Seasonal Changes in Bluegill Metabolism[1]

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ABSTRACT

A one-year study of bluegill metabolism in a California reservoir indicated that field determinations of oxygen uptake rates and multivariate analyses of results with respect to weight, activity, and temperature during each season were feasible in the form,

$$Y_i = \text{constant} + b_1 X_2 \quad b_3 X_3$$

where Y, is the expected log milligrams of oxygen consumed per hour, X_1 is the log weight in grams, x_2 is the swimming velocity in meters per minute, X_3 is the temperature in degrees centigrade, and where b_1, b2, and b_3 are the respective partial regression coefficients. By delimiting "seasons" on the basis of thermal and related limnological characteristics, the data yield the equations:

Apr.-June	$Y_i =$	$-0.6954 + 0.8036X1$	$0.0250X_2$	$0.0069X_3$
July-Aug.	$Y_i =$	$-2.1951 + 1.0621X_1$	$0.0138X2$	$0.0567X_3$
Sept.-Dec.	$Y_i =$	$-0.9242 + 0.8494X_1$	$0.0142X2$	$0.0198X_3$
Jan.-Feb.	$Y_i =$	$-1.9310 + 0.8624X_1$	$0.0427X_2$	$0.1153X_3$

The multiple correlation coefficients for these equations are highly significant as are all the partial regression coefficients, excepting the low spring $b_3 = 0.0069$.

The weight relationships expressed by b_1 are remarkably close to Krogh's constant of approximately 0.85 except in the summer when the calculated higher rate may be due to the spawning condition of the larger fish and the post-spawning condition of the smaller fish.

There are similar relationships of respiratory rates with respect to swimming movements over the spring, summer, and autumn seasons, but during winter it appears that relatively higher oxygen consumption is required for comparable swimming activity.

The respiratory rates with respect to temperature appear to be of the same order during spring and autumn when they are lower than in summer and much lower than in winter. The high respiration-temperature regressions in winter, and possibly in summer, may be due to excessive spontaneous activity not reflected as swimming motion at temperature extremes.

Females during each season have higher metabolic rates than the males over the range of temperatures and activities encountered, but the differences are not statistically significant.

Groups of fish during the spawning season have higher than average respiratory rates than do single fish, other conditions being equal. Limited data suggest that social facilitation exists during the summer after spawning.

Variations in Felt Lake limnological conditions are considered from the standpoint of about a 50 per cent reduction in volume from spring to autumn, the absence of a well developed littoral zone, and the rather drastic spring to autumn and winter declines in bottom fauna and average weights of the larger fish. A comparison of the above regressions over average spring and autumn conditions reveals that metabolic rates would be about equal,

although in spring the fish grow rapidly and spawn, while in autumn and winter they lose weight. Similarly the calculated winter metabolic rates are higher at comparable temperatures than those of spring or autumn due possibly to cold adaptation.

While the potential growing season in Felt Lake would be about twice as long as that for the northern portion of the native bluegill range, the growth rates are of the same order. The biological productivity of the bluegill in Felt Lake and similar western U. S. waters is interpreted to be much poorer than in eastern areas because of the longer growing season without adequate food (especially bottom fauna) production and because there appears to be no adaptive mechanism for lowering the metabolic requirements during seasons of poor food supplies.

INTRODUCTION

The purpose of this study is to describe quantitatively seasonal changes in respiratory rates of the bluegill, *Lepomis macrochirus* (Centrarchidae), in relation to seasonal limnological variations of Felt Lake, a small California reservoir.

Included among the physiological and limnological factors which influence the respiratory (oxygen consumption) rate are: the direct temperature effect, effect of temperature acclimation, oxygen and carbon dioxide content of the water, body weight, body fat content, cruising speed or activity, recency and amount of feeding or degree of starvation, extent of social facilitation, sex, sexual development and spawning, excitement, injury, shock, parasitism, disease, and perhaps many other factors. Fry (1957) has given a comprehensive account of the literature dealing with the effects of these factors on fish respiration and metabolism, and Wohlschlag (1957) has noted that body weight, swimming velocity, and temperature accounted for most of the variability in oxygen consumption rates of an arctic whitefish. Gerking (1954) has emphasized the importance of fish metabolism data by showing how metabolism and biological production are related in a natural environment.

Customarily respiratory rates are expressed as log oxygen consumed per hour, and metabolic rates are expressed as log oxygen consumed per hour per kilogram of body weight, either in total weight or in protein weight units. Respiratory or metabolic rates are also expressed as "standard" rates which approach basal rates, as "active" rates which pertain to fish with sustained "maximum" swimming velocities, and as "routine" or intermediate rates which pertain to fish exhibiting spontaneous activity other than swimming (Fry 1957). Most of the published data on fish metabolism refer to determinations for fish carefully acclimated to controlled laboratory conditions, although Pritchard (1955) has made determinations for two small marine species held in concrete cisterns, and Wohlschlag (1957) has made determinations on whitefish in their natural habitats. There is very little information available to suggest to what extent metabolism of fish varies with seasonal limnological conditions.

On the assumption that bluegills in their natural state were "acclimated" to currently existing limnological conditions, a field study was set up at Felt Lake to evaluate any seasonal changes that might occur in the respiratory rates with respect to body weight, various swimming rates, temperature, sex, and grouping.

DESCRIPTION OF FELT LAKE

Felt Lake is a reservoir, retained by an earth-fill dam, on the Stanford University campus. It is about five miles west of Palo Alto, California, at Lat. 37° 24' N and Long. 122° 14' W. The inflow is via a one-half mile diversion ditch from Los Trancos Creek. Above the diversion the drainage basin consists of about 5.4 square miles; immediately tributary to the lake, the drainage basin consists of about 110 acres. Rainfall to the extent of about 15 inches per year occurs mostly from November through March. These winter rains maintain the reservoir at a 300 million gallon capacity with a surface area of 46 acres until about May. The level declines with irrigation needs about 10-12 feet by late summer when the volume is about 125 million gallons. In 1956-57 the lake was full from March to June. From June to October the level dropped regularly a total of 10 feet.

During the very dry November and December period the level dropped only one foot. The lake filled during January and February, 1957.

The 1956-57 surface water temperatures ranged from 8.0-26.5°C. Formation of a partially stable thermocline in summer and partial hypolimnetic oxygen depletion can occur; however, the oxygen content of the surface waters remained near saturation levels during 1956-57.

From spring through autumn the littoral areas tend to have a fairly dense growth of weeds which follow lakeward the declining water level. Consequently the littoral fauna, which reaches its peak in late spring, is poorly developed in comparison to lakes with constant levels. It is estimated that an average volume of stomach contents for spring and early summer would be at least 1-2 cc. Frymire (unpublished M.S. thesis) has shown that the bottom fauna as a food supply for bluegills whose fork lengths were 125 mm and over is severely curtailed by autumn when the average volume of stomach contents declined to 0.20 cc per fish. By early winter the average volume had declined to 0.17 cc, with mollusk and plant remains making up a large portion of the stomach contents. By late March insects were again important foods, and the average volume of stomach contents rose to 0.52 cc.

On the basis of several hundred length and weight measurements taken in early May and again in early November, 1956, for fish in the fork-length classes of 125-149 mm and 150 mm and over, it is apparent that there is a marked decline in condition (weight per unit length). In the spring the smaller class had respective averages of length and weight of 138.4 mm and 54.8 g, while the respective averages for the larger class were 158.5 mm and 90.1 g. The corresponding data for autumn were 139.7 mm and 50.5 g, and 157.4 mm and 75.5 g.

The bluegill is the dominant species in the lake. From unpublished population dynamics studies, the growth and recruitment is rapid only in the spring and early summer when the population of fish whose fork lengths are 125 mm and over varies from 20 to 25 thousand. Following the late summer and autumn periods of poor growth and high mortality rates accompanied by a high incidence of parasitism, this population is reduced by as much as one-half. The adverse winter conditions persist until March warming when the smaller fish, especially, start to grow rapidly and begin to spawn in April to May. The larger bluegills start to grow somewhat later and begin to spawn from May to June and continue spawning as late as August.

Felt Lake also has a small population of largemouth bass *(Micropterus salmoides)* and very small populations of the brown bullhead *(Ictalurus nebulosus)* and the sculpin *(Cottus asper).*

FIELD PROCEDURES

Bluegills were obtained by seining or trapping in surface waters. They were retained in a live car for a period of at least one hour before measurement of their respiratory rates in a respiration chamber. All respiratory measurements were carried out in the field from March, 1956, through February, 1957.

The respiration chamber, described by Wohlschlag (1957), is a circular, completely enclosed, transparent plastic chamber which can be rotated. Rotation was effected by suspending the chamber from an inverted, spring-wound, phonograph motor whose velocity could be controlled by a manually regulated governor. In the earlier determinations the motor and chamber were suspended from a four-legged derrick set up in shallow water near shore. Later determinations were made when the rig was suspended through a deck hatch of a raft located at the center of the lake. Approximate dimensions of the chamber are: outside diameter, 45 cm; inside diameter, 25 cm; depth, 10 cm; and volume, 10,400 ml. A complete revolution by a swimming fish would equal a distance of about one meter.

For each determination fresh surface lake water was added to the chamber through a funnel-like reservoir and connecting plastic tube. Fish were introduced through a lid which was then sealed. Runs were made with single large fish due to space limitations within the chamber, but smaller fish were

often used in groups of two to eighteen depending upon their size and availability. Bubbles were removed through the connecting tube of the reservoir and the entire chamber was lowered by a pulley system so that it was barely immersed in the lake. The chamber was then rotated at whatever approximately constant velocity the fish would tend to maintain.

Samples of water for oxygen analyses were withdrawn through an outlet tube after the chamber was raised above lake level. Simultaneously fresh water from the reservoir replaced the withdrawn water without the introduction of bubbles. These samples were taken initially and at 10- to 15-minute intervals over a period of one-half to one hour. The oxygen contents of the samples were determined by the modified Winkler method. Except for the spring months of 1956 all oxygen analyses were completed in the field.

While respiratory rate determinations were underway, temperature and rotation velocities were periodically recorded; after the run these data were averaged, the fish were weighed, and notes were taken on sex, sexual development, stomach contents, and visible parasites.

RESULTS AND COMPUTATIONS

Field data

To determine the rate of oxygen consumption, or respiration, the oxygen content of the chamber was calculated for the time of each water sampling. A systematic correction was made to allow for the additional oxygen introduced into the chamber by the fresh water which replaced the withdrawn water. For each respiration run the corrected oxygen contents of the chamber were plotted against elapsed time. The least squares calculation of the slope of the best straight line through these four or five points yielded the respiratory rate in milligrams of oxygen consumed per hour for the total weight of the fish. In Appendix Tables A—D are listed the respiratory rates in logarithms (Y), the log total weights (X_1), the swimming velocity in meters per minute (X_2), the temperatures (X_3), and the metabolic rates (Y_1) expressed as log

milligrams of oxygen consumed per hour per kilogram. The four "seasons" into which these data are separated are arbitrary delimitations of: (1) a period of rapidly increasing temperature and spawning activity in spring; (2) a warm summer period with declining water levels; (3) a long, late summer and autumn period of low water level characterized by declining temperature and benthos and by a rising incidence of starvation and parasitism; and (4) a cold winter period of winter rains with high and turbid waters.

Multiple regressions

The interrelationships of the expected log oxygen consumption (Y_e), which is dependent on the log body weight in grams (X_1), the activity (X_2) in meters per minute, and temperature (X_3) in degrees centigrade, can be expressed as a multiple regression (Wohlschlag 1957). Routine procedures in most standard statistics books, *e.g.,* Goulden (1952) and Snedecor (1956), are available for the calculation of the multiple regression,

$$Ye = \text{constant} + b_1 \qquad b_2 X_2 + b_3 X_3$$

where b_1 is the partial regression coefficient of Y on X_1 with constant X_2 and X_3, b_2 is the partial regression coefficient of Y on X_2 with constant X_1 and X_3, and b_3 is the partial regression coefficient of Y on X_3 with constant X_1 and X_2.

The regressions based on data in Appendix Tables A—D have been calculated in two ways. The first method involved the values Y and X_1 as tabulated for the total oxygen consumed for the total weight of fish in the chamber; the second method involved Y as the log average milligrams of oxygen consumed per hour per fish and X_1 as the log of the average weight per fish in cases where more than one fish was enclosed in the chamber. Regressions based on the first method are given in Equations 1-5 in Table 1, while the regressions calculated on a "per fish" basis are given in Equations 6-11. Calculated values have been rounded to four decimal places. Reasons for the various seasonal breakdowns are discussed below. Other useful regression statistics

TABLE 1.   *Regression equations for Felt Lake bluegills relating log oxygen consumption rates (Y,) to log body weight (X_1), swimming velocity (X_2), and temperature (X_3)*

Season	Number of determinations	Regression equation
		For total weights
March-June	31	$Y_1 = -0.7248 + 0.8232X_1 + 0.0158X_2 + 0.0132X_3$ (1)
Apr.-June	23	$Y_e = -1.6459 + 1.3132X_1 + 0.0167X_2 + 0.0107X_3$ (2)
July-Aug.	22	$Y_, = -1.9808 + 0.9571X_1 + 0.0140X_2 + 0.0557X_3$ (3)
Sept.-Dec.	40	$Y_, = -0.6912 + 0.7167X_1 + 0.0107X_2 + 0.0235X_3$ (4)
Jan.-Feb.	22	$Y_g = -1.7517 + 1.2167X_1 + 0.0091X_2 + 0.0439X_3$ (5)
		For average weights
Apr.-June	23	$Y_e = -0.6954 + 0.8036X_1 + 0.0250X_2 + 0.0069X_3$ (6)
July-Aug.	22	$Y_e = -2.1951 + 1.0621X_1 + 0.0138X_2 + 0.0567X_3$ (7)
Sept.-Dec.	40	$Y_i = -0.9242 + 0.8494X_1 + 0.0142X_2 + 0.0198X_3$ (8)
Jan.-Feb.	22	$Y_e = -1.0603 + 0.9630X_1 - 0.0002X_2 + 0.0251X_3$ (9)
Jan.-Feb. (active fish)	15	$Y_i = -1.9310 + 0.8624X_1 + 0.0427X_2 + 0.1153X_3$ (10)
Jan.-Mar.	30	$Y_i = -0.6799 + 0.8235X_1 \qquad 0.0063X_3 \qquad 0.0107X_3$ (11)

TABLE 2.   *Felt Lake bluegill oxygen consumption regression statistics*
(See Text and Table 1.)

Equation	Degrees of freedom	Standard error of estimate	Multiple correlation		Standard errors of estimate, s_b, for partial regression coefficients					
					Log wt., x_1		Activity, x_2		Temp, x_3	
			$R_{y.123}$	P	s_{b1}	P	s_{b2}	P	s_{b3}	P
1	27	0.1351	0.7010	<0.01	0.1872	<0.001	0.0060	<0.02	0.0099	<0.20
2	19	0.1472	0.6070	<0.05	0.4786	<0.02	0.0082	<0.10	0.0123	<0.40
3	18	0.1021	0.8414	<0.001	0.2413	<0.001	0.0063	<0.05	0.0170	<0.01
4	36	0.1662	0.5867	<0.01	0.3174	<0.05	0.0067	<0.20	0.0071	<0.01
5	18	0.1742	0.5970	<0.05	0.4336	<0.02	0.0170	<0.70	0.0327	<0.20
6	19	0.1737	0.9067	<0.001	0.1274	<0.001	0.0113	<0.05	0.0161	<0.70
7	18	0.0582	0.9914	<0.001	0.0337	<0.001	0.0035	<0.01	0.0095	<0.001
8	36	0.1631	0.8468	<0.001	0.1037	<0.001	0.0070	<0.05	0.0076	<0.02
9	18	0.1932	0.6495	<0.05	0.3432	<0.02	0.0188	>0.90	0.0366	<0.60
10	11	0.1119	0.8787	<0.001	0.2050	<0.01	0.1054	<0.02	0.0316	<0.01
11	26	0.1547	0.5943	<0.01	0.2393	<0.01	0.0084	<0.50	0.0093	<0.30

for these equations are given in Table 2 with probabilities *(P)* indicated for the overall multiple correlation (RŸ.123) and the individual partial regression coefficients (b_1, b_2, and b_3). Probabilities are referred to tabulated values at levels 0.001, 0.01, 0.02, 0.05, and 0.1 to 0.9 by tenths.

Sex *and metabolic rates*

While the experiments on single fish were not designed specifically for a comparison of male and female metabolism, the following schedule for the comparisons of the Y_1 (log O_2 consumption rate per unit body weight) in the Appendix is of interest:

Season	Average Y_i	
	Males	Females
Apr.-June	2.2378	2.2590
July-Aug.	2.2942	2.4693
Sept.-Dec.	2.1674	2.2209
Jan.-Feb.	2.1006	2.1598

In all seasons the females have the higher metabolic rates, but none of the differences between sexes is statistically significant.

Effect of grouping

Indirect comparisons between oxygen consumption rates (Y) of single fish and of

two or more fish may be made by utilizing the Table 1 regressions (based on average weights) to calculate the expected values of oxygen consumption for the experiments in which groups of fish were used. A comparison of expected Y_v and observed Y_d values is then possible.

For example, in the April-June period Y_v values may be calculated from Equation 6 (Table 1) and compared with the observed rates Y_v in Appendix Table A as follows:

Experiment No.	Y_v	Y_e
11	1.143	1.050
18	1.312	1.118
19	1.258	1.056
20	1.332	1.114
23	1.277	1.143
26	1.088	0.970
27	1.034	0.987
28	1.352	1.118
29	1.336	1.205
30	1.241	1.078

All ten observed values are higher than expected.

By utilizing Equation 7 (Table 1) and the data of Appendix Table B, the following comparisons for the July-August period obtain:

Experiment No.	Y_v	Y_e
47	1.075	1.207
48	1.481	1.569
49	1.268	1.277
50	1.300	1.258

Only the comparison for Experiment No. 50 indicates a higher value for the Y_v, and this is very likely explained by the agitation among the three fish which included a small ripe male and a small ripe female.

The September-December comparisons based on Equation 8 and Appendix Table C data are:

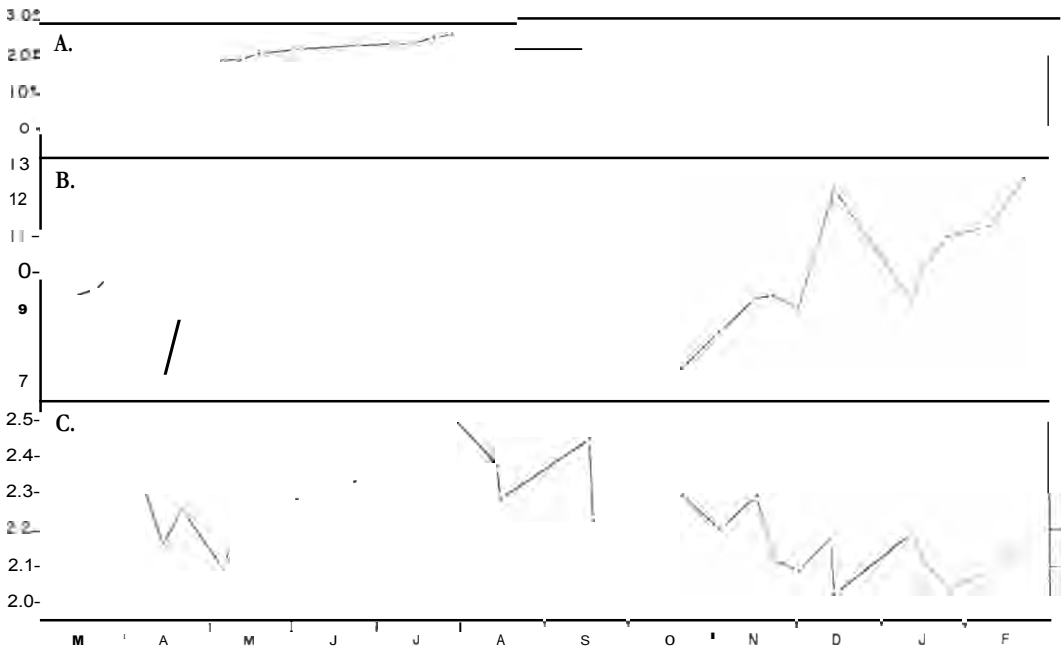| Experiment No.	Y_v	Y_e
56	1.353	1.111
57	1.105	0.872
64	1.192	1.170
65	1.268	1.161
69	1.100	1.140
76	0.989	1.053
78	1.108	1.078
95	1.157	1.065
96	1.118	1.196

FIG. 1. Trends of 1956-57 Felt Lake averages for selected days. Surface temperatures in degrees centigrade (Panel A), milligrams oxygen per liter at surface (Panel B), and log milligrams oxygen consumed by blueells per hour per kilogram (Panel C).

That six of the nine Y_0 are higher than expected hardly provides a significant indication of difference.

The January—February data contained only one group determination. The March data were inadequate due to temperature variations.

Limnological conditions

Shown in Figure 1 is the trend of averages of Felt Lake surface temperatures and oxygen contents and of the bluegill metabolic rates for the days during 1956-57 when field determinations were made.

EVALUATION OF DATA

Methodology

Fry (1957) gives excellent critiques of laboratory methods for measurement of respiration or metabolism. Wohlschlag (1957) gives a critique of the field methodology pertinent to this study. There appears no evidence to indicate that manipulation of gear or determination of the oxygen consumption rates should involve any systematic biases.

The oxygen content of the chamber declined linearly on the average during each run, and ordinarily did not drop below about 70 per cent of saturation. There was thus no indication that respiratory rates decreased with time due to lower oxygen tension as might be expected with relatively large fish (Job 1955, Fry and Hart 1948a, Fry 1957) or with relatively very active fish (Graham 1949). The initial oxygen consumption rate during the first 10-15 minutes was not higher than average due to excitement (Black et al. 1939), nor did the fish show any symptoms of irritability except in winter. In January—February some of the inactive fish tended to have excessively high respiratory rates (see Equations 9 and 10, Table 1). Otherwise the bluegills were fairly placid whether swimming or not.

There is the possibility that hour-to-hour oxygen consumption rates could vary with endogenous daily cycles as demonstrated by Clausen (1936) and others for standard metabolic rates. However, all observations in this study were from day-light hours and are quite likely comparable. Another source of hour-to-hour variation occurred during the March, 1956, determinations when the respiration chamber was in shallow water, and shoreline water temperatures increased rapidly during the day to the extent of 2-3° above the temperatures to which the fish were acclimated. From Fry's (1957) review of thermal stimulation and acclimation data related to metabolic rates, it would appear that the March data are apt to be unusually variable. A comparison of the January—February with the January—March regressions (Equations 9 and 11) or a comparison of the March—June with the April—June regressions (Equations 1 and 2) based on Table 2 statistics indicates the pronounced effects of the March data. Hence it would seem desirable to omit these data from further consideration.

From Figure 1 it will be observed that April and May metabolic rates fluctuated with surface water oxygen contents. The significance of this relationship is unclear. Since the oxygen contents for each run were initially above 7 mg O_2/L, it is unlikely that respiratory dependence on oxygen would be involved.

Linearity

Not only would interseasonal variation be expected for some of the partial regression coefficients, but there would also be expected intraseasonal variation over the individual seasonal ranges of limnological conditions. Should intraseasonal variations be pronounced, curvilinear and time-series analyses of the data would be necessary. However, there are several reasons why the linear analysis used here is satisfactory.

It is well known, at least since the time of Krogh's (1916) studies, that the log oxygen consumption rate plotted against log weight is nearly linear. There may be some exceptions at extremes of size ranges (Zeuthen 1947, 1953), temperatures, activities, and low oxygen levels. Fry (1957) discusses these interrelationships at length. Since extremes were not encountered, and since the partial regressions coefficients b_1 are highly significant (Table 2), there is good reason to consider the log oxygen

consumption rate-log body weight relation-
ships essentially linear.

Linearity of the log oxygen consumption-
swimming velocity rate is harder to evalu-
ate. A few workers, *e.g.,* Spoor (1946) and
Sullivan (1954), have utilized "spontaneous
activity" measurements of relatively sta-
tionary fish. Spoor's data would be es-
sentially linear if oxygen consumption rates
were plotted logarithmically, while Sulli-
van's data would not. Most other workers
have considered activity as being negligible
in determinations of "standard" or "resting"
metabolism or as being maximal on a
sustained basis. In the Appendix it will
be noted that the range of activity is small
and that the maximum swimming velocities
are much lower than would be expected had
the fish been stimulated to maximum pos-
sible activity. Because the range of swim-
ming velocities is small and of a low order
the log oxygen uptake-velocity regressions
appear essentially linear, even though the
relationships over a wider range of possible
activities and temperatures would be curvilin-
ear (Fry and Hart 1948b). One pro-
nounced exception to a linear rate did
occur during the January—February period
when some of the non-swimming fish ap-
peared especially irritable. For the 22
observations summarized by Equations 5
and 9 (Table 1) the partial regression co-
efficients b2 and the multiple correlation
coefficients have a lower order of probability
(Table 2) than they do when the seven in-
active fish (Appendix Table D) are not
considered as in Equation 10. The ob-
served oxygen consumption rates for five
of the seven non-swimming fish are higher
than the expected values from Equations
9 or 10. Besides appearing irritable and
refusing to swim, four of these seven fish
were definitely thinner than the average for
this season when their physiological con-
dition was already poor. Thus it would
seem desirable during the colder periods to
consider for regression analysis on a linear
basis only the fish whose activities can be
measured.

Besides its effect on activity, temperature
also influences directly the oxygen uptake
rate of poikilotherms. From data based on
standard and routine metabolism assembled
by Fry (1957) it would appear that the log
metabolic or respiratory rates plotted
against temperature might be at least
slightly curvilinear over a wide temperature
range. The annual temperature range at
Felt Lake is fairly small, and by breaking
up the data into seasons, each with a still
smaller temperature range, it is reasonable
that the log oxygen consumption-tempera-
ture regressions b_3 are essentially linear.

From the above considerations on the
effects of log weight, swimming velocity,
and temperature variables on the log oxygen
uptake, from the relatively high multiple
correlation coefficients, and from the in-
dividual partial regression coefficients with
small standard errors (Table 2) it may be
concluded that these variables may justi-
fiably be treated on a linear basis.

Total versus average weights of fish

For the determinations involving more
than one fish in the chamber, a question
arises on the soundness of treating the data
either in terms of the total oxygen con-
sumed for the aggregate weight of the fish
or in terms of the average amount of oxygen
consumed per average weight of fish. If
totals are used the regressions (Equations
1-5) are restricted to smaller weight ranges
than is the case when averages are used
(Equations 6-11). If a very small single
fish were in the chamber, its oxygen con-
sumption rate would have been too small
for adequate detection. If averages for
small fish are compared with individual
measurements for larger fish, a question
arises as to the valid measurement of
statistical precision. By the season, com-
parisons of equations based on totals with
those based on averages of Y and X_1 (Tables
1 and 2), indicate that equations based on
averages are "better" with respect to the
statistical significance of parameters. How-
ever illusory the statistical advantages of
the choice may be, Equations 6, 7, 8, and
10 are selected as best representing seasonal
relationships among the variables.

LIMNOLOGICAL CONSIDERATIONS

The choice and interpretations of Equa-
tions 6, 7, 8, and 10 of Tables 1 and 2 be-
come simplified if the limnological data of

Figure 1 and the seasonal changes in the behavior of bluegills are considered together. These equations apply only within the range of tabulated values in the Appendix Tables A—D, and they apply to "population averages" under natural conditions in contrast to most published information on laboratory acclimated fish.

Seasonal delimitations

For the 1956-57 period, the utilization of water temperature change or stability as criteria for seasonal grouping of the data is not altogether arbitrary, since changes in water level, abundance of aquatic invertebrate food supply, and condition of the fish also corresponded closely to the thermal characteristics. Since little is known of seasonal changes in respiratory or metabolic rates of fishes, it is thus premature to use changes in these rates themselves as criteria for delimitation of "physiological seasons." Seasonal variation in respiration has been reported by Wells (1935), and endocrine changes associated with gonadal development and spawning, which is seasonal for the bluegill, would undoubtedly influence metabolism (see review by Hoar 1957). Although some of the individual partial regression coefficients do change from season to season (Table 1), usefulness of the seasonal breakdown is evident from the relatively high multiple correlations (Table 2), which would not occur if there were large intraseasonal variations in respiratory rates.

Effects of weight

The partial regressions b_1 of Equations 6, 8, and 10 relating log oxygen consumption rate to log weight are remarkably close to the standard values of $ca.$ 0.85 given by Krogh and many later workers. Scholander *et al.* (1953) observed approximately the same value for a wide variety of tropical and arctic poikilotherms. The summer value of 1.06 (Equation 7) is high, quite possibly because several of the larger fish were in spawning condition and might have higher metabolic rates than the smaller fish which had passed their spawning season (Fry 1957, Hoar 1957). For future studies the feasibility of adding another independent variable, such as gonad weight, to provide a measure of sexual development should be investigated.

There are many arguments for expressing weights on a nitrogen or protein weight basis (Gerking 1952, 1954, 1955; Prosser *et al.* 1950; Zeuthen 1947, 1953), especially for the purpose of reducing variability due to wide seasonal variations in fat content. Since the respiratory quotient for fat is lower than for protein, the respiratory rate of a fat fish would be lower than for a lean one, all other conditions being equal (Prosser *et al.* 1950). In this study, however, the magnitude of seasonal variations in respiratory rates is perhaps better clarified by the use of total weights which reflect seasonal variations associated with growth conditions.

Effects of swimming velocity

The relationships of the log oxygen consumption rate to swimming velocity $(b_2$ in Equations 6, 7, and 8) are approximately the same, considering the fairly large standard errors involved. For these equations, the spring, summer, and autumn average velocities are 3.43, 9.06, and 6.85 meters per minute corresponding to respective average temperatures of 19.51°, 24.07°, and 15.30°C. No attempt was made to calculate a winter average velocity due to "spontaneous" activity of the non-swimming fish. Direct observations from spring through autumn indicate that activity of the fish follows this same pattern. The spring increase in activity, while coinciding with rising temperatures, may also be influenced by the increased output of gonad stimulating hormones. Hoar *et al.* (1955) note that this phenomenon can increase swimming activity and thereby increase oxygen consumption rates instead of increasing metabolism directly. The apparently high rate of swimming in the autumn is a real phenomenon possibly associated with increased efforts in seeking for the dwindling food supply. Although swimming velocity varies considerably over the spring-autumn period, the fact that the partial regressions coefficients do not is a point of considerable interest, inasmuch as the same level of respiration with respect to swimming

movements is implied over this period. The high coefficient for the winter period, however, may mean that movement can be accomplished only at the expense of a much higher relative respiratory rate. Job's (1955) data for *Salvelinus fontinalis* show that the standard rate as a percentage of the active rate of oxygen consumption at 5°C is considerably less than the corresponding percentage for temperatures up to about 14°C. If Job's active rates are for similar swimming velocities at these two temperatures, then the regression of oxygen consumption on swimming velocity from standard conditions to a given active condition would also have to be greater at the lower temperatures.

Effects of temperature

From the considerable literature on temperature acclimation and preferenda it would appear that the partial regression coefficients b_3 would vary so much that they could be statistically significant only if the bluegills were actually acclimated to the temperatures at which the respiratory rates were determined. This condition appears to be generally realized except for the spring data. Since the March data are inadequate because of wide temperature fluctuations from hour to hour, it is important to examine also the temperature conditions during the April—June period for which the temperature coefficient 0.0069 is not significant and is probably too low. During this period bluegills will remain over the shallow spawning beds in spite of wide day-to-day or hour-to-hour temperature variations. Unless there is adequate wind-driven circulation of surface waters, these shallow waters can vary an estimated 5°C diurnally from hot calm days to cool nights. That spawning fish actually confine themselves to the spawning beds during such fluctuations is evident from observations during May and June, 1955, when there was an extensive kill due to oxygen depletion in the inshore areas of the lake. At this time only spawning bluegills were killed; the non-spawning largemouth bass and bluegills were presumably neither killed nor confined to the areas of temporary oxygen depletion and wide temperature fluctuation. Thus there is good reason to believe that spawning bluegills during the spring period are not always thermally acclimated in the classical sense of laboratory determinations.

From a comparison of Equations 6, 7, 8, and 10 in Tables 1 and 2, it appears that the log oxygen consumption rate-temperature regressions are definitely greater during the summer and winter. Fry (1957) discusses this phenomenon in terms of routine and active metabolism for *Salvelinus fontinalis* acclimated to various temperatures. Job's (1955) and Sullivan's (1954) data for this species show that oxygen consumption rates can be relatively higher at temperature extremes. Fry believes that the physiological basis for this condition at temperature extremes is possibly due to increases in spontaneous movements which are not reflected in increased swimming velocities. Irritability and an increase in spontaneous movements mentioned above did occur in the winter but were not especially noticeable during the summer field work at temperatures of about 23-26°C. A high level of spontaneous movements did occur, however, for bluegills in an aquarium at about 30°C.

Effects of sex

There is little in the literature to indicate that sex of fish has an appreciable effect on metabolism. However, much of the experimental work applies to sexually immature fish. For many larger fish in the laboratory there would also not be expected the usual seasonal sexual cycle that occurs in nature. From the inconclusive results of this study, it would seem that any effect of sex on metabolism could be established in the field only by confining experiments to more limited environmental fluctuations.

Effects of grouping

The phenomenon of "social facilitation" for animals including fishes is generally recognized (Allee *et al.* 1949) at least on the basis of laboratory experimentation. From the field study of bluegills, however, it would appear that the respiratory rates for groups are not correspondingly lower than

the rates for single fish in all seasons. The groups of bluegills during the spring and the one group in the summer that contained sexually mature specimens had higher than average oxygen consumption rates. The other three summer groups consisting of immature or post-spawning fish had lower than average oxygen consumption rates as would be expected on the basis of goldfish experiments by Schuett (1934), Escobar *et al.* (1936), and Shlaifer (1938, 1939). Pritchard (personal communication) found that groups of bluegills in late summer consumed oxygen per unit weight at significantly lower rates than did single fish, while in winter there was no difference in the rates between groups and individuals. Direct observations of bluegills and information from seining indicated that both spawning and non-spawning fish of all sizes largely confined themselves to shallow waters during the spring and early summer in concentrations 10 to 100 times denser than in late summer and autumn when the fish tended to disperse. Earlier in the season the fish were wary and antagonistic toward each other; later, when in loose schools and more widely distributed, they appeared much more placid. Both Schuett and Shlaifer noted that the numbers in the groups within a given volume would influence the rate of oxygen consumption but not in a straightforward inverse relationship. Shlaifer (1939) found that vision was directly involved. While the results from the bluegill experiments would appear to agree with direct observations under natural conditions, the results are insufficient to indicate effects of varying numbers and the possibilities of acclimating the spring and early summer fish within the chamber so that they would exhibit social facilitation rather than antagonism.

SEASONAL EFFECTS ON BIOLOGICAL PRODUCTIVITY

Gerking (1954) has shown how data for bluegill metabolism and population dynamics can be combined for an estimate of the total protein turnover in a population. He defined protein turnover as the amount of protein that is required by the population for growth, for the metabolic expenditure of energy, and for the replacement of proteins broken down during the normal course of living. Although the weight data in this study are expressed as live weight, and not as protein weight, Gerking's concepts can be applied at least qualitatively to an interpretation of Equations 6, 7, 8, and 10 (Table 1) with respect to limnological variables affecting the Felt Lake bluegill population.

In a general way the seasonal trend of metabolic rates varies with the temperature (Fig. 1). Yet in the spring and early summer the fish not only grow rapidly and get fatter, but their gonads also develop rapidly in contrast to the autumn period at similar temperatures when the fish tend to lose weight. Since the obvious cause of the weight decline in autumn and winter is lack of food, it would seem that the population could maintain weight at this time if metabolic "efficiency" increased, if metabolic rates dropped, or if the population decreased so that competition for food was eliminated. Only the last condition appears to be even partially realized, and there is no evidence to indicate that adverse autumn and winter conditions reduce the reproductive potential in the spring. If there were any kind of "metabolic adaptation" (akin to hibernation or aestivation) to these seasonal extremes, it would seem that the metabolic rates would thus change markedly from spring through autumn and winter.

A comparison of Equations 6 and 8 for an intermediate spring or autumn temperature of, say, 17°C for observed weights and activities yields expected respiratory (or metabolic) rates of the same order for the two periods. Furthermore, the expected rates, calculated from Equations 6, 8, and 10 over pertinent weight and activity ranges for a winter temperature of, say, 10°C, are also of comparable magnitude. There thus is no evidence from these equations that the respiratory or metabolic rates decline during the adverse growing seasons much more than would be expected solely on the basis of the decline in temperature, and possibly activity. There is,

however, some physiological basis for the apparent lack of metabolic adaptation to poor food conditions.

In the spring the addition of fat can be explained not only by the increased food supplies and the greater feeding intensities, but also by the fact that at increased feeding rates there tends to be an increase in fat content (Gerking 1955). Gerking (1954) reported that fat content could rise to about 33 per cent for northern Indiana bluegills. On this basis and on the basis that the respiratory quotients for carbohydrate, protein, and fat are respectively 1.00, 0.79, and 0.71 (Prosser *et al.* 1950), adjustment of the spring rates for fat fish (Equation 6) to a protein basis would be but slightly upward. In a similar manner the increased plant consumption (and carbohydrate intake) in the autumn and winter might be responsible for higher rates. However, there appears no conclusive evidence that carbohydrate is actually digested, although the herbivorous propensities of the bluegill during food shortages have been widely reported (Ball 1948, among others). Gerking (1952) also noted that while two centrarchids absorbed protein efficiently at all ages, younger fish utilized protein for growth more efficiently than did older fish. Inasmuch as most all of the fish in this study were a full growing season older in the autumn and winter than in the spring, this "aging" phenomenon would also account for higher rates by the end of the growing season. When Equation 10 for winter is used to estimate respiratory rates at spring or autumn temperatures, it is evident that the comparably high rates are probably explained by "cold adaptation" as defined by Scholander *et al.* (1953).

With aging, with cold adaptation, and with the increasing carbohydrate consumption along with a poorer protein diet and declining fat reserves, it is likely that the metabolic rates of bluegills on a live weight basis would tend to increase during autumn and winter, other factors being constant.

From the standpoint of biological productivity, it may be noted that the annual growth rates of Felt Lake bluegills are estimated to be of the same order as those reported for northern Indiana bluegills 90 millimeters and longer by Gerking (1954). From Figure 1 data, it appears that the Felt Lake growing season (at temperatures above 15-16°C, say), during which the environment is reduced to about half its maximum with an accompanying decrease in the production of bottom fauna, is *potentially* at least twice as long as in northern Indiana. Allowing for the inherent dangers in basing calculations on variously derived data, a generalized comparison of Gerking's (1954) Gordy Lake, Indiana, protein turnover data with calculated values from Felt Lake is possible assuming that the annual growth of the larger bluegills in these diverse environments is of the same order. This assumption is justified to the extent that Felt Lake bluegills from ages I to IV have instantaneous growth rates roughly equivalent to those of ages II to V in Gordy Lake (Gerking 1954, Fig. 2). While Felt Lake bluegills grow as much in their first year as Gordy Lake bluegills grow in their first two years, the poor feeding conditions and the high mortality rates make survival and growth rates beyond age IV very poor. Hence the average instantaneous growth rate in each population would be of the same order.

For an average Gordy Lake summer population of 8979 fish weighing 420.0 kg the average weight of a fish would be 46.78 g. By interpolation from Gerking's (1954) Table I and Figure 3, a fish of this size would require about 19 g protein for seasonal growth at a 31 per cent efficiency of protein utilization for growth alone. On this basis, for growth, metabolic energy expenditure, and protein replacement the total seasonal protein requirement would be about 61 g for a 46.78 g fish. Since there are, crudely, 5.65 Cal/g protein and 1 L oxygen consumed in generating 4.82 Cal upon the oxidation of mixed protein (Brody 1945), there are consumed 1.172 L oxygen per gram of oxidized protein. Thus the oxidation of 61 g protein per fish would require about 71 L oxygen. Since Gerking's growth experiments with presumably inactive fish at a temperature of 25.9°C indicated that 150 days would be

required to account for the seasonal growth, a direct comparison with Equation 7 (Table 1) for Felt Lake is possible. From this equation the log mg oxygen uptake per hour for a 46.78 g fish at 25.9°C and zero velocity would be 1.0472, or 11.14 mg/hr, or 7.803 cc/hr. At the average summer swimming velocity of 9.06 m/min in Felt Lake, the oxygen consumption would be increased to 10.41 cc/hr. In 150 days 28 L oxygen would be consumed at zero velocity or 38 L at the average observed velocity. Both of these Felt Lake values are much lower than the 71 L calculated for Gordy Lake and indicate that Felt Lake bluegills with a long potential growing season have a much lower production rate per unit weight of fish.

Therefore, without apparent mechanisms for suppressing maintenance metabolic requirements after the growing season or for maintaining adequate food supplies to allow for potential growth over the entire growing seaon, the biological productivity of the bluegill in western U. S. waters of the Felt Lake type would be necessarily poor compared to the productivity attained in its native eastern U. S. habitats.

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APPENDIX TABLE *A-Continued*

(1)	(2)	(3)	X_1 (4)	X_2 (5)	X_3 (6)	(7)	(8)
21 IV 56	18	1.312	2.072	0.5	19.7	2.240	5
	19	1.258	2.004	0.0	20.5	2.254	8
	20	1.332	2.065	0.0	21.9	2.269	5
5 V 56	21	1.022	1.881	8.5	18.8	2.141	
	22	0.946	1.944	0.0	19.0	2.001	
	23	1.277	2.124	0.0	19.0	2.154	5
12 V 56	24	1.229	1.982	1.1	17.0	2.247	1
	25	1.206	1.954	6.7	21.0	2.252	
19 V 56	26	1.088	1.863	1.2	20.0	2.224	8
	27	1.034	1.903	0.6	20.0	2.131	7
	28	1.352	2.076	0.0	21.0	2.276	6
2 VI 56	29	1.336	2.000	5.8	21.5	2.336	3
	30	1.241	2.009	0.0	23.0	2.233	2
23 VI 56	31	0.925	1.924	8.5	22.8	2.000	
	32	1.452	1.978	12.5	22.8	2.474	
	33	1.511	1.982	10.3	23.0	2.529	

APPENDIX

Felt Lake bluegill data tabulations by seasons. Code for Tables A to D.

Column 1-Date of experiment.

Column 2-Experiment number.

Column 3-Log milligrams oxygen consumed per hour.

Column 4-Log weight of fish in grams.

Column 5-Activity of fish (meters per minute).

Column 6-Temperature of water (°C).

Column 7-Log milligrams oxygen consumed per hour per kilogram.

Column 8-Sex: M, male; F, female; or number of small fishes (usually immature).

APPENDIX TABLE A: *March-June Data*

(1)	(2)	(3)	X_1 (4)	X_2 (5)	X_3 (6)	y_1 (7)	(8)
12 III 56	1	1.493	2.511	0.0	14.8	1.982	4
	2	1.534	2.339	7.8	17.8	2.197	3
	3	1.533	2.210	10.1	17.8	2.322	2
	4	1.312	2.072	12.0	17.0	2.240	2
24 III 56	5	1.292	2.137	1.5	17.6	2.155	2
	6	1.316	1.924	5.5	15.5	2.393	2
27 III 56	9	1.330	2.225	1.5	16.4	2.104	3
	10	1.008	2.025	0.0	15.0	1.983	
7 IV 56	11	1.143	1.973	1.5	17.7	2.170	5
	12	1.127	1.954	0.0	19.3	2.173	
	13	1.112	1.892	1.1	18.5	2.219	
	14	1.624	1.924	7.7	18.5	2.700	
14 IV 56	15	1.234	2.045	6.0	14.0	2.189	
	16	1.131	2.021	6.0	14.9	2.109	
	17	1.148	1.954	1.0	14.9	2.194	

APPENDIX TABLE B: *July-August Data*

(1)	(2)	Y (3)	X_1 (4)	X_2 (5)	X_3 (6)	Y_1 (7)	(8)
7 VII 56	34	1.454	2.100	8.4	23.5	2.353	F
	35	1.060	1.845	1.0	24.2	2.214	M
	36	1.352	1.833	1.0	24.5	2.519	M
13 VII 56	37	1.468	1.991	12.4	23.1	2.477	F
	38	1.426	1.991	14.4	23.2	2.435	F
21 VII 56	39	1.393	1.914	9.7	24.5	2.480	M
	40	1.324	1.973	3.0	24.5	2.351	F
	41	1.478	1.886	11.5	25.8	2.592	F
28 VII 56	42	1.491	2.004	13.0	25.0	2.487	F
	43	1.461	1.964	12.3	25.2	2.497	F
	44	1.428	1.881	12.0	25.2	2.547	F
	45	1.490	2.017	11.7	26.0	2.473	F
	46	1.549	2.000	6.7	26.5	2.549	F
14 VIII 56	47	1.075	1.748	9.3	25.0	2.327	10
	48	1.481	2.083	9.7	25.0	2.398	18
	49	1.268	1.875	8.7	24.0	2.393	5
	50	1.300	1.908	9.3	22.9	2.391	3
15 VIII 56	51	1.260	1.924	9.3	22.0	2.336	F
	52	0.868	1.785	8.3	22.2	2.083	M
	53	1.327	1.792	11.7	22.2	2.535	F
	54	1.224	2.025	7.0	22.5	2.199	M
	55	1.103	1.833	9.0	22.5	2.270	M

APPENDIX TABLE C: *September-December Data*

(1)	(2)	Y (3)	X_1 (4)	X_2 (5)	X_3 (6)	Y_1 (7)	(8)
17 IX 56	56	1.353	1.806	5.3	21.5	2.547	8
	57	1.105	1.602	0.0	22.0	2.503	9
	58	1.299	1.919	14.3	22.0	2.380	F
	59	1.294	1.935	13.3	22.0	2.360	F
	60	1.264	1.778	11.3	22.4	2.486	M

APPENDIX TABLE C—Continued

(1)	(2)	Y (3)	X₁ (4)	X₂ (5)	X₃ (6)	Y₁ (7)	(8)
18 IX 56	61	1.108	1.813	8.3	21.3	2.295	M
	62	0.935	1.833	10.7	21.5	2.102	F
	63	1.229	1.820	11.3	22.0	2.410	1
20 X 56	64	1.192	1.924	7.3	18.0	2.268	11
	65	1.268	1.869	9.7	18.2	2.399	2
	67	1.198	1.833	6.7	19.0	2.366	F
	68	1.234	1.935	10.3	19.1	2.300	M
	69	1.100	1.973	0.0	19.6	2.127	2
3 XI 56	70	0.960	1.892	0.0	14.9	2.068	F
	71	1.250	1.863	6.0	15.0	2.387	M
	72	0.938	1.792	1.3	15.5	2.146	F
17 XI 56	74	1.057	1.839	10.7	13.9	2.218	F
	75	1.299	1.833	10.7	13.9	2.466	M
	76	0.989	1.851	9.0	14.0	2.138	2
	77	1.341	1.820	7.3	13.9	2.521	M
	78	1.108	2.000	2.0	13.9	2.108	2
13 XI 56	79	0.831	1.813	11.3	12.0	2.019	F
	80	0.944	1.756	10.0	12.0	2.189	F
	81	0.921	1.820	12.3	12.5	2.102	M
	82	1.117	1.799	5.7	12.5	2.317	F
	83	0.720	1.748	8.7	12.5	1.972	M
1 XII 56	84	1.046	1.973	7.0	11.0	2.073	F
	85	1.018	1.929	4.3	11.1	2.089	M
	86	0.555	1.845	0.3	11.9	1.709	M
	87	0.995	1.839	6.0	12.5	2.156	M
	88	1.109	1.845	8.0	12.5	2.264	M
	89	1.104	1.869	6.3	12.0	2.235	F
13 XII 56	90	1.207	1.924	10.7	11.7	2.283	F
	91	1.046	1.898	4.3	12.0	2.148	M
	92	1.032	2.017	0.3	12.3	2.015	M
	93	1.163	1.903	0.0	12.3	2.260	F
14 XII 56	94	0.427	1.826	2.8	11.4	1.601	M
	95	1.157	1.973	5.3	12.0	2.184	2
	96	1.118	2.097	7.0	12.1	2.021	2
	97	1.166	1.869	8.2	12.2	2.297	F

APPENDIX TABLE D: *January–February Data*

(1)	(2)	(3)	X₁ (4)	X₂ (5)	(6)	(7)	(8)
12 I 57	98	0.995	1.881	9.0	8.2	2.114	M
	99	1.097	1.826	0.0	8.4	2.271	F
16 I 57	100	0.795	1.845	5.3	9.0	1.950	M
	101	1.131	2.076	1.7	9.1	2.055	F
	102	1.095	1.785	6.3	10.0	2.310	F
	103	0.938	1.813	0.7	10.0	2.126	F
	104	0.964	1.869	4.3	10.0	2.094	M
	105	0.977	1.806	4.5	9.5	2.170	M
25 I 57	106	0.953	1.881	6.7	8.5	2.072	F
	107	0.630	1.716	2.7	8.5	1.914	2
	108	0.663	1.732	5.0	8.4	1.930	M
	109	0.940	1.699	6.2	8.5	2.241	F
9 II 57	110	1.057	2.025	1.7	9.2	2.031	F
	111	1.073	1.833	0.0	9.2	2.241	M
	112	0.806	1.792	0.0	9.4	2.013	M
22 II 57	113	1.125	1.863	0.7	11.9	2.262	M
	114	1.082	1.833	0.8	12.0	2.249	F
	115	0.638	1.806	0.0	12.0	1.832	F
	116	1.162	1.875	0.0	11.9	2.287	F
	117	0.985	1.903	0.5	11.9	2.082	M
	118	1.141	1.857	0.0	11.9	2.284	F
	119	0.899	1.748	0.0	11.9	2.150	M