OXYGEN REQUIREMENTS OF THIRTEEN SPECIES OF FISHES IN RELATION TO EXERCISE

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INTRODUCTION

Oxygen requirements of fishes have been reported to vary with: (1) size (Job, 1955), (2) life history stage (Alderdice et al., 1958), (3) concentration of oxygen in the water (Gibson & Fry, 1954), (4) ability of the hemoglobin of the blood to bind and release oxygen (Black, 1940), (5) length of time the fishes were acclimated to waters of low oxygen content (Shepard, 1955), (6) temperature (Downing & Merkens, 1957), (7) pH (Powers, 1922), (8) carbon dioxide content (Basu, 1959), (9) dissolved substances (Southgate et al., 1933), and (10) activity of the fishes (Graham, 1949). The primary purpose of the study, herein reported, was to measure the ability of each of nine species of fishes to survive low oxygen levels while actively releasing energy by swimming, more or less continuously, in flowing waters (approximately 0.8 ft/sec), for a six-hour period.

Oxygen concentrations necessary for some fishes during forced activity have been estimated by measurements of (1) the ability of the fishes to survive low oxygen levels in flowing waters (Katz et al., 1959, constructed an apparatus which controlled the rate of flow and oxygen content of water and determined how long fishes could swim in currents of 0.8 and 1.2 ft/sec at oxygen levels of 2 mg/L and higher), and (2) the quantity of oxygen consumed by fishes (Fry & Hart, 1948, estimated the minimum oxygen level from the active metabolic rate by determining the oxygen level at which the oxygen uptake was reduced to no more than the oxygen uptake required in active metabolism).

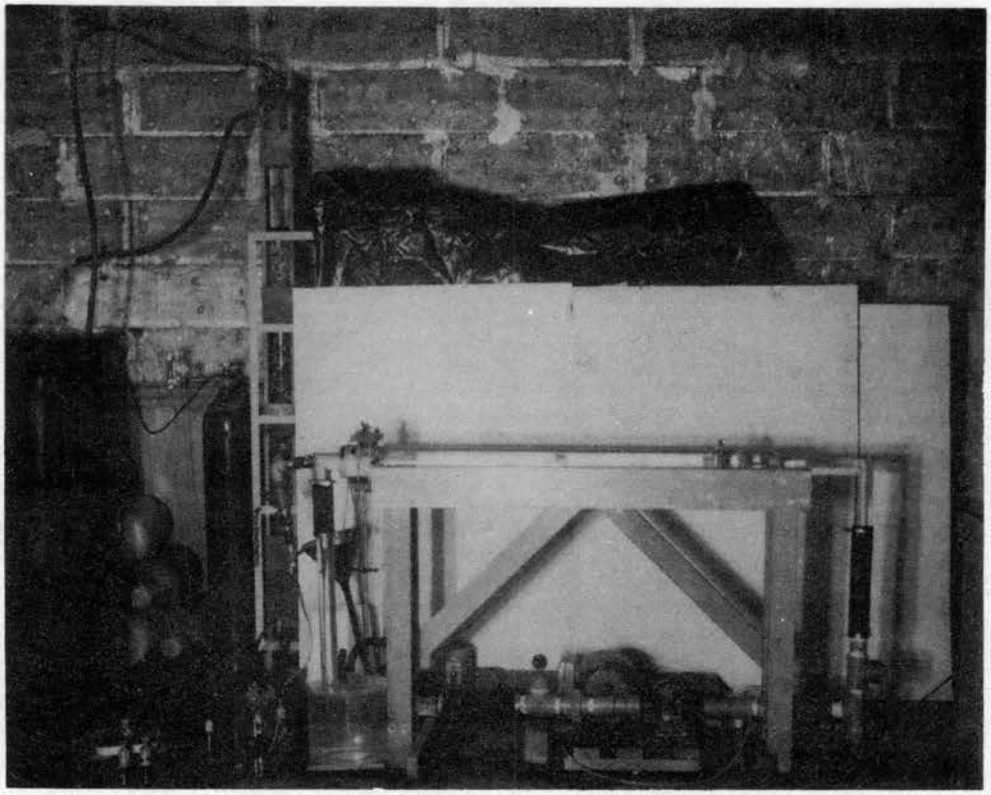
In the process of obtaining the information some measurements were obtained concerning the (1) oxygen consumption and opercular rates of some fishes, (2) ability of some fishes to tolerate low oxygen levels in standing waters, and (3) ability of specimens of Cottus carolinae (which refused to swim against a current of water), to live in flowing waters of low oxygen content. Observations were also made concerning the collection, maintenance, and behavior of the fishes.

A pressing need for water quality criteria, especially dissolved oxygen, can be realized only when pertinent information regarding the affected aquatic forms is available. Oxygen concentrations necessary for fishes have been estimated by determining the oxygen content of the water and observing the numbers and kinds of fishes present (Thompson, 1925, and Odum & Caldwell, 1955). Because it is extremely difficult to measure activity and oxygen consumption of fishes in the field, information obtained from laboratory experiments must be judiciously applied to field situations, even though the ecological significance of laboratory experimentation is not fully understood.

MATERIALS AND METHODS

An apparatus (Figure 1) was constructed in which the rate of water flow and concentration of dissolved oxygen could be controlled (similar in principle to that of Katz et al., 1959). Water was pumped from a six-hundred-gallon redwood vat to the top of a vertical stripping column (a 66x4 in. glass cylinder filled with marbles, with a 12x1 in. tube connected to an upper 12x4 in. tubular section). Excess water was returned to the vat through a tube from the upper section of the column. Nitrogen gas was introduced at the base while water flowed through the column. The rate of displacement of oxygen from the water was regulated by the rate of water and/or nitrogen flow through the stripping column (see Carpenter & Cargo, 1957, for a discussion of the principles of a stripping column). The water was forced from the base of the stripping column to a reservoir, then pumped through a swimming chamber back to the reservoir. The amount of water withdrawn from the system was regulated, by a ball valve, to attain the desired temperature and oxygen content. The water withdrawn from the system passed either (1) into an oxygen sample bottle, (2) directly to discard, or (3) into a jar, then through an oxygen sample bottle. The system contained approximately 35 liters of water.

The swimming chamber occupied approximately 48 in. of a 60x4 in. plexiglass cylinder. Near one end of the cylinder nylon netting restricted movement forward into baffle plates. Near the other end of



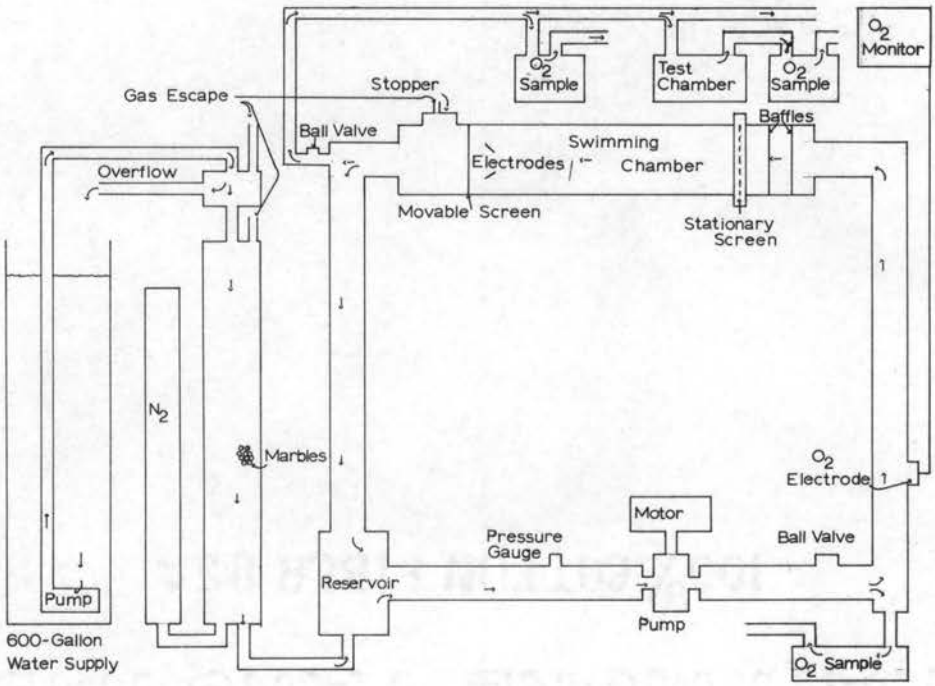


Figure 1. Types of apparatus used in measuring the oxygen requirements of fishes. Upper, photograph; lower, diagrammatic drawing.

the cylinder nylon netting mounted on a movable stainless steel stand confined fish to the swimming chamber. Fish could be introduced or removed by withdrawing a rubber stopper from a two-inch opening on the upper surface of the cylinder, approximately 6 in. from the outflow, and the movable screen pushed back into the 2-in. outflow. Then the movable screen and stopper were replaced and secured. Two platinum electrodes were installed in the swimming chamber approximately 2 in. in front of the movable screen.

Oxygen was gradually reduced after (1) the fish were introduced, (2) the swimming chamber was secured, (3) the water flow started, and (4) the fish allowed an adjustment period in their new environment. The number of fish introduced into the swimming chamber was dependent upon the following criteria: (1) if most of the specimens were swept onto the screen, the screen area covered would be less than the area of the 2-in. outflow, and (2) the number of specimens available. Fish were generally introduced into the swimming chamber the day of the test. Specimens of two species, on three occasions, were introduced into the swimming chamber the afternoon before the test. The results revealed little or no difference when compared to tests in which a similar acclimation period was not employed. Shepard (1955) also observed that acclimation to the test chamber resulted in no appreciable difference in the resistance of young Salvelinus fontinalis to low oxygen levels. The recorded time period began when oxygen had stabilized at the desired level and was terminated in six hours, or when the fish were no longer able to swim against the current. The fish still swimming at the close of the recorded time period were shocked into immobility to more easily remove them from the swimming chamber. The

fish then were weighed (wet), measured, preserved, and a condition index calculated for each specimen, as described in Carlander, 1950. (see Tables I and II for a summarization of certain measurements of the test conditions and fishes).

Once the recorded time period began, dissolved oxygen was measured at approximate half-hour intervals employing the Alsterberg (Azide) modification of the Winkler method, and the iodine concentration measured with a Bausch and Lomb Spectronic 20 Colorimeter (the results obtained from the Colorimeter were periodically checked by titration). The oxygen content was also measured with a continuous recording Beckman model 764 oxygen monitor electrode installed between the pump and the swimming chamber.

It was necessary to lightly shock (1-3 A.C. volts), some individuals of some species to enforce swimming when oxygen levels approached or fell within the critical zone (delineated by almost complete survival at one extreme and almost complete extermination at the other extreme). Electrical stimuli were not used until an individual rested frequently on the movable screen. In most instances those individuals who rested frequently, succumbed early.

Fish were also placed in the test chamber near the outlet of the system to determine if they, when not forced to exercise, would survive at approximately the same oxygen level as the individuals in the swimming chamber, and to obtain a measurement of their oxygen consumption. Dissolved oxygen was measured as the water entered and left the chamber. Unfortunately a sufficient number of specimens were not always available to place enough biomass in the chamber to obtain a valid measurement of the oxygen used by the fish. Oxygen consumption was calculated, using

TABLE I

AVERAGES AND RANGES OF CERTAIN CHARACTERISTICS OF THE LABORATORY ENVIRONMENT AND TEST CONDITIONS

ATMOSPHERE	Temperature (°F)	Pressure (mm Hg)	Relative Humidity (%)
July	----------	----------	----------
August	77.44 (77-79)	762.63 (760.3-767.8)	----------
September	76.5 (73-79)	766.86 (761.0-767.7)	----------
October	77.4 (71-85)	763.67 (755.0-775.8)	60.9 (42.5-70.8)
November	74.28 (66.5-81)	765.74 (755.1-773.9)	52.39 (48-61)
December	74.77 (62-80)	766.48 (760.1-781.4)	52.07 (43.5-61)

WATER	Tap Water pH	Water After Standing in Vat at Least 24 Hours[1] pH	Water After Standing in Vat at Least 24 Hours[1] Temperature (°F)	Water in Fish Tanks[2] Temp.(°F)
July	----------	8.35 (8.3-8.4)	76.88 (74-79)	73 (70-76)
August	7.86 (7.75-7.9)	8.43 (8.3-8.6)	75.59 (73-77.5)	73.31 (72-76)
September	7.84 (7.5-8.05)	8.41 (8.3-8.6)	75.06 (74.5-75.5)	74.07 (71-78)
October	7.87 (7.5-8.05)	8.44 (8.4-8.5)	74.43 (73-77)	75.06 (70-80)
November	7.98 (7.7-8.2)	8.42 (8.15-8.49)	70.05 (68-72.5)	69.78 (66-75)
December	7.97 (7.65-8.2)	8.22 (8.15-8.3)	69.4 (67.75-72)	70.06 (64-74)

WATER ANALYSIS [3]

Na 35 ppm Mg 14 ppm Fe 0.01 ppm So_4 26 ppm F 1 ppm HCO_3 174 ppm SiO_2 3 ppm

Ca 45 ppm Mn 0 ppm Al 0 ppm Cl 54 ppm OH 0 ppm CO_2 5 ppm Total solids 348 ppm

Specific conductance 410 Microohms Total alkalinity as $CaCO_3$ 143 ppm Total hardness 168 ppm

TEST CONDITIONS	Water in the Test Chambers Temperature (°F)	Water in the Test Chambers pH	Time 1[4] (min)	Time 2[5] (min)	Time 3[6] (min)
T. nilotica	76.9 (70.5-80)	8.4 (8.2-8.6)	16.9 (5-50)	29.3 (15-68)	116.7 (58-245)
H. nigricans	76.29 (71.5-80)	8.44 (8.3-8.6)	14.4 (5-45)	31.9 (5-60)	101.9 (50-175)
H. storeriana	78.25 (75.5-80.5)	8.49 (8.45-8.55)	12.25 (5-20)	29.0 (15-55)	98.0 (60-155)
C. anomalum[7]	75.7 (70.5-78.5)	8.43 (8.23-8.49)	11.2 (5-40)	30.56 (5-70)	89.13 (50-140)
C. anomalum[8]	78.0 (77.5-78.5)	8.46 (8.45-8.48)	13.57 (5-40)	34.29 (5-70)	80.0 (50-140)
C. anomalum[9]	73.92 (70.5-77.3)	8.41 (8.23-8.49)	9.13 (5-17)	27.67 (10-65)	96.22 (70-125)
M. dolomieui	76.03 (71.5-80)	8.44 (8.3-8.55)	13.69 (5-45)	59.8 (15-197)	96.8 (30-210)
N. cornutus	78.3 (75.5-80.5)	8.49 (8.45-8.55)	9.75 (5-20)	22.13 (15-43)	113.38 (80-155)
N. camurus	78.0 (76.5-80)	8.44 (8.4-8.475)	9.7 (5-30)	23.1 (13-35)	92.8 (50-175)
L. sicculus	74.5 (71-80)	8.28 (8.15-8.45)	8.9 (5-15)	34.6 (15-65)	92.0 (50-173)
H. biguttata	75.4 (73-80)	8.45 (8.4-8.5)	6.9 (5-10)	29.6 (8-50)	90.6 (50-150)
D. cepedianum	73.6 (72-74.5)	8.21 (8.15-8.29)	7.0 (5-10)	62.0 (45-75)	92.33 (70-117)
C. carolinae	78.25 (76-80)	8.4 (8.3-8.5)	11.25 (0-240)	68.5 (0-240)	159.8 (34-480)
A. calva	72.25 (71.5-73)	8.35 (8.3-8.4)			
P. caprodes	75.25 (74.5-76)	8.37 (8.2-8.55)			

Average Oxygen Deviation, All Tests (ppm)

L. sicculus	± 0.237 (0.08-0.32)	H. nigricans	± 0.105 (0.06-0.14)
M. dolomieui	± 0.248 (0.07-0.5)	N. camurus	± 0.145 (0.04-0.275)
H. biguttata	± 0.212 (0.07-0.335)	N. cornutus	± 0.082 (0.05-0.105)
C. anomalum	± 0.127 (0.02-0.215)	T. nilotica	± 0.106 (0.01-0.225)
H. storeriana	± 0.115 (0.09-0.185)	D. cepedianum	± 0.237 (0.08-0.32)
C. carolinae	± 0.135 (0.075-0.195)		

1. Chlorine was less than 2 ppb.
2. The pH of the water in the fish tanks usually dropped from 8.2-8.4 down to 7.4-7.6 in 1-2 weeks and then stabilized.
3. Sample taken 12-17-62, analyzed by C. E. Moutrey & Associate Inc., Tulsa, Oklahoma.
4. Time from introduction of fish to starting of pump.
5. Time from starting pump to starting of nitrogen flow.
6. Time from starting nitrogen flow to beginning of test.
7. All specimens.
8. Specimens 112 to 148 mm in length.
9. Specimens 50 to 91 mm in length.

TABLE II

A SUMMARIZATION OF CERTAIN MEASUREMENTS OF THE FISHES

Species	Type of Test[1]	No. Fish	No. Tests	Weight[2] (grams)	Length[2] (millimeters)	Condition[2] Index	Fishes That Would Not Swim No.	Wt.(gm)	Lt.(mm)	K	Opercular Rate[3] No./min
Tilapia nilotica	I	85	13	2.74 (1.2-4.4)	57.8 (44.0-69.0)	1.394 (1.18-1.77)					183.2 (155.0-232.7)
	II	56	8	1.72 (0.9-3.0)	49.44 (39.0-58.0)	1.394 (1.18-1.733)					190.0 (158.6-231.5)
Hybopsis storeriana	I	21	8	12.15 (10.0-14.4)	119.8 (112.0-125.0)	.704 (.639-.833)	1	14.4	129.0	.670	188.1 (152.0-212.2)
	II	7	6	13.72 (11.0-16.2)	123.8 (118.0-130.0)	.719 (.669-.750)					192.7 (191.5-193.8)
Campostoma anomalum[4]	I	98	16	10.61 (0.9-28.0)	95.1 (50.0-148.0)	.836 (.582-1.091)					223.2 (182.6-242.1)
	II	57	15	10.56 (0.6-24.0)	98.01 (39.0-148.0)	.813 (.596-1.027)					231.5 (199.1-257.1)
Campostoma anomalum[5]	I	15	7	21.15 (12.0-28.0)	131.2 (112.0-148.0)	.923 (.764-1.091)					212.5 (182.6-240.5)
	II	6	6	20.9 (17.7-24.0)	134.17 (127.0-148.0)	.867 (.740-.935)					222.6 (215.8-240.0)
Campostoma anomalum[6]	I	83	9	2.41 (0.9-5.7)	66.96 (50.0-91.0)	.769 (.582-1.022)					230.7 (212.1-242.1)
	II	51	9	3.66 (0.6-10.3)	73.9 (39.0-115.0)	.778 (.596-1.027)					238.9 (199.1-257.1)
Hypentelium nigricans	I	23	7	15.64 (2.9-79.7)	104.42 (70.0-178.0)	.991 (.830-1.413)					250.2 (233.5-270.8)
	II	6	4	16.84 (6.0-29.9)	118.8 (84.0-145.0)	.918 (.800-1.024)					244.8 (227.6-259.5)
Micropterus dolomieui	I	56	14	8.12 (2.1-22.1)	88.9 (57.0-125.0)	1.033 (.563-1.660)	26	8.84	90.1	1.079	160.9 (120.0-193.8)
	II	15	6	12.15 (2.3-24.8)	98.9 (65.0-134.0)	1.044 (.731-1.157)					163.0 (130.9-202.0)
Notropis cornutus	I	20	8	10.89 (5.2-21.6)	105.88 (83.0-128.0)	.857 (.713-1.029)					178.1 (176.6-180.7)
	II	6	6	24.42 (16.5-33.3)	138.33 (126.0-163.0)	.911 (.768-1.030)					167.4 (132.6-196.7)
Notropis camurus	I	54	10	2.38 (1.0-5.6)	67.14 (52-94)	.751 (.565-.873)	2	2.7	68.5	.817	232.9 (214.8-247.8)
	II	24	7	2.05 (0.8-6.3)	64.3 (50-94)	.675 (.457-.836					234.2 (218.3-245.8)
Labidesthes sicculus	I	125	15	1.8 (0.7-3.2)	76.03 (60-92)	.383 (.243-.470)	2	.75	67.5	.243	218.4 (195.0-231.2)
	II	115	12	1.75 (0.3-3.1)	76.7 (59-89)	.368 (.227-.455)					224.1 (218.0-239.5)
Hybopsis biguttata	I	73	10	3.11 (1.0-8.4)	69.24 (53-96)	.874 (.568-1.034)	1	2.7	78.0	.568	191.1 (180.0-201.0)
	II	34	7	10.58 (0.7-29.4)	96.34 (50-147)	.816 (.539-.951)					181.7 (172.0-191.0)
Dorosoma cepedianum	I	24	5	7.36 (4.6-9.6)	104.47 (92-114)	.639 (.452-.802)					182.4 (151.9-204.2)
	II	11	5	6.31 (4.1-9.8)	100.33 (85-112)	.608 (.504-.756)					176.6 ----------
Cottus carolinae	I	33	5	----------	----------	----------	33	1.16	44.35	1.179	----------
	II	15	3	0.74 (0.4-1.1)	40.73 (36-49)	1.103 (.78-1.27)					----------
Amia calva	II	2	2	58 (39.7-76.3)	163.5 (145-182)	1.284 (1.265-1.302)					36.6 (36.4-36.8
Percina caprodes	II	6	2	6.12 (3.2-10.2)	94.9 (80-111)	.667 (.583-.745)					----------

1. I represents the swimming chamber and II represents the test chamber.
2. The average is of all tests, while the range includes all observations.
3. The average is of all tests, and the range is of the test averages.
4. All specimens.
5. Specimens 112 to 148 mm in length.
6. Specimens 50 to 91 mm in length.

the following equation:

$$X = \frac{A\left(\frac{60}{B-C}\right)}{\frac{D}{E}}$$

where X = the oxygen consumption (ppm/gm/hr), A = the difference in the oxygen content (ppm) of the inflowing and outflowing waters of the chamber, B = the capacity of the chamber (3750 ml), C = the volume of water displaced by the fish (1.05 ml/gm of fish), D = the rate of water flow through the chamber (ml/min), and E = the weight of the fish (gm). Correction of water volume in the chamber for introduced fish was obtained by 23 measurements of displacement, which included forty specimens of eleven species (average of 1.05 ml/gm of fish, range 1.01 to 1.12 ml/gm of fish). The rate of flow ranged from 217 to 300 ml/min.

The opercular rates of the fishes in the swimming chamber and test chamber were obtained whenever possible by measuring the time required to open and close the opercles ten times. The results were expressed on a per minute basis.

The fishes tested in the swimming chamber were: Notropis camurus (Jordan & Meek), the bluntface shiner; Labidesthes sicculus (Cope), the brook silverside; Notropis cornutus (Mitchill), the common shiner; Hypentelium nigricans (LeSueur), the northern hogsucker; Cottus carolinae (Gill), the banded sculpin; Micropterus dolomieui Lacépède, the smallmouth bass; Campostoma anomalum (Rafinesque), the stoneroller; Tilapia nilotica (Linneaus), the Nile tilapia; Hybopsis storeriana (Kirtland), the silver chub; Hybopsis biguttata (Kirtland), the hornyhead chub; and Dorosoma cepedianum (LeSueur), the gizzard shad. Some information of the oxygen requirements of Percina caprodes (Rafinesque),

the logperch, and Amia calva Linneaus, the bowfin, was obtained while they were confined in the test chamber. After fishes were obtained they were held in the laboratory and fed at least once a day. The fishes were tested when, to all appearances, they had adjusted to the new environment, i.e. ate readily and were not unduly excited.

In calculating averages and ranges of dissolved oxygen for tests, the readings obtained by using the Alsterberg method were used because (1) the monitor was calibrated to the Alsterberg method, and (2) the scale on the monitor was not as finely calibrated as that of the Spectronic 20.

Results obtained for each species tested in the swimming chamber, expressed as percent surviving the six-hour period, were plotted against the average oxygen concentration for each test and a regression line was calculated.

The selected physical and chemical measurements were obtained at irregular times throughout the test period (see Table I).

COLLECTION AND CARE OF FISHES

All fishes, except A. calva and T. nilotica, were collected with woven-mesh nylon seines, and brought to the laboratory in plastic bags or rectangular tanks carried in a pickup truck. Tilapia nilotica were sent from a federal hatchery in Marian, Alabama, November, 1961, and A. calva were sent from LaCrosse, Wisconsin, November, 1962. Notropis cornutus and H. storeriana were collected from Skunk River, Story County, Iowa, September, 1962. Notropis camurus, P. caprodes, and D. cepedianum were collected from Fourteen Mile Creek, Cherokee County, Oklahoma, September through December, 1962. Cottus carolinae were collected from Tyner Creek, Adair County, Oklahoma, July, 1962. Labidesthes sicculus, C. anomalum, H. biguttata, and H. nigricans were collected from Barren Fork River and Fourteen Mile Creek, Cherokee County, Oklahoma, September through December, 1962. Micropterus dolomieui were collected from Barren Fork River, Cherokee County, Oklahoma, July and August, 1962.

Hybopsis storeriana and N. cornutus were collected in pools (6 in. to 3 ft deep) over sand bottoms; P. caprodes and C. carolinae were obtained in shallow riffles (2 to 12 in. deep); and N. camurus, C. anomalum, H. biguttata, L. sicculus, M. dolomieui, D. cepedianum, and H. nigricans were captured in pool and riffle areas (6 in. to 3 ft deep). Although most fishes were easily seined, collection of H. nigricans and large M. dolomieui, H. biguttata, and C. anomalum

required the use of drivers moving toward the seine. Cottus carolinae were captured at night, and the other fishes obtained throughout the day. Extreme care was required while seining and removing specimens of D. cepedianum from the seine to prevent abrasions and subsequent death.

Specimens of N. camurus, N. cornutus, and H. storeriana were extremely nervous, and when placed in carrying containers, many would "freeze" momentarily. If startled many would swim wildly against the sides of the container, and often leap 12 to 14 in. from the water.

All fishes adapted rapidly to the laboratory environment and most apparently ate dried food successfully. All, except M. dolomieui and A. calva, were fed a mixture of poultry lay-pellets and fifty percent protein meal, ground alfalfa pellets, and only on rare occasions Daphnia sp and/or white worms. Micropterus dolomieui and A. calva were fed a variety of minnows. Forage minnows were occasionally treated with terramycin and acriflavin, in both the field and the laboratory.

All fishes, except M. dolomieui that gained weight and A. calva that remained the same, showed a decrease in general body condition when held for extended periods (up to 13 months). With the exception of the following, a decrease in general body condition apparently did not adversely affect the fishes. Specimens of D. cepedianum died after 2 to 4 weeks in the laboratory. No reduction in general body condition was noted, although great variation existed within the population when collected. Labidesthes sicculus deteriorated after 6 to 8 weeks in the laboratory and many died.

REACTIONS OF FISHES TO FLOWING WATERS AND TO LOW OXYGEN CONCENTRATIONS

When fishes are placed in a confined channel their general reaction to a current is to swim in order to maintain a position with respect to some fixed reference point, usually detected by sight (Fry, 1957). Some specimens of M. dolomieui would not swim, even when an electrical stimulus was applied. No apparent difference could be observed between the individuals that would, and would not swim. Basu (1959) reported similarly for some specimens of Catostomus commersoni while they were being tested in an annular rotating chamber.

Initial reactions of most specimens tested to water flow were to swim rapidly from one screen to the other, making one or two trips, then all specimens orientated to meet the current. A general reaction of most specimens to low oxygen levels (near critical), was to restrict activity to an area 6 to 12 in. from the movable screen (except for brief excursions forward).

After an initial, violent swim, H. nigricans settled to the lower surface of the swimming chamber, spread the pectorals, bent the body to form an arc, and remained quietly with only an occasional movement of the caudal and no perceptible movement of pelvics or pectorals. They maintained the position for a short period, then were carried slowly backward toward the movable screen. Before the caudal touched the screen the fish swam strongly forward and continued to swim for a brief period. Specimens reacted similarly in water of

low oxygen content. A few individuals occasionally required a light electrical stimulation, particularly when oxygen levels were in the critical zone.

Campostoma anomalum (112 to 148 mm, length), reacted similarly to H. nigricans, but were able to maintain position for only a short period after settling to the lower surface of the swimming chamber, after which they drifted backward toward the movable screen. Prior to touching the movable screen they swam forward to the stationary screen, swam at the screen for a brief period, dropped to the lower surface, and repeated. When the oxygen content dropped, near 2 ppm, the specimens swam forward, allowed the current to move their anterior end upward until a vertical position was reached, often turning completely over, and then carry them toward the movable screen. After some repetition of the action, the fish returned to the previous routine. The same type of reaction was noted in the test chamber with approximately the same oxygen concentrations, i.e. letting the body fall into a vertical position and turning over. Smaller specimens (50 to 91 mm, length), attempted to settle to the lower surface of the swimming chamber and maintain their position in a manner similar to the larger specimens, but were immediately swept backward to the movable screen area. Some specimens braced themselves for brief moments on the screen, or electrodes, or occasionally were swept backward onto the screen. Except for brief moments of the above reactions the fish swam rather steadily. The activity of larger specimens at 2 ppm was, if observed at all, noted in smaller specimens at oxygen levels between 1.2 to 1.5 ppm. Slight electrical stimulation was required with a few individuals when oxygen levels were in the critical zone, particularly with smaller specimens.

After an initial, violent reaction to the current, N. camurus swam steadily and only occasionally drifted back toward the movable screen. Most individuals swam near the stationary screen until oxygen levels approached the critical zone. The general pattern of swimming near the movable screen was then followed. Some specimens swam near the movable screen for the entire test period with only rare excursions forward. Specimens reacted in a similar manner to waters of low oxygen content. Weak electrical stimulation was required with only 2 or 3 individuals when oxygen levels were in the critical zone.

The initial reaction of specimens of N. cornutus to the current often times involved an attempt to get behind the movable screen. After a few moments of effort the fish swam rather steadily, and only occasionally allowed the current to carry them backward toward the movable screen. They swam throughout all areas of the swimming chamber until oxygen levels approached the critical zone, when they swam near the movable screen. No other reactions to low oxygen levels prior to death were noted. Weak electrical stimulation was required with only 1 or 2 individuals when oxygen levels were in the critical zone.

Labidesthes sicculus maintained a position near the stationary screen and swam steadily for long intervals, 30 minutes or more. Occasionally they drifted backward and swam at a different position. As the oxygen content approached the critical level they were gradually carried backward until they were swimming near the movable screen. They swam there steadily until swept against the screen, unable to recover. They died shortly after coming to rest on the screen. No electrical stimulation was required.

Specimens of T. nilotica swam rather steadily near the stationary screen, except when drifting backward with the current. Some specimens occasionally bit and chased each other. They favored the inflow end of the swimming chamber when oxygen levels were high and gradually drifted backward as the oxygen content reached critical levels. Small specimens swam more in the rear half of the swimming chamber regardless of the oxygen concentration. No other definite reactions to low oxygen levels were noted, prior to death. Weak electrical stimulation was required with some individuals regardless of the oxygen concentration, but more generally when oxygen dropped below 1 ppm.

Micropterus dolomieui was extremely violent when first exposed to the current. Some individuals did not swim and allowed the current to sweep them against the screen. After the initially violent reaction, some specimens also fell backward against the screen. After a few minutes to two hours, some, or all specimens commenced swimming. They swam near the stationary screen when oxygen levels were above the critical zone and near the movable screen when oxygen levels were near, or in the critical zone. Prior to death no other definite reactions to low oxygen concentrations were observed. Electrical stimulation was not used as it failed to produce the desired effects.

Specimens of H. biguttata reacted to the current by swimming slowly, and soon were forced backward onto the movable screen. They braced themselves a few minutes on the screen and gradually began swimming near it. After a short time they swam forward to the stationary screen area and continued to swim rather steadily. Periodically they allowed the current to bring the anterior part of their bodies upward until they almost reached a vertical position, which stopped their forward motion and

caused them to be swept backward toward the movable screen. Prior to touching the screen the fish regained equilibrium and swam forward. Specimens rested on the screen by bracing their tails or caudal peduncles on it or the electrodes when oxygen levels approached the critical zone. They swam in the movable screen area once oxygen levels became critical and required frequent electrical stimulation, but no other noticeable reactions to low oxygen levels were observed prior to death.

After an initially violent reaction to the current, H. storeriana swam near the lower surface of the swimming chamber and favored no particular area. They swam near the movable screen after the oxygen content approached the critical zone. No other definite reactions to low oxygen levels were observed, prior to death. Weak electrical stimulation was required with only 1 or 2 specimens after oxygen levels fell into the critical zone.

Dorosoma cepedianum swam back and forth between the screens when first exposed to the water flow, and then began swimming rather steadily near the stationary screen. They swam near the movable screen as oxygen levels approached the critical zone and died shortly after being swept onto it. No electrical stimulation was required.

Specimens of C. carolinae reacted to the water flow by attempting to cling to the lower surface of the swimming chamber, then clinging to the screen or bracing their caudal peduncles on the screen or electrodes. Some specimens swam briefly, less than thirty seconds. When water flow was only 1/8 ft/sec the fish could maintain a position anywhere in the swimming chamber and apparently were not affected by the current. No other reactions to low oxygen levels were noted prior to

death. Electrical stimulation was not used because it did not affect their reactions, i.e. they would move forward, drift backward, and then stay on the screen regardless of the strength of the electrical shock.

TOLERANCE OF FISHES TO LOW OXYGEN LEVELS WHILE FORCED, AND NOT FORCED TO SWIM

The oxygen concentration at which 75% of the specimens survived was arbitrarily selected from the calculated regression line as an estimate of the level at which oxygen became limiting for a species. Confidence intervals, of means of percent survival, were calculated to obtain the expected range of means of populations, tested at the selected oxygen level, in which not more than one mean of 20 might fall outside the calculated range (see Table III).

Data obtained from specimens tested in the swimming chamber showed that oxygen concentrations approaching 2 ppm were required to maintain populations of most fishes when water temperatures were in the 70 to 80 F range. Micropterus dolomieui would succumb as oxygen levels approached 3 ppm and few would be expected to tolerate 2 ppm. Labidesthes sicculus and H. biguttata would succumb at oxygen levels below 3 ppm. Few specimens of L. sicculus might tolerate levels below 2 ppm, while some H. biguttata would survive at lower levels. Specimens of H. nigricans, N. cornutus, N. camurus, C. anomalum, T. nilotica, and H. storeriana would succumb at oxygen levels below 2 ppm. Few large C. anomalum would survive oxygen levels of 1 ppm. Many T. nilotica would survive levels of 1 ppm and lower. The data also revealed, as did the voluminous literature, that most fishes not stimulated to activity tolerated oxygen levels approaching 1 ppm for varying

TABLE III

LOW OXYGEN LEVELS OF FISHES

	Forced to Swim		Not Forced to Swim	
	Oxygen Level[1] (ppm)	Confidence[2] Interval	Minimum Oxygen Level Reached	Tolerance Level (ppm)
A. calva	-	-	No	less than 1.5
H. nigricans	1.6	44-100	Yes	1.0
N. camurus	1.85	56-94	No	less than 1.26
N. cornutus	1.5	45-100	No	less than 1.0
H. storeriana	1.7	43-100	Yes	between 1.0-1.5
H. biguttata	2.2	52-98	No	less than 1.6
C. anomalum (All)	1.6	44-100	No	less than 1.0
112-148 mm	1.65	48-100	No	less than 1.0
50-91 mm	1.26	37-100	No	less than 1.0
L. sicculus	2.7	49-100	Yes	between 1.0-1.5
M. dolomieui	3.3	0-100	Yes	1.0
T. nilotica	1.2	38-100	No	less than 0.5
P. caprpdes	-	-	No	less than 1.5

1. Calculated 75% survival level.
2. Mean would be in range 95% of the time.

periods, when water temperatures were in the 70 to 80 F range (see Figure 2 and Table III).

Preliminary testing of D. cepedianum in the swimming chamber and the test chamber revealed extreme variation in oxygen requirements. It seems, from the data obtained, that oxygen levels of 2 ppm, or greater, would be required for specimens when not forced to exercise and 4 ppm, or greater, would be required in the swimming chamber (Figure 3).

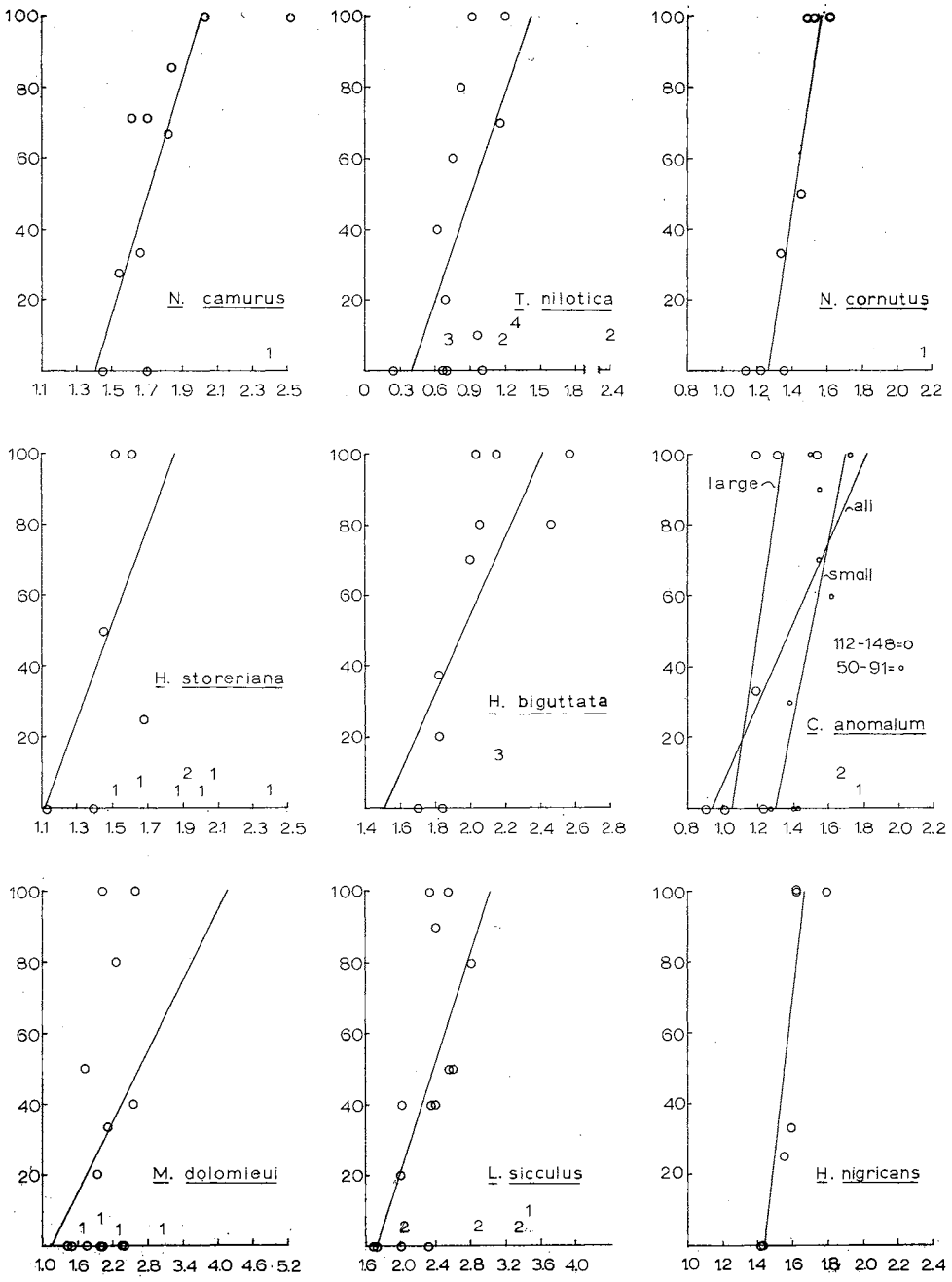


Figure 2. Tolerances of fishes to low oxygen levels while swimming in flowing waters. Oxygen content in ppm on ordinate, and percent surviving the recorded time period on abscissa. Circles represent percent surviving the recorded time period. Numbers represent individuals that succumbed prior to reaching the oxygen level of a test. Lines were computed by linear regression.

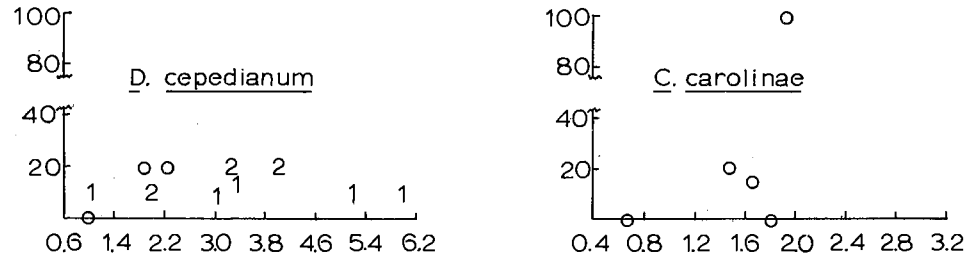


Figure 3. Preliminary testing of D. cepedianum and C. carolinae in flowing waters of low oxygen content. Oxygen content in ppm on ordinate, and percent surviving the recorded time period on abscissa. Circles represent percent surviving the recorded time period. Numbers represent individuals that succembed prior to reaching the oxygen level of a test.

Specimens of C. carolinae tested in the swimming chamber did not swim but were tested to measure their abilities to live in flowing and standing waters of reduced oxygen content. Specimens tested in standing waters indicated an ability to tolerate oxygen levels of 1 ppm, and lower, whereas specimens tested in the swimming chamber required oxygen levels approaching 2 ppm (Figure 3).

OXYGEN CONSUMPTION AND OPERCULAR RATES OF FISHES

Oxygen consumption values have been considered an index of fish activities, reflecting the speed of expenditure of energy, and to some extent measuring the oxygen requirements of fishes. Data obtained concerning oxygen consumption of fishes (see Table IV), were presented for the use of investigators, but few conclusions were drawn from the results because the experiments were not designed to yield information required for standard or active oxygen consumption. Although the fishes were not intentionally stimulated in the test chamber, they were undoubtedly metabolizing at a faster rate than required for standard metabolism. The low oxygen levels tolerated by specimens in the test and swimming chambers suggest slower metabolism in the test chamber because lower oxygen levels were tolerated in the test chamber. The values were generally consistent with current opinions concerning the relationships between oxygen consumption, body size, and muscular activity (Winberg, 1956), and were considered an estimate of routine metabolism.

The fishes, with the exception of A. calva, are associated with fairly clear streams. Specimens of A. calva are associated with sluggish rivers and backwater areas. There was a definite difference between oxygen consumption rates of specimens of A. calva and other fishes. There was also a definite difference between oxygen consumption rates of specimens of N. camurus and other fishes. Specimens of N. camurus have been observed swimming in fast water areas more frequently

TABLE IV

A SUMMARIZATION OF THE TESTS IN WHICH OXYGEN CONSUMPTION VALUES WERE OBTAINED

No. of Fish	Weight (gm)	O_2 (ppm) Inflowing Water	Temp (°F)	O_2 Consumed (ppm/gm/hr)	Ave. O_2 Consumed (ppm/gm/hr)
Tilapia nilotica					
5	2.2 (1.9-2.3)	0.91 (0.8-1.05)	78.5	.0423	
5	1.62 (1.3-2.3)	0.62 (0.43-0.74)	78.5	.0318	
5	1.4 (1.1-1.7)	0.7 (0.68-0.72)	78.0	.0577	
5	1.7 (1.5-1.9)	0.67 (0.66-0.68)	75.5	.0203	.0412
10	2.2 (1.4-3.0)	0.96 (0.9-1.05)	73.5	.0390	
10	1.61 (1.1-2.5)	1.19 (1.16-1.23)	70.5	.0437	
10	1.61 (1.0-2.4)	0.98 (0.9-1.06)	73.0	.0384	
6	1.4 (0.9-1.8)	1.16 (1.05-1.23)	73.0	.0563	
Hypentalium nigricans					
1	24.4	1.61 (1.5-1.67)	79.0	.0419	
1	7.1	1.43 (1.3-1.56)	77.5	.0908	
1	17.7	1.55 (1.35-1.7)	73.0	.0572	.0518
1	18.2	1.55 (1.35-1.7)	73.0	.0435	
2	17.95 (6.0-29.9)	1.61 (1.5-1.67)	74.0	.0256	
Micropterus dolomieui					
4	4.9 (3.10-7.00)	1.52 (1.46-1.56)	78.0	.0492	
5	3.26 (2.30-4.50)	1.94 (1.63-2.21)	72.0	.0461	
1	24.8	2.55 (2.08-3.09)	71.5	.0444	.0387
1	20.3	2.43 (2.24-2.57)	71.5	.0380	
1	15.4	2.02 (1.78-2.31)	71.5	.0376	
3	4.23 (3.7-5.0)	2.25 (1.94-2.57)	72.0	.0170	
Campostoma anomalum					
1	24.0	1.54 (1.35-1.70)	78.0	.0337	
1	17.7	1.19 (1.05-1.30)	77.5	.0296	
1	20.8	0.90 (0.8-0.98)	77.5	.0260	
1	18.9	1.01 (0.88-1.13)	78.0	.0241	
1	22.0	1.23 (1.1-1.3)	78.5	.0333	
1	22.0	1.31 (1.16-1.42)	78.5	.0372	
4	2.6 (1.0-7.2)	1.73 (1.62-1.87)	77.0	.0794	.0417
5	2.16 (1.5-3.0)	1.51 (1.33-1.64)	75.5	.0522	
3	2.17 (0.9-4.0)	1.43 (1.42-1.46)	77.5	.0957	
12	1.08 (0.6-1.4)	1.28 (1.1-1.36)	74.0	.0252	
4	6.58 (5.8-7.8)	1.55 (1.35-1.78)	73.5	.0285	
7	4.36 (2.6-8.1)	1.41 (1.39-1.48)	73.25	.0331	
10	1.86 (1.2-2.9)	1.39 (1.3-1.5)	70.5	.0436	
3	7.23 (5.7-10.3)	1.62 (1.48-1.85)	71.0	.0416	

TABLE IV (Continued)

No. of Fish	Weight (gm)	O_2 (ppm) Inflowing Water	Temp (°F)	O_2 Consumed (ppm/gm/hr)	Ave. O_2 Consumed (ppm/gm/hr)
Dorosoma cepedianum					
2	4.75 (4.6-4.9)	2.23 (2.04-2.4)	74.0	.0547	.0539
1	5.1	2.04 (1.25-2.86)	72.0	.0531	
Hybopsis storeriana					
1	13.3	1.14 (1.05-1.32)	80.0	.0208	
1	12.7	1.05 (0.96-1.16)	80.0	.0780	.0421
2	13.6 (11.0-16.2)	1.92 (1.84-2.08)	77.0	.0276	
Notropis cornutus					
1	33.3	1.61 (1.53-1.72)	80.0	.0705	
1	16.5	1.48 (1.34-1.56)	78.0	.0487	
1	29.5	1.33 (1.25-1.42)	75.5	.0396	.0505
1	25.5	1.22 (1.16-1.27)	75.5	.0427	
1	21.4	1.14 (1.05-1.32)	80.0	.0509	
Percina caprodes					
3	5.8 (3.2-10.2)	1.68 (1.6-1.78)	76.0	.0634	.0589
3	6.43 (4.4-9.7)	1.88 (1.64-2.06)	74.5	.0544	
Notropis camurus					
3	1.6 (1.5-1.8)	1.82 (1.74-1.92)	78.0	.1258	
2	1.3 (1.3-1.3)	1.66 (1.51-1.77)	78.5	.0796	
4	1.63 (0.8-3.4)	1.84 (1.64-1.98)	78.0	.1222	
6	2.47 (1.1-6.1)	1.54 (1.42-1.68)	77.0	.0822	.1216
3	3.6 (1.2-6.3)	1.61 (1.5-1.78)	78.0	.0666	
3	1.47 (1.2-1.8)	1.45 (1.42-1.5)	78.0	.1284	
2	1.15 (1.1-1.2)	1.7 (1.5-1.78)	76.5	.2465	
Labidesthes sicculus					
5	0.52 (0.3-0.7)	2.31 (2.24-2.43)	74.0	.1654	
5	2.40 (1.3-3.1)	2.11 (1.7-2.4)	75.5	.0586	
9	1.75 (1.2-2.5)	2.4 (2.24-2.57)	75.0	.0573	
10	1.98 (1.6-2.3)	2.83 (2.72-2.9)	71.0	.0442	
10	1.55 (0.9-2.4)	2.43 (2.21-2.58)	72.0	.0742	.0696
10	1.94 (1.5-2.3)	2.38 (2.24-2.58)	73.0	.0564	
10	1.98 (1.6-2.4)	2.6 (2.42-2.88)	73.0	.0538	
10	1.79 (1.2-2.2)	2.59 (2.4-2.88)	72.0	.0514	
10	1.52 (0.9-2.1)	2.83 (2.61-3.09)	72.0	.0631	
8	1.95 (1.6-2.4)	2.6 (2.24-2.58)	73.0	.0718	
Amia calva					
1	39.7	1.55 (1.35-1.74)	73.0	.0105	
1	76.3	1.59 (1.47-1.74)	71.5	.0137	.0121

TABLE IV (Continued)

No. of Fish	Weight (gm)	O_2 (ppm) Inflowing Water	Temp (°F)	O_2 Consumed (ppm/gm/hr)	Ave. O_2 Consumed (ppm/gm/hr)
Hybopsis biguttata					
5	1.18 (0.7-2.4)	1.84 (1.78-1.92)	73.0	.0822	
1	29.4	2.46 (2.31-2.63)	73.0	.0519	
11	1.62 (0.8-2.6)	2.05 (1.74-2.22)	73.0	.0509	
2	14.7 (7.0-22.4)	1.82 (1.64-2.17)	74.0	.0343	.0525
1	19.7	2.15 (1.92-2.31)	75.0	.0552	
4	5.98 (4.1-8.5)	1.82 (1.66-2.04)	75.5	.0464	
10	3.33 (0.8-8.6)	1.99 (1.67-2.38)	75.5	.0463	

than any other fishes tested. The data obtained agrees with Winberg's (1956) conclusion that the routine metabolic rates of fishes of different ecological groups, if they do differ, do so only to a slight degree, and we do not have sufficient data to draw conclusions.

Investigators have observed that opercular rates increased when oxygen levels decreased. Mount (1961) reported that the opercular rate in *M. dolomieui* increased from 85/min at 6 ppm to 135/min at 1 ppm. The present study revealed no significant differences between the average opercular rates at different oxygen levels. Probably because the measurements were obtained in a relatively narrow oxygen range, near or in the critical zone. Belding (1929) observed that the opercular rate was faster in small specimens of most species, and my observations coincided with his.

No significant differences between the average opercular rates of specimens tested in the test and swimming chambers were noted. Specimens of *H. nigricans*, *C. anomalum*, *N. camurus*, and *L. sicculus* had average opercular rates greater than 200/min in both test chambers, while *H. storeriana*, *T. nilotica*, *N. cornutus*, *H. biguttata*, *M. dolomieui*,

and D. cepedianum had average opercular rates less than 200/min. The average opercular rates of specimens of D. cepedianum, N. cornutus, H. nigricans, and H. biguttata increased slightly in the swimming chamber over those in the test chamber, and the average rates for C. anomalum, T. nilotica, H. storeriana, N. camurus, M. dolomieui, and L. sicculus decreased slightly in the swimming chamber below those in the test chamber. Because of variation within a species the differences could not be judged significant without performing a series of carefully designed experiments (see Table II for a summarization of the average opercular rates).

DISCUSSION

Data obtained from tests in the swimming chamber indicated a relatively narrow oxygen range (the critical zone), in which fish mortality occurred. Shepard (1955) also observed a relatively narrow oxygen range in which mortality occurred with young specimens of Salvelinus fontinalis, i.e. at 1.86 ppm all survived and at 1.5 ppm all died. Although it is thought that a probit transformation would probably provide a more precise estimate of the minimum oxygen levels required to maintain populations of a species, the variation of oxygen measurements during a test, often exceeding 0.5 ppm, provided numerous opportunities for variation of response at the same average oxygen level when tests were performed in the critical zones. A regression line, which biased estimates of the minimum oxygen level required by a species upward, rather than downward, provided useable and logical results for all species tested except M. dolomieui. It was felt that a more rigorous statistical treatment was not justified for the data obtained from specimens of M. dolomieui because the wide variation in response of the specimens tested could not be attributed to fluctuations of oxygen levels throughout a test, and no explanation was apparent for the failure of some specimens to swim in the swimming chamber. The calculated 75% survival level for specimens of M. dolomieui seems to be a logical, but high, estimate of the upper extreme of the critical zone, but the regression technique failed to provide adequate information, i.e. the prediction that the range of means of populations tested

at the selected oxygen level would be expected to lie between 0 and 100%, is of little value.

Data obtained from specimens of C. anomalum showed a definite difference in the tolerance of two size groups to low oxygen levels while forced to swim against a water flow. Results obtained with specimens of T. nilotica also suggested that for fish below a certain size, either oxygen requirements increased or current became a limiting factor. The swimming speed required of the fishes in the swimming chamber was much less than the speeds reported by Dow (1962), and less than the cruising speeds reported by many authors (Bainbridge, 1961).

Data obtained from specimens of H. storeriana were not considered as valid as data obtained from other species, because in the last two tests specimens succumbed at oxygen levels well above the levels that specimens in previous tests tolerated. The lengths, weights, and K factors of the fish in the last two tests were similar to the preceding tests and no visible differences in specimens could be seen. Two possible explanations were (1) the first specimens tested were stronger individuals with a greater resistance to low oxygen levels, and (2) the latter specimens were actually not in good condition. Unfortunately specimens were not readily available to continue the testing program. Because the same oxygen range appeared critical in the swimming and test chambers, the first explanation seems most plausible, i.e. fish swimming should need more oxygen than fish not required to swim.

Preliminary testing with D. cepedianum showed they would be difficult to test with the methods employed. Specimens that were swept against the screen during a test were easily descaled, necessitating

complete cleaning of the system after each test. If only one specimen was employed per test that problem might have been averted.

Unfortunately there was no method of measuring the physical and psychological health of the fishes tested, and except for the results obtained with H. storeriana, D. cepedianum, and M. dolomieui, the techniques employed provided good results. Although the nutritional requirements of many of the species may not have been adequately fulfilled, specimens of L. sicculus, which wasted away after 6 to 8 weeks captivity, provided consistent results from 1 to 2 days, to, 4 to 5 weeks after capture.

It seems improbable that fishes, in nature, would be required to actively metabolize by swimming against a current for six hours. By combining information obtained in studies of the standard, routine, and active oxygen requirements of fishes at different life history stages, and under different environmental conditions, the influence of oxygen on the fish populations of a community should be better understood.

Contributions to our knowledge of the oxygen requirements of some of the fishes here studied, have been made by other investigators. Black et al. (1954) reported lethal oxygen levels for specimens of Micropterus dolomieui and Notropis cornutus, at low carbon dioxide levels, of approximately 1 ppm (temperature range of 15 to 20 C). Burdick et al. (1954) reported that specimens of two populations of Micropterus dolomieui had lethal oxygen levels of 1 ppm and lower, at 80 F (mean survival time was approximately 8 hours). Summers (1954) reported that specimens of Micropterus dolomieui and Dorosoma cepedianum were living in water having a dissolved oxygen content of spproximately 1 ppm.

Mount (1961) recorded lethal limits of 1 ppm for specimens of Micropterus dolomieui. Cooper (1960) reported lethal oxygen levels for specimens of Notropis cornutus of 1.23 ppm (0.56 to 6.2 ppm) at 80 F, and 1.05 ppm (0.46 to 6 ppm) at 75 F.

A challenging problem for future research would be the construction of an apparatus that would simulate a portion of a stream. Fishes could then be placed in the apparatus for life cycle studies exposed to various combinations and levels of environmental factors that previous research had shown to be tolerable for at least some life history stages. By correlating information gained with judicious field observations and the simulated natural environments, we may better propose adequate minimum oxygen standards for aquatic habitats, concomitant with existing environmental conditions. Another area that would provide useful information regarding oxygen standards would be the area of fish behavior. Although the majority of researchers have reported that oxygen is a nondirective stimulus, and fish will normally swim into areas of low oxygen content with no hesitation (Hoglund, 1961), Whitmore et al. (1960) reported that fish are able to detect and avoid areas of low oxygen content. The chemical changes that take place within a fish as a result of muscular activity may also affect fish behavior (see Black, 1957, for a review of our knowledge of the effects of muscular activity on metabolism).

SUMMARY

1. Tolerances of each of nine species of fishes to low oxygen levels while forced to swim against a water flow of approximately 0.8 ft/sec for a six-hour period were measured.
2. An apparatus was constructed in which the rate of water flow and concentration of dissolved oxygen was controlled.
3. Observations were made concerning the collection, maintenance, and behavior of the fishes.
4. Oxygen consumption values when specimens were not forced to swim against a water flow were obtained for twelve species.
5. Opercular rates while specimens were, and were not forced to swim against a water flow were obtained for twelve species.
6. The ability of specimens of Cottus carolinae (which refused to swim against a current of water) to live in flowing waters of low oxygen content was measured.
7. Observations were made of the ability of thirteen species of fishes to survive low oxygen levels while not forced to swim against a water flow.
8. The importance of studying the respiratory requirements of fishes is discussed and areas for future research are suggested.

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