

Gas Exchange and Metabolism in the Sirenidae (Amphibia, Caudata)

By

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This work is dedicated to my wife, Sandra, for the many years of work to support a student husband, and to my daughter, Julie, who must have wondered at times if she actually had a father.

## ACKNOWLEDGMENTS

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Abstract of Dissertation Presented to the Graduate Council  
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GAS EXCHANGE AND METABOLISM IN THE SIRENIDAE (AMPHIBIA, CAUDATA)

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Chairman: B. K. McNab  
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All members of the family Sirenidae (Amphibia, Caudata) are usually found in areas of aquatic vegetation. They are particularly abundant in water hyacinth communities, which were found to have low concentrations of dissolved oxygen and high concentrations of dissolved carbon dioxide.

Field studies indicated that the Sirenidae do not select microhabitats on the basis of dissolved respiratory gases, and that they choose hyacinth areas over open water within the same pond.

Sirenids above 800 g are obligate air-breathers at 25°C in air saturated water. Theory and experiments had predicted this weight closely when body size, metabolic rate, and permeability of the skin to oxygen were considered.

Siren lacertina was found to adapt to the hyacinth community by breathing air in response to low levels of dissolved oxygen and by eliminating carbon dioxide to the air and tolerating a high blood  $p\text{CO}_2$  in response to elevated levels of carbon dioxide in the water.

A model is presented that shows the advantage in attaining a large size of a decreasing weight-specific metabolic rate with increasing size. It is suggested that metabolic rate is limited by the  $O_2$  exchange capacity of an organism.

## INTRODUCTION

Animals that utilize both aerial and aquatic gas exchange are particularly interesting subjects for studies of respiratory adaptations. Differences within the two fluids in gas concentrations, medium density, types of exchange organs, and diffusion and solubility constants of the respiratory gases contribute to a complex set of alternatives for meeting various respiratory demands. If the organisms exhibit a large range in body sizes and inhabit waters with varying concentrations of dissolved oxygen and carbon dioxide, one can expect to observe various types of adaptations for metabolism and gas exchange.

A family of aquatic salamanders, the Sirenidae, is such a group of animals. It is comprised of three species, Siren lacertina, S. intermedia, and Pseudobranchius striatus. The wide range of body sizes is indicated by the maximum weights of adults collected: S. lacertina, 1698 g, S. intermedia, 45 g, and P. striatus, 5 g. Considerable attention will be paid to S. lacertina in this paper, which was studied over a weight range of greater than three orders of magnitude.

The Sirenidae are effective air and water breathers (Czopek, 1962; Freeman, 1963; Goin, 1941; Guimond, 1970). They possess highly vascularized lungs (Guimond, 1970), and surface to breath air regularly. Although external gills are present, the aquatic mode of respiration is almost entirely cutaneous (Czopek, 1962; Guimond, 1970). Therefore no effort was made in this study to evaluate the role of the gills as separate from that of the skin in aquatic gas exchange.

These salamanders are found in waters that offer some degree of refuge, usually in the form of aquatic vegetation. Pseudobranchius has become particularly abundant in the water hyacinth (Eichhornia crassipes) community and is usually associated with some form of dense vegetation. Both species of Siren are also usually associated with relatively dense vegetation, although S. lacertina appears to venture into more open waters frequently, perhaps because its large size makes it less susceptible to predation.

Aquatic animals that live in such vegetated areas are usually subject to unfavorable concentrations of dissolved oxygen and carbon dioxide. Data from Lynch et al. (1947), for water samples from areas with various types of aquatic vegetation, indicate that oxygen is usually below saturation levels and carbon dioxide concentrations are elevated. They found that this was especially true for water covered by water hyacinths, which makes this community a particularly hostile environment for aquatic gas exchange.

The effects of Eichhornia on dissolved gases was one of the factors considered in the choice of a field study site. The pond used was on the edge of Payne's Prairie, Gainesville, Alachua County, Florida. Approximately 95% of the water surface was covered with water hyacinths, leaving an area of about 1/2 acre of "open" water (meaning the surface was not covered by Eichhornia, although the submerged aquatic Ceratophyllum was often dense). All three of the species of Sirenidae were present in large numbers, especially P. striatus. The two available aquatic microhabitats provided an excellent field laboratory for studies of behavioral adaptations associated with habitat selection.

The purpose of this study was to investigate some of the behavioral and physiological adaptations of the Sirenidae that enable them to cope with the respiratory stress placed on them by the low levels of dissolved oxygen and high levels of dissolved carbon dioxide associated with water hyacinth communities. As the extent of the effects of Eichhornia on the aquatic microenvironment were rather poorly documented, it was also necessary to study certain environmental parameters in detail in order to properly plan and evaluate the laboratory studies. Temperature, pH, dissolved oxygen and dissolved carbon dioxide in both the "open" and hyacinth-covered portions of the pond were the factors chosen for investigation.

## MATERIALS AND METHODS

### Field Work

Temperature, pH, dissolved O<sub>2</sub> and dissolved CO<sub>2</sub> were measured in the hyacinth mat and "open" water at the surface and bottom. Temperature was measured to the nearest 1/2°C. Water samples were drawn through a water-saturated cloth, which excluded most of the detritus, into a glass tube that was stoppered at both ends with rubber stoppers. The samples were placed in an ice chest and returned to the laboratory, where they were warmed to 25°C. A Radiometer PHA 27 pH meter and Gas Monitor, calibrated at 25°C, was used to determine pH, pCO<sub>2</sub> and pO<sub>2</sub> for each sample. The pCO<sub>2</sub> scale could only be read down to 7 mmHg; any readings below this value were assigned a value of 3.5 mmHg (7 ppm). Partial pressure readings were converted to parts per million by weight (ppm) by multiplying the pCO<sub>2</sub> readings by 1.96 ppm/mmHg and the pO<sub>2</sub> readings by 0.053 ppm/mmHg.

It was found that some gas was being exchanged between the rubber stoppers and the water samples between the times of collecting and measuring. This change was predictable and was corrected for by a table of correction factors derived from observing changes in water samples of known concentrations treated in the same manner as the field samples.

The environmental parameters were measured throughout the year as a function of time of day, depth of the water column, season, and

thickness of vegetation. All measurements intended for use in describing annual cycles were taken on sunny days to prevent the effect of cloud cover from masking the effect of season.

In order to determine the location of the animals in the pond, extensive collections were made with a dredge in the hyacinths and with seines in the "open" water. Water samples were taken prior to all collections.

In addition to animals collected at the Payne's Prairie site, experimental animals were also collected from the River Styx in Alachua County and from a culvert passing under SR-121 near Biven's Arm in Gainesville.

#### Maintenance of Animals

All animals used in the laboratory work were maintained at least two weeks at  $25 \pm 2^{\circ}\text{C}$  with a 12-12 light-dark photoperiod. Animals were not fed within three days of the start of any experiment. If fecal material was visible in an experimental chamber at the end of an experiment, the results were discarded because of the possibility of oxygen consumption by decomposition of the feces.

#### Surface Area Determinations

Surface area determinations were made initially by anesthetizing animals with MS-222 (tricaine methanesulfonate) and wrapping them in aluminum foil. The foil was cut to fit the body contours, unrolled and the outline traced on graph paper ruled in  $\text{mm}^2$ . Surface area was determined by counting squares. It was later found that a good approximation could be made by treating the animal as a cylinder from the head to the vent and then considering the remainder as a triangle with a base

equal to the distance from the vent to the tip of the tail. Six comparisons of the techniques were made, with animals of 21 - 690 g. Considering the square-counting method to represent the actual surface area, the geometrical approximation averaged an error of only + 1.8%. Most of the additional determinations utilized the geometrical technique.

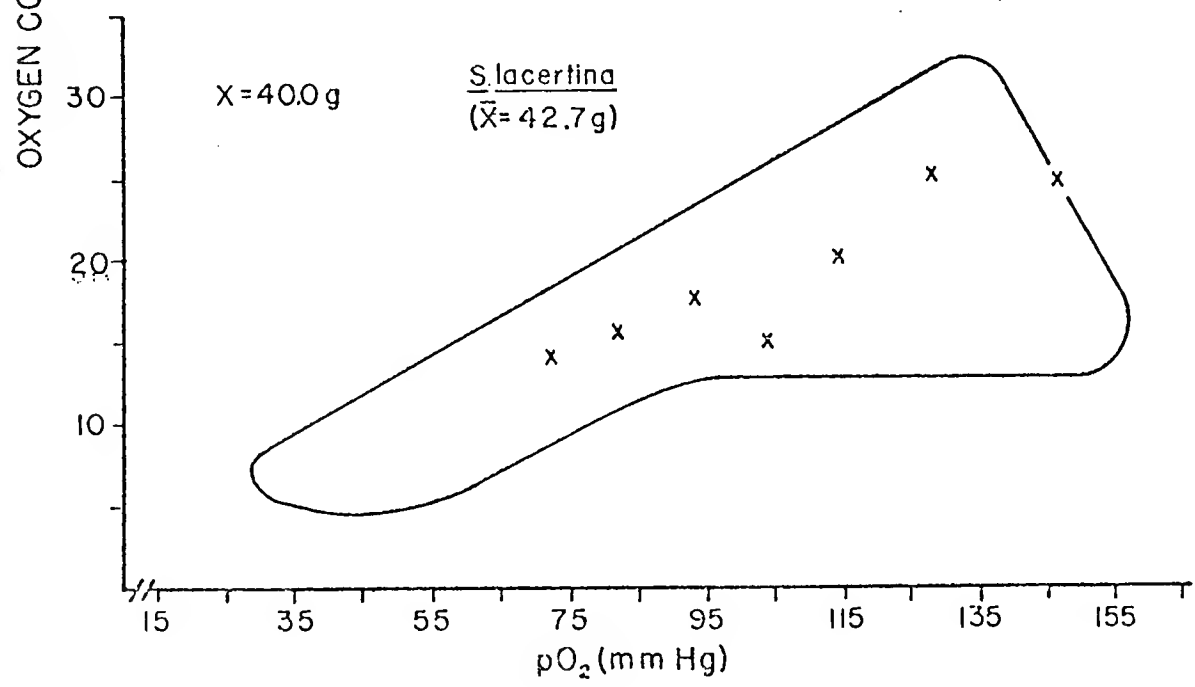
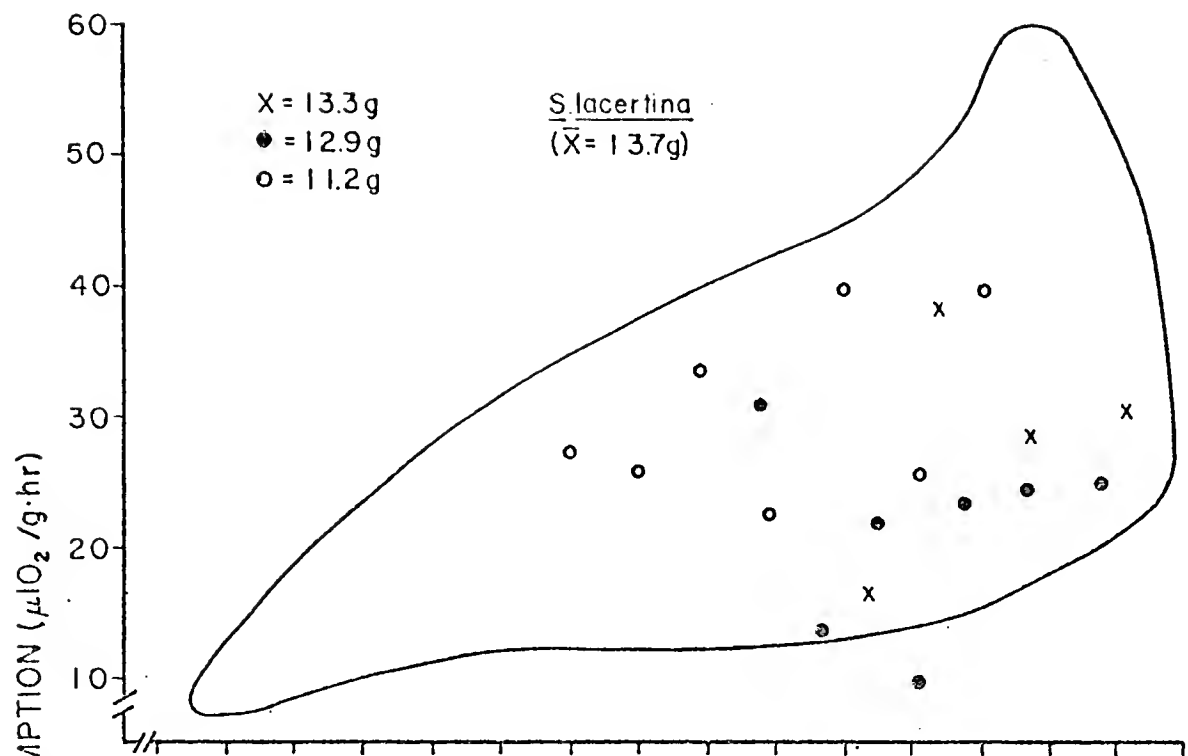
#### Metabolic Rates of Submerged Animals

Animals used in these experiments were placed in the experimental containers with access to air the night before use to become accustomed to the chamber. The type of container used varied with the size of the animal, but was usually a jar or Erlenmeyer flask with a volume that would result in a drop of  $pO_2$  of about 10 mmHg/hr when the animal was in a relatively inactive state. The water was changed the next day to eliminate any accumulated fecal material, skin, etc. Well water was used rather than distilled water, to alleviate osmoregulatory stresses. Controls indicated the biochemical oxygen demand of the well water was insignificant (decreases in  $pO_2$  of 0.0 - 0.5 mmHg/hr).

At the start of an experiment the container was filled with water supersaturated with  $O_2$  at 25°C. The animal was then submerged in the filled and sealed chamber and allowed to respire for about two hours before an initial oxygen determination was made, in order to deplete the lungs of oxygen. Figure 1 shows a test of this assumption. The enclosed areas represent metabolic rates measured during experiments that were preceded by the two-hour submergence period. The scores indicate metabolic rates of submerged animals after six days of submergence. Presumably, all available  $O_2$  in the



Figure 1. Comparison of aquatic  $\dot{V}_{O_2}$  of S. lacertina submerged for approximately two hours (enclosed area) and for 145 hours. Scores represent metabolic rates after 145 hours of submergence.



15 35 55 75 95 115 135 155  
 $pO_2$  (mm Hg)

lungs would have been utilized by this time. The metabolic rates after 145 hours of submergence are similar to those after only two hours of submergence, indicating that the animals are functioning only as water breathers in the submerged metabolism experiments. Metabolic rate was determined by allowing the animal to consume oxygen from the water for at least one hour, and converting the decrease in  $pO_2$  to oxygen consumption in  $\mu l O_2/g \cdot hr$ . The animal was considered to have exhibited that metabolic rate at an oxygen tension equal to the average tension for the interval.

Determinations of metabolic rate as a function of oxygen tension were made for S. lacertina of average weight groups from 0.36 g to 1310 g, for S. intermedia from 3.3 to 29.6 g, and for P. striatus from 0.51 to 2.88 g.

#### Gas Exchange Partitioning Experiments With S. lacertina

Gas exchange partitioning experiments were conducted in two-section plexiglas chambers. The lower portion of a chamber contained the animal and was filled with water; the upper portion was filled with air. A small opening connected the two sections to allow the animal to air breathe. The surface of the water at the opening was covered with a 1 cm layer of heavy duty paraffin oil to minimize gas exchange between the air and water. The chamber was painted a dull gray except for the area above the breathing hole. Observation showed that the animals located the breathing hole much more readily when it was the only source of light. In practice, the animals usually stayed near the opening, and air breathing merely necessitated raising the upper third of the body to be able to protrude the mouth into the aerial chamber.

Gas concentrations were set at the desired levels by bubbling CO<sub>2</sub>, O<sub>2</sub>, or N<sub>2</sub> through the water. Gas exchange between the air and water in controls was nil (0.006 vol%/hr for CO<sub>2</sub> and 0.022 vol%/hr for O<sub>2</sub>). The animals were acclimated to the experimental conditions for at least 24 hours before the start of a series of experiments by placing them in the chamber at 25°C and with the appropriate set of concentrations of dissolved gases and leaving the aerial portion open to the atmosphere. Immediately prior to an experiment, the water was changed and the desired gas concentrations re-established in the water. One to two hours were allowed before the aerial portion was sealed from the atmosphere, after which the tank was completely submerged in the water bath at 25°C. Generally, two experiments were run per day, after which the gas concentrations would be reset to the desired levels, and the animals would be left in the chamber overnight. The same procedure was followed for the next day and thereafter until a series of experiments for a particular set of conditions was complete. Any acclimation was apparently complete at the end of 24 hours, since there was no significant change in metabolic rates or partitioning between first and final days of experimentation for a particular set of conditions.

Changes in the vol% of CO<sub>2</sub> and O<sub>2</sub> in the aerial phase were measured with a Scholander 1/2 cc gas analyzer. Dissolved O<sub>2</sub> was measured with the Radiometer PHA 27 and Gas Monitor. Dissolved CO<sub>2</sub> was determined by calculation from an RQ of 0.91 (SE = 0.03) reported by Guimond (1970) for S. lacertina at 25°C.

All gas volumes are reduced to STPD.

## RESULTS AND DISCUSSION OF FIELD STUDIES

Curves were constructed for pH, CO<sub>2</sub>, O<sub>2</sub> and temperature for a 24-hour sunny day of each month. Measurements in the hyacinth area were made during September and October of 1969, and for all other months in 1970. "Open" water measurements were made monthly from February, 1970, to January, 1971. Each curve was averaged over the 24-hour period, and these average values were plotted as single points. Figure 2 shows the results for temperature and pH, and Figure 3 for dissolved O<sub>2</sub> and CO<sub>2</sub>. Figure 4 gives profiles for O<sub>2</sub> and CO<sub>2</sub> in summer and winter, and as a function of time of day. The profiles reveal that depth is not an important factor in selection of a favorable respiratory microenvironment for a sirenid in the hyacinths, since once the depth reaches only 20 cm, dissolved gases remain rather constant. Therefore, the bottom measurements in the hyacinth area of the pond may be considered to be roughly equivalent to the general conditions existing anywhere within the water column under a hyacinth mat. However, Figure 5 clearly indicates that horizontal movements from hyacinth areas to open water can have a marked effect on the respiratory microenvironment.

The growing season for water hyacinths in the Gainesville area is March-October. It is during this period that conditions become particularly unfavorable for aquatic gas exchange in the water covered by hyacinths. Table 1 shows the average O<sub>2</sub> for this period to be only

Figure 2. Temperature and pH at the surface and bottom in "open" water and hyacinths. Each point is the average value for a 24-hr sunny day for a given month.

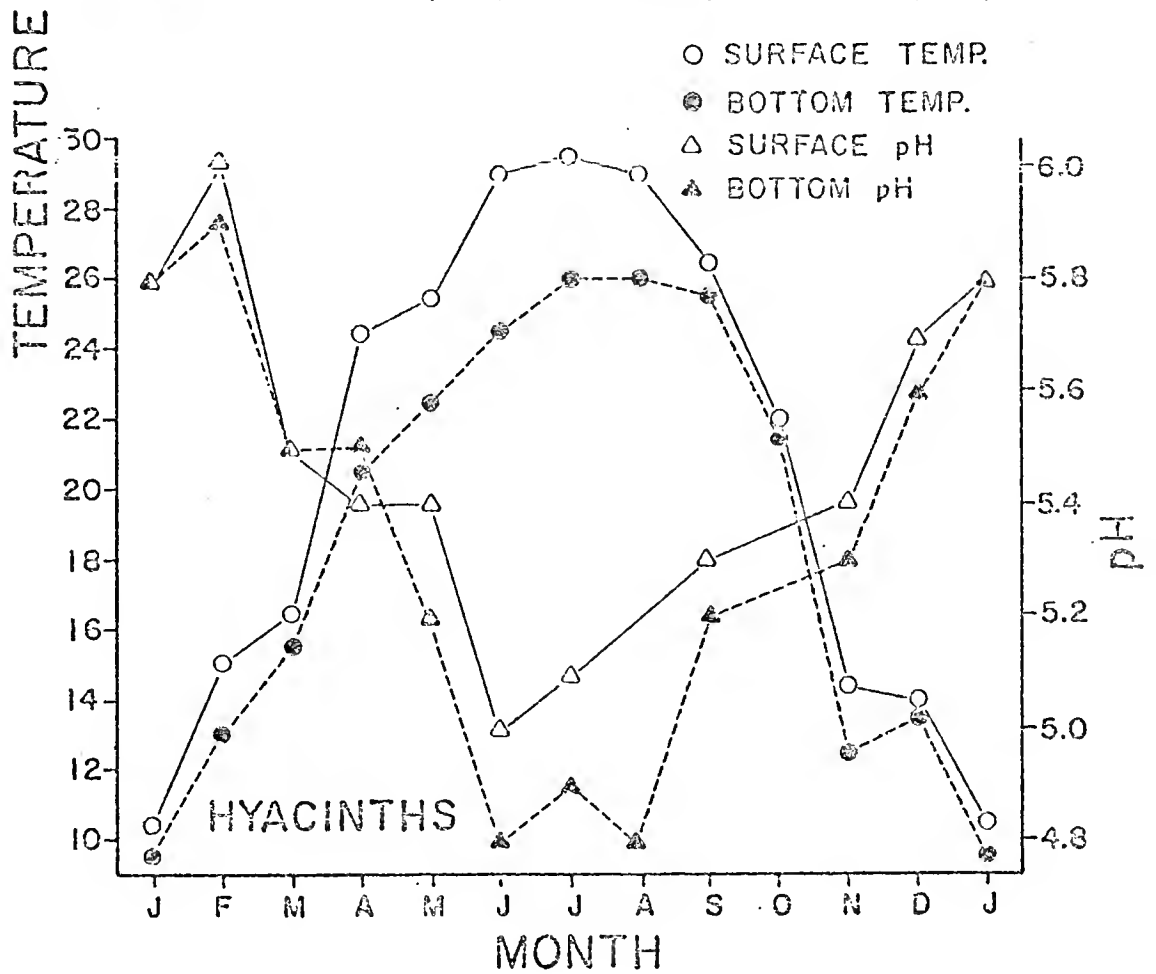
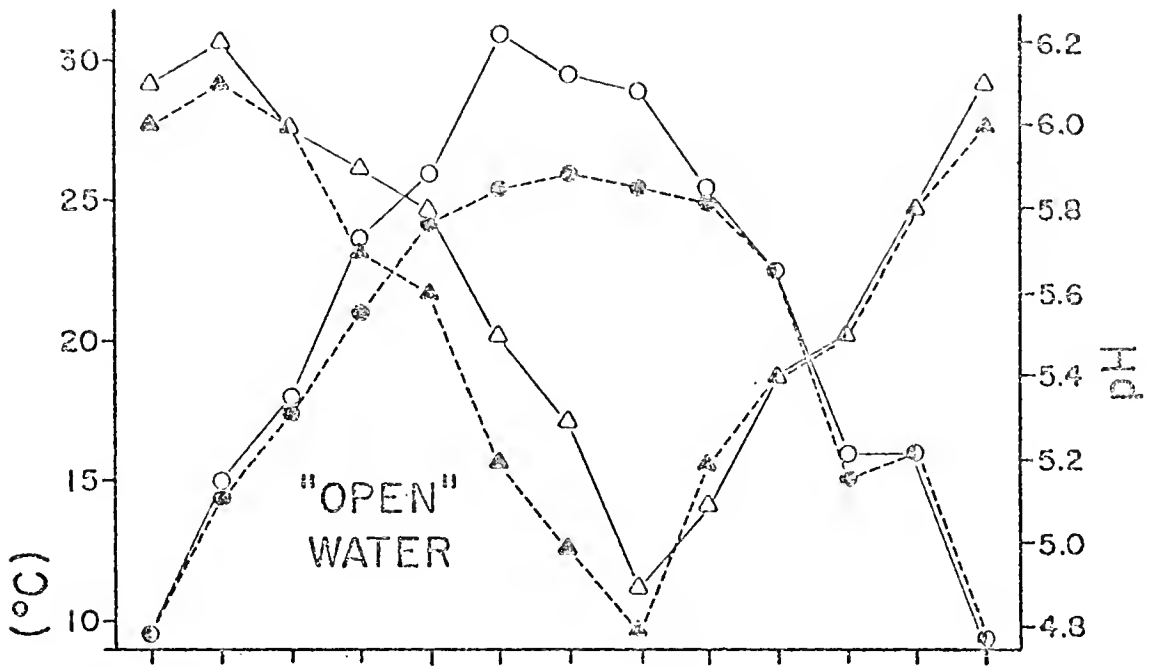


Figure 3. CO<sub>2</sub> and O<sub>2</sub> concentrations at the surface and bottom in "open" water and hyacinths. Each point is the average value for a 24-hr sunny day for a given month.



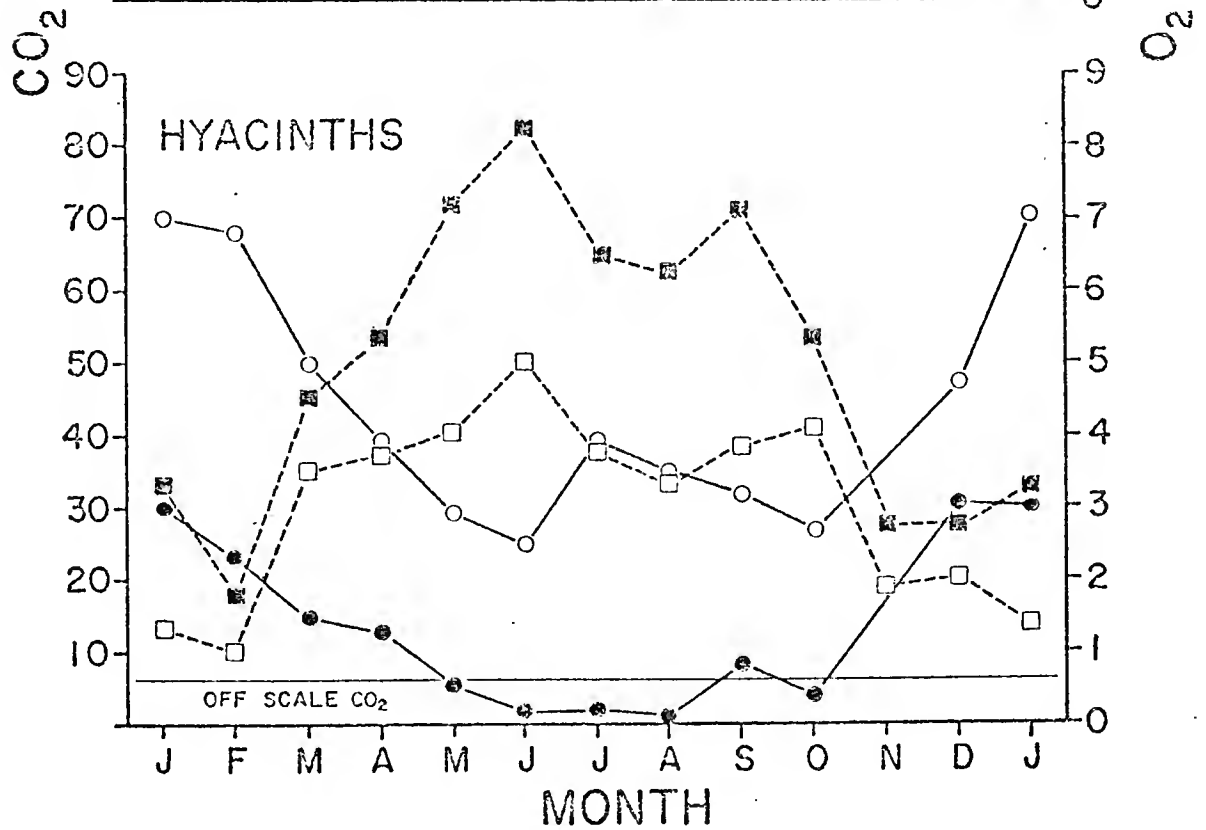
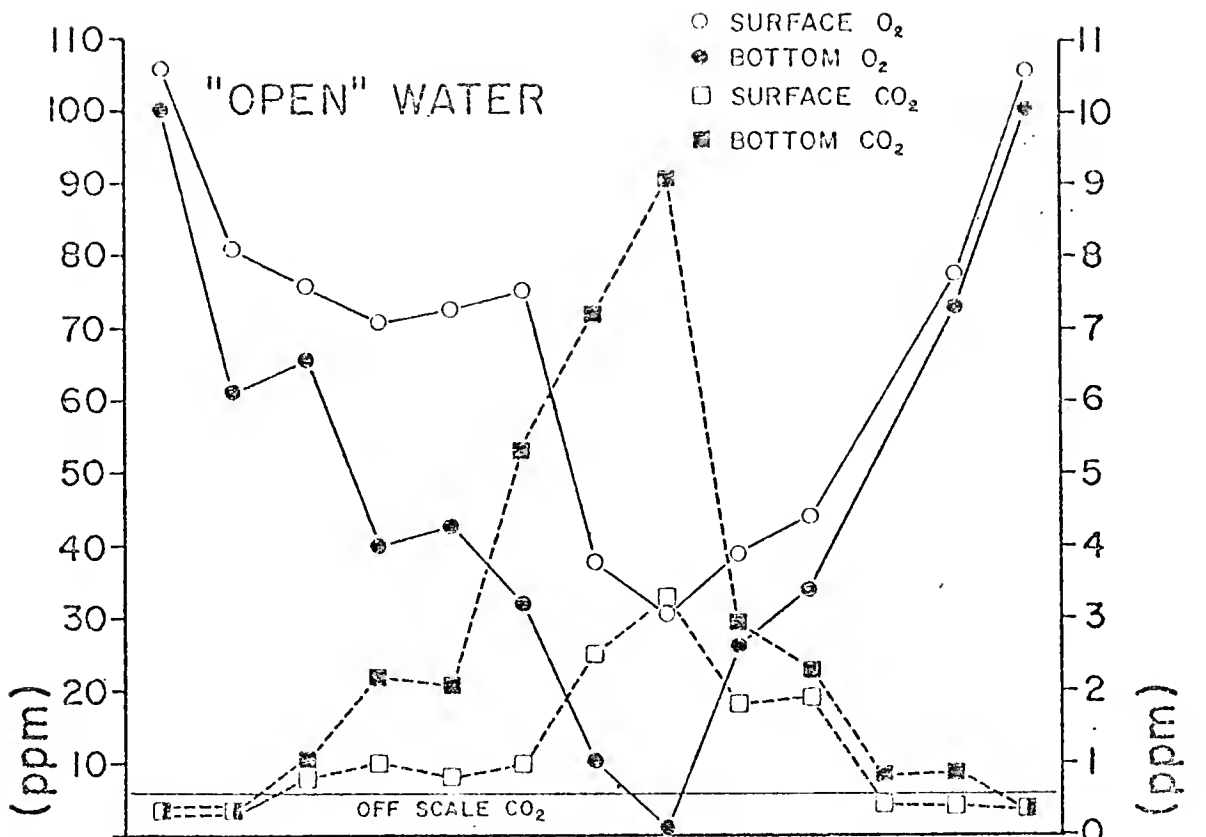


Figure 4. CO<sub>2</sub> and O<sub>2</sub> profiles for different thicknesses of hyacinth cover, times of day, and times of year.

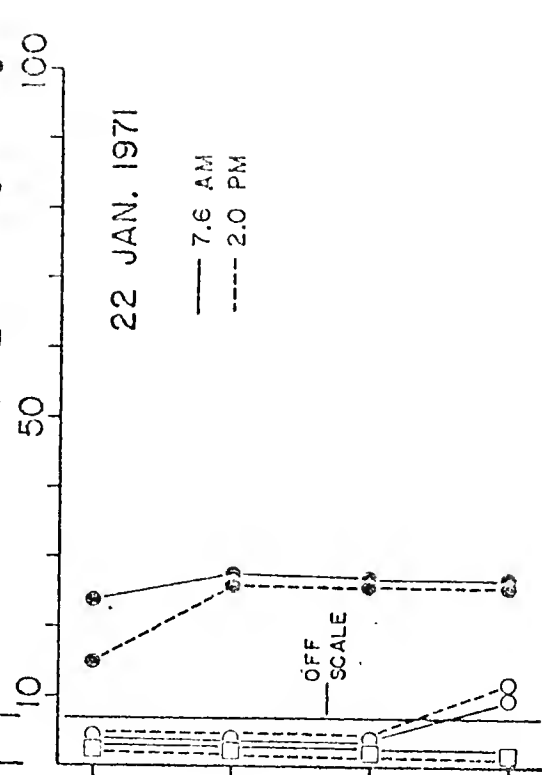
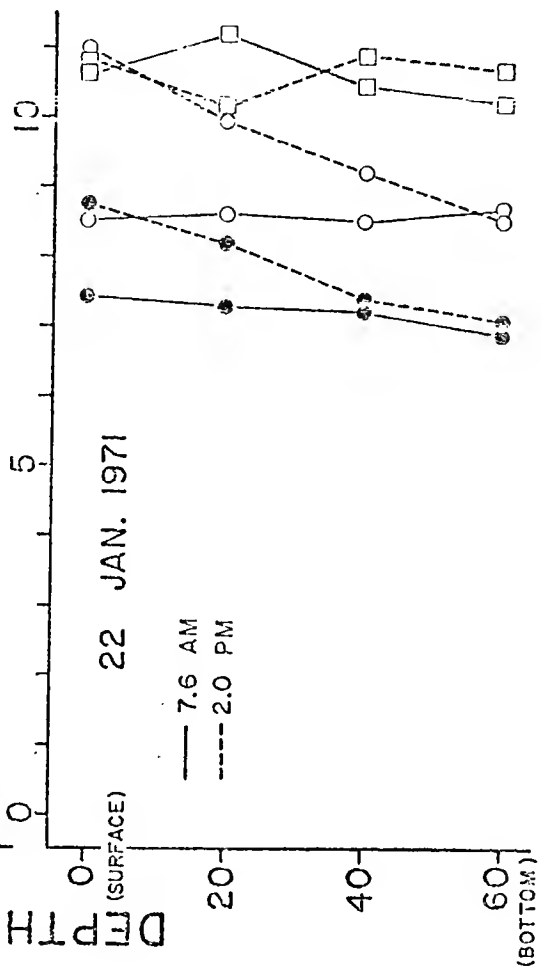
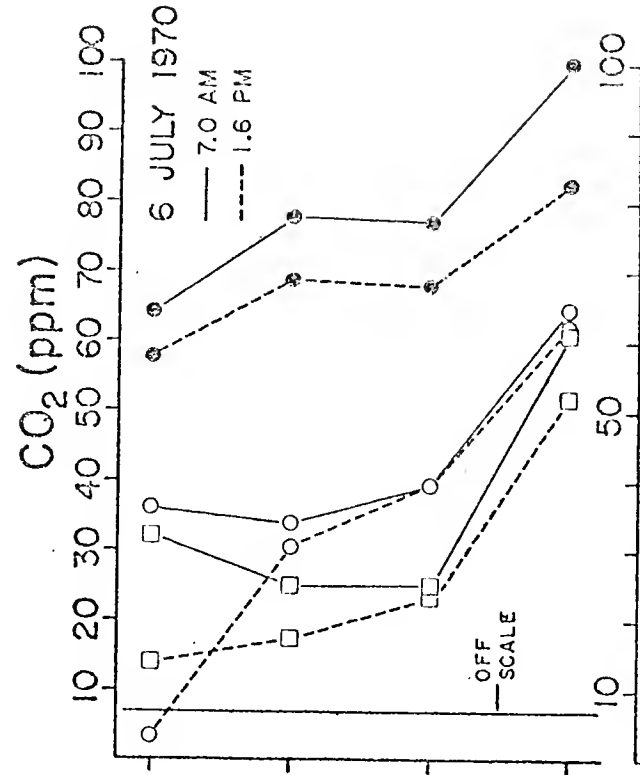
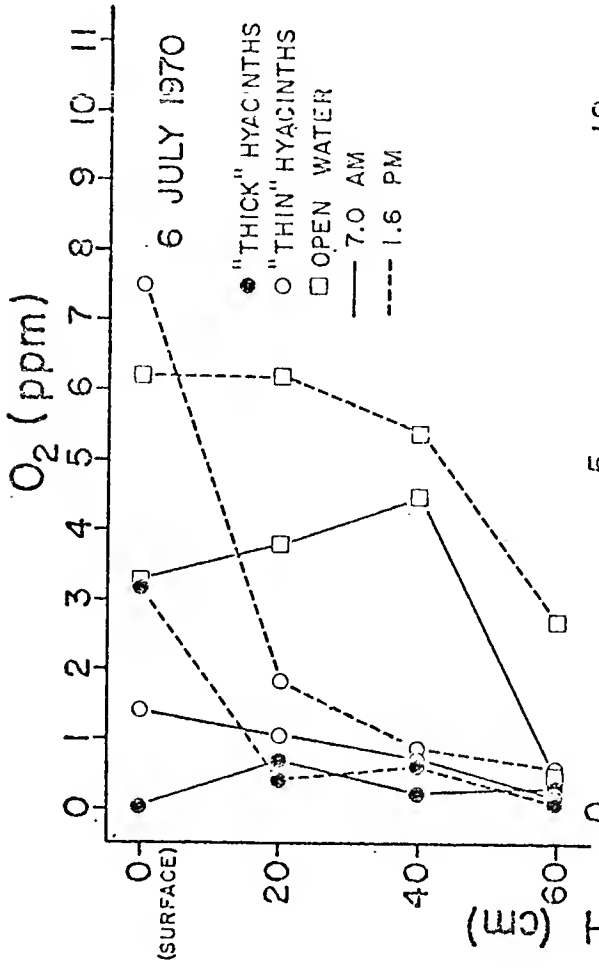
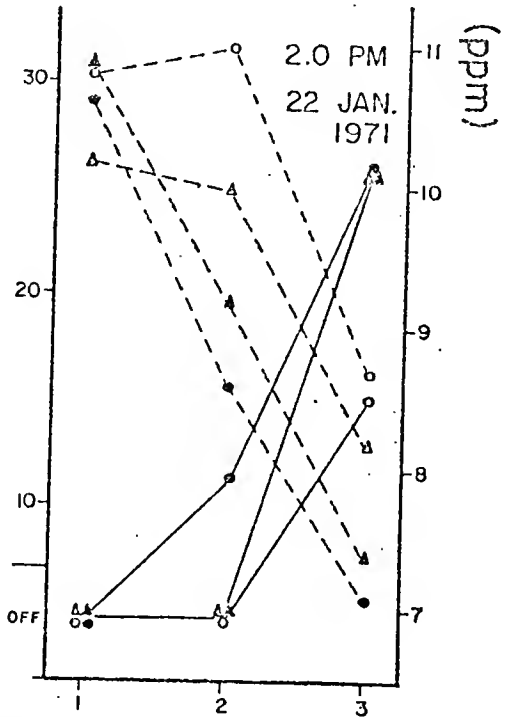
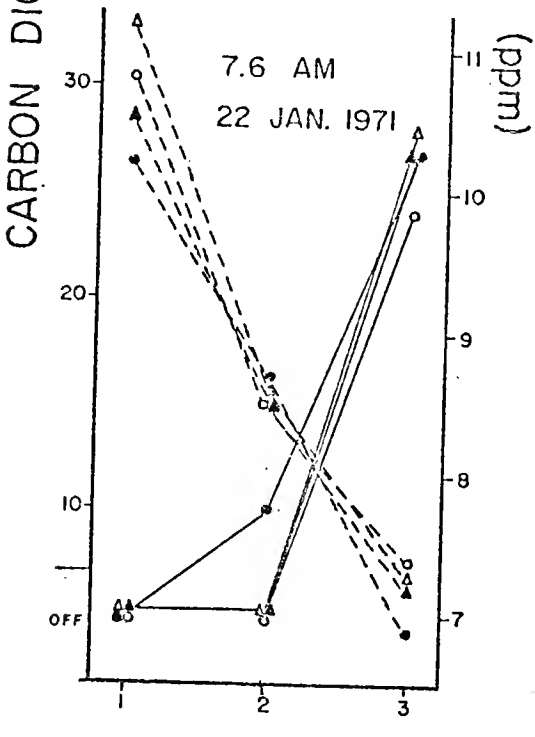
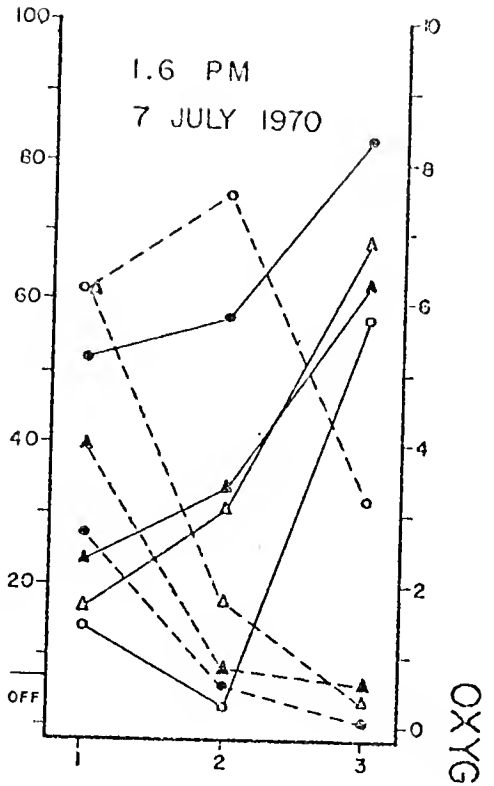
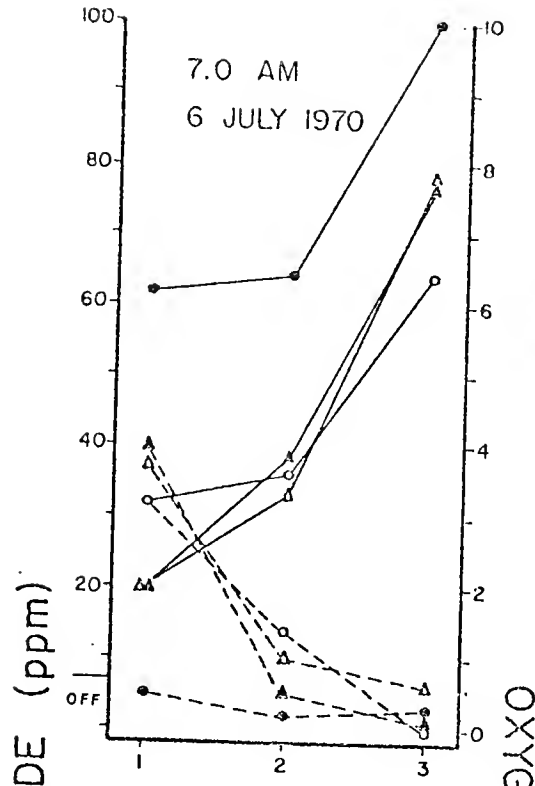


Figure 5. Concentrations of dissolved oxygen and carbon dioxide as a function of thickness of hyacinth cover, time of day, and time of year. Station 1 is "open" (no hyacinths, but considerable Ceratophyllum in summer), Station 2 is "thin" hyacinths (no accumulation of detritus in root mass), and Station 3 is "thick" hyacinths (larger plants characteristic of a mature mat, with considerable accumulation of detritus in the root mass).



STATION NUMBER

Table 1. Comparisons of pH, temperature, dissolved O<sub>2</sub> and dissolved CO<sub>2</sub> in hyacinth and "open" water areas. March-October is the growing season of Eichhornia in Gainesville, Florida.

	HYACINTHS				"OPEN" WATER		
	Yearly	Nov.-Feb.	March-Oct.	Yearly	Nov.-Feb.	March-Oct.	
Top Temp. (°C)	21.5	13.5	25.5	21.5	13.0	25.5	
Bottom Temp. (°C)	19.0	12.0	23.0	20.0	13.0	23.5	
Top pH	5.4	5.7	5.2	5.6	5.9	5.5	
Bottom pH	5.3	5.6	5.1	5.5	5.8	5.4	
Top O <sub>2</sub> (ppm)	4.2	5.6	3.5	6.4	8.1	5.6	
Bottom O <sub>2</sub> (ppm)	1.2	2.5	0.6	4.5	7.2	3.2	
Top CO <sub>2</sub> (ppm)	31	16	39	13	7	16	
Bottom CO <sub>2</sub> (ppm)	51	26	63	29	8	40	

0.6 ppm under the hyacinths, while the  $\text{CO}_2$  is 63 ppm. For an organism dependent upon aquatic respiration, the "open" water is a refuge during this period. In fact, larger fish such as the centrarchids are found only in the open water during the summer, while they are also in the hyacinth areas in winter. Some fish, therefore, migrate horizontally due to respiratory stress.

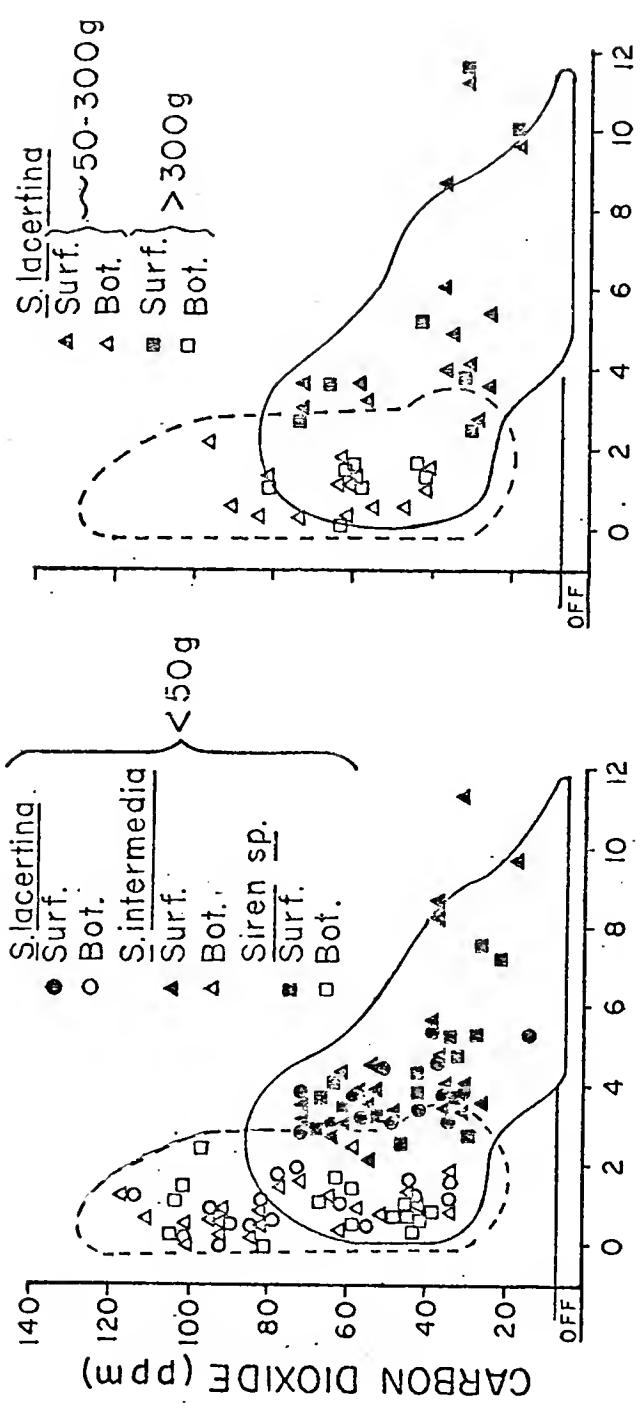
Extensive collections were made in both the "open" water and hyacinth areas to determine where sirenids were located. Regardless of the time of year, no P. striatus and only one Siren (probably lacertina) were collected in "open" water. The hyacinth areas are definitely the preferred microenvironment.

To determine if the animals were selecting areas within the hyacinth portion of the pond, successful collecting attempts were paired with the corresponding gas concentrations at the site of collection and compared to the set of all available gas concentrations within the hyacinth portion of the pond. These results are shown in Figures 6-8 as a function of the size of the animal (for Siren) and the time of the year. In all cases, the animals are not avoiding any particular gas concentrations, regardless of species, size, or time of year.

The conclusion drawn from the field work is that aquatic gas exchange considerations are not limiting in habitat selection in the Sirenidae. This evidence is in agreement with the results of a previous study for P. striatus (Ultsch, 1971). A probable corollary is that the Sirenidae must depend heavily upon aerial respiration as a source of oxygen, and perhaps as a method of carbon dioxide elimination.

Figure 6. Location of S. lacertina and S. intermedia within the hyacinth area of the pond during the hyacinth growing season (March-October), as a function of concentrations of dissolved respiratory gases. Areas enclosed by solid and dashed lines represent concentrations of dissolved  $O_2$  and  $CO_2$  at the surface (Surf.) and bottom (Bot.), respectively, for all March-October field determinations (exclusive of determinations made concurrently with collections).





O X Y G E N ( p p m )

C A R B O N D I O X I D E ( p p m )

Figure 7. Location of P. striatus within the hyacinth area of the pond during the growing season of Eichhornia (March-October), as a function of concentrations of dissolved respiratory gases. Enclosed areas are as in Figure 6.

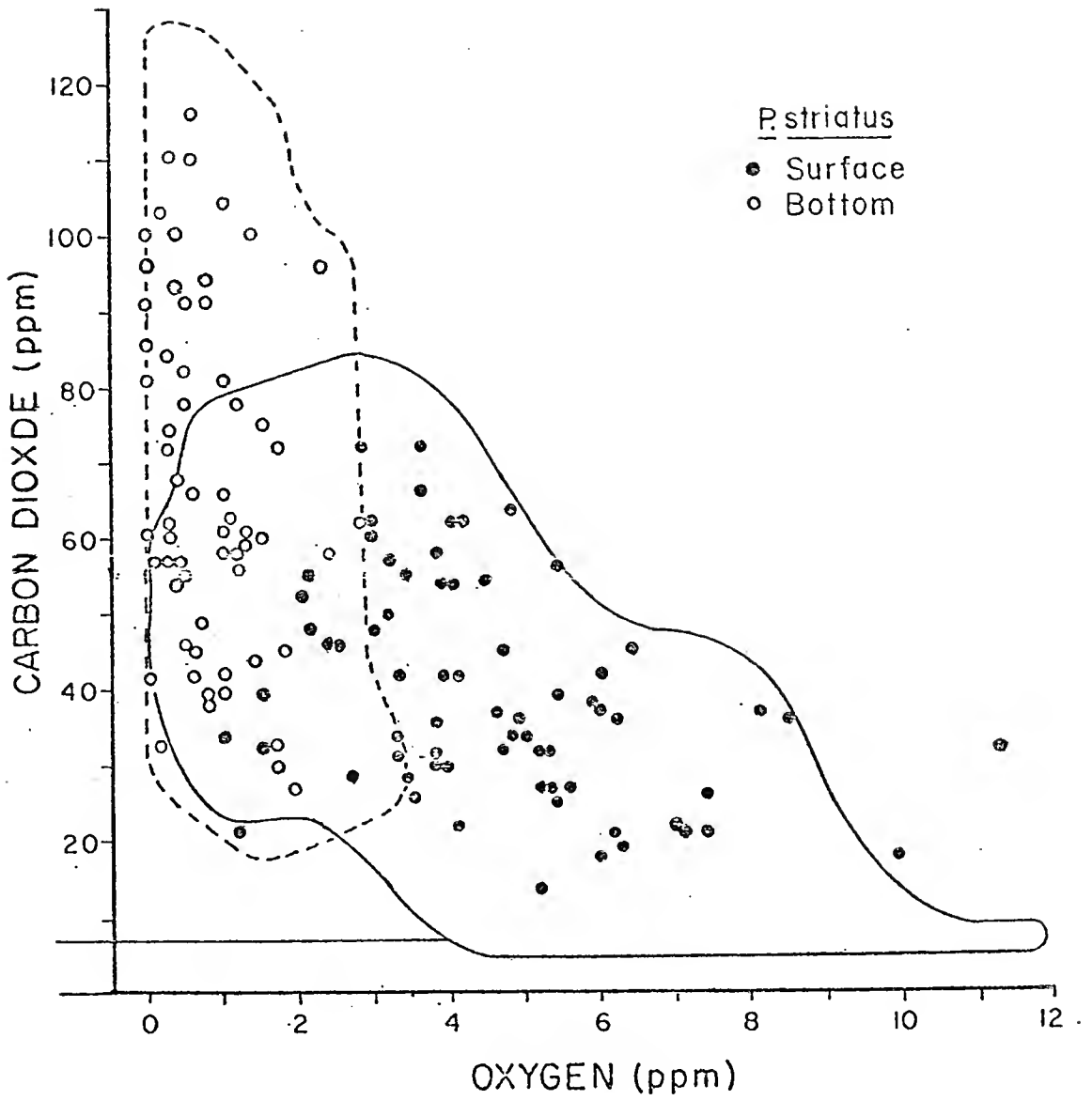
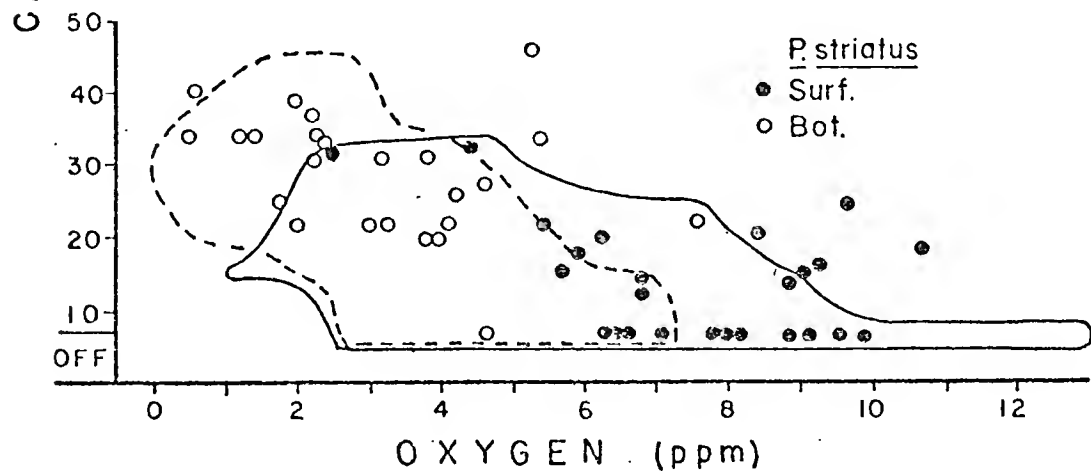
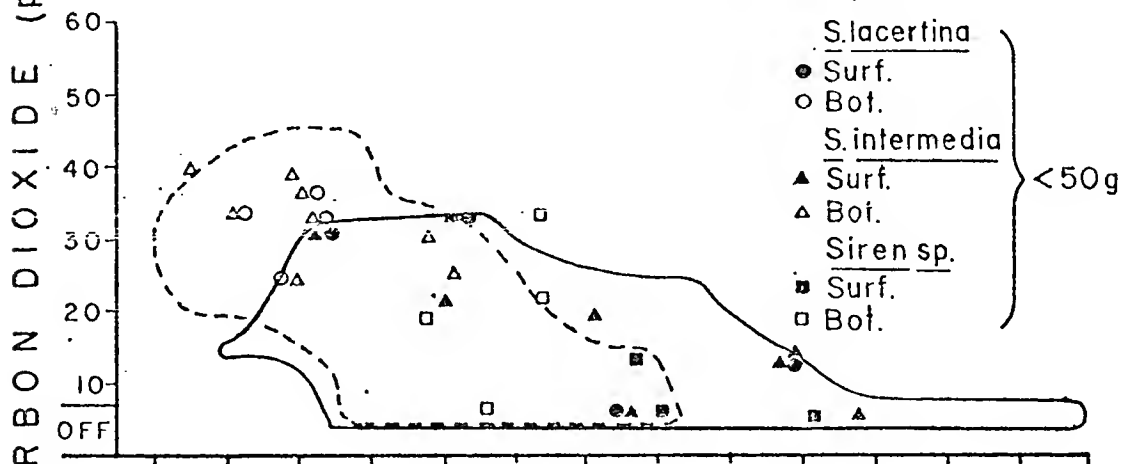
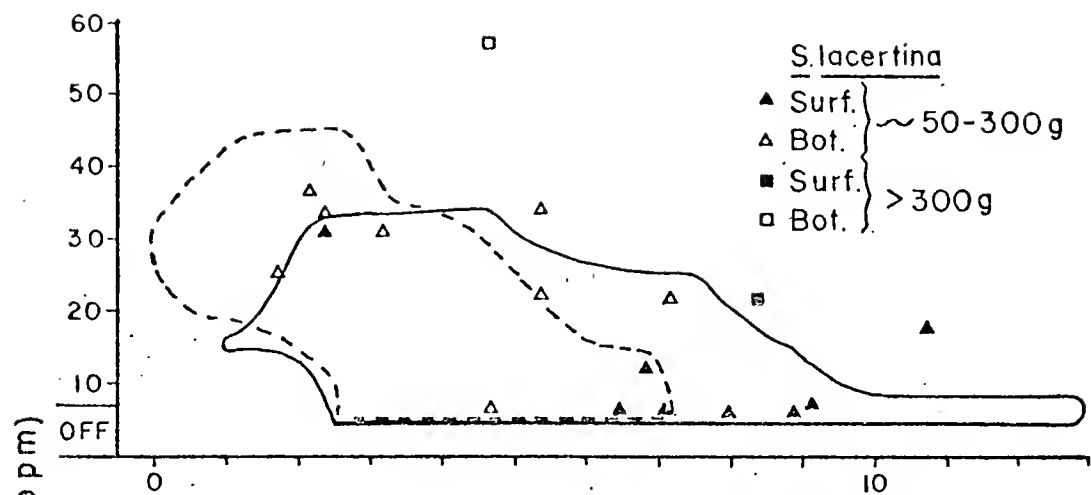


Figure 8. Location of Siren and Pseudobranchus within the hyacinth area of the pond during the non-growing season of Eichhornia (November-February), as a function of concentrations of dissolved respiratory gases. Enclosed areas are as in Figure 6, except for determinations being for November-February.

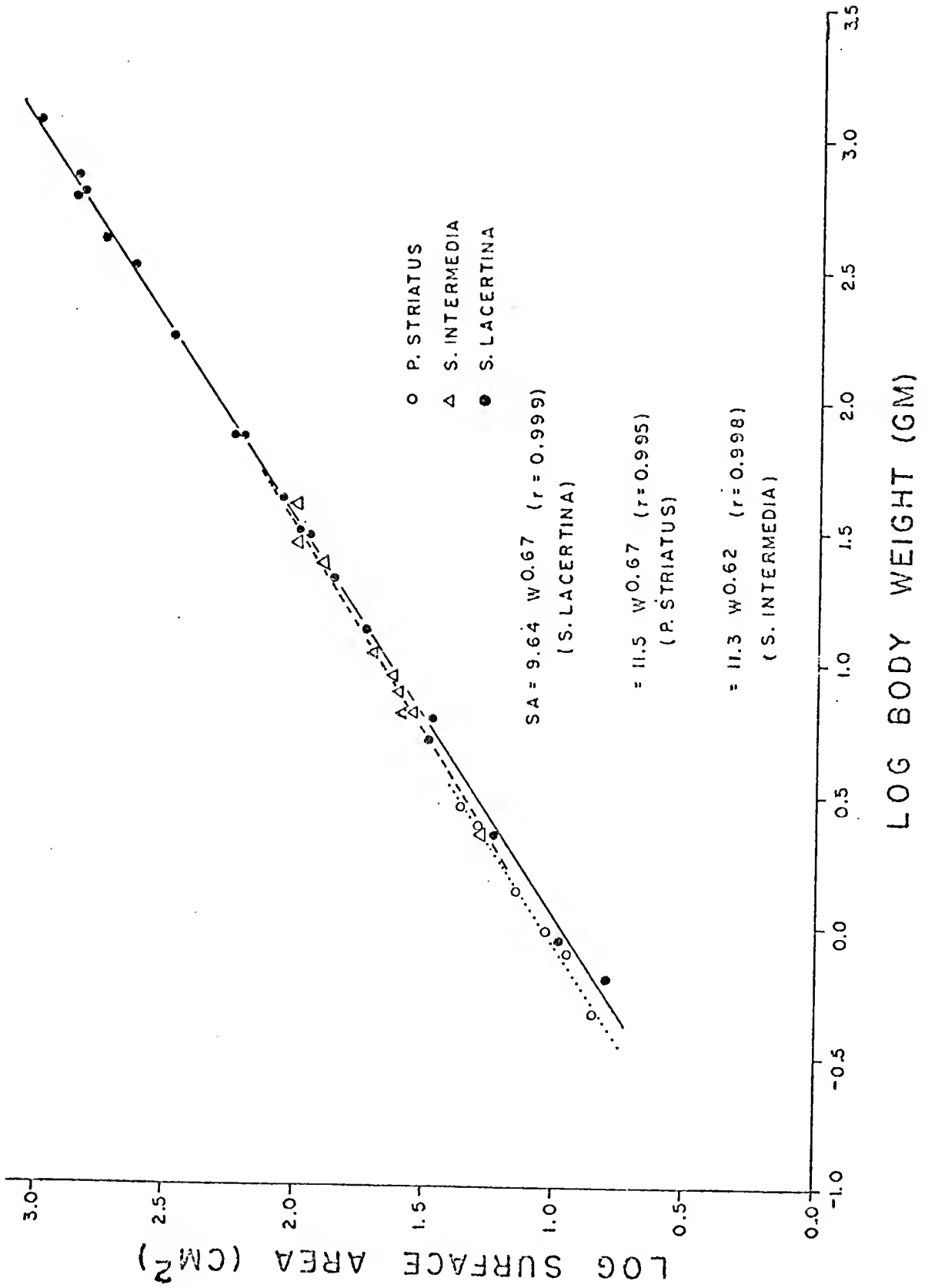


## RESULTS OF LABORATORY STUDIES

The results of determinations of skin area at various body sizes comprise Figure 9.

The results of progressive hypoxia experiments on submerged animals are given in Figures 1A-11A in Appendix A. The animals are definitely oxygen conformers at low  $O_2$  tensions and regulators at high tensions. Two methods of evaluating the metabolic rate data are presented. In both cases, a point R on the  $pO_2$  axis was chosen such that it was obvious that metabolic rate had no significant dependence upon  $pO_2$  at tensions greater than R. For all metabolic rates at oxygen tensions greater than or equal to R, two levels were determined: the average value ( $\bar{x}$ ), and a level where 10% of the points fell below and 90% above (10/90 level). Once these levels of metabolism had been determined, that level was extended graphically from the highest  $pO_2$  through lower ones as a straight line. In the case of the mean value, the line was continued until 75% or more of the values fell below the line for a given interval of 10 mmHg and for all following intervals. The point at which this occurred (to the nearest 5 mmHg) was deemed to indicate that the animal had given up regulation of oxygen consumption and is labeled  $P_c$  (critical oxygen tension). A line was then fitted by eye for the values remaining below  $P_c$ . The same approach was used to fix a  $P_c$  for the 10/90 level, except 50% of the values falling below the line was the arbitrary level picked to indicate the abandon-

Figure 9. Surface area of the skin in the three species of Sirenidae as a function of body weight.





ment of regulation. Some comparative use might be derived from considering the minimal metabolic rates given by the 10/90 line, but since the animals were relatively inactive in the metabolism chambers, the mean metabolic rate while the animal is regulating is probably the most realistic estimate of the standard metabolic rate while submerged and is the value that will be used in all further discussions and calculations.

Pseudobranchus and small Siren can survive submerged in air-equilibrated water indefinitely. Siren lacertina of various body weights were submerged at 23-24°C to determine if there was an upper limit to the size at which a submerged Siren could survive. Table 2 shows that animals 800 g or larger cannot survive without access to air, while smaller ones can function as water breathers only.

This observation led to an investigation of the effect of body size on gas partitioning in S. lacertina. Two large individuals (the largest one very near the maximum size for the species: Conant, 1958) and one relatively small individual were studied. The conditions for these experiments are given in Table 3, and the results in terms of absolute values and percentages in Table 4. It is possible for a particular partition to be significantly different between large and small animals without the absolute values being different, depending on the absolute value of the total gas exchange. Figure 10 presents a statistical interpretation of the absolute values for each partition for comparison to Table 4, which gives a statistical presentation of the percentage of the total gas exchange represented by each partition.

Table 2. Survival of submerged S. lacertina at 23-24°C in air-equilibrated water ( $pO_2$  approximately 155 mmHg). Animals removed at 336<sup>7</sup> hours were in no difficulty. Other times indicate the first observance of death, and are therefore maximum estimates of survival time.

Weight (g)	Survival time (hr)
83	336 +
191	336 +
277	336 +
463	336 +
670	336 +
805	114
998	30
1046	48

Table 3. Conditions of gas exchange partitioning experiments for two large and one small S. lacertina. The duration of the runs was 2.75-5.00 hrs (aerial) and 3.08-5.50 hrs (aquatic) for large animals, and 3.25-6.25 hrs (aerial) and 2.00-6.33 hrs (aquatic) for the small animal. All experiments were at 25°C. Values are given as  $\bar{x} \pm 2$  S.E.

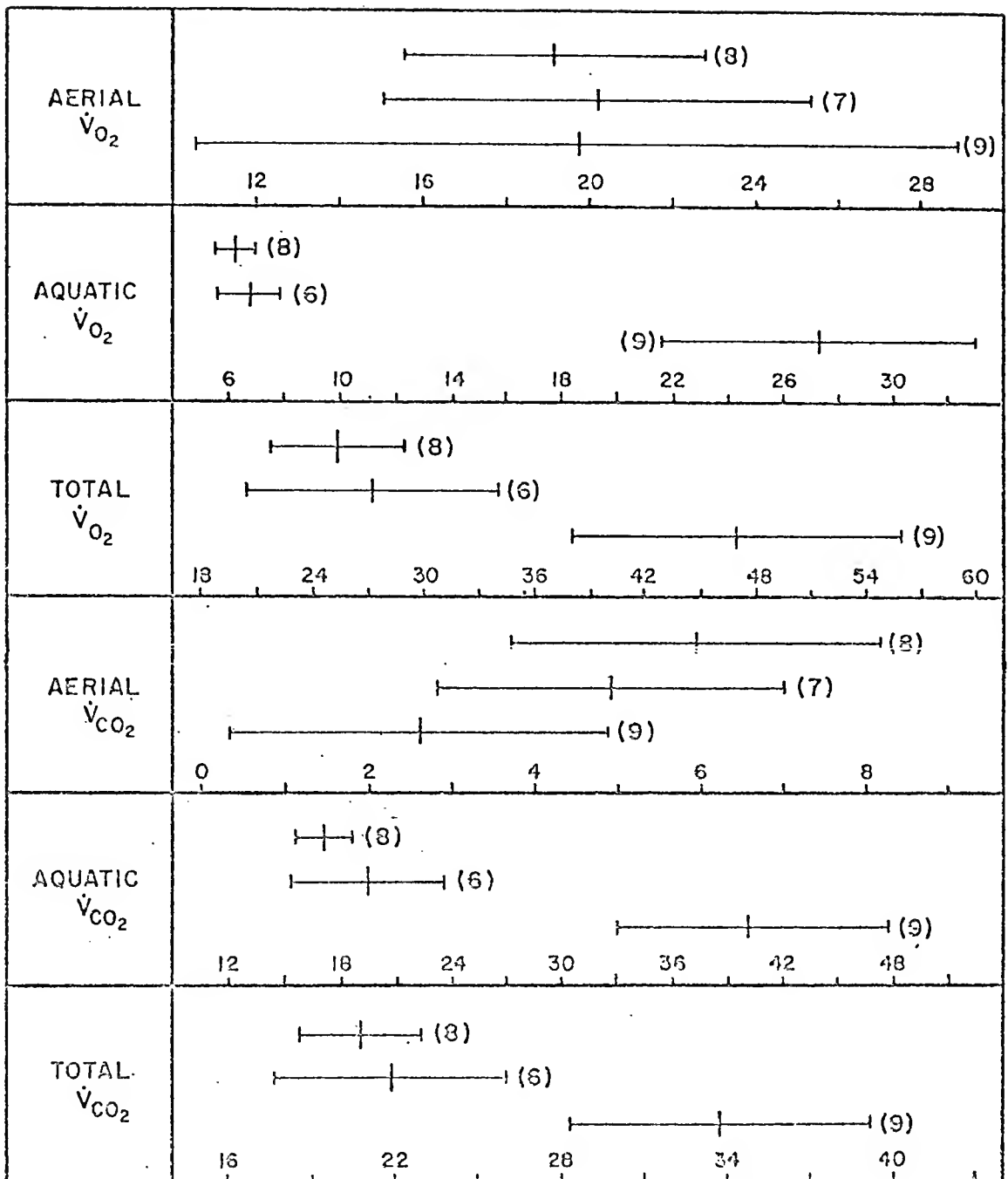
Dates of Experiment	Weight (g)	Final Air O <sub>2</sub> (vol%)	Mean Water pO <sub>2</sub> (mmHg)	Mean Water pCO <sub>2</sub> (mmHg)
2/26/72- 3/4/72	1489 $\pm 26$	15.6 $\pm 1.0$	145 $\pm 8$	less than 7
2/22/72- 3/2/72	1182 $\pm 9$	15.2 $\pm 1.4$	144 $\pm 3$	less than 7
3/28/72- 4/3/72	89.6 $\pm 0.7$	18.3 $\pm 0.8$	143 $\pm 4$	less than 7

Table 4. Gas exchange partitioning between air and water for large and small *S. lacertina* under conditions of high  $O_2$  and low  $CO_2$  in the water (see Table 3). Absolute values are  $\mu\text{l gas/g}\cdot\text{hr}$  ( $\bar{x} \pm 2 \text{ S.E.}$ ); values below this are percentages for each partition expressed as the mean and 95% confidence interval.  $N = 8$  for 1489 g,  $N = 9$  for 90 g,  $N = 6$  for aquatic and total results and 7 for aerial results for 1182 g.

	LARGE		SMALL	
	1489 g	1182 g	90 g	
Aerial	$\dot{V} O_2$	19.10 $\pm$ 3.00 75(61-89)	20.15 $\pm$ 4.20 75(56-94)	19.68 $\pm$ 7.94 42(22-60)*
	$\dot{V} CO_2$	5.93 $\pm$ 1.88 26(16-35)	4.91 $\pm$ 1.72 20(12-29)	2.61 $\pm$ 1.98 6(1-11)*
Aquatic	$\dot{V} O_2$	6.22 $\pm$ 0.62 25(22-27)	6.68 $\pm$ 0.88 25(21-29)	27.25 $\pm$ 4.94 58(46-70)*
	$\dot{V} CO_2$	17.16 $\pm$ 1.28 74(68-81)	19.49 $\pm$ 3.22 80(63-97)	40.05 $\pm$ 6.12 94(77-100)
Total	$\dot{V} O_2$	25.32 $\pm$ 3.02	27.22 $\pm$ 5.34	46.93 $\pm$ 7.78
	$\dot{V} CO_2$	23.09 $\pm$ 2.74	24.77 $\pm$ 4.86	42.57 $\pm$ 6.98

\*Significantly different from large animals at the 95% level of confidence.

Figure 10. Aerial-aquatic gas exchange partitioning in a high  $O_2$ -low  $CO_2$  aquatic phase (see Table 3) as a function of body size. For each partition the upper line is for  $W = 1489$  g, the middle line for  $W = 1182$  g, and the lower line for  $W = 90$  g. Results are shown as  $\bar{x}$  and the 95% confidence interval. Non-overlap of confidence intervals yields statistical difference in the mean values at the 95% level. Numbers in parentheses are sample sizes.



$O_2$  CONSUMPTION OR  $CO_2$  ELIMINATION ( $\mu l/g \cdot hr$ )

Since the field data determined that Siren could be found in a number of different aquatic situations with various combinations of dissolved respiratory gases, the final study dealt with the partitioning of aerial and aquatic gas exchange as a function of the levels of dissolved  $O_2$  and  $CO_2$ . The largest animal available was chosen for this study, since the submergence experiments had determined that large animals are most affected by the levels of dissolved respiratory gases (Table 2). The various conditions used are given in Table 5. The low  $O_2$ -high  $CO_2$  condition is most similar to the actual environment of vegetated waters. Animals are occasionally found in high  $O_2$ -low  $CO_2$  situations, such as when some move into streams to breed in February and March. The other conditions were investigated to determine the relative importance of low oxygen and high carbon dioxide separately. The results are presented in terms of percentages in Table 6 and absolute amounts in Figure 11.

Table 5. Conditions of gas exchange partitioning experiments in a single, large S. lacertina. The duration of the runs were 2.75-4.50 hrs (aerial) and 3.00-5.50 hrs (aquatic). All experiments were at 25°C. Values are given as  $\bar{x} \pm 2$  S.E.

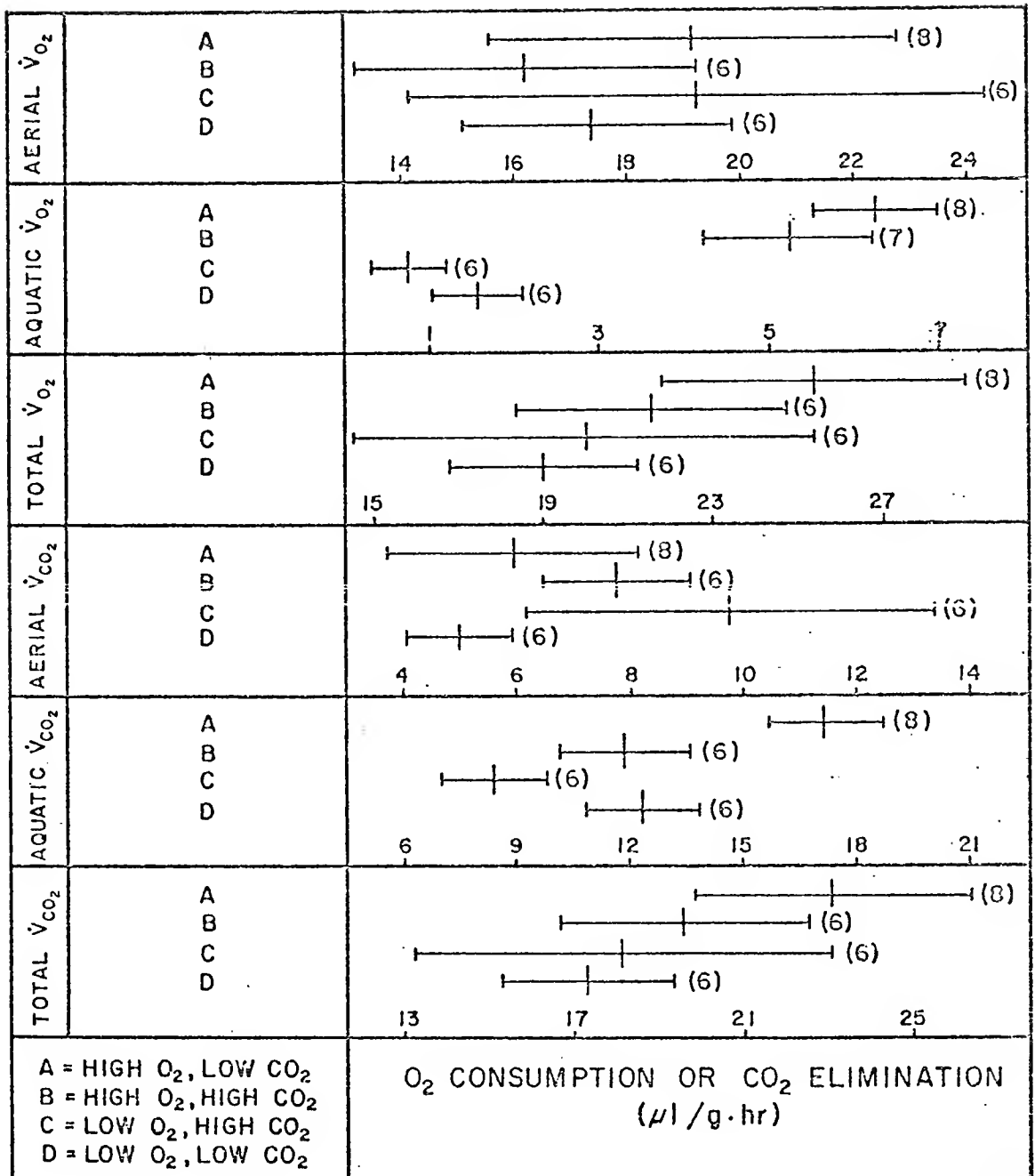
Dates of Experiment	Weight (g)	Final Air O <sub>2</sub> (vol%)	Mean Water pO <sub>2</sub> (mmHg)	Mean Water pCO <sub>2</sub> (mmHg)
2/26/72- 3/4/72	1489 $\pm 26$	15.6 $\pm 1.0$	145 $\pm 8$	less than 7
3/17/72- 3/20-72	1454 $\pm 10$	15.7 $\pm 0.5$	145 $\pm 2$	40 $\pm 2$
3/8/72- 3/11/72	1464 $\pm 4$	15.3 $\pm 1.2$	24 $\pm 5$	39 $\pm 2$
3/13/72- 3/15/72	1453 $\pm 2$	15.5 $\pm 0.9$	22 $\pm 4$	less than 7



Table 6. Gas exchange partitioning between air and water for an individual, large S. lacertina (1453-1489 g) as a function of concentrations of dissolved O<sub>2</sub> and CO<sub>2</sub> in the water phase. Values are expressed as in Table 4. N = 8 at all high O<sub>2</sub>-low CO<sub>2</sub> values, N = 7 for aquatic  $\dot{V}O_2$  at high O<sub>2</sub>-high CO<sub>2</sub>, N = 6 for all other conditions. All experiments were at 25°C.

	HIGH O <sub>2</sub>		LOW O <sub>2</sub>		
	Low CO <sub>2</sub>	High CO <sub>2</sub>	Low CO <sub>2</sub>	High CO <sub>2</sub>	
Aerial	$\dot{V}O_2$	19.10 ± 3.00 75(73-78)	16.16 ± 2.34 76(61-89)	17.44 ± 1.86 92(79-100)	19.21 ± 3.94 96(71-100)
	$\dot{V}CO_2$	5.93 ± 1.88 26(16-35)	7.78 ± 1.02 40(33-46)	5.00 ± 0.78 26(23-29)	9.76 ± 2.80 54(34-74)
Aquatic	$\dot{V}O_2$	6.22 ± 0.62 25(22-27)	5.21 ± 0.80 24(20-29)	1.56 ± 0.42 8(5-11)	0.75 ± 0.34 4(2-6)
	$\dot{V}CO_2$	17.16 ± 1.28 74(65-84)	11.82 ± 1.40 60(51-69)	12.32 ± 1.16 74(63-80)	8.41 ± 1.12 46(38-54)
Total	$\dot{V}O_2$	25.32 ± 3.02	21.54 ± 2.48	19.00 ± 1.74	19.96 ± 4.20
	$\dot{V}CO_2$	23.09 ± 2.74	19.60 ± 2.26	17.32 ± 1.58	18.17 ± 3.82

Figure 11. Aerial-aquatic gas exchange partitioning in a large S. lacertina (1453-1489 g) under various conditions of dissolved O<sub>2</sub> and CO<sub>2</sub> (see Table 5). Results are shown as  $\bar{x}$  and the 95% confidence interval. Non-overlap of confidence intervals yields statistical difference in the mean values at the 95% level. Numbers in parentheses are sample sizes.



## DISCUSSION OF LABORATORY STUDIES

### Metabolic Rate, Gas Exchange and Body Weight

Hemmingsen (1960) has shown that the metabolic rate as a function of body size for a large number of organisms can be expressed by

$$(1) \quad M = k W^{0.75}$$

where M is the rate of oxygen consumption and W is the body weight.

This equation was the result of interspecific comparisons, and Kleiber (1961) has argued that the relationship also holds for large intra-specific ranges of body weight, although supporting data are scarce.

Why is the power function of weight in Eq. (1) 0.75 rather than 1.0? One possibility often mentioned is a disproportionate increase of non-metabolizing (or low-level metabolizing) tissues with an increase in body size. The W in Eq. (1) is actually  $W_T$ , the whole body weight, which is composed of  $W_A$  (active tissue) and  $W_I$  (relatively inactive tissue). Even without any actual change in the metabolic rate of the active tissues, a disproportionate increase in  $W_I$  with increasing  $W_T$  would result in an apparent decrease in weight-specific metabolic rate. Appendix B shows calculations that indicate that only a minor percentage (at least for mammals) of the decrease in weight-specific metabolic rate with size can be accounted for as apparent and that the power of  $W_A$  in this relationship is close to 0.75 (about 0.77), even when disproportionate increases in  $W_I$  are taken into account.

Another explanation has been offered by Kleiber (1961) which considers heat exchange. He points out that a 60 g mouse with the same weight-specific metabolic rate as a steer would need a 20 cm thick fur coat to maintain its body temperature if the air temperature were 3°C. He uses this example to point out why it is advantageous for mammals to have an increasing weight-specific metabolic rate with decreasing size. However, this cannot be considered the cause in the general case, since poikilotherms, which do not regulate their body temperature, and small aquatic organisms, which would obviously have no problem in dissipating heat, also have metabolic rates proportional to  $W^{0.75}$ . Therefore it would appear that insulation is adapted to  $W^{0.75}$ , rather than vice versa, and some other factor is responsible for  $M = k W^{0.75}$ .

Hemmingsen also showed that unicellular organisms, poikilotherms and homeotherms have rates of metabolism that are quite different for a given weight. Poikilotherms had metabolic rates about eight times those that would be predicted from considerations of the metabolic rates of unicellular organisms, and homeotherms had metabolic rates about 28.6 times those of poikilotherms of the same size. However, since the poikilotherm data was for 20°C, and the homeotherm data for 39°C, we can say that the poikilotherm values (considering  $Q_{10} = 2$  and the temperature correction to be about 20°C) should have been some four times higher than shown. This means that homeotherms generally have metabolic rates about seven times greater than poikilotherms of the same size. Hemmingsen then argued at considerable length that higher levels can be directly related to the increase in respiratory

surface area per unit weight that occurs as one follows the phylogenetic sequence from unicellular organisms to homeotherms.

This viewpoint has been supported by several workers. Anderson (1970) showed that for two species of spiders of similar body weight, there was a close correlation between metabolic rate and book lung surface area. Tenney and Remmers (1963) compared the manatee with the porpoise at approximately the same body weights. The porpoise had the greater metabolic rate and the greater lung diffusing area. Whitford and Hutchison (1967) demonstrated that lungless salamanders have lower metabolic rates than salamanders of the same size with lungs (see Table 7 for a re-interpretation of their data).

These observations suggest that the metabolic rate of an organism is correlated with its life style, and that the surface area of the gas exchanger will be adapted to help meet the metabolic demands for oxygen. I suggest that there is a limitation to the ability of an organism to obtain oxygen, and that this limitation is a function of body size and is responsible for organisms showing a decrease in weight-specific metabolic rate with increasing body size. The surface area of the gas exchanger is one of the two factors determining this  $O_2$  exchange capacity; permeability to  $O_2$  is the other.

A model will illustrate this point. Assume that the surface area (SA) of the external gas exchanger is the only factor determining the rate of oxygen delivery to the tissues. The equation relating surface area to volume for objects of similar shape but varying sizes is

$$(2) \quad SA = k_1 W^{0.67}$$

where  $W$  has been substituted for the volume by assuming the average

density of an organism to be 1.0, and where  $k_1$  depends on the shape of the object. The exponent of  $W$  in Eq. (2), which relates weight to SA and therefore to the ability to supply  $O_2$ , is less than the exponent of  $W$  in Eq. (1), which relates weight to oxygen demand. Therefore, as an animal increases in size, the demand for  $O_2$  will increase more than the ability to supply it. At the theoretical maximum size, the demand and supply of oxygen would be equal.

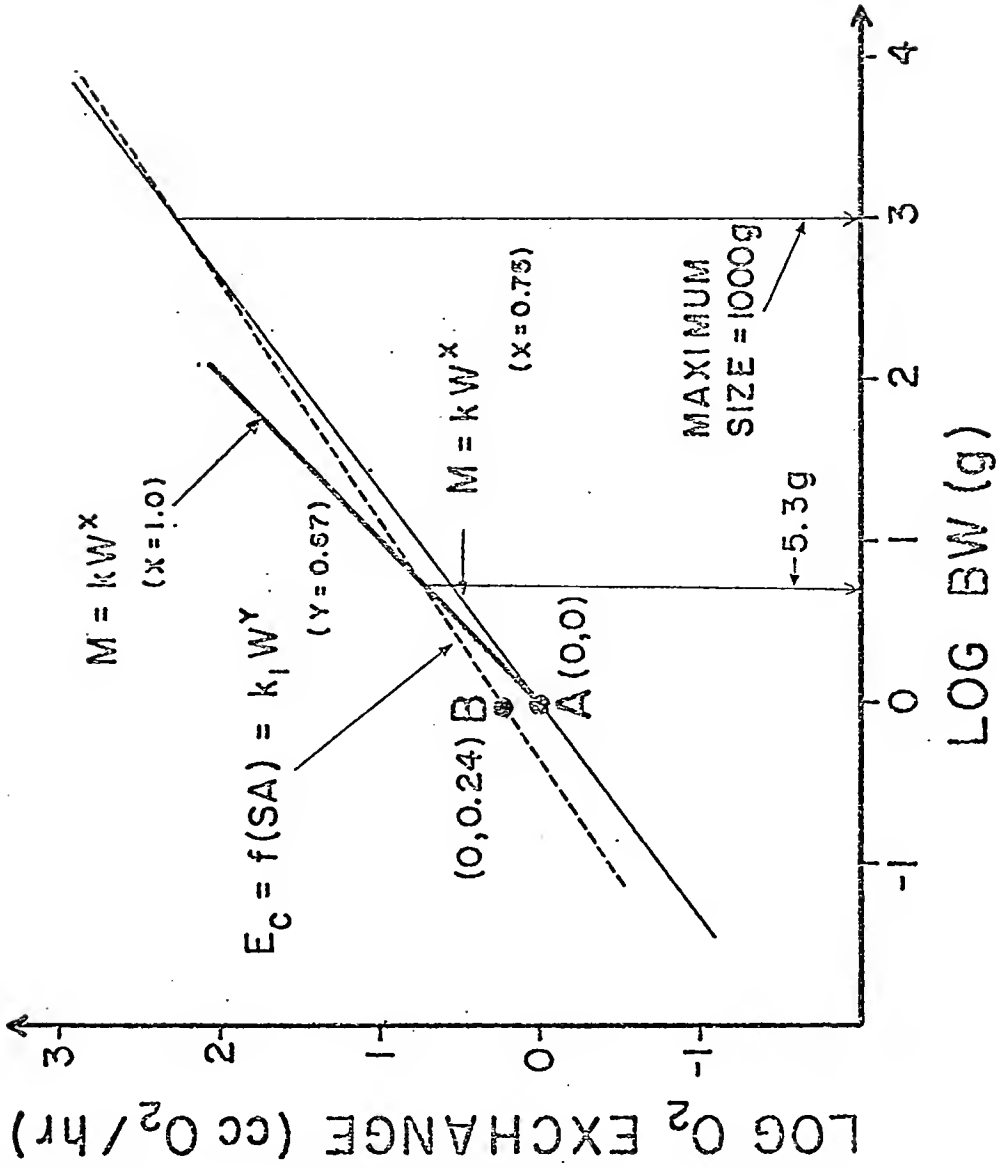
The model is illustrated in Figure 12. For an immature (small) animal, the ability to supply  $O_2$  under the conditions set above must be greater than the demand expressed by the standard metabolic rate, since it does grow to a larger size, and must also maintain some scope for activity regardless of size. For some given differential in  $pO_2$  across the external gas exchanger, assume the permeability to oxygen to be  $1 \text{ cc } O_2/\text{hr}\cdot\text{cm}^2$  and constant with body size. This makes the  $O_2$  exchange capacity ( $E_c$ ) a function of surface area of the gas exchanger only. By choosing a starting weight of 1 g, the values of  $k$  and  $k_1$  in Eq. (1) and (2) will be the antilogs of the y-intercepts of these equations when they are plotted in logarithmic form. For convenience, points A and B are chosen to give values of  $1.0 \text{ cc } O_2/\text{hr}\cdot\text{g}$  for  $k$  and  $1.74 \text{ cm}^2/\text{g}$  for  $k_1$ . If the power of  $W$  on  $M$  in Eq. (1) were 1.0, then for a 1 g animal,  $M = 1.0 \text{ cc } O_2/\text{hr}$  and  $SA = 1.74 \text{ cm}^2$ . The same values are obtained for a 1 g animal if  $M$  is proportional to  $W^{0.75}$ .

The capacity of the external gas exchanger to take up  $O_2$  for a given differential in  $pO_2$  is

$$(3) \quad E_c = SA (P)$$

Figure 12. Predicted maximum size attainable by a 1 g organism whose surface area of the gas exchanger is  $(f) W^{0.67}$  and whose metabolic rate is either  $(f) W^{1.0}$  or  $(f) W^{0.75}$ . Points A and B and permeability of the gas exchanger to  $O_2$  are given terms (see text).





where  $E_c$  is the oxygen exchange capacity, i.e., the oxygen uptake that would occur across the gas exchanger if the animal consumed all of the oxygen that crossed the exchanger. For a 1 g animal  $E_c = (1.74 \text{ cm}^2) (1.0 \text{ cc O}_2/\text{hr}\cdot\text{cm}^2) = 1.74 \text{ cc O}_2/\text{hr}$  which is 74% greater than his resting metabolic rate. This difference  $\overline{AB}$  may be termed "reserve  $\text{O}_2$  exchange capacity" and would be related to the scope for activity.

The maximum weight that can be achieved can be calculated for power functions of  $W^{1.0}$  and  $W^{0.75}$  by setting  $E_c = M$ . These weights are 5.3 and 1000 g respectively, and represent a large difference in maximal body size, associated with having a decreasing weight-specific metabolic rate with increasing body size. Actually, the maximal attainable weight would be less than these values since some reserve  $\text{O}_2$  exchange capacity must be maintained by the organism for those times when its metabolic rate exceeds the average resting value.

This analysis points out an advantage of having a metabolic rate proportional to a power less than 1.0. Figure 12 can also be used to point out other strategies which would enable an animal to reach a large size. Generally, any adaptation that will move the intersection of the  $E_c$  and  $M$  curves to the right will permit a larger body size.

A decrease in the exponent of weight on metabolism is one strategy; others deal with increasing the slope of the  $E_c$  curve. Since

$$(4) \quad E_c = SA(\text{cm}^2) P(\text{cc O}_2/\text{hr}\cdot\text{cm}^2\cdot\text{mmHg}) \Delta p\text{O}_2(\text{mmHg})$$

where  $SA$  is the surface area of the gas exchanger,  $P$  the permeability, and  $\Delta p\text{O}_2$  the difference in partial pressure of oxygen across the gas exchanger, changes in any of these factors will affect the slope of the  $E_c$  curve.

One adaptation would be microhabitat selection resulting in increasing the differential in partial pressure across the exchanger. The field results showed that Sirenidae do not do this.

A morphological adaptation which would affect  $O_2$  exchange capacity would be to maintain a constant ratio of the surface area of the gas exchanger to metabolic demands for oxygen. For example, consider a cylindrical organism whose metabolic rate is a function of  $W^{0.75}$ . Ignoring the area of the ends of the cylinder which are small in relation to the area of the curved surface, the ratio of surface area to metabolism can be held constant if

$$(5) \quad \frac{SA}{M} = \frac{2\pi rL}{k W^{0.75}} = k_o,$$

or combining constants,

$$(6) \quad rL = k_1 W^{0.75}.$$

This means that if the increase in the product of radius and length is greater than the increase in metabolic rate, a cylindrical animal can grow indefinitely large.

When a sirenid is submerged, it is essentially a cutaneous breather. Figure 9 indicates that the larger sirenids do not change their skin surface area with increasing body weight in a manner different from the relation predicted in Eq. 2.

A more general statement regarding the relationship between the power functions of weight on surface area and on metabolism can be made: there will be no limitation to body size due to limitations of oxygen supply if the power of weight against  $O_2$  exchange capacity is greater than the power of weight against metabolic rate. Since the surface area of the gas exchanger is an important determinant of  $O_2$  exchange capacity, one might expect the relationship to hold for

it also. Table 7 presents a number of values for these two exponents from the literature for various groups of animals. In all cases except fresh-water turtles, the exponent of weight against surface area is equal to or greater than that of weight against metabolism. While this does not prove a cause and effect relationship between  $E_c$  and  $M$ , it certainly supports the conclusion that the two are closely correlated.

One might ask why the exponent for weight vs. the exponent for the  $E_c$ -related factor (usually surface area of the gas exchanger) is usually greater than that of weight vs. metabolism. It is possible that the permeability of the external gas exchanger to oxygen decreases with body size in many organisms, especially those using the skin as a respiratory organ. Table 8 indicates that this is the case for large ranid frogs, due to an increase in the thickness of the epidermis without a compensatory increase in the vascularization of the skin. Since  $E_c$  is both a function of surface area and permeability, a decreasing permeability with increasing body size could be partly compensated for by the increase in  $O_2$  exchange area being greater than the increase in metabolic rate as body size increases.

The permeability to oxygen of the gas exchanger in a living animal is difficult to measure directly, but it can be inferred for the skin of submerged sirenids from the data of Figures 1A-11A. When  $O_2$  tensions are high and an animal is regulating oxygen consumption, permeability will vary according to oxygen needs. But as the  $O_2$  tension in the water falls toward the critical  $O_2$  tension, whatever adjustments can be made to increase the effective permeability of the skin to  $O_2$  will come into play. Such changes could include

Table 7. Relationships between metabolic rate and weight and O<sub>2</sub> exchange capacity and weight for various groups of animals.

Group	Approximate Size Range	E <sub>c</sub> -Related Measurement	Meta-bolism	Power of Weight		Source and Comments
				vs. E <sub>c</sub> -Related factor		
Spiders	25-970 mg	surface area of book lungs	0.63	0.84		Anderson, 1970. Six species at 20°C.
	25-23,120 mg	-----	0.70	-----		Anderson, 1968. Seven species at 20°C.
Anura	3-90 g	-----	0.71	-----		Hutchison, Whitford and Kohl, 1968. Various species at 5-25°C.
	2-150 g	-----	0.67	-----		Davison, 1955. Seven species at 25°C.
	0.5-291 g	total capillary length of all respiratory surfaces	-----	0.85		Calculated from data of Czopek, 1965. 19 species.
Lunged salamanders	~3-30 g	-----	0.856	-----		Whitford and Hutchison, 1967. Six species at 15°C.
	1.3-38 g	total capillary length of all respiratory surfaces	-----	0.864*		Calculated from data of Czopek, 1965. Ten species.
Lungless salamanders	~3-23 g	-----	0.72	-----		Whitford and Hutchison, 1967. Four species at 15°C.

Table 7. continued

Group	Approximate Size Range	E <sub>C</sub> -Related Measurement	Meta- bolism	Power of Weight vs.		Source and Comments
				E <sub>C</sub> -Related factor	E <sub>C</sub> -Related factor	
Lungless salamanders	0.5-13.6 g	total capillary length of all respiratory surfaces	----	0.735*	0.735*	Calculated from data of Czopek, 1965. Seven species.
Amphibia	35-398 g	respiratory surface area (skin + lungs)	----	0.98	0.98	Tenney and Tenney, 1970. Seven species.
Fish	0.1-50 g	----	0.70	----	----	Kayser and Huesner, 1964 (from Stussi, et al., 1963). Four species at 25°C.
	0.2-3487 g	----	0.81	----	----	Winberg, 1956 (from Ivlev, 1954). 22 species of freshwater fishes at 18-22°C.
	0.0032-10,400 g	----	0.81	----	----	Winberg, 1956. Many freshwater species, corrected to 20°C by Winberg.
	1.4-116 g	----	0.71-0.79	----	----	O'Hara, 1968. Two freshwater species at 25-30°C.
	0.08-870 g	----	0.79	----	----	Winberg, 1956. Various marine species, corrected by Winberg, to 20°C.
	1-1000 g	gill surface area	----	0.78	0.78	Muir, 1969 (from Price, 1931). <u>Micropterus dolomieu</u> .

Table 7. continued

Group	Approximate Size Range	Ec-Related Measurement	Meta- bolism	Power of Weight		Source and Comments
				vs. Ec-Related factor	factor	
Fish	71-5216 g	gill surface area	----	0.82		Ursin, 1967 (from Gray, 1954). Marine species.
	5.2-39.5 kg	gill surface area	----	0.94		Muir and Hughes, 1969. Bluefin tuna.
	1-1000 g	gill surface area	----	0.9		Muir and Hughes, 1969. Tench.
Reptilia	22-100,000 g	pulmonary surface	----	0.75		Tenney and Tenney, 1970. 15 Species.
Lizards	1-1300 g	----	0.62	----		Bartholomew and Tucker, 1964. 11 genera at 30°C.
Snakes	351-22,502 g	----	0.60	----		Dmi'el, 1972. 15 species at 30°C.
Freshwater turtles	3-1000 g	----	0.86	----		Kayser and Huesner, 1964. 25°C.
Mammals	21-600,000 g	----	0.75	----		Kleiber, 1961. Many species.
	10-1,000,000 g	alveolar surface area	----	0.75		Tenney and Remmers, 1963.
	10-300,000 g	lung weight	----	0.99		Stahl, 1967 (from Brody, 1945).
	20-800,000 g	lung capacity	----	1.06		Stahl, 1967.

Table 7. continued

Group	Approximate Size Range	E <sub>c</sub> -Related Measurement	Meta- bolism	Power of Weight vs.		Source and Comments
				E <sub>c</sub> -Related factor	E <sub>c</sub> -Related factor	
Birds	.003-100 kg		0.72	----		Lasiewski and Calder, 1971.
	.005-125 kg	lung weight	----	0.95		Lasiewski and Calder, 1971.
	.006-88 kg	lung volume	----	0.94		Lasiewski and Calder, 1971.

\*Values reported were 0.794 for lunged and 0.614 for lungless, calculated by using Czopek's data of 1960, 1961, and 1962 for respiratory surface area. However, using total capillary length gives a measure of vascularization, which is a step closer to O<sub>2</sub> exchange capacity, and therefore a better estimate of E<sub>c</sub>.

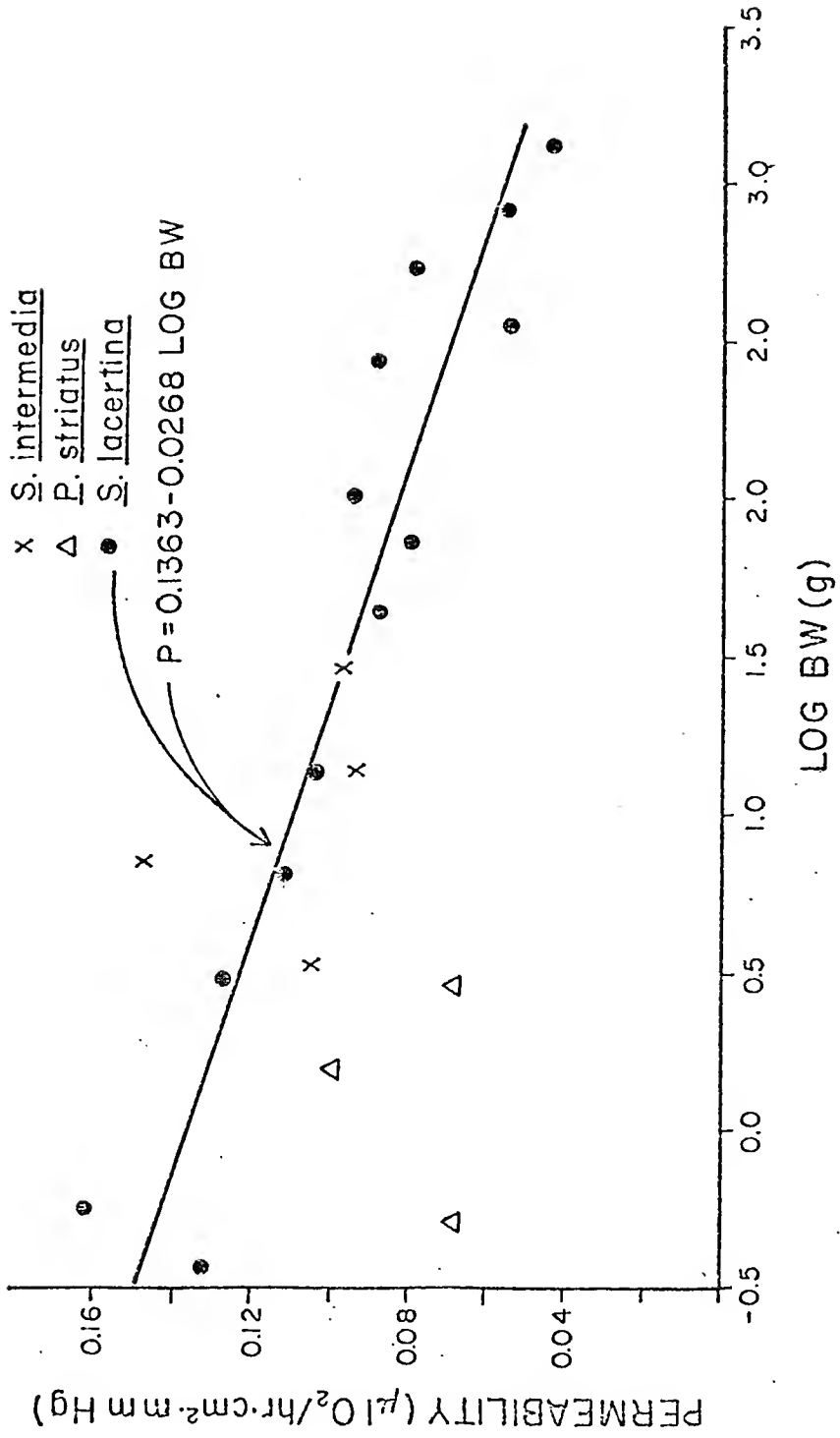


Table 8. Skin vascularization and epidermal thickness in ranid frogs (data from Czopek, 1965).

Species	W (g)	Epidermal Thickness ( $\mu$ )	# meshes capillary net per $\text{mm}^2$ skin
<u>Rana</u> <u>escuelenta</u>	1.7	35.0	204
<u>Rana</u> <u>escuelenta</u>	53.0	39.1	220
<u>Rana</u> <u>escúelenta</u>	250.0	62.3	225
<u>Rana</u> <u>grylio</u>	4.5	24.5	103
<u>Rana</u> <u>grylio</u>	24.0	----	106
<u>Rana</u> <u>grylio</u>	291.0	32.3	107
<u>Rana</u> <u>pipiens</u> <u>sphenocephala</u>	0.6	12.7	132
<u>Rana</u> <u>pipiens</u> <u>sphenocephala</u>	127.0	37.0	100

vasodilation of the peripheral arterioles and shunting of blood to the skin. At  $P_c$ , the permeability of the skin to oxygen should be maximal, and at this time exchange capacity ( $E_c$ ) will equal metabolic rate. Therefore the  $O_2$  consumption at  $P_c$  is equal to (maximal permeability)(surface area), and permeability can be solved for directly in terms of  $\mu l O_2/cm^2 \cdot hr$ . To express permeability in terms of  $\mu l O_2/cm^2 \cdot hr \cdot mmHg$ , one need only to know the  $pO_2$  of the blood, since the  $pO_2$  of the water is known (i.e.,  $P_c$ ). A reasonable estimate can be made by assuming that the  $O_2$  tension of the blood is close to the  $p50$  when the blood returns to the skin to pick up oxygen. The  $p50$  values for the large aquatic salamanders Necturus, Amphiuma and Cryptobranchus range from 14.5 - 29 (Lenfant and Johansen, 1967; McCutcheon and Hall, 1937; Scott, 1931). Even small (0.36 - 0.56 g) submerged S. lacertina die at  $pO_2$  tensions between 10 and 20, indicating that such tensions are not enough to saturate the blood to a degree permitting survival and are probably below the  $p50$ . Therefore, the loading tension of the blood of a Siren will be considered to be 25 mmHg for purposes of calculation. For example, for S. lacertina with  $W = 0.36$  g,  $M = 35.3 \mu l O_2/hr$ ,  $SA = 4.886 cm^2$  and  $P_c = 80$  mmHg, permeability would have units of  $\mu l O_2/hr \cdot cm^2 \cdot mmHg$  or  $M/SA(P_c - 25)$ . We are calculating maximal permeability ( $P_{max}$ ) and have  $P_{max} = 35.3 \mu l O_2/hr \cdot 4.886 cm^2 \cdot 55 mmHg$  or  $0.1313 \mu l O_2/hr \cdot cm^2 \cdot mmHg$ . Utilizing this method, permeabilities were calculated for each size of sirenid for which submerged metabolism data were taken, and the results are shown in Figure 13.

Figure 13. Permeability of the skin to oxygen in the Sirenidae as a function of body size. The regression line is fitted to the data for S. lacertina only.



Oxygen exchange capacity can now be calculated as

$$(7) \quad E_c (\mu\text{l O}_2/\text{hr}) = P_{\text{max}} (\mu\text{l O}_2/\text{cm}^2 \cdot \text{hr} \cdot \text{mmHg}) \quad \text{SA} (\text{cm}^2) \quad \Delta p\text{O}_2 (\text{mmHg})$$

where  $\Delta p\text{O}_2$  is the differential between whatever the oxygen tension of the water happens to be and the 25 mmHg loading tension assumed for the blood. All S. lacertina were compared at 155 mmHg of  $\text{O}_2$  in the water, which makes  $\Delta p\text{O}_2 = 130$  mmHg. In the example this means that  $E_c = (0.1313 \mu\text{l O}_2/\text{hr} \cdot \text{cm}^2 \cdot \text{mmHg}) (4.886 \text{ cm}^2) (130 \text{ mmHg})$  or  $83.4 \mu\text{l O}_2/\text{hr}$ . This is the  $E_c$  for a 0.36 g S. lacertina submerged in air-equilibrated water ( $p\text{O}_2 = 155$  mmHg of oxygen) at  $25^\circ\text{C}$ . Table 9 gives  $E_c$ , M and  $P_c$  values for 13 sizes of S. lacertina. No  $P_c$  could be determined for the 178 g size class, therefore no  $E_c$  could be calculated. Note that  $\text{O}_2$  exchange capacity fell behind metabolic demand for the largest size class. Regression lines are fitted to log-log plots of the data in Figure 14. The slope of the metabolism plot is 0.65, which is less than the 0.67 found for the surface area of the skin in Figure 9, but the decrease in permeability with size caused the slope of the  $E_c$  line to become 0.54, and, as predicted by the model in Figure 12, there is a theoretical maximum size, which is 2908 g. This would mean that a S. lacertina of up to 2908 g could survive submerged in water at  $25^\circ\text{C}$  and  $p\text{O}_2 = 155$  if it continually maintained only his standard metabolic rate. However, some scope for activity must be maintained by retaining a reserve  $\text{O}_2$  exchange capacity. Thus we would expect death to occur in submerged animals at a size smaller than 2908 g. Table 9 indicates that large animals have standard metabolic rates close to their  $\text{O}_2$  exchange capacities. Using the data from that table, a plot is shown in Figure 15 of the

Table 9. Standard metabolic rate, O<sub>2</sub> exchange capacity, and critical oxygen tension of S. lacertina of various body sizes (for submerged animals).

Body weight ( $\bar{x}$ and range)	Average Metabolic Rate ( $\mu\text{l O}_2/\text{hr}$ )	O <sub>2</sub> exchange capacity at 25°C, 155 mmHg ( $\mu\text{l O}_2/\text{hr}$ )	P <sub>c</sub> (mmHg)
0.36(0.32-0.42)	35.3	83.4	80
0.56(0.49-0.63)	47.6	137	70
3.0 (2.7-3.6)	153	331	85
6.5 (5.0-8.5)	280	485	100
13.7(11.0-17.1)	438	759	100
42.7(40-45)	769	1334	100
73(67-76)	1080	1756	105
103(93-112)	1710	2616	110
178(170-191)	2083	-----	---
269(233-280)	3040	4652	110
357(346-375)	3034	3432	140
541(472-590)	5031	6543	125
825(770-857)	5692	6165	145
1310(1090-1451)	7467	6696	170

Figure 14. Metabolic rate and  $O_2$  exchange capacity of submerged S. lacertina  
as a function of body weight.

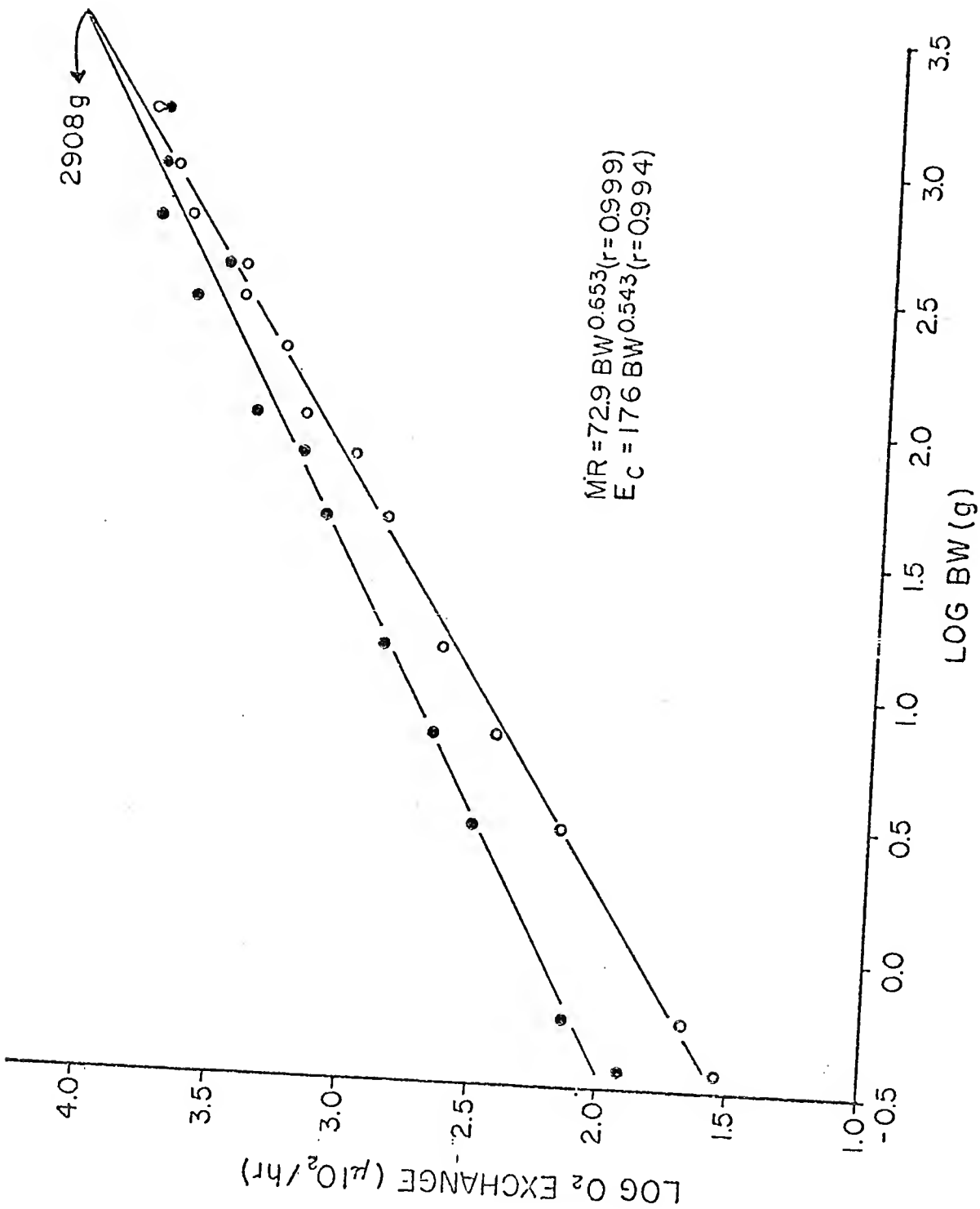
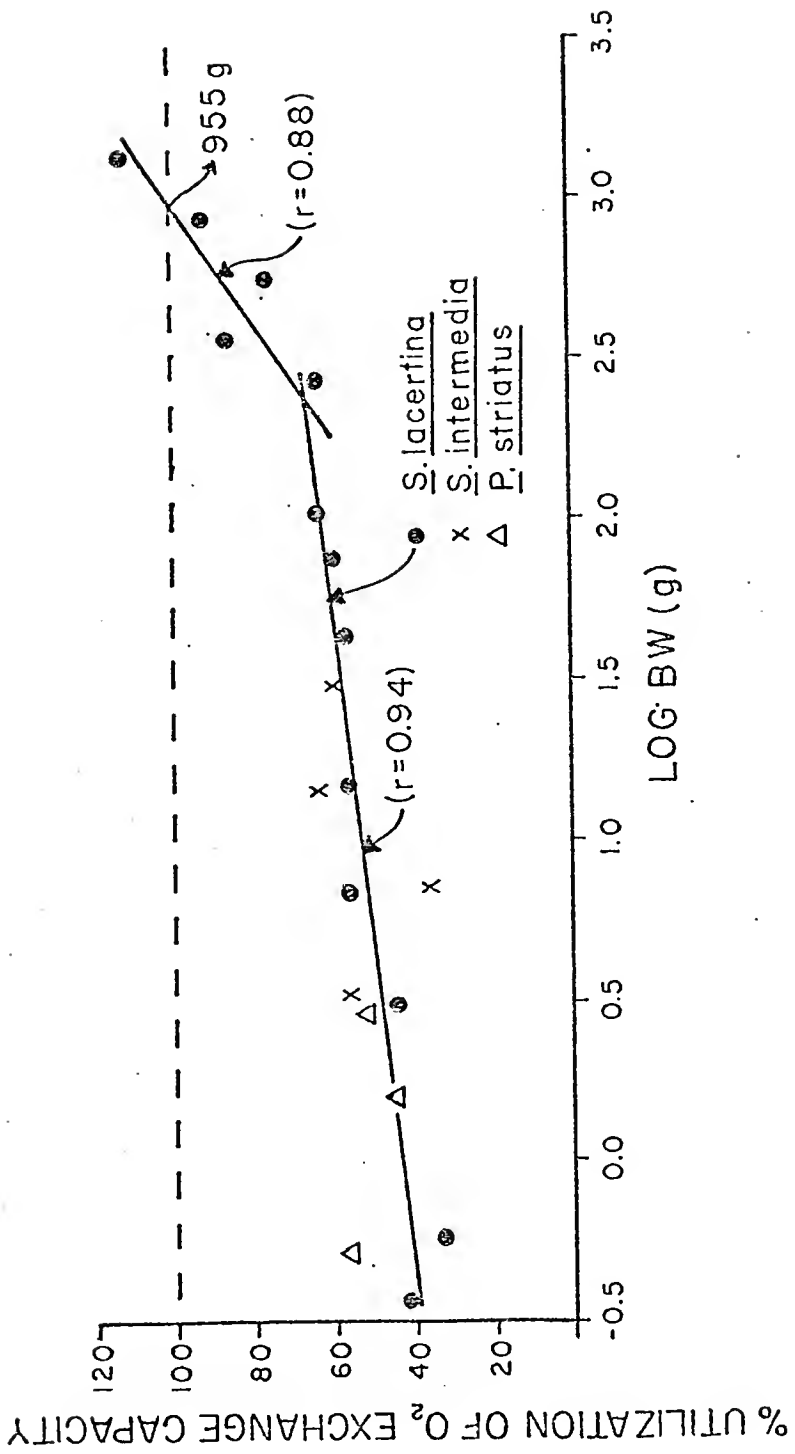




Figure 15. Per cent utilization of oxygen exchange capacity as a function of body weight in the Sirenidae. Regression lines are for S. lacertina only.



per cent utilization of  $E_c$  for each body weight. It is obvious that there is a more rapid increase in the per cent utilization at larger body weights. This approach predicts a maximum body weight of 955 g for submerged survival, and shows that animals of 825 g are using 92% of their  $O_2$  exchange capacity just to maintain their standard metabolic rate.

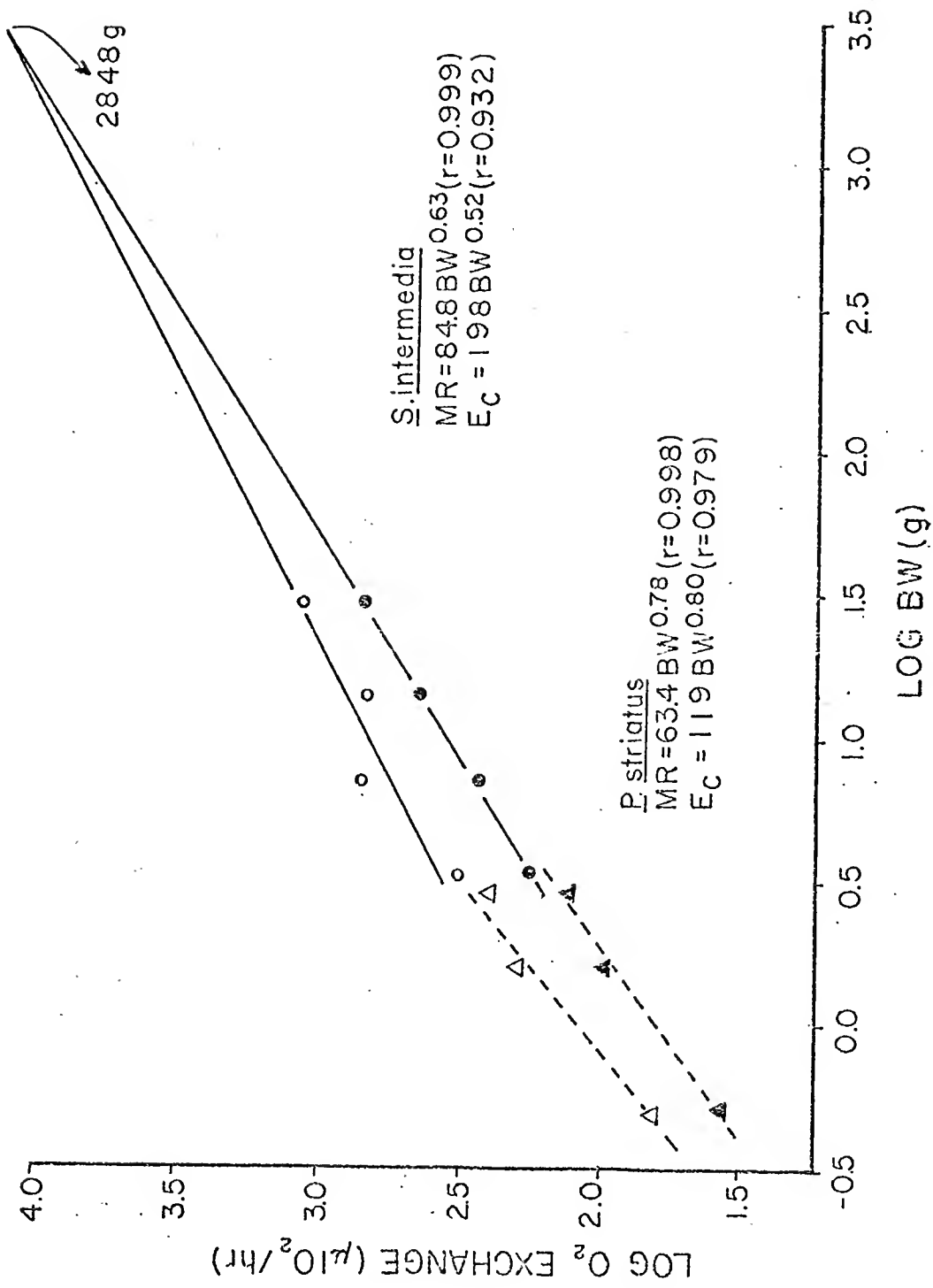
Actual survival was tested by submerging animals and checking them periodically for up to 336 hours. If they were still alive at that time, they were removed and considered to be able to survive indefinitely. The results were given in Table 2, and it is clear that animals of 800 g were in trouble, and that larger ones could not survive.

The smaller size ranges available for P. striatus and S. intermedia make similar calculations more tenuous. The results are given in Figure 16, and qualitatively agree with the observation that all sizes of these sirenids can survive in air-saturated water at 25°C. It is interesting that although the predicted maximum size for S. intermedia is essentially identical to that of S. lacertina, S. intermedia reaches a much smaller maximum size than S. lacertina where the two are sympatric than it does where S. lacertina does not occur. For the few sizes of P. striatus studied, the  $O_2$  exchange capacity is increasing faster than the metabolic rate with increasing body size.

#### Gas Exchange Partitioning

The previous discussion has centered on S. lacertina as a water breather, but it must be borne in mind that this organism also uses

Figure 16. Metabolic rate and  $O_2$  exchange capacity as a function of body weight for submerged P. striatus and S. intermedia.



aerial gas exchange. Even small individuals in an aerated tank will breathe air if allowed to surface, and certainly large individuals must do so to survive. Therefore to gain a more complete understanding of what the animal is actually doing in his natural habitat, the partitioning of gas exchange between the air and water must be considered. This will, however, still be a function of body size, regardless of the environmental conditions.

The results of experiments dealing with the effect of body size on gas partitioning were given in Table 4 and Figure 10. Large animals are obligate air breathers, due mainly to their inability to obtain sufficient  $O_2$  from the water. Most aquatic amphibians eliminate the majority of their  $CO_2$  into the water, and Siren is no exception. The increase from 6% to 26% in aerial  $CO_2$  elimination associated with large size is probably caused largely by the increase in aerial  $O_2$  consumption from 42% to 75%. Assumably, Siren smaller than the 90 g individual studied obtain even less than 42% of their  $O_2$  from the air. Guimond (1970) studied S. lacertina at 25°C and found the per cent aerial  $\dot{V}_{O_2}$  for three individuals to be 56% (1200 g), 53% (907 g), and 42% (482 g). For 11 S. lacertina averaging 628 g he found the aerial  $\dot{V}_{O_2}$  to be 50%, and the per cent aerial  $\dot{V}_{CO_2}$  to be 78%. This body size lies between the 90 g and 1489 g used here, and the percentages for the aerial partition of each gas lie between the corresponding results for this study, even though the absolute values given by Guimond are much lower.

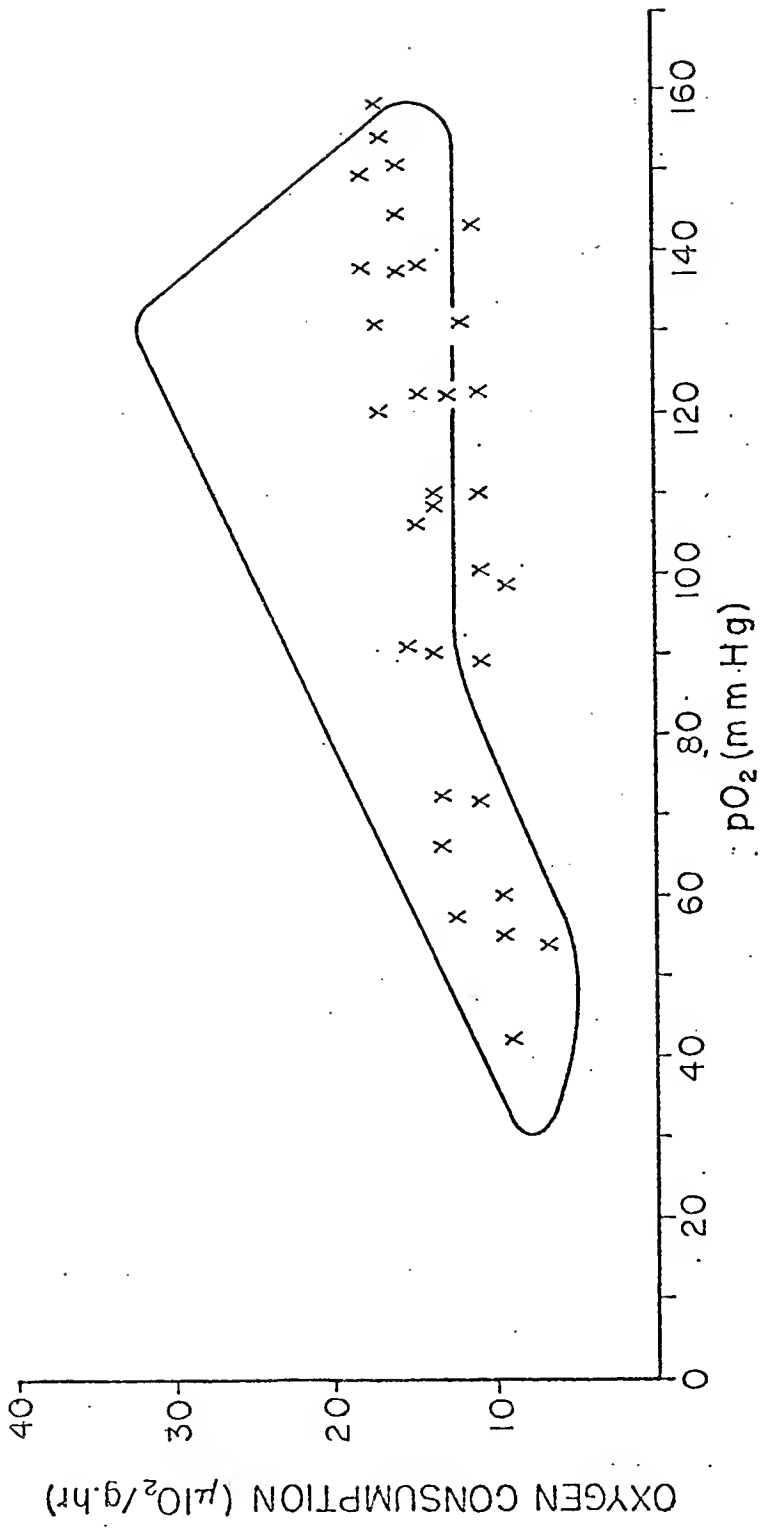
The total  $\dot{V}_{O_2}$  for animals allowed to breathe air was about 3-5 times greater in S. lacertina than the average metabolic rate for the

same size animals submerged at the same aquatic  $pO_2$ . This is particularly relevant in the case of the 90 g Siren, which can live submerged indefinitely. Some of this increase in oxygen consumption can be associated with an increase in activity connected with air breathing, but it has already been mentioned that the increase in activity was of no obviously great importance. It appears that the Siren is functioning essentially like the lunged and lungless salamanders studied by Whitford and Hutchison (where lunged salamanders had higher metabolic rates), and that at least part of the increase in metabolic rate can be attributed directly to the presence in the air and water breathing Siren of the additional surface area for gas exchange added by the lungs. This interpretation fits with the original suggestion made earlier that the exchange capacity for  $O_2$  may limit the level of metabolic rate of an organism.

It was assumed that the submerged animals were extracting all the  $O_2$  they needed from the water while they were regulating metabolic rate. To determine if air breathing effects the level of aquatic  $\dot{V}_{O_2}$ , a 44 g animal was placed in a container similar to that used for the submergence experiments and allowed to breathe air through a layer of paraffin oil. The results (Figure 17) show that the aquatic  $\dot{V}_{O_2}$  was unchanged. Therefore all of the increase in total  $\dot{V}_{O_2}$  in an air-breathing animal is due to pulmonary respiration. The results appear to strongly suggest that the presence of an additional amount of respiratory surface area resulted in an elevation of the standard metabolic rate. However, metabolic rates of animals breathing both air and water over a large range of body sizes will have to be determined

Figure 17. Aquatic  $\dot{V}_{O_2}$  of a 44 g S. lacertina breathing air and water. The enclosed area represents aquatic  $\dot{V}_{O_2}$  values for submerged S. lacertina of 40-45 g (see Figure 7A).





before it can definitely be stated that the metabolic rate of Siren depends upon the surface area for gas exchange, rather than being fixed by some other variable.

Finally, to combine the effect of body size with the effect of the concentrations of dissolved respiratory gases in the water, partitioning experiments were carried out for a large S. lacertina at various partial pressures of  $O_2$  and  $CO_2$  in the water phase. The results were given in Table 6 and Figure 11. There was no difference in the level of aerial  $\dot{V}_{O_2}$  for any set of aquatic conditions. Oxygen consumption from the water was significantly higher for conditions of high  $O_2$  tensions than for low, and the aquatic  $\dot{V}_{O_2}$  was lower for high levels of  $CO_2$  (for a given level  $O_2$  tension) than for low levels of  $CO_2$ . Although the latter differences were not significant, they suggest the presence of a Bohr shift in Siren blood.

The results for  $CO_2$  were somewhat surprising. The absolute levels of  $CO_2$  elimination to the water were highest when the  $CO_2$  in the water was low, but at high  $O_2$  tensions there was no difference in the percentage of  $CO_2$  eliminated to the water whether the  $CO_2$  tension was high or low. Even though there was a significant decrease in the absolute amount eliminated to the water, 60% of the total  $\dot{V}_{CO_2}$  was aquatic at tensions of 145 mmHg for  $O_2$  and 40 mmHg for  $CO_2$ . For conditions of low  $O_2$  tension,  $CO_2$  elimination to the water was significantly less in terms of both absolute amounts and percentages for high  $CO_2$  as compared to low. However, even for those conditions most favoring aerial respiration (low  $O_2$ -high  $CO_2$ ), resulting in 96% aerial  $\dot{V}_{O_2}$ , the  $CO_2$  eliminated to the water was 46%. This means that a Siren must be able

to tolerate a  $p\text{CO}_2$  in the blood greater than 40 mmHg, which is high for an aquatic animal. This adaptation, coupled with the use of lungs to obtain  $\text{O}_2$  from the air, accounts for the ability of Siren (and presumably Pseudobranchus) to tolerate the hostile respiratory environment of the water hyacinth community.

## SUMMARY

1. All three species of the family Sirenidae were commonly found under water hyacinths.
2. The physical conditions under water hyacinths in terms of pH, temperature, dissolved carbon dioxide and dissolved oxygen were determined and compared to those of water not covered by hyacinths in the same pond. Generally, dissolved  $O_2$  was lower, dissolved  $CO_2$  higher, pH lower, and temperature lower under the hyacinths as compared to the "open" (no hyacinths, but often with submerged Ceratophyllum) water.
3. There is no avoidance of areas of low  $O_2$  and/or high  $CO_2$  by any of the three species.
4. Siren, and probably Pseudobranchus, adapt to conditions of low  $O_2$  by air breathing. They adapt to conditions of high  $CO_2$  partially by air breathing and partially by tolerating high levels of blood  $pCO_2$ .
5. Siren lacertina above 800 g cannot survive as water breathers at  $25^\circ C$  in air-equilibrated water. Smaller Siren, and Pseudobranchus, can.
6. All three species were found to have little or no change in body proportions with increasing body weight.
7. All three species were found to be  $O_2$  regulators at high  $O_2$  tensions and conformers at low  $O_2$  tensions. Large sirenids have higher critical oxygen tensions than smaller ones.

8. The permeability of the skin to oxygen decreases as a function of body size in S. lacertina.
9. The oxygen exchange capacity of submerged S. lacertina increases at a slower rate than does the metabolic rate, both as functions of increasing body weight.
10. A model is presented that shows the advantage in attaining large size of a decreasing weight-specific metabolic rate with increasing size. It is suggested that metabolic rate is limited by the  $O_2$  exchange capacity of an organism.

## APPENDIX

APPENDIX A

Metabolic rates of submerged sirenids as a function of oxygen tension.

Figure 1A. Metabolic rate of submerged P. striatus (0.51 and 1.58 g)  
as a function of oxygen tension.



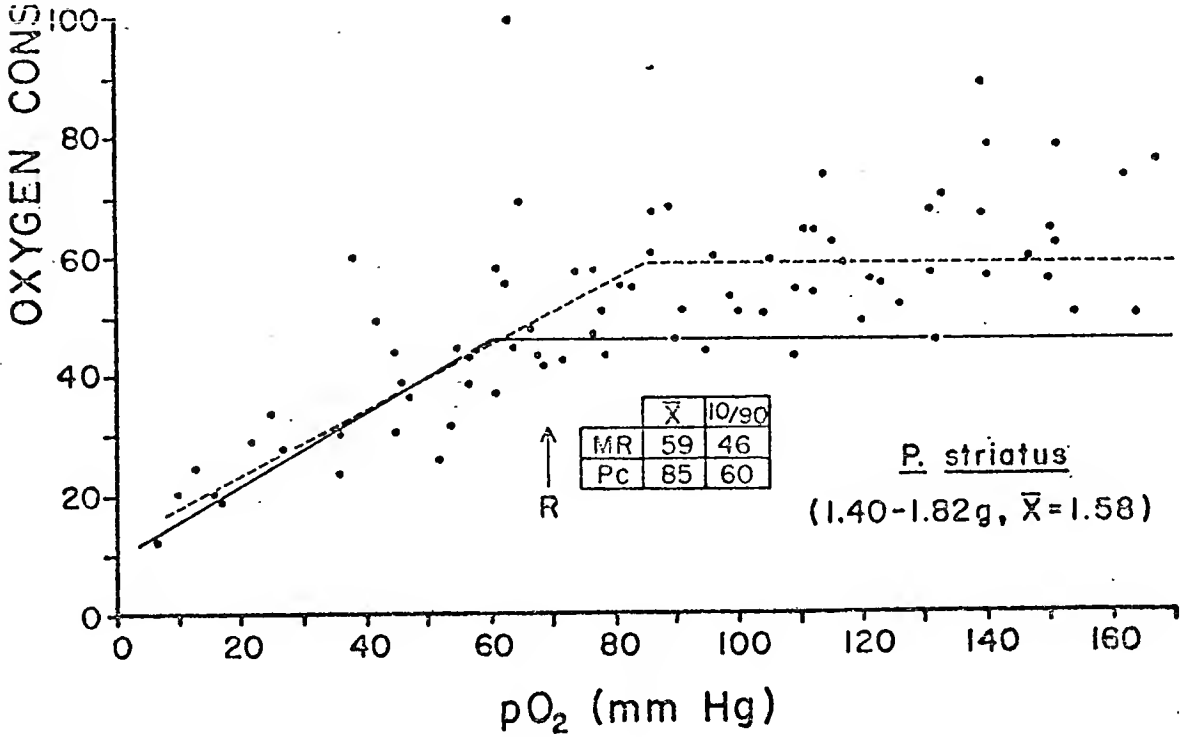
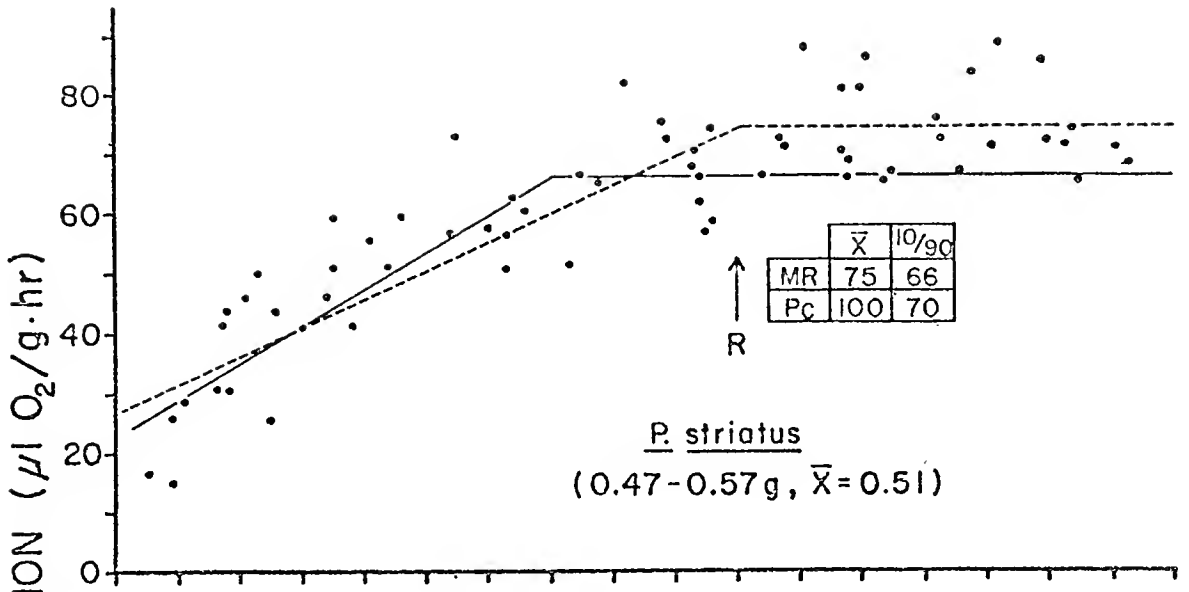


Figure 2A. Metabolic rate of submerged P. striatus (2.88 g) as a function of oxygen tension.

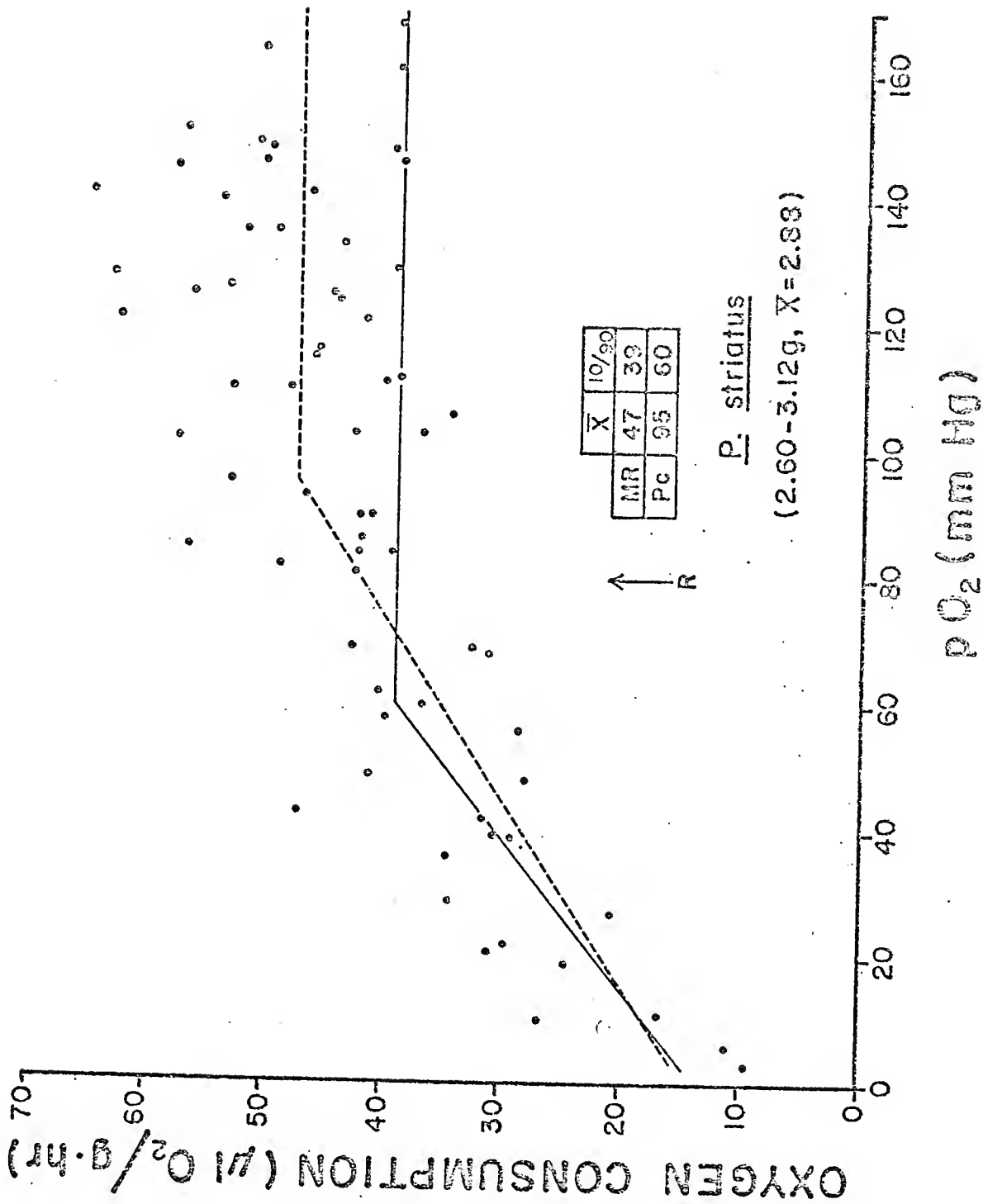


Figure 3A. Metabolic rate of submerged S. intermedia (3.3 and 7.0 g)  
as a function of oxygen tension.

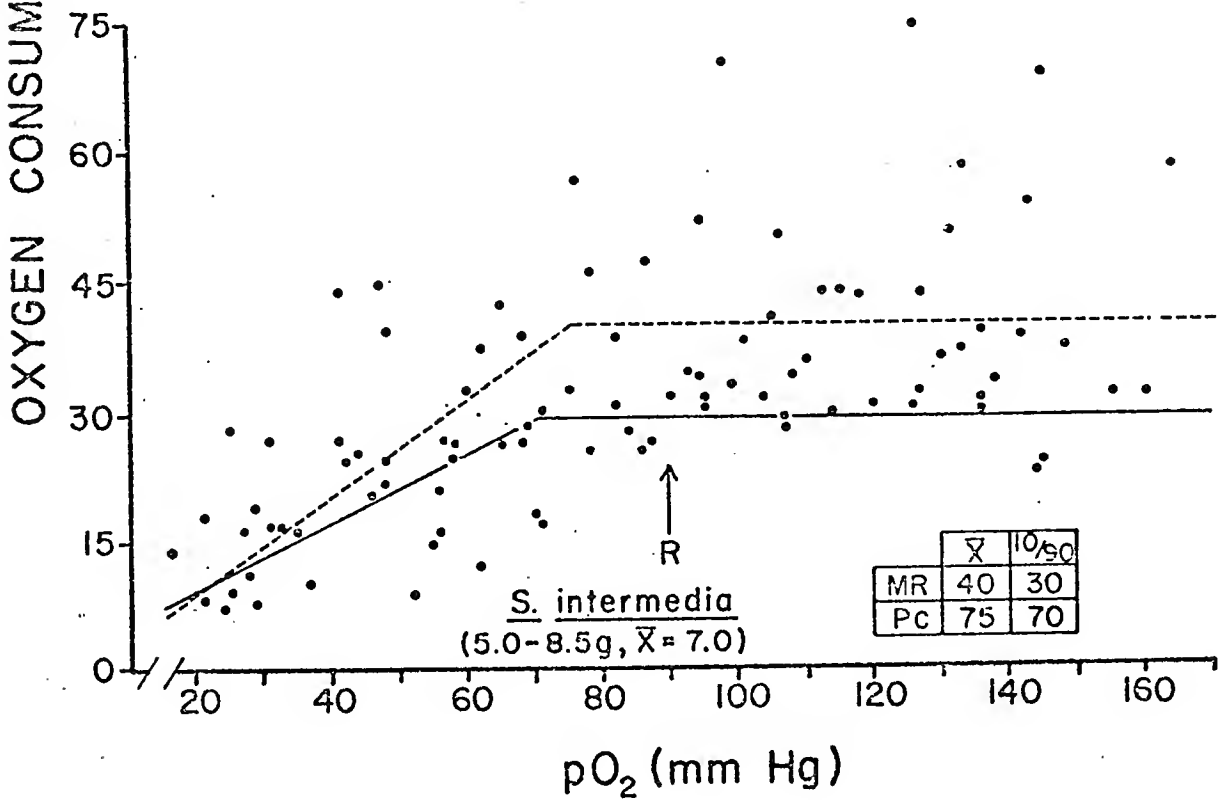
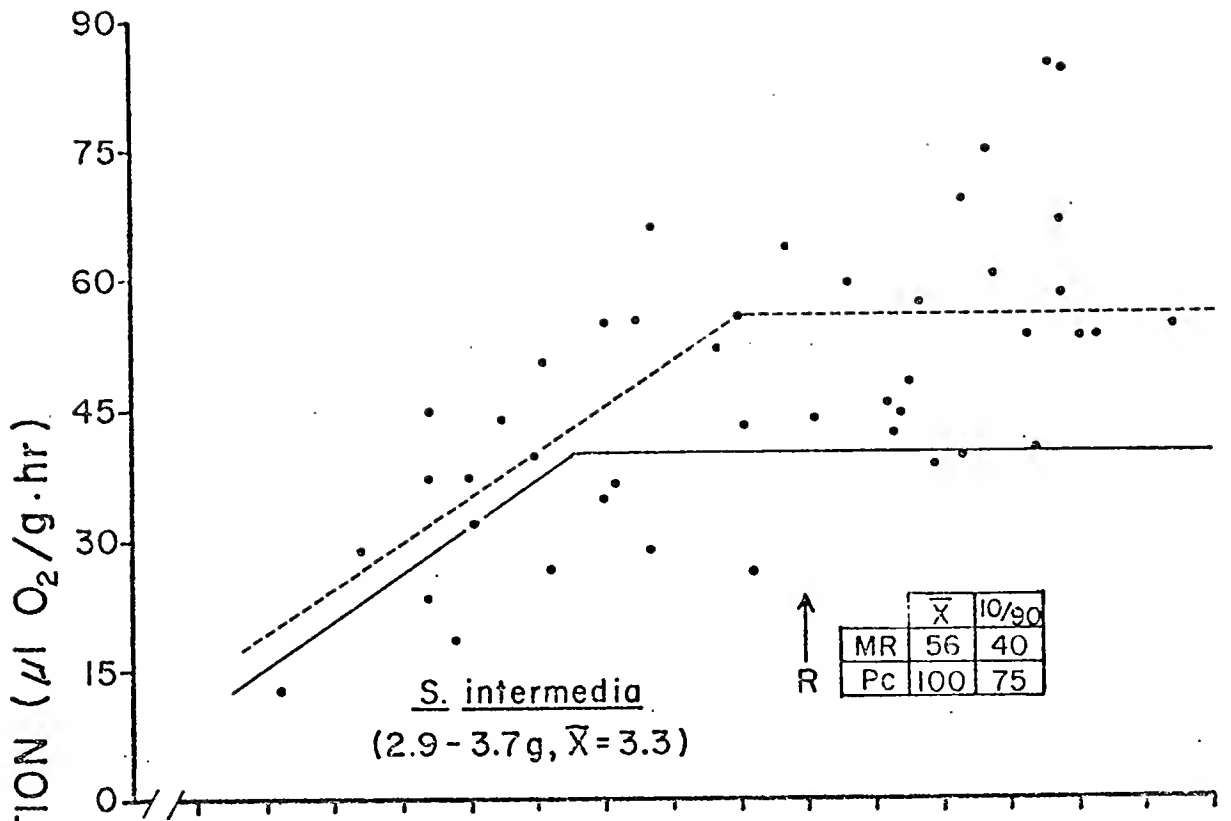


Figure 4A. Metabolic rate of submerged S. intermedia (13.7 and 29.6 g)  
as a function of oxygen tension.

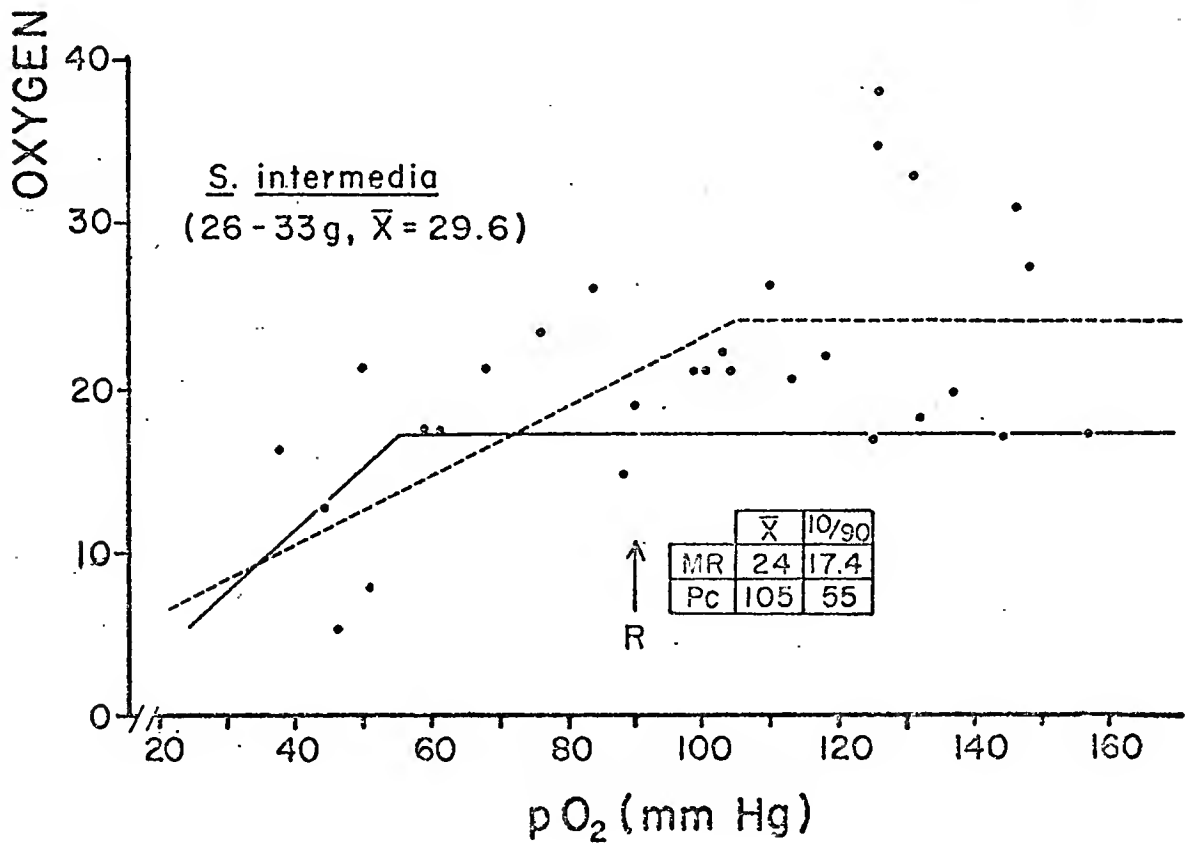
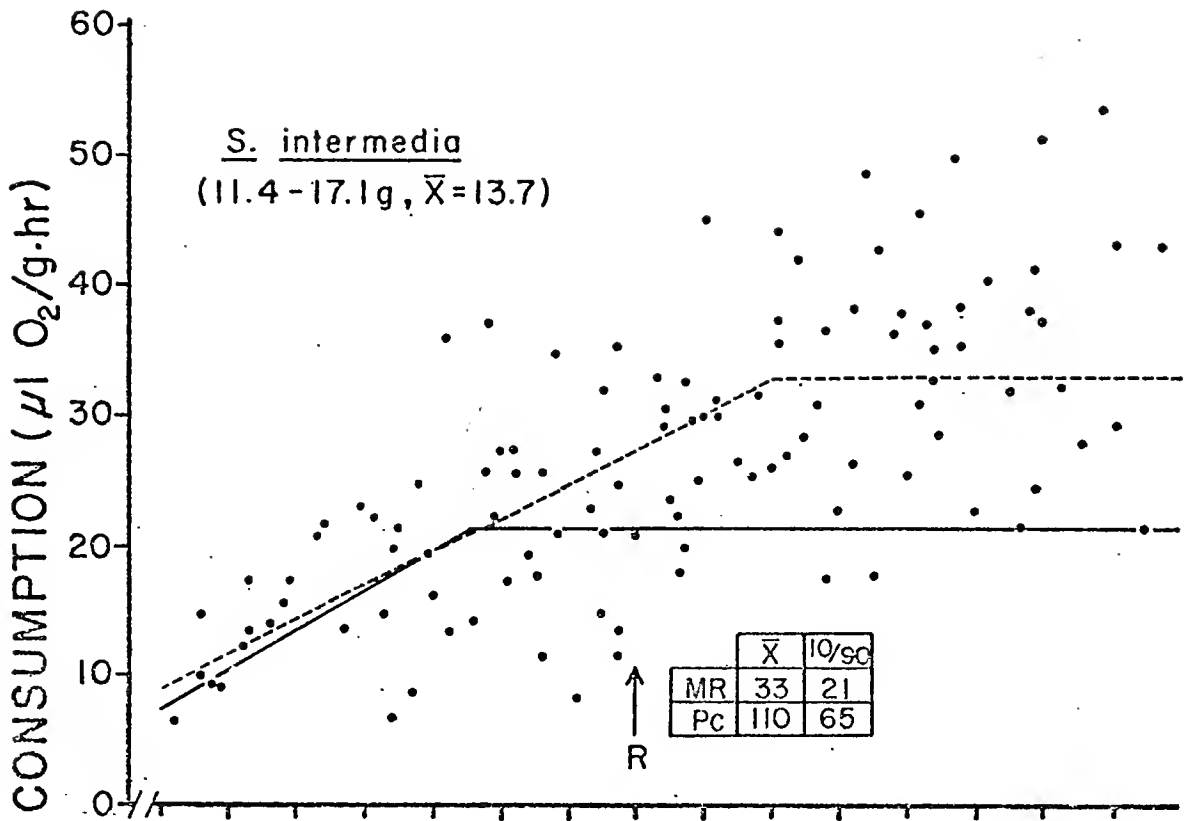


Figure 5A. Metabolic rate of submerged S. lacertina (0.36 and 0.56 g) as a function of oxygen tension.



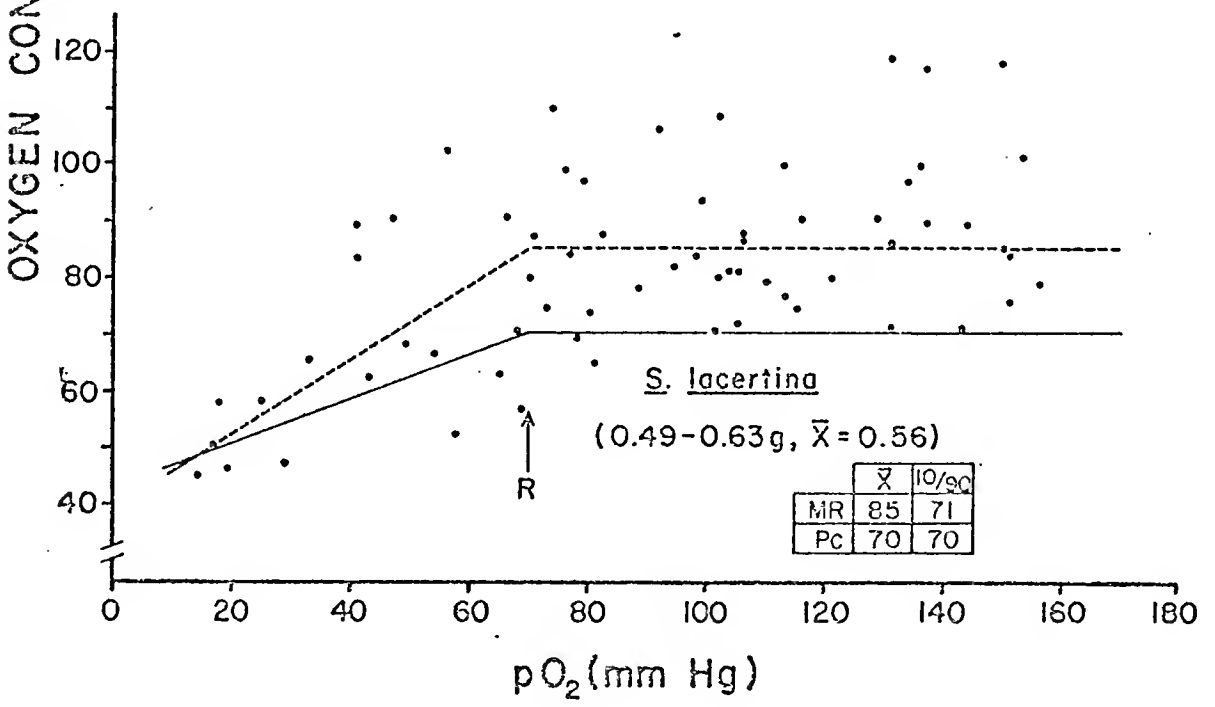
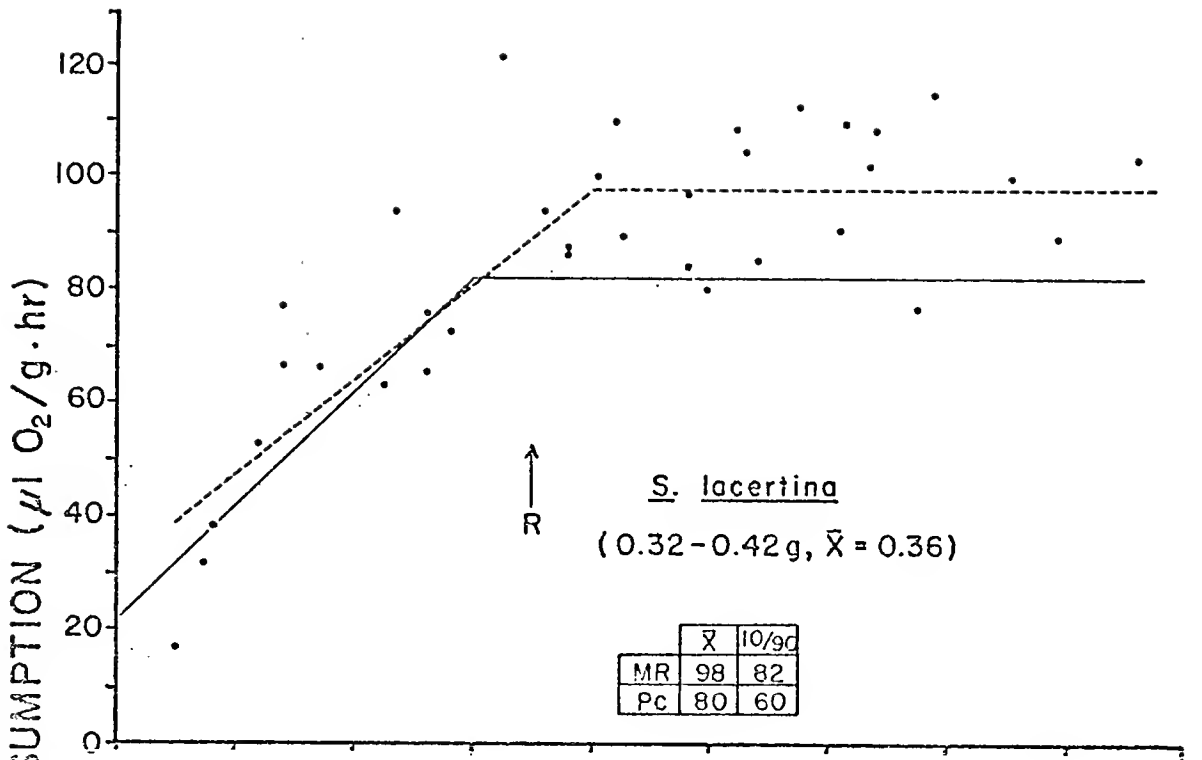


Figure 6A. Metabolic rate of submerged S. lacertina (3.0 and 6.5 g) as a function of oxygen tension.

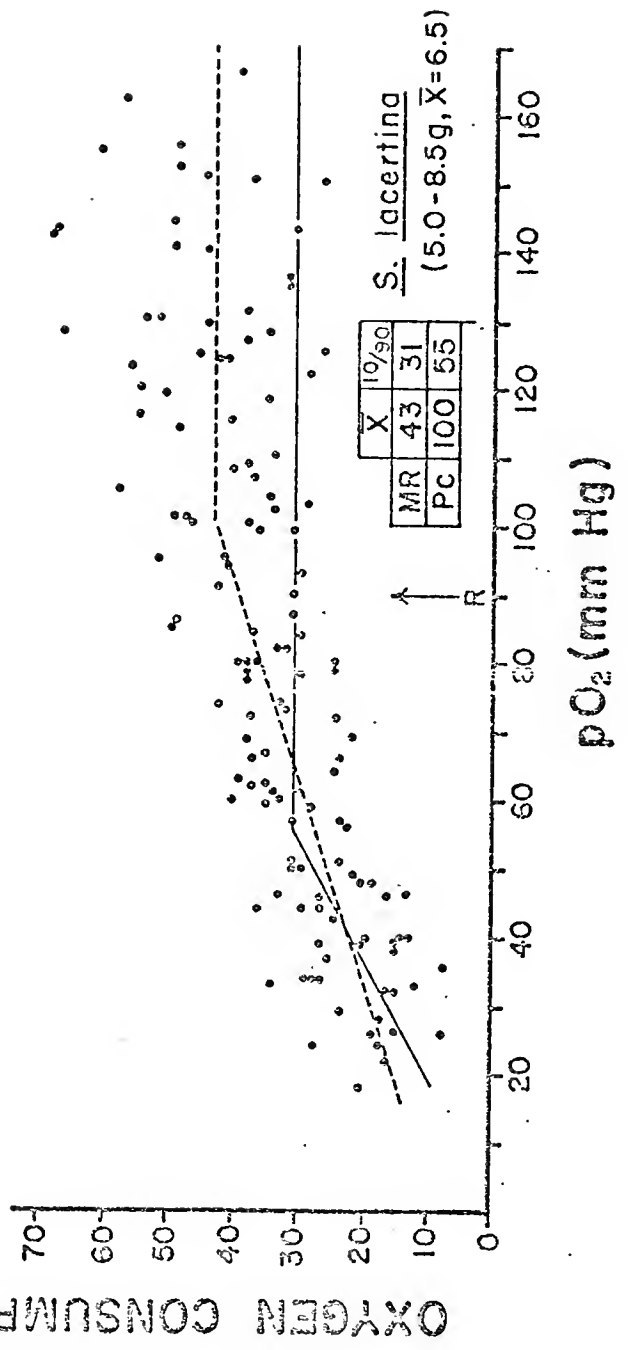
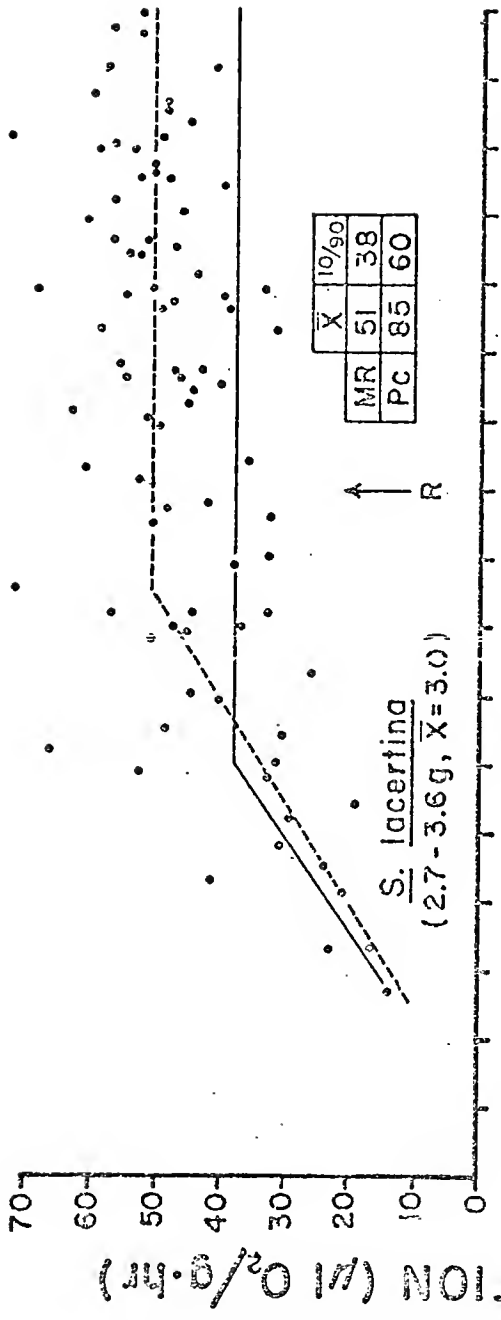


Figure 7A. Metabolic rate of submerged S. lacertina (13.7 and 42.7 g)  
as a function of oxygen tension.

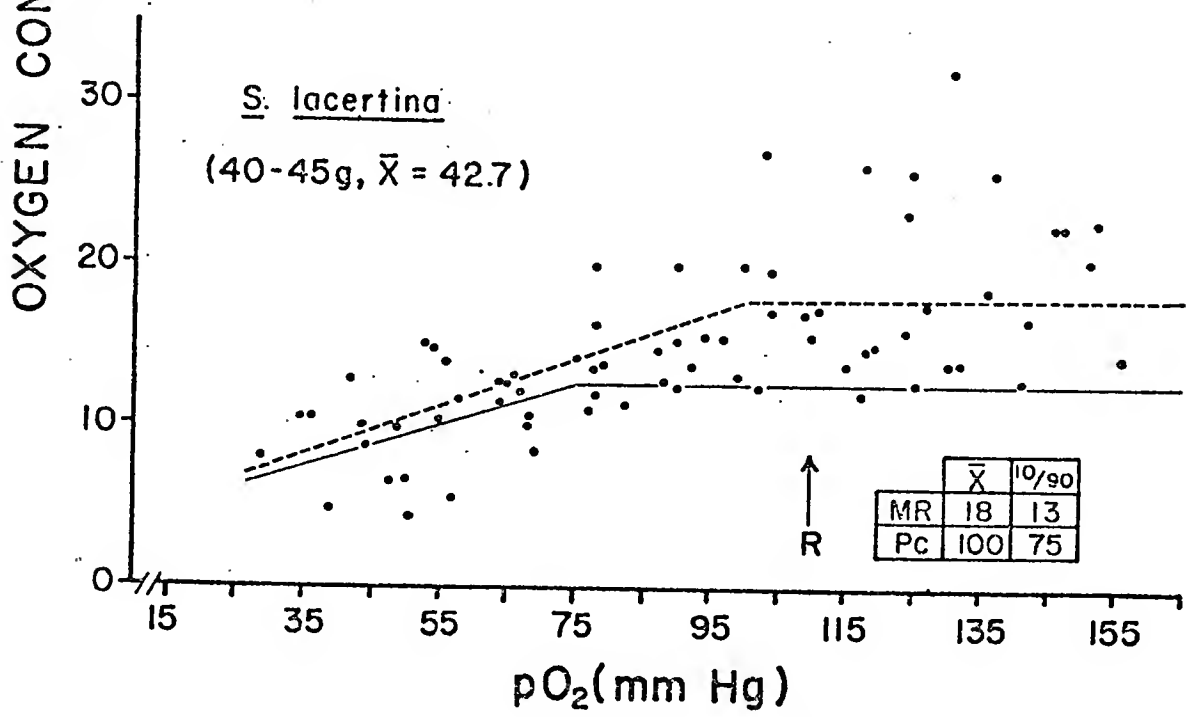
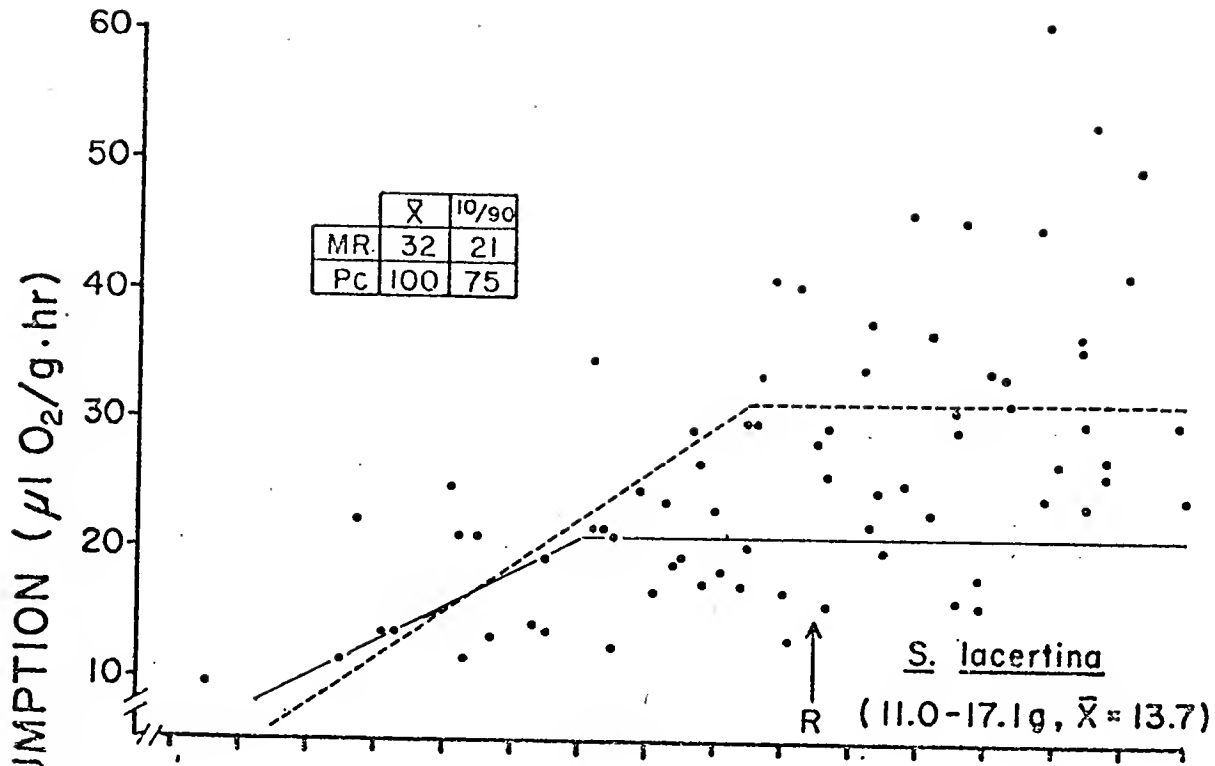


Figure 8A. Metabolic rate of submerged S. lacertina (73 and 103 g)  
as a function of oxygen tension.

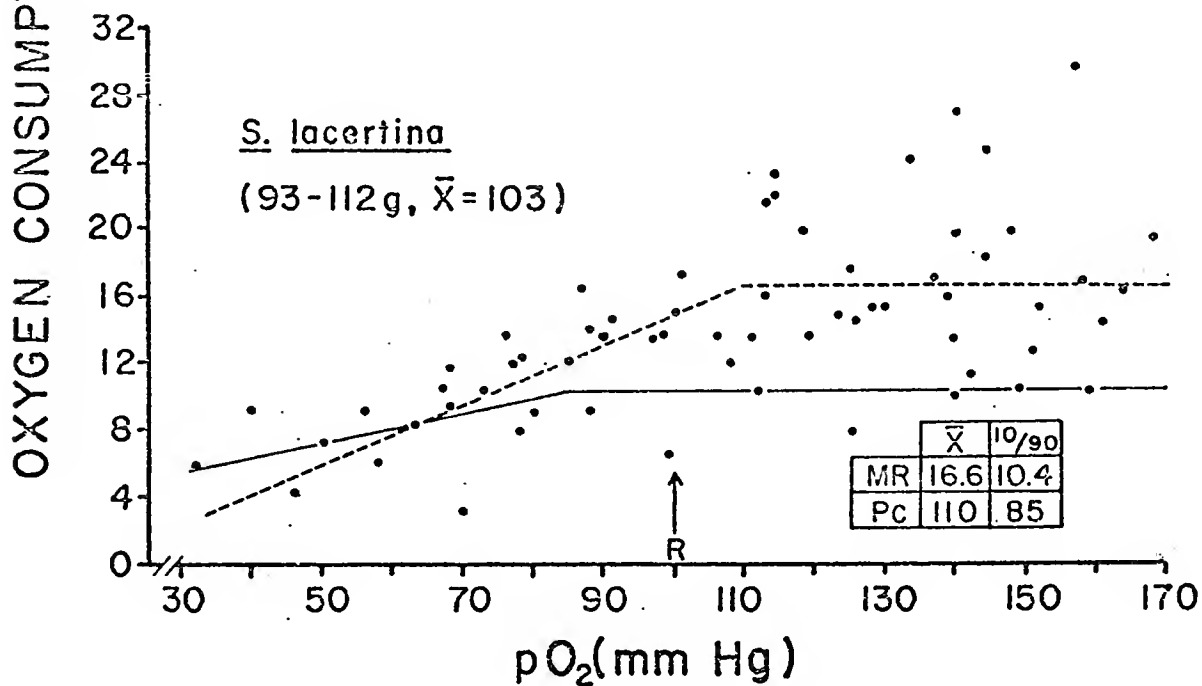
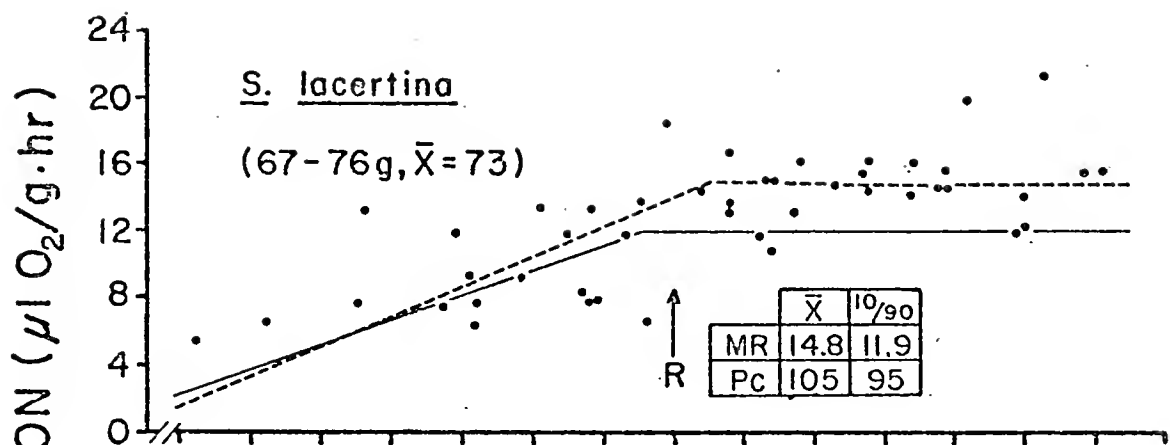


Figure 9A. Metabolic rate of submerged S. lacertina (178 and 269 g) as a function of oxygen tension.



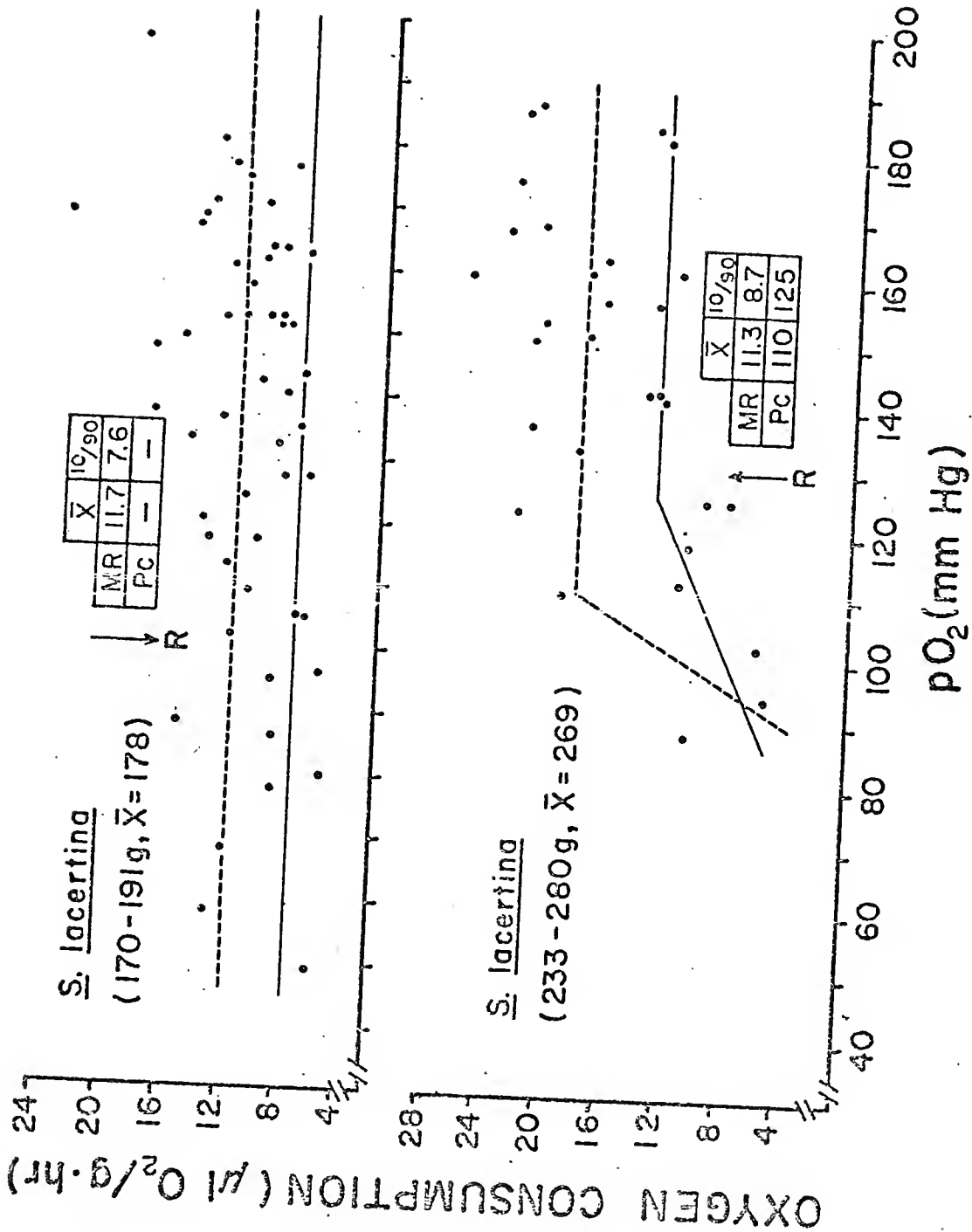


Figure 10A. Metabolic rate of submerged S. lacertina (357 and 541 g)  
as a function of oxygen tension.

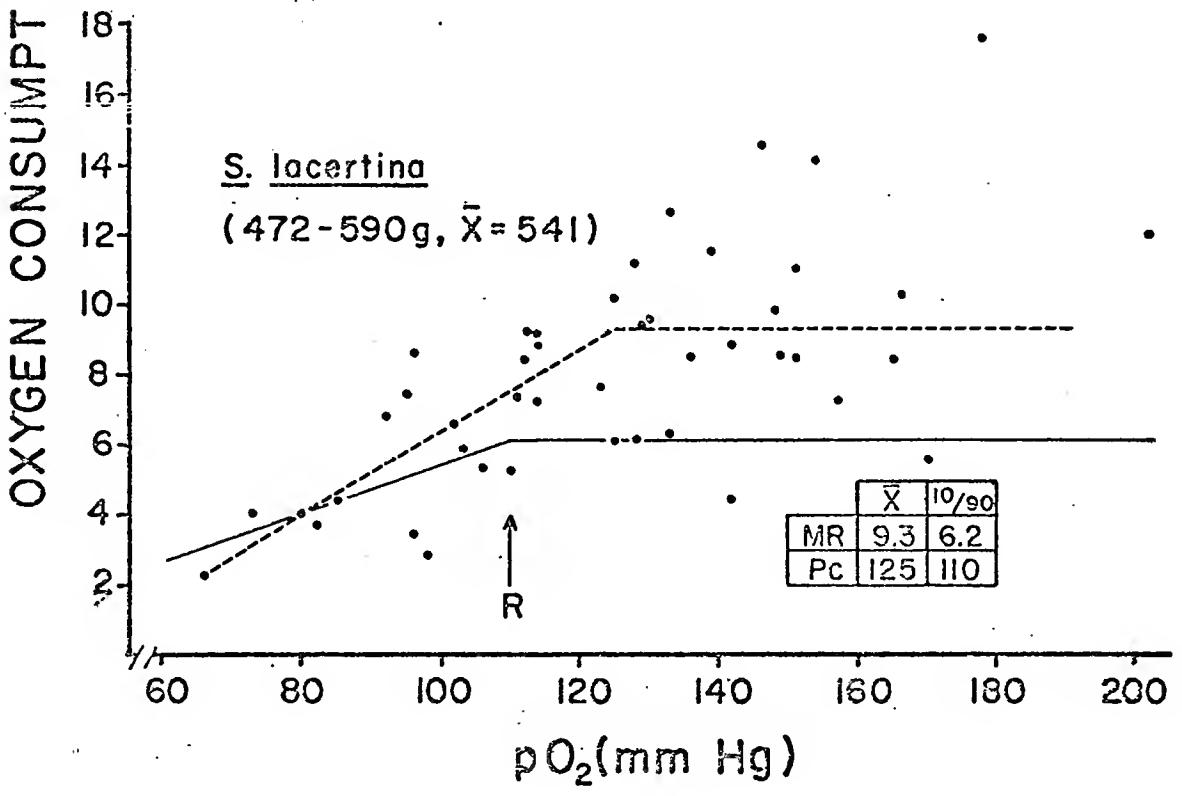
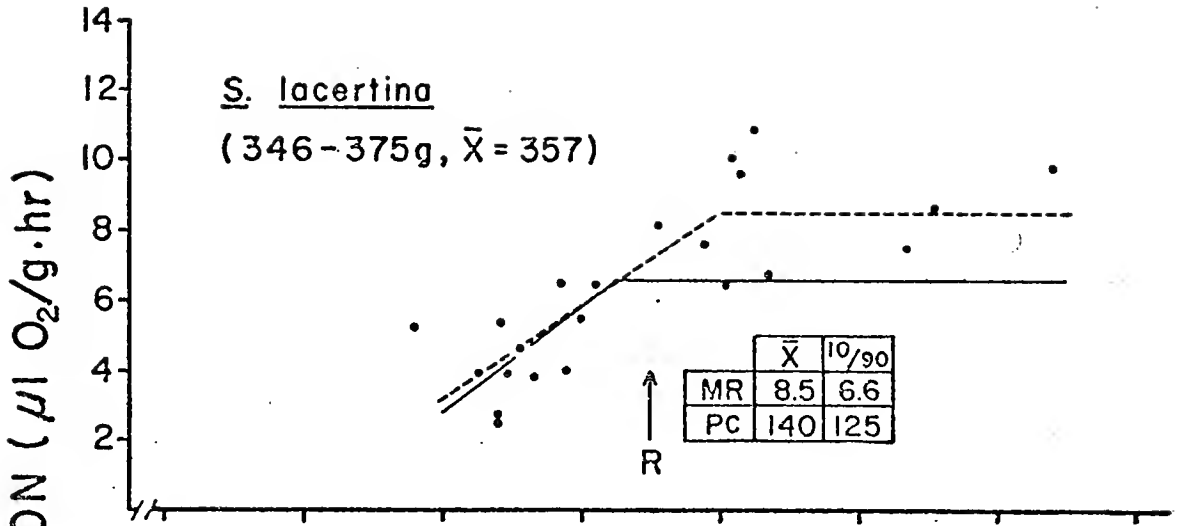
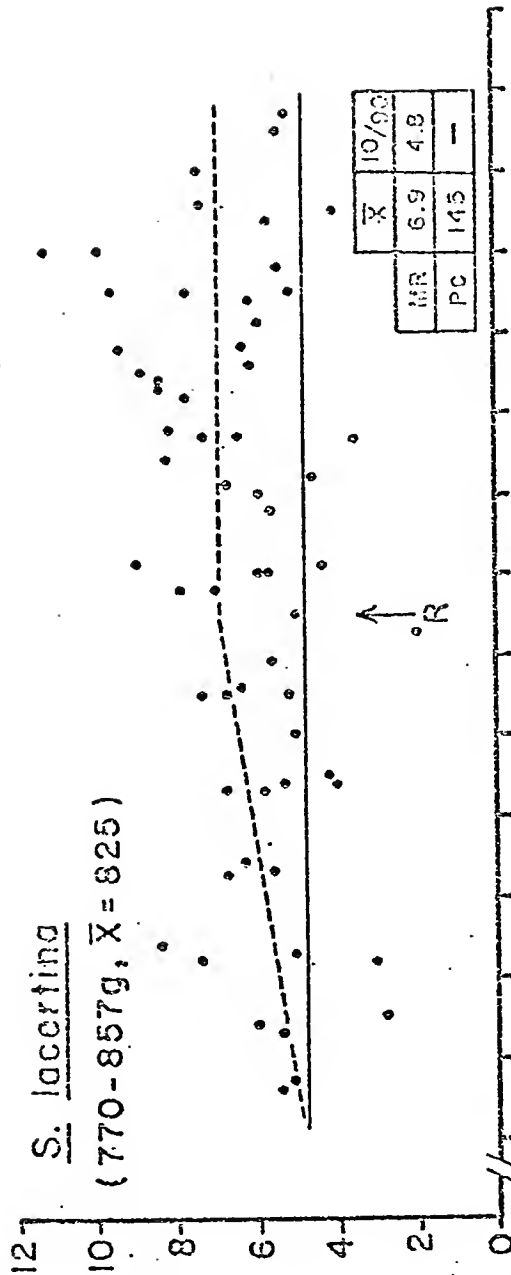


Figure 11A. Metabolic rate of submerged S. lacertina (825 and 1310 g)  
as a function of oxygen tension.

OXYGEN CONSUMPTION ( $\text{ml O}_2/\text{g} \cdot \text{hr}$ )

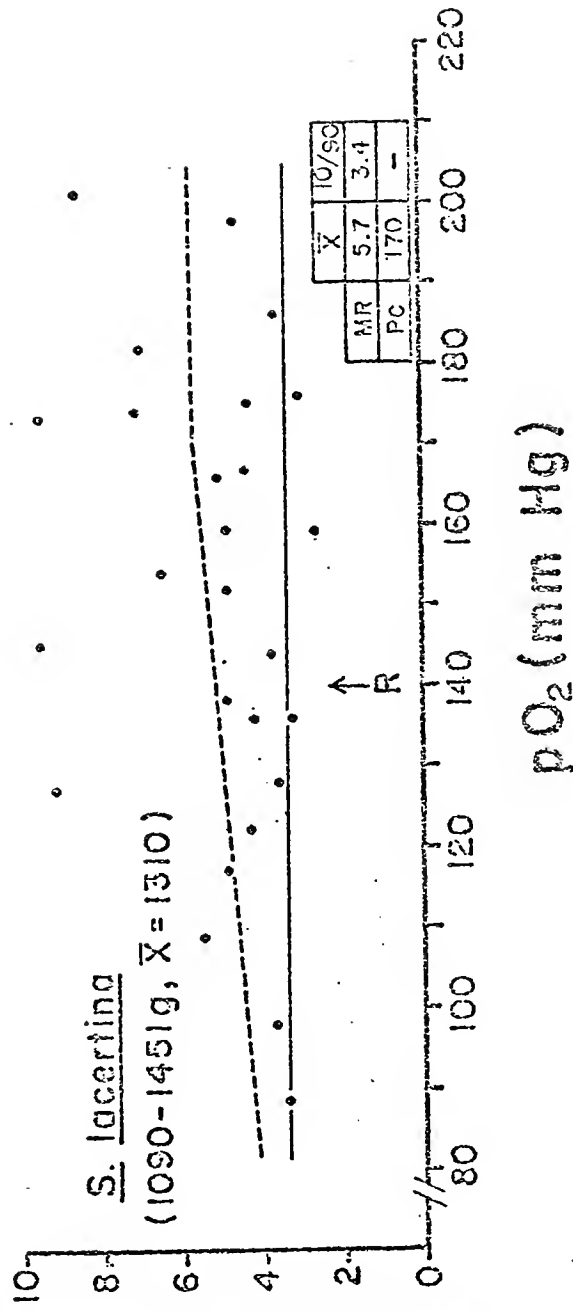
S. lacertina

(770-857g,  $\bar{X} = 825$ )



S. lacertina

(1090-1451g,  $\bar{X} = 1310$ )



$p\text{O}_2$  (mm Hg)

## APPENDIX B

### The Effect of Inactive Tissues on Metabolic Rate

More data is available for the metabolic rate of mammals than for any other group, where the relation between metabolic rate and weight is

$$(1B) \quad M = 70 W^{0.75} \text{ (Kleiber, 1961),}$$

with  $W$  in kg and  $M$  in kcal/day. The weight in Eq. (1B) is actually  $W_T$ , the whole body weight, which is composed of  $W_A$  (active tissues) and  $W_I$  (inactive tissues). For purposes of this discussion,  $W_I$  will be equated to  $W_S$ , the skeletal weight of mammals, which is known to increase disproportionately with body size.

Assume that one of the two following cases is correct:

$$(a) \quad M = k W_A^{1.0}, \text{ or}$$

$$(b) \quad M = k_1 W_A^{0.75}.$$

In case (a) metabolism of the active tissues shows no weight-specific change with changes in body size. Given a very small mammal, what increase in skeletal weight with increasing size would be necessary if case (a) were true to give the results observed from Eq. (1B)?

To answer this question, skeletal weights were determined for seven shrews (Sorex and Blarina) of  $W_T$  from 3.3 to 11.0 g. The mean  $W_T$  was 0.0062 kg, with  $W_S = 0.0003$  kg, about 5% of the total body weight. Using these data to approximate the smallest mammals, it is possible to determine the effect of inactive tissues on metabolic rate.

When the observed metabolic rate is both a function of  $W_T^{0.75}$  and  $W_A^{1.0}$ , then

$$(2B) \quad M = 70 W_T^{0.75} = k W_A^{1.0}.$$

Solving for  $k$  at  $W_T = 0.0062$  and  $W_A = 0.0059$ ,  $k = 262$ . Then substituting  $(W_T - W_S)$  for  $W_A$ , and solving for  $W_S$ , gives

$$(3B) \quad W_S = W_T - 0.267 W_T^{0.75}.$$

Figure 1B shows this relationship. Obviously,  $W_S$  would have to become the major portion of the total weight, for the skeletal weight to account entirely for the decrease in the weight-specific rate of metabolism given by Eq. (1B). Figure 1B also shows the actual skeletal weight of mammals (Kayser and Huesner, 1964). The equation for their data is

$$(4B) \quad W_S = 0.089 W_T^{1.13},$$

and the point for the shrews fits well. Since the power of  $W_T$  is greater than one, a portion of the decrease in weight-specific metabolic rate with increasing size is due to the influence of disproportionate increases in skeletal weight.

How much of the difference between  $W_T^{1.0}$  and the observed  $W_T^{0.75}$  of Eq. (1B) can be accounted for by Eq. (4B)? In Figure 2B the shrews are used as a starting point to predict metabolic rates when metabolism is proportional to either  $W_A^{1.0}$  or  $W_A^{0.75}$ . Calculating constants at the starting weight of 0.0062 kg, we already have the case where  $M = k W_A^{1.0}$ , with  $k = 262$ . For the case where  $M = k_1 W_A^{0.75}$  (i.e., the observed change in weight-specific metabolic rate actually is due to a change in the metabolic rate of active tissues),

$$(5B) \quad M = 70 W_T^{0.75} = k_1 W_A^{0.75} = k_1 (0.0059)^{0.75},$$

Figure 1B. Predicted relationship between total weight and skeletal of mammals required to give  $M = 70 W_T^{0.75}$  when metabolism of active tissues does not change with body size (black circles). Open circles are actual skeletal weights of mammals (Kayser and Huesner, 1964), and x is a point for shrews.



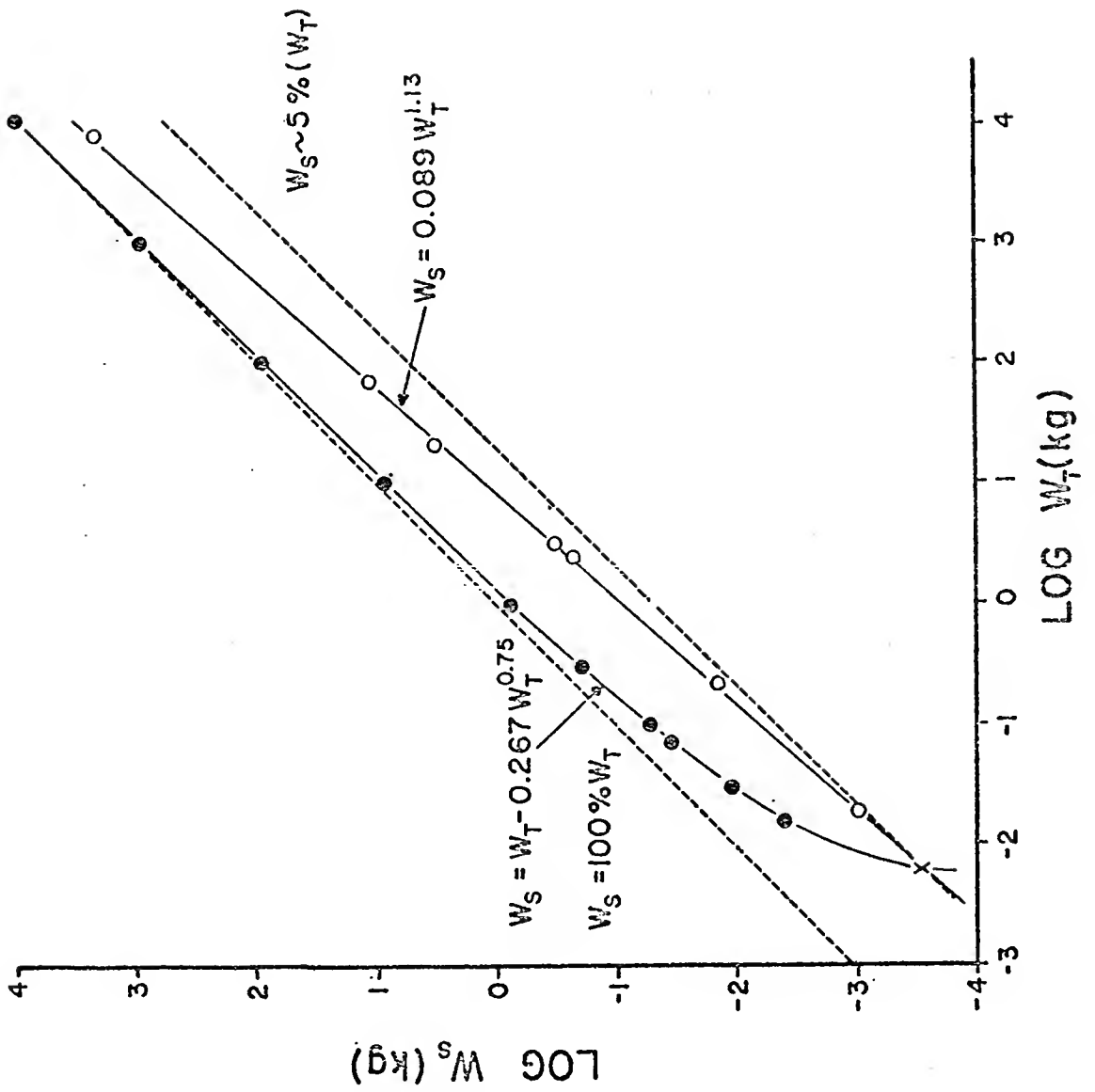
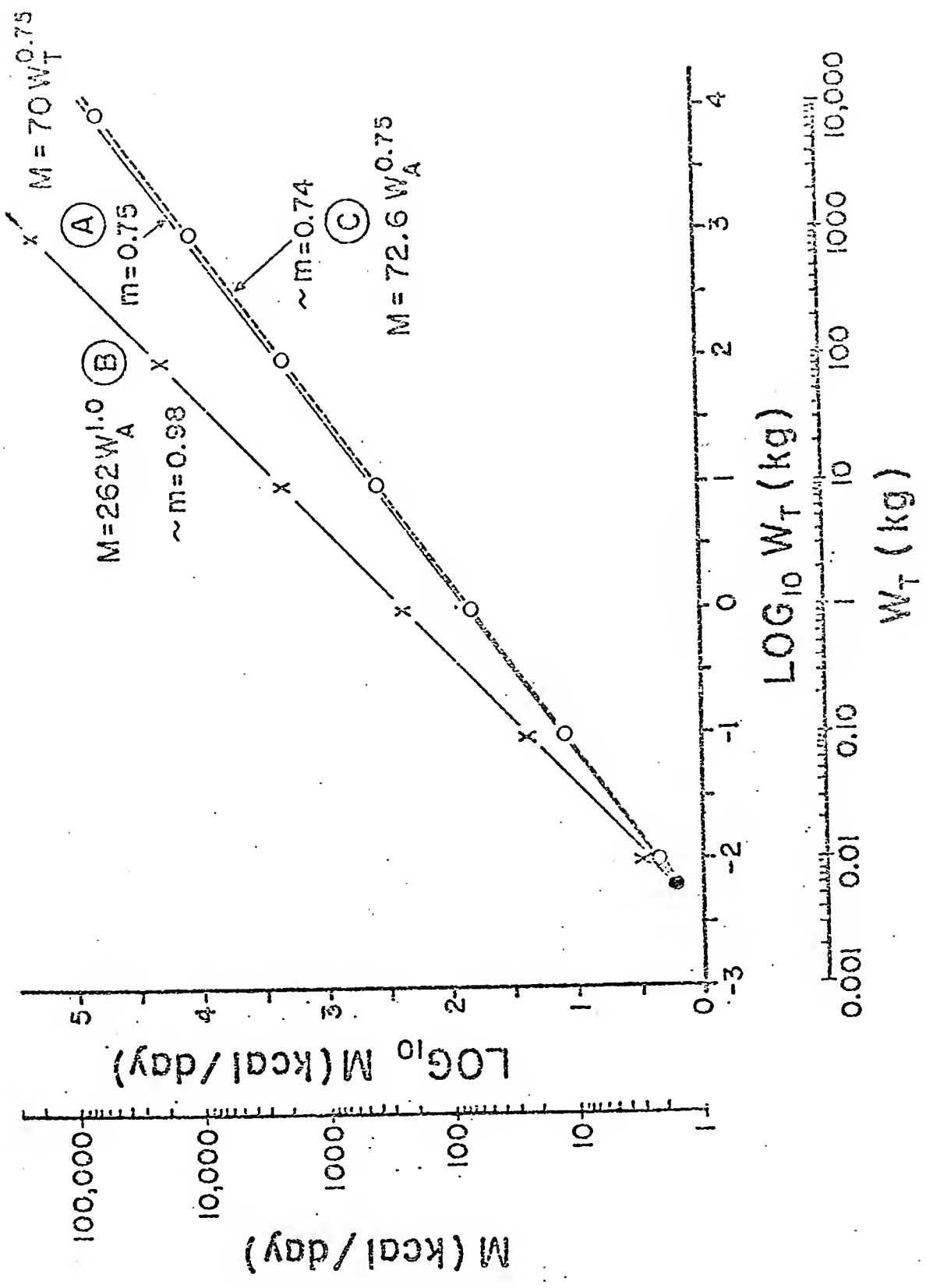


Figure 2B. Metabolic rate of mammals as a function of body size for:

(A) observed data,

(B) as a function of  $W_A^{1.0}$  (active tissue weight),

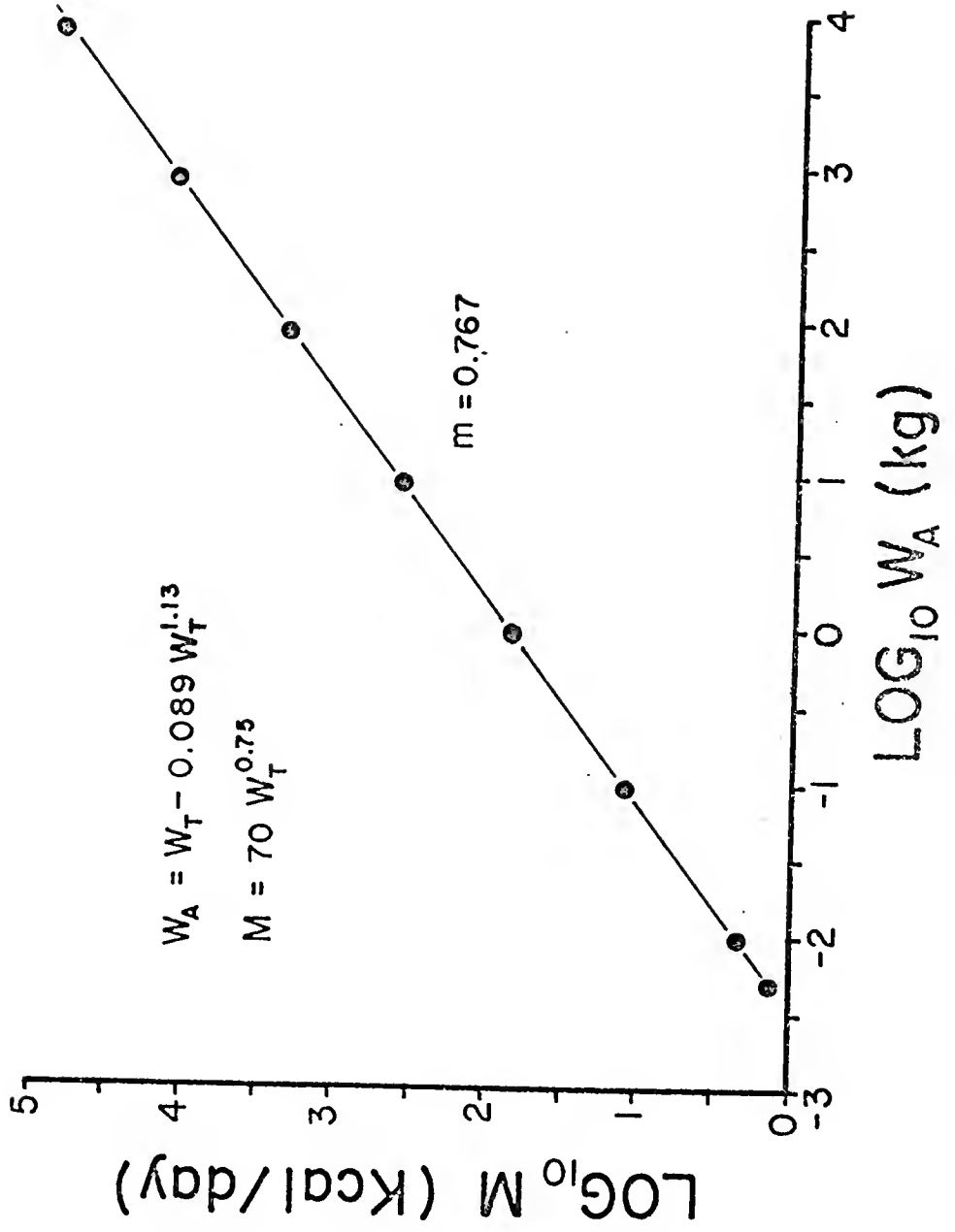
(C) as a function of  $W_A^{0.75}$ .



and  $k_1$  is 72.6. Line A on Figure 2B is the actual relationship between metabolic rate and body size as given by Eq. (1B). Line C, representing metabolic rate as  $(f) W_A^{0.75}$  is a much better approximation of the actual results than line B, which represents metabolic rate as  $(f) W_A^{1.0}$ . Note that both lines B and C are corrected for increasing skeletal weights which are disproportionate to increasing total weights.

It is obvious from Figure 2B that most of the 0.25 units difference from 1.0 in the weight exponent is actually due to a decrease in weight-specific metabolic rate of active tissues. However, curves B and C in that figure are not exactly linear, since  $W_A$  was calculated from  $W_A = W_T - 0.089 W_T^{1.13}$ , which is not a linear function. Therefore, C cannot be fitted perfectly to A merely by increasing the exponent of  $W_A$ . To find what the actual difference between 0.75 and some slightly higher exponent of active weight should be to account for  $M = 70 W_T^{0.75}$ , one need only plot the actual metabolic rate against  $W_A$ . This is done in Figure 3B, where the slope of the line represents the exponent of  $W_A$ , and gives a power of 0.767. This can be interpreted as meaning that approximately 0.017 units of the 0.25 units, or only about 7%, of the decrease in weight-specific metabolic rate with increasing size can be accounted for by a disproportionate increase in skeletal weight.

Figure 3B. Relationship between weight of active tissues ( $W_A$ ) and metabolic rate in mammals.  $W_T$  = total weight.



## LITERATURE CITED

- Anderson, J. 1968. Metabolic rates in spiders. Ph.D. Dissertation. Univ. of Fla., Gainesville, Fla.
- Anderson, J. 1970. Metabolic rates of spiders. *Comp. Biochem. Physiol.* 33(1): 51-72.
- Bartholomew, G. and V. Tucker. 1964. Size, body temperature, thermal conductance, oxygen consumption, and heart rate in Australian varanid lizards. *Physiol. Zool.* 37: 341-354.
- Brody, S. 1945. Bioenergetics and growth. Reinhold Pub. Corp., New York.
- Conant, R. 1958. A field guide to reptiles and amphibians. Houghton Mifflin Co., Boston.
- Czopek, J. 1960. Unaczynienie powierzchni oddechowych u salamandry plamistej (*Salamandra salamandra* L.) w rozwoju ontogenetycznym. *Zeszyty Nauk. UMK, Torun. Biol.* 5: 3-16.
- Czopek, J. 1961. Vascularization of respiratory surfaces in some Plethodontidae. *Zoöl. Pol.* 11: 131-150.
- Czopek, J. 1962. Vascularization of respiratory surfaces in some Caudata. *Copeia*, 1962(3): 576-587.
- Czopek, J. 1965. Quantitative studies on the morphology of respiratory surfaces in amphibians. *Acta anat.* 62: 296-323.
- Davison, J. 1955. Body weight, cell surface, and metabolic rate in anuran amphibia. *Biol. Bull.* 109(3): 407-419.
- Dmi'el, R. 1972. Relation of metabolism to body weight in snakes. *Copeia* 1972(1): 179-181.
- Freeman, J. 1963. Studies of respiratory mechanisms of the salamander *Pseudobranchius striatus*. Ph.D. Dissertation. Univ. of Fla., Gainesville, Fla.
- Goin, C. 1941. "The striped siren, *Pseudobranchius striatus* (LeConte)." Master's Thesis. Univ. of Fla., Gainesville, Fla.
- Gray, I. 1954. Comparative study of the gill area of marine fishes. *Biol. Bull.* 107: 219-225.
- Guimond, R. 1970. Aerial and aquatic respiration in four species of paedomorphic salamanders: *Amphiuma means means*, *Cryptobranchus alleganiensis alleganiensis*, *Necturus maculosus maculosus*, and *Siren lacertina*. Ph.D. Dissertation. Univ. of Rhode Island, Kingston, Rhode Island.

- Hemmingsen, A. 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rept. Steno Mem. Hosp. Nord. Insulin Lab. 9 (Part II).
- Hutchison, V., W. Whitford and M. Kohl. 1968. Relation of body size and surface area to gas exchange in anurans. *Physiol. Zool.* 41(1): 65-85.
- Ivlev, V. 1954. The relation of metabolic rate to size in fish. *Fiziologich. zhurnal* 40: 717-721.
- Kayser, C. and A. Heusner. 1964. Étude comparative du métabolisme énergétique dans la série animale. *J. Physiol. (Paris)* 56: 489-524.
- Kleiber, M. 1961. The fire of life. John Wiley & Sons, Inc., New York.
- Lasiewski, R. and W. Calder. 1971. A preliminary allometric analysis of respiratory variables in resting birds. *Resp. Physiol.* 11: 152-166.
- Lenfant, C. and K. Johansen. 1967. Respiratory adaptations in selected amphibians. *Resp. Physiol.* (1967)2: 247-260.
- Lynch, J., J. King, T. Chamberlain and A. Smith. 1947. Effects of aquatic weed infestations on the fish and wildlife of the Gulf States. U. S. Dept. Int. Spec. Sci. Rept. 39: 1-71.
- McCutcheon, F. and F. Hall. 1937. Hemoglobin in the amphibia. *J. Cell and Comp. Physiol.* 9: 191-197.
- Muir, B. 1969. Gill dimensions as a function of fish size. *J. Fish Res. Bd. Canada.* 26: 165-170.
- Muir, B. and G. Hughes. 1969. Gill dimensions for three species of tunny. *J. Exp. Biol.* 51: 271-285.
- O'Hara, J. 1968. The influence of weight and temperature on the metabolic rate of sunfish. *Ecology* 49(1): 159-161.
- Price, J. 1931. Growth and gill development in the smallmouthed black bass, Micropterus dolomieu, Lacépède. *Studies, Ohio State Univ.* 4: 46.
- Scott, W. 1931. Oxygen and carbon dioxide transport by the blood of the urodele, Amphiuma tridactyla. *Biol. Bull.* 61(2): 211-222.
- Stahl, W. 1967. Scaling of respiratory variables in mammals. *J. Appl. Physiol.* 22(3): 453-460.
- Stussi, T., A. Huesner, C. Kayser, C. Marx and M. Harmelin. 1963. Relation entre le poids et la consommation d'oxygène. III. Étude interspécifique chez les poissons. *C. R. Soc. Biol., Paris,* 157: 667-669.



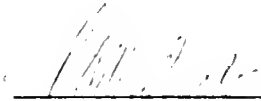
- Tenney, S. and J. Remmers. 1963. Comparative morphology of the mammalian lung: diffusing area. *Nature* 197: 54-56.
- Tenney, S. and J. Tenney. 1970. Quantitative morphology of cold-blooded lungs: amphibia and reptilia. *Resp. Physiol.* 9: 197-215.
- Ultsch, G. 1971. The relationship of dissolved carbon dioxide and oxygen to microhabitat selection in Pseudobranchius striatus. *Copeia*, 1971(2): 247-252.
- Ursin, E. 1967. A mathematical of some aspects of fish growth, respiration, and mortality. *J. Fish. Res. Bd. Canada.* 24: 2355-2453.
- Whitford, W. and V. Hutchison. 1967. Body size and metabolic rate in salamanders. *Physiol. Zool.* 40(2): 127-133.
- Winberg, G. 1956. Rate of metabolism and food requirements of fishes. (Original in Russian) Translation Series No. 194 (*J. Fish. Res. Bd. Canada*).

## BIOGRAPHICAL SKETCH

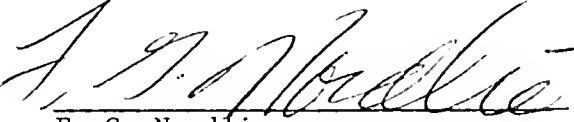
Gordon Richard Ultsch was born in Waltham, Massachusetts on June 30, 1942. He graduated from Fitch Senior High School in Groton, Connecticut in 1960, and attended the University of Connecticut from 1960 to 1963, when he was married to Sandra Lawrence. He returned to the University of Connecticut in 1966 and graduated with a B.A. in 1967. That year he entered the University of Florida as a graduate student and has since pursued work leading to the Ph.D.

Gordon and Sandra have one child, Julie Anne.

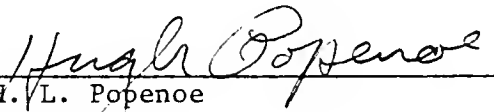
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B. K. McNab, Chairman  
Professor of Zoology

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F. G. Nordlie  
Associate Professor of Zoology

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Professor of Soils

This dissertation was submitted to the Department of Zoology in the College of Arts and Sciences and to the Graduate Council, and was accepted as partial fulfillment of the requirements for the degree of Doctor of Philosophy.

August, 1972

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