates, standard metabolism measurements of rainbow trout were subject to considerable variation. Some experiments involved "excited" or "nervous" fish that exhibited high levels of activity. Prolonged habituation of the fish to the chamber, exclusion of light from the chamber, and other precautions taken to reduce the fish to a quiescent state were unsuccessful. Smit (1965) and Brett (1964, 1965) discussed how such behavioural characteristics as excitability, restlessness, and spontaneous movement can contribute to the variability of estimates of standard metabolism. Beamish and Dickie (1967) considered that this variability in behaviour was mainly responsible for the "unavoidably high experimental error" usually associated with estimates of standard oxygen consumption.

STARVATION AND CONTROLLED LIGHTING

Hatchery trout acclimated to 15 C were starved for 1, 2, 3, 6, and 9 days. Fish were forced to swim at 91 cm/sec velocity (3.0-4.0 lengths/sec) except that those starved for 9 days were unable to swim at the higher velocities and were exercised at 67–91 cm/sec velocities (2.5–3.6 lengths/sec). Active and standard metabolism rates of starved fish were measured from 7:00 AM to 5:00 PM and from 7:00 AM to 2:00 PM, respectively.

Active and standard metabolic rates were determined using wild trout subjected to continuous light (2–12 ft-c) and to light controlled to coincide with natural day length. A light-proof enclosure was erected around two acclimation tanks, and the photoperiod adjusted to coincide with natural length of day. Fish were exposed to periods of different light intensities in succession as follows: 30 min of 28–60 ft-c, 9 hr of 380–450 ft-c, 30 min of 28–60 ft-c, and 14 hr of darkness. The effect of light on active and standard metabolism was investigated during morning (7:00 AM–1:00 PM) and afternoon (1:00 PM–7:00 PM).

STATISTICAL TREATMENT

Weights of fish were adjusted by covariance analysis to a common mean and, unless otherwise indicated, these and other statistical results of active and standard metabolism experiments are reported at P = 0.05. In some instances, statistical analyses without covariance were employed to compare scope for activity values, and standard and active metabolic rates. However, these respiratory rates were compared only when mean weights of fish were not significantly different at P =0.05. Based on the z distribution described by Ostle (1963), respiratory rates were significantly different at $P = 0.05_{2}^{*}$ if the calculated z value exceeded 1.96.

Results and Discussion

EFFECTS OF TEMPERATURE

Scope for activity

Scope for activity increased from 348 and 324 mg O_2/kg per hr at 5 C to a maximum of 498 mg O_2/kg per hr at 15 and 20 C for hatchery and wild trout, respectively (Table 2). At 25 C, scope for

activity was unchanged for wild trout, but was significantly decreased for hatchery trout. Lowest scope for activity for hatchery and wild trout occurred at 25 and 5 C, respectively. Scope for activity of hatchery trout was less at 5 C than at 10, 15, or 20 C ($z \ge 4.03$) and lower at 10 C than 15 and 20 C ($z \ge 2.30$). Similarly, scope for activity of wild trout was less at 5 C than at 10 and 15 C $(z \ge 4.38)$, and was less at 10 C and 20 C (z = 2.03). Hatchery and wild trout acclimated to the lower temperatures weighed significantly more than those at higher temperatures, and this prevented statistical comparison of scope for activity between these temperatures. However, in accordance with Job's findings (1955) any increase in mean weight of fish acclimated to higher temperatures would tend to further decrease scope for activity at these higher temperatures. Job (1955) studied the effect of weight on respiratory metabolism of brook trout (Salvelinus fontinalis) and found that the rate of increase in scope for activity with rising temperatures was progressively reduced for larger fish.

Scope for activity was similar for hatchery and wild trout at each temperature except 25 C, at which it was significantly higher (z = 3.88) for wild trout. This markedly different response at 25 C suggests that wild trout may be the more active in warm water. Increased activity of wild trout would be expected, as increased scope for

TABLE 2. Active and standard metabolism and scope for activity (mg O_2/kg per hr) of hatchery and wild rainbow trout at five temperatures. Values (active and standard rates only) joined by underline are not significantly different from each other at P = 0.05 (Newman-Keuls multiple range test).

	Date (1967)	No. testsª	Wt (g)	Length (<i>mm</i>)	Swimming speed (<i>lengths/</i> sec)	Temp (<i>C</i>)				
Trout						5	10	15	20	25
				Active m	netabolism					
Hatchery	Apr. 22-June 24	54	137–249	230-285	2.3-3.8	384(15)ь	468(11)	576(22)	570(22)	478(18)
Wild	Sept. 28-Oct. 30	65	79–398	198-300	2.9-4.7	366(16)	492(20)	552(37)	592(19)	588(19)
				Standard	metabolism					
Hatchery	Apr. 17-June 29	48	148-264	235-290	-	36(2)	42(5)	78(6)	84(7)	138(12)
Wild	Sept. 25-Oct. 27	55	85-396	208-318	-	42(2)	54(4)	60(5)	94(10)	120(18)
				Scope fo	r activity					
Hatchery						348(16)	426(21)	498(37)	486(20)	336(23)
Wild						324(16)	438(20)	492(37)	498(22)	468(26)

^aNumber of tests at each temperature ranged from 8 to 15 and averaged 12. ^bNumerals in parentheses represent one standard error of the mean. activity indicates more "available energy" for swimming (Brett 1964). This additional energy available to wild trout may be an important survival mechanism during times of stress. If scope for activity may be used to assess environmental stress as Brett (1958) has suggested (a decreased scope indicating stress conditions), wild trout in water of high temperature may be better able to cope with temperature stress and have greater potential for survival than hatchery trout under these conditions.

The difference in scope for activity between hatchery and wild trout may be attributed to differential effects of hatchery and natural selection on their genetic compositions. Hatchery trout were produced from brood stock maintained in Utah hatcheries, and had experienced hatchery selection since 1880 (Dollar and Katz 1964). Eggs for the wild stock were obtained from De Smet Lake, Wyoming, where wild trout have been exposed to natural selection processes since as early as 1912. Differences observed by Flick and Webster (1964) and Smith (1957) in behaviour, growth, and survival of hatchery and wild trout suggest genetic implications. Unlike hatchery trout maintained in water of relatively constant temperature, wild trout exposed to the temperature extremes and fluctuations encountered in nature may have adapted to high water temperatures.

Active metabolism

Temperature had a significant effect on active metabolic rates of hatchery trout (P = 0.01;F = 20.05) and wild trout (P = 0.01; F = 23.70). Highest active metabolic rates for hatchery and wild trout occurred at 15 and 20 C, and were 576 and 592 mg O2/kg per hr, respectively. Active rates for hatchery trout at 5 and 10 C were significantly lower than those at other temperatures, and active metabolism of wild trout was significantly different at 5, 10, 20, and 25 C (Table 2). Active metabolism of wild trout was significantly higher than active metabolism of domestic trout at 25 C (z = 4.35) and this accounted for the higher scope for activity for wild trout at 25 C. Mean rates of active metabolism of hatchery and wild trout did not differ significantly at other temperatures $(z \ge 1.05).$

The decrease in active metabolic rates of hatchery trout at temperatures greater than 15 C may be explained by lowered dissolved oxygen concentrations at these higher temperatures. This, however, does not acount for the difference in active metabolism between hatchery and wild trout at 25 C. Active metabolic rates of wild trout at 25 C were not significantly lowered at 20 C. Similarly, Brett

(1964) found no statistical difference between active metabolic rates of sockeye salmon (*Oncorhynchus nerka*) acclimated to 15, 20, and 24 C, although the mean rates tended to decrease at temperatures above 15 C. He attributed this decline in active metabolism of sockeye salmon at high temperatures to the reduced oxygen available in solution at high temperatures, and "other factors of a physiological nature."

Standard metabolism

Temperature had a significant effect on standard metabolism of hatchery trout (P = 0.01; F = 17.65) and wild trout (F = 6.17). Standard metabolic rates of hatchery trout at 5 and 10 C were significantly lower than those at higher temperatures and were significantly higher at 25 C than at other temperatures (Table 2). Standard metabolic rates of wild trout at 5, 10, and 15 C were significantly lower than those at higher temperatures. Standard metabolism increased progressively from a low of 36 and 42 mg O2/kg per hr at 5 C to a high of 138 and 120 mg O2/kg per hr at 25 C for hatchery and wild trout, respectively. Standard metabolic rates of hatchery and wild trout showed similar increases with temperature except at 15 C, at which standard metabolic rates of hatchery trout were higher (z = 2.29).

In standard metabolism measurements, the relation between water temperature and the logarithm of oxygen consumption rate was linear for hatchery and wild trout over the range of temperatures investigated (Fig. 2). Least squares fitted to the points were: $\log Y = 1.388 + 0.029 X$ and $\log Y = 1.492 + 0.023 X$ for hatchery and wild trout respectively, where $Y = \log_{10} oxygen$ uptake rate (mg O₂/kg per hr) and X = water temperature (C).

The semilogarithmic relation between standard oxygen consumption and temperature for hatchery and wild rainbow trout differs somewhat from the slightly convex curvilinear relation reported for warmwater species (Beamish 1964c), but appears

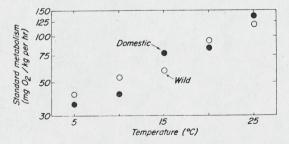


FIG. 2. Relation of temperature and standard metabolism of hatchery and wild rainbow trout.

typical for cold-water species (Gibson and Fry 1954; Beamish 1964c; and Brett 1964).

Temperature increased the ratios of active and standard metabolic rates approximately 9-11 times at 15 C, and decreased these ratios to three to five times the standard rate at 25 C for hatchery and wild trout, respectively. The maximum active rate was about 16 times the lowest standard rate. Brett (1964) reported similar ratios to describe the effect of temperature on active and standard metabolic rate of sockeye salmon.

EFFECTS OF STARVATION

Scope for activity

Starvation increased scope for activity of hatchery trout from a low of 414 mg O_2/kg per hr at 1 day's starvation to a high of 486 mg O_2/kg per hr after 6 days' starvation. Scope decreased at 9 days' starvation to 456 mg O_2/kg per hr (Table 3). Although mean active metabolic rates were not significantly different for different levels of starvation, these individual means were used in preference to a common mean in calculations of scope for activity. Scope for activity at 6 days' starvation differed significantly from that at 1 and 3 days' starvation ($z \ge 2.42$). The increased scope for activity after starvation for 6 days suggests that more oxygen may be available for metabolic functions that demand maximum energy.

Active metabolism

Starvation had no significant effect on rates of active metabolism of hatchery trout. Mean active rates of oxygen consumption ranged from a low of 498 mg O_2/kg per hr after 3 days' starvation to a high of 558 mg O_2/kg per hr after 6 days' starvation (Table 3).

The effect of starvation on active metabolism of fish has received little attention. Fry (1957) reported results obtained by Barrett who investigated the effect of starvation on active metabolism of rainbow trout. Fish were maintained at approximately 11 C and were starved for 100 days. Barrett found "no essential difference" between the active rates of starved and control animals.

Standard metabolism

Standard metabolic rates of hatchery trout decreased after 2 days' starvation but increased slightly with continued starvation (Table 3). Highest standard oxygen consumption was 96 mg O_2/kg per hr after 1 day's starvation, and the lowest 60 mg O_2/kg per hr after starvation for 2 days. Standard metabolism differed significantly between 1 and 2 days' starvation (F = 3.42).

Beamish (1964a) reported a decrease in standard metabolism of fish during the first 2 or 3 days of starvation, and he attributed this decrease to the reduced oxygen required for assimilation of food. A decreased oxygen requirement for food assimilation would explain the significant reduction in standard metabolism of rainbow trout after 2 days' starvation.

EFFECTS OF DAYLIGHT HOURS

Scope for activity

Scope for activity of wild trout maintained under controlled conditions of light and dark coinciding

TABLE 3. Active and standard metabolism and scope for activity of starved hatchery rainbow trout at 15 C.

	Date	No. testsª	Wt (g)	Length (mm)	Swimming speed (<i>lengths</i> / – sec)					
						1	2	3	6	9
					Active me	etabolism				
July	6-25	50	146-328	230-255	2.5-4.0	510(21)ь	510(12)	498(23)	558(16)	528(17)
					Standard n	netabolism				
June	28-Aug. 14	45	150-311	235-305		96(5)	60(7)	84(7)	72(7)	72(5)
					Scope for	activity				
						414(22)	450(14)	414(24)	486(17)	456(18)

*Number of tests for each starvation period ranged from 9 to 10.

^bNumerals in parentheses represent one standard error of the mean.

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with the natural photoperiod was 450 ± 20 mg O_2/kg per hr in the forenoon and 480 ± 25 mg O_2/kg per hr in the afternoon. Scope for activity of fish maintained under constant light was 456 ± 25 mg O_2/kg per hr in the forenoon and 462 ± 25 mg O_2/kg per hr in the afternoon. Forenoon and afternoon periods had no significant effect on scope for activity.

There appears to be no general agreement concerning the existence of diurnal differences in the metabolic rate of fish (Winberg 1956). In the present study, the absence of differences in respiratory metabolism of wild rainbow trout during the daylight hours suggests that any diurnal differences must occur at night.

Active and standard metabolism

Active and standard metabolic rates of wild trout were not significantly different (F = 0.74) between forenoon and afternoon periods (Table 4). Endogenous daily cycles of activity during the diurnal period may affect respiratory metabolism measurements, particularly standard metabolism measurements, in spite of maintenance of constant conditions (Fry 1957). In the present study, however, the influence of spontaneous activity on oxygen consumption was quantified and eliminated from estimates of standard metabolism of rainbow trout and could not contribute to diurnal differences in the metabolic rate. Clausen (1933, 1936), Oya and Kimata (1938), and Graham (1949) described diurnal influence on fish metabolism by measuring

oxygen consumption throughout a 24-hr period. The influence of spontaneous activity on oxygen consumption was not determined, although precautions were taken to reduce external stimuli and induce the fish to a quiescent state. Higginbotham (1947) found that the respiratory metabolism of channel catfish (*Ictalurus punctatus*) was higher in the afternoon than in the morning and attributed this to increased spontaneous activity during the afternoon.

EFFECTS OF SEASON AND SEX ON ACTIVE METABOLISM

Ten to 49 measurements of active metabolism of mature hatchery rainbow trout acclimated to 15 C were made on five separate occasions: October-November 1966, and February, April, July, and August 1967 (Table 5). This provided an opportunity to investigate seasonal influence on active rates of oxygen consumption and seasonal effects on active metabolism of the sexes.

Season

For males, the minimum active rate of oxygen consumption was 546 mg O_2/kg per hr during October-November 1966, and increased to a high of 618 mg O_2/kg per hr in February 1967. Active rates remained relatively high in April, but decreased to a low of 522 mg O_2/kg per hr in July. Mean active metabolic rates for the five test periods were not significantly different (F = 1.38).

TABLE 4. Active and standard metabolism of wild rainbow trout at 15 C during forenoon and afternoon periods of controlled lighting.

Light conditions	Daytime period	Wt (g)	Length (mm)	Swimming speed (lengths/sec)	Mean metabolic rate (mg O ₂ /kg per hr)
		Active metal	bolism		
Controlled light and dark ^a Continuous light (2–12 ft-c)	Forenoon Afternoon ^b Forenoon Afternoon	153–261 88–247 86–325 100–576	240–292 195–328 190–306 210–360	3.1-4.33.1-5.32.5-4.82.5-4.8	534(19)° 558(24) 528(24) 534(23)
		Standard met	abolism		
Controlled light and dark ^a Continuous light (2–12 ft-c)	Forenoon Afternoon Forenoon Afternoon	110–306 86–309 105–381 116–330	230–297 200–296 217–310 220–305		84(7) 78(8) 72(6) 72(9)

*Light intensities in succession as follows: 30 min of 28–60 ft-c, 9 hr of 380–450 ft-c, 30 min of 28–60 ft-c, and 14 hr of darkness.

^bEleven fish used in this test, and 12 in each of the others.

Numerals in parentheses represent one standard error of the mean.

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