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The Response of the Bivalve *Mercenaria mercenaria* to Declining Oxygen Tensions

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THE RESPONSE OF THE BIVALVE MERCENARIA MERCENARIA
TO DECLINING OXYGEN TENSIONS.

A Thesis

Presented to

The Faculty of the School of Marine Science
The College of William and Mary in Virginia

In Partial Fulfillment
Of the Requirements for the Degree of
Master of Arts

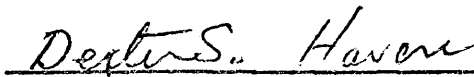
By
Dennis Walsh
1974

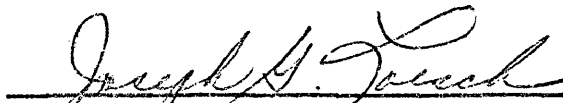
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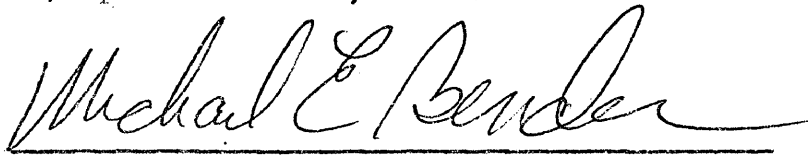
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Dennis Walsh

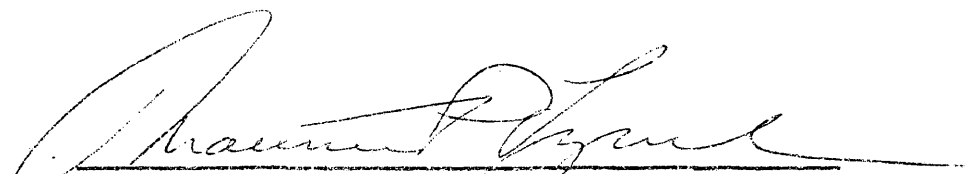
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Abstract

The oxygen consumption, pumping rate and filtration efficiency of Mercenaria mercenaria L., from the York River, Virginia, U.S.A., were measured at low oxygen tensions and compared to the same measurements taken at high oxygen tensions. All experiments were conducted under naturally fluctuating conditions of salinity, temperature, turbidity, and food levels. Analysis of results from 58 clams indicated Mercenaria could maintain a constant oxygen consumption in declining oxygen tension, but the critical oxygen tension (P_c) at which this respiratory regulation ceased appeared to depend on the clam's size and sex. Gravid females, dry tissue weight 1.20 - 5.03 g, displayed a P_c near an oxygen tension of 40 mm Hg (25% sat.). Male clams with gametes, whose dry tissue weight was less than 3.0g had a P_c near 80 mm Hg oxygen tension (50% sat.). Some evidence^c is offered that larger males have a P_c similar to females. Three modes of respiratory regulation were observed. In the first, oxygen utilization and pumping rate remained unchanged at all oxygen levels above P_c such that the oxygen consumption, the product of these two variables, remained unchanged. In the second mode a decrease in pumping rate was compensated by a sufficient increase in oxygen utilization to give a constant oxygen consumption. In an anomalous third mode, an increase in pumping rate was not fully compensated by a decrease in oxygen utilization, but oxygen consumption remained constant. The efficiency with which the gill's cilia were able to remove particles in the 3-20 μ range was found to be independent of the pumping rate, oxygen consumption and the oxygen tensions. Multiple linear regression analysis showed that the observed values of temperature, salinity turbidity and food level showed little effect on either male or female Mercenaria at high or low oxygen tensions. Sexual differences were again evident at high versus low oxygen tensions when size and the oxygen utilization of the clam was analyzed by MLR analysis.

THE RESPONSE OF THE BIVALVE MERCENARIA
MERCENARIA TO DECLINING OXYGEN TENSIONS

Introduction

Oxygen is relatively scarce in water and thus often an important limiting factor to aquatic organisms (Odum, 1971). Considerable research has indicated that with regard to respiration marine invertebrates can be placed in two broad categories regarding their reaction to a decline in dissolved oxygen. Those with independent respiration maintain a constant rate of oxygen consumption over a wide range of oxygen tensions until reaching a certain critical oxygen tension (P_c), below which the rate of oxygen consumption drops precipitously. In organisms with dependent respiration oxygen consumption falls continuously with decreasing oxygen tension (Beadle, 1961). Prosser and Brown (1961) have designated these two categories "regulators" and "conformers" respectively.

Most marine bivalves regulate their oxygen consumption, but different P_c and regulatory mechanisms are found (Galtsoff and Whipple, 1931; Van Dam, 1938, 1954; Bayne, 1967, 1971a, 1973). Regulatory mechanisms involve manipulation of the two factors governing bivalve respiration: pumping (ventilation) rate and the oxygen utilization (Ghiretti, 1964). The volume of oxygen consumed per unit time is obtained when the oxygen utilization (reduction in oxygen content between incurrent and excurrent water) is multiplied by the pumping rate (the amount of water passing over the clam's gill per unit time). Because by the defini-

tion.

of respiratory regulation the product of these two variables must be constant at all oxygen tensions above P_c , three modes of regulation are theoretically available to a regulating bivalve: (1) The oxygen utilization and pumping rate are both held constant at all oxygen tensions above P_c . (2) A decrease in pumping rate is coupled with an increase in the oxygen utilization. (3) A decrease in the oxygen utilization is coupled with an increase in the pumping rate.

Examination of the literature on bivalve respiration revealed most studies on bivalve respiration were done under conditions of constant temperature, salinity and food levels in closed-system respirometer (Galtsoff and Whipple, 1931, Nazawa, 1929, and Bayne, 1967). In many of these studies the bivalve was allowed to reduce the oxygen level in a closed container and the point at which oxygen was no longer consumed at a constant rate was defined as P_c . These experiments could not be conducted over long time periods because of oxygen depletion and waste accumulation. In other experiments the water in the chamber was replaced with water of a given oxygen tension and the animals respiration was measured for a given period of time (Bayne, 1971b, 1973). In only one study was an open flow-through system used (Hamwi, 1969). However, in this latter study the bivalve's respiration was measured under conditions of rapid fluctuations in oxygen tension.

In all of the above studies the period of exposure to a given oxygen level was a few minutes to a few hours at most. A chronic exposure to low oxygen tensions under condition of naturally fluctuating environmental variables might give a value for P_c closer to that value occurring in nature. For example, Prosser, Barr, Pinc and Lauer (1957) demonstrated goldfish responded to chronic exposure to low oxygen by a shift of P_c to lower oxygen tensions. Odum (1971) pointed out that organisms which are normally subjected to variable temperatures in nature were found to be depressed, inhibited or slowed down by constant temperature. The pattern of mortality of the oyster drill, Urosalpinx in fluctuating salinities was reported to be quite different from mortality patterns in constant salinity (Zachary and Haven, 1973). Organisms in situ respond to their total environment rather than to a single factor. Hence, "monofactorial analysis may lead to conclusions that are ecologically invalid (Kinne, 1964).

Accordingly, the purposes of this study were (1) to determine the critical oxygen tension (P_c) of the hard clam, Mercenaria mercenaria exposed to reduced oxygen tensions for a minimum 48 hour period, (2) to determine the mode of regulation governing oxygen consumption, and (3) to analyze the effects of fluctuating environmental variables which might modify the clams response to declining oxygen tensions.

Materials and Methods

1. Collection and Preparation of Clam Stock

Adult Mercenaria were collected from tongers operating in the York River near Gloucester Point, Virginia or from clam beds located near the laboratory. The salinity ranged from 12 ‰ to 21 ‰ during the course of this study; the average salinity was 17 ‰. A total of 68 clams were used in this study and except for two clams that had spawned, all clams had developing gametes. Clams were maintained in the laboratory in sand-filled boxes to prevent possible infestation by the annelid Polydora (Landers, 1967). Unfiltered York River water flowed past the animals continuously so that the clams experienced the natural fluctuations of the estuarine environment.

Because the York River estuary exhibited abnormally low salinities during the winter, several experiments were performed to study the response of Mercenaria to declining oxygen tensions at reduced salinities. During the winter (1972-1973), the clams were thermally acclimated a minimum of two weeks at fluctuating temperatures of 22-26°C. No other environmental factors were controlled. Widdows and Bayne (1971) determined it took a minimum of two weeks for Mytilus edulis to completely acclimate their oxygen consumption and filtration rate to temperature changes. Copious production of feces and the presence of growth rings indicated food sources were not limiting in the winter water.

2. Apparatus

The apparatus used to maintain clams under variable oxygen tensions (Figure 1) consisted of a submersible pump (A) supplying a continuous flow of unfiltered water to two polyvinyl chloride water/gas exchange columns (C). Water for all studies was pumped through plastic pipes from a source 0.5 m above the bottom, 90 m. offshore in the York River, to a constantly overflowing overhead trough in the laboratory.

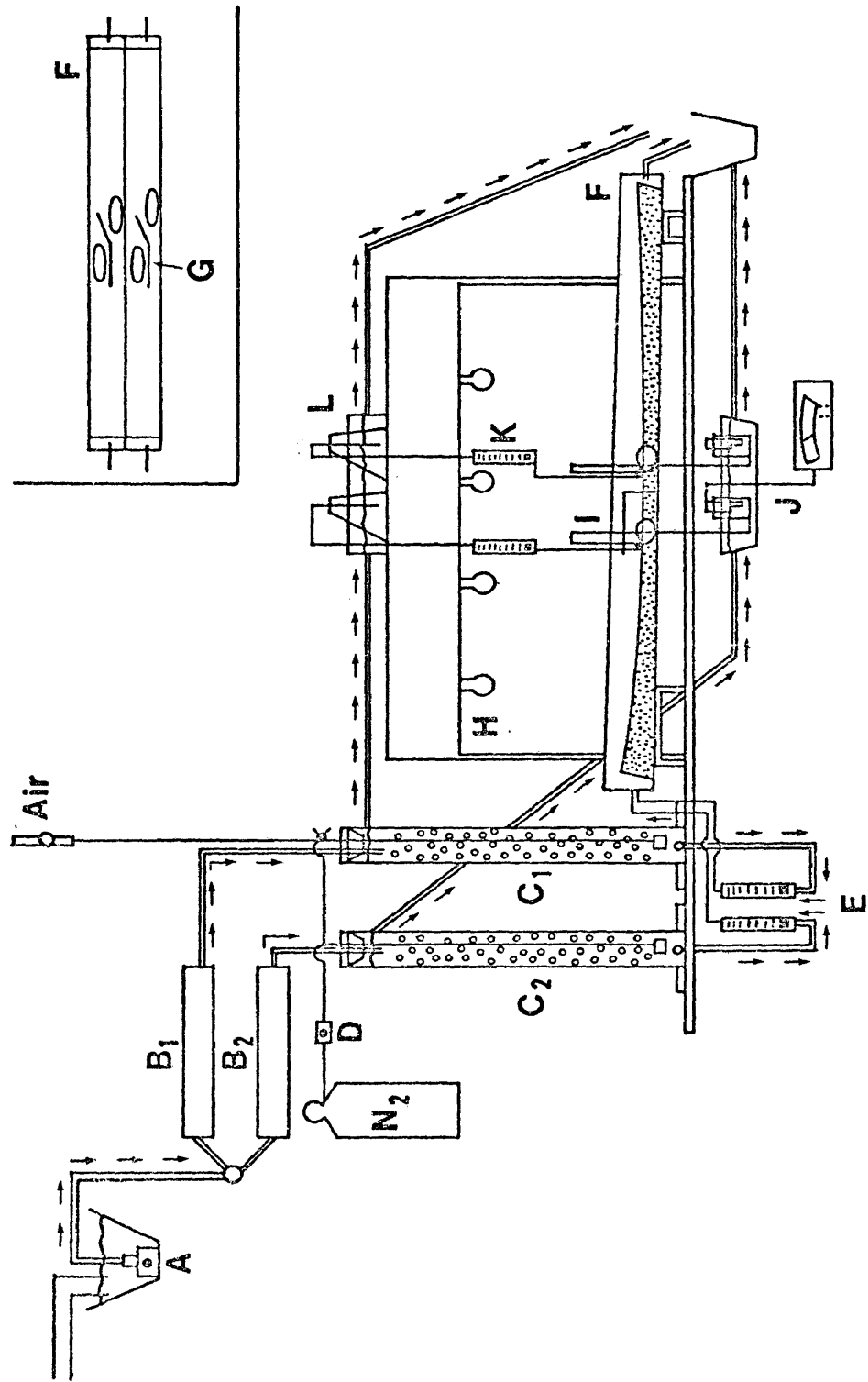
For the winter experiments the water was heated by two glass heat exchange units (B) to the experimental temperatures (22-26°C) before entering the exchange columns. One column furnished high oxygen tension water for the control (C₁), while the other column (C₂) furnished water stripped of oxygen by oxygen-free nitrogen (N₂) bubbling upwards. Oxygen supersaturation of the water during the winter was prevented in the controls by bubbling a small stream of nitrogen into the control column.

The desired level of oxygen for the various studies was maintained by adjusting the amount of nitrogen entering the column by use of a micrometer valve (D). Flowmeters (E) gave a controlled flow of 560-600 ml/min of river water into a twin chambered trough (F) that had four clams buried in coarse beach sand. The sand was packed in a concave configuration to minimize turbulence and recirculation and produce a near laminar flow past the animals. The clams were positioned with their inhalent

Figure 1.

Flow-through environmental system employed in the measurement of pumping rate, oxygen consumption and filtration efficiency of Mercenaria

A, Pump; B, Heat exchange coils; C, PVC water-gas exchange columns; D, Nitrogen regulation valve; E, Flowmeters; F, Twin chambered trough; G, Partitions; H, Light bank; I, Capillary collecting tubes; J, Oxygen probe unit; K, Lab-Crest Flowmeters; L, Ambient water bath.



siphon facing upstream. Plastic partitions (G) insured that each clam received clean unfiltered water. A blue-green light bank (H) provided light from 0600-1800 hours daily.

1 mm I.D. glass capillary tubes (I) were used to collect water samples from the clam's siphons. The oxygen content of the water was measured by a self-stirring polarographic probe (J) (Model 54, Yellow Springs Instrument Company, Yellow Springs, Ohio). Lab Crest Flowmeters (K) (Fisher Scientific Company, Pittsburg, Penn.) were used to measure the clams pumping rate. Water for the pumping rate determination was collected in flasks and placed in an ambient temperature water bath (L).

3. Experimental Procedure

a. Time Table

An experiment lasted for one week and consisted of three phases. Phase one was a two day adjustment period to the trough. Phase two lasted approximately two and one half days, during which time measurements of the pumping rate and oxygen consumption for all four animals were monitored at high oxygen tensions of 120-160 mm Hg (75-100% saturation). At the beginning of phase three the oxygen tension in the experimental trough was lowered to a designated level over a one hour period. The designated oxygen tensions were 80 mm Hg (50% sat.), 40 mm Hg (25% sat.) and 18 mm Hg (12% sat.). The control chamber remained at high oxygen tensions. Once the oxygen level was stabilized in the experimental trough, measurements of oxygen consumption and pumping rate were continued daily from 0800-1700 hr on both the controls and experimental animals for at

least 48 hours. At the end of phase three the clam's length (maximum distance between external surface of the valves), tissue wet weight and tissue dry weight, were recorded. Tissue dry weight was obtained by heating the tissue in a drying oven at 87°C until a constant weight was recorded.

b. Measurement of Oxygen Consumption and Pumping Rate

A capillary tube, withdrawing water by gravity at a rate of 8-10 ml/min, was positioned over the animals incurrent siphon. This water collected in a chamber situated in a water bath at ambient temperature, and was recorded as the incurrent oxygen concentration. The oxygen probe was calibrated at least twice daily with air saturated water using the tables of oxygen saturation of sea water (Green and Carritt, 1967).

Using the method of Coughlan and Ansell (1964), the instantaneous pumping rate was read from the calibrated flowmeter when the dyed water just began to overflow the incurrent siphon. In all experiments, the soluble nontoxic dye used was green food coloring (C.F. Sauer Company, Richmond, Va.; the dye contained propylene glycol, water and 2.5% pure green food dye).

Immediately after the pumping rate determination, the capillary tube collected excurrent water by gravity at a rate one half or less than the previously determined pumping rate. The oxygen content of this water was recorded over several minutes as the average excurrent oxygen concentration. Next,

the incurrent oxygen concentration was recorded again and the two readings averaged. The difference between the averaged incurrent and excurrent oxygen concentration is the oxygen utilization ($d [O_2]$). Finally, the pumping rate was measured again and the two readings averaged. The oxygen consumption was then determined by multiplying the average pumping rate by the oxygen utilization. Weight-specific oxygen consumption (QO_2 :ml O_2 (STP)/hr/g dry wt.) and weight specific pumping rate (SPR:LH₂O/hr/g dry wt.) were calculated at the end of the experiment. The oxygen utilization coefficient (O.U.C.) (Hazelhoff, 1938):

$$\text{O.U.C.} = \frac{[O_2]_{in} - [O_2]_{ex} \times 100}{[O_2]_{in}}$$

was also determined for each set of measurements. This coefficient measures the percentage of oxygen removed for respiration as the water passes over the gills.

The efficiency (E):

$$E = \frac{\text{pumping rate}}{\text{Oxygen consumption}} = \text{L H}_2\text{O/ml O}_2$$

defines the amount of water pumped to gain one milliliter of oxygen (Dejours, Cary, Rahn, 1970)

c. Measurement of Filtration Efficiency

Several experiments were performed to measure the effect of low oxygen tension on the gills' particle filtering capacity. The filtration efficiency is defined by the following equation:

$$\text{Filtration Efficiency} = \frac{\text{Particle}_{in} - \text{Particle}_{ex}}{\text{Particle}_{in}} \times 100$$

The filtration efficiency was measured by carefully sampling incurrent and excurrent water simultaneously with a capillary collecting tube. The capillary was always positioned inside the siphon and water was withdrawn slowly by gravity. Particles in the water sample in the size range 3-20 μ were measured and counted using the Coulter Electronic Particle Counter (Model B, Coulter Electronics Inc., Franklin Park, Illinois). The pumping rate was determined by the method of Coughlan and Ansell (1964) before or after the collection of these samples.

The pumping rate (amount of water passing over the gills per unit time) and the filtration rate (amount of water cleared of particles per unit time) are related (Rice and Smith, 1958). Both are expressed in the same units: liters of water (pumped or filtered) per unit time. If the filtration efficiency is 100%, then the volume filtered is the volume pumped and the

pumping rate and filtering rate are equal. If the filtration efficiency is 50%, then the filtration rate is one-half the pumping rate. Therefore, the filtration rate is directly proportional to the pumping rate and the filtration efficiency is the proportionality factor:

$$\text{Filtering rate} = (\text{filtration efficiency}) \times (\text{pumping rate})$$

Thus, by measuring the pumping rate and filtration efficiency, the filtration rate was calculated.

d. Measurement of environmental variables.

The following environmental variables were monitored throughout each experiment: temperature, salinity, turbidity and chlorophyll "A". Temperature was measured by a Yellow Springs Instrument Thermistor whenever oxygen consumption was measured. Salinity was recorded hourly during the day with a Beckman induction salinometer. (Beckman Instruments, Inc., Fullerton, California.)

Turbidity and chlorophyll "A" were determined at 0900, 1200, and 1600 hours each day of the experiment. A volume of 400 ml was collected from an area immediately in front of the animals; 200 ml was filtered through a 0.45 μ pre-weighed Gelman filter, dried overnight and weighed to give the turbidity weight (mg particulate matter per liter). The standard method of Strickland and Parsons (1968) was used to extract the chlorophyll from the remaining 200 ml of water. No corrections were made for phaeopigments because living and dead phytoplankton

are probably filtered from the water by bivalves.

4. Statistical Analysis

Analysis of variance (ANOVA) and multiple linear regressions were applied to the data using the statistical formulas and methods of Snedecor and Cochran (1967).

Pumping rate (SPR), oxygen consumption (QO_2), oxygen utilization ($d O_2$), oxygen utilization coefficient (O.U.C.) and efficiency (E) of individual clams were compared by ANOVA. ANOVA for individual clams were used to determine significant differences ($P < 0.05$) or highly significant differences ($P < 0.01$) between the mean value of observations at high oxygen tensions (Phase two) with mean values of observations at a given low oxygen tension (Phase three). The data on oxygen utilization coefficient, a percentage, was first transformed into degrees using the arcsin transformation. Data from the individual control clams were likewise divided into two data blocks corresponding in time to phase two and phase three of the experimental animals. ANOVA was applied to see if there was any change in the control caused by environmental variables other than oxygen tension.

Next, the experimental clams were pooled into five arbitrarily defined weight classes. (eg., Table I). Each weight class covered 0.99 grams from 1.00 to 5.99 grams. Individuals of a given weight class were divided into three subsets: (1)

those animals exposed to high oxygen tensions (120-160 mm Hg) throughout the experiment (controls); (2) those animals exposed to high oxygen tension followed by an average oxygen tension of 80 mm Hg (50% sat.), and (3) those animals exposed to high oxygen tension followed by an average oxygen tension of 40 mm Hg (25% sat.). Data on animals exposed to 18 mm Hg (12.5% sat.) was not pooled because so few data points were collected at this low oxygen tension due to the animal not pumping. Lastly, the pooled data in each subset were divided into two other data blocks: high (Phase two) vs. experimental oxygen tension (Phase 3) and significant differences between the means were found by ANOVA.

Multiple linear regression (MLR) with ANOVA was employed to determine if such environmental factors as temperature, salinity, turbidity and food level (chl. "A") or such factors as body weight and oxygen utilization had an effect on the animals' response to a decline in oxygen level as measured by pumping rate and oxygen consumption. MLR was used only to discover which X variables are related to Y (pumping rate or oxygen consumption) and, if possible, to rank the variables in order of their importance.

All measurements taken at high oxygen tensions (120-160 mm Hg) and low oxygen tensions (40 mm Hg) were pooled and analyzed by MLR. Comparison of a variable's partial regression coefficient (b) at high oxygen tension and 40 mm Hg were made to see if the variable's effect on the clam is altered by changes in oxygen tension.

Results

1. The Critical Oxygen Tension (P_c)

Unless otherwise indicated "oxygen consumption" refers to weight specific oxygen consumption (QO_2) and "pumping rate" refers to weight specific pumping rate (SPR). Gravid females of the five weight classes studied maintained a constant oxygen consumption down to an oxygen tension of 40 mm Hg (25% sat.) (Tables 1-5). The only exceptions were a single female that had spawned (Table 1) and two females that were subjected to an oxygen tension of 40 mm Hg when a red tide (Cochlodinium heterolabotum) was present in late summer (Table 3). In these three cases regulation broke down above 40 mm Hg oxygen tension. In all other cases female regulation disappeared between an oxygen tension of 40 mm Hg and 18 mm Hg (contrast figure 2 with figure 6).

The response of male Mercenaria to declining oxygen tension differed significantly from female clams. Male Mercenaria, whose dry tissue weight was under three grams, were able to regulate only down to an oxygen tension of 80 mm Hg (50% sat.). Oxygen consumption declined rapidly between an oxygen tension of 80 mm Hg and 40 mm Hg (Tables 6-7). Above three grams dry tissue weight the P_c for males is uncertain because by chance only one

Figure 2

Female Mercenaria displaying the first mode of respiratory regulation while exposed to low oxygen levels. (23% sat.)

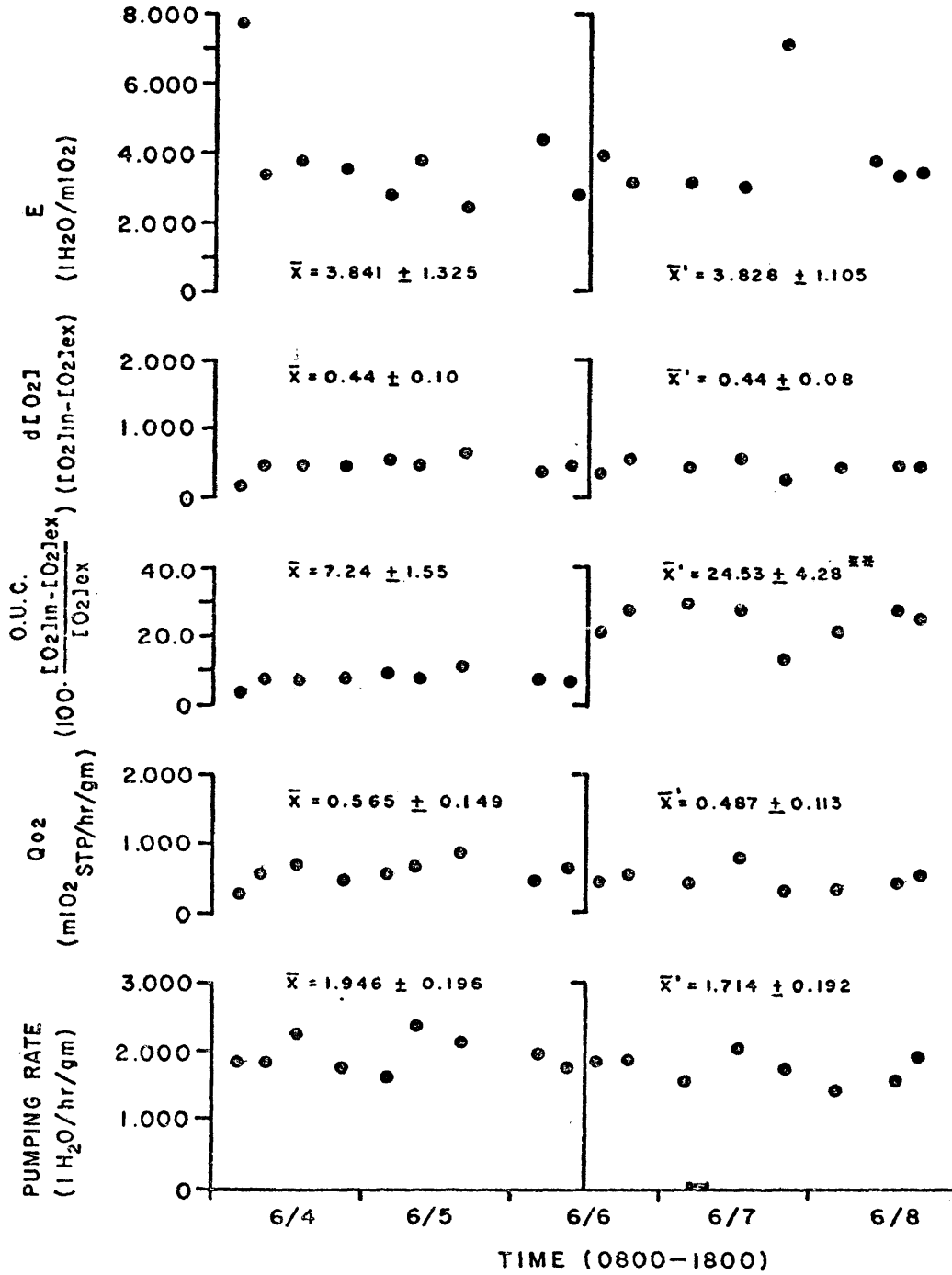
CLAM 18-~~XIV~~

SEX: Q

Length: 72.0 mm Wet tissue wt. 22.32 gm Dry tissue wt. 3.90 gm

$\bar{p}O_2 = 124$ mmHg

$\bar{p}O_2 = 37$ mmHg



experimental male was tested whose dry tissue weight exceeded three grams. This individual male, 4.16g dry weight, regulated its oxygen consumption down to 40 mm Hg (Table 8).

The oxygen consumption of the control male and female clams showed no change during the course of the experiments (Table 1-8), except in the case of small female clams (mean weight: 1.67 g) where there was a significant decrease in oxygen consumption (Table 1). In several cases the control clams' pumping rate declined during the course of the experiment, but the oxygen consumption was maintained (Tables 2,8).

2. Modes of Respiratory Regulation

When the pumping rate remained unchanged at oxygen tensions above P_c , the oxygen utilization likewise did not change in its value. As a result the oxygen consumption remained constant (Figure 2). In this mode of regulation the amount of water pumped to gain one milliliter of oxygen, the efficiency (E), also remained constant at all oxygen tensions above P_c (Figure 2).

A second response of the pumping rate was that it decreased in declining oxygen tension. This was compensated by an increase in the oxygen utilization such that the oxygen consumption remained constant (Figure 3). In this second mode of regulation the amount of water pumped to extract one milliliter of oxygen (E) was reduced at low oxygen tensions above P_c :

In several cases the clams' pumping rate increased as oxygen tension declined. However, the oxygen utilization did not show a significant decline in value, nor did the oxygen consumption show a significant increase. In this anomalous third mode of regulation the amount of water pumped to extract one milliliter increased at low oxygen tensions above P_c (Figure 4).

The oxygen utilization coefficient (O.U.C.) always showed a highly significant increase at low oxygen tensions, (Figures 2-6, Tables 1-8). This coefficient increased regardless of which mode of regulation was in effect.

Oxygen consumption declined precipitously below P_c (Figures 5,6, Table 7). At an oxygen tension of 18 mm Hg (12% sat.) the amount of water that would have to have been pumped to gain one milliliter of oxygen was at least three times the normal amount at high oxygen tensions (Figure 6).

3. Filtration Efficiency

Preliminary experiments indicated Mercenaria's filtration efficiency in the size range of 1-3 μ was 10-25% over a wide range of oxygen tensions. However, when this size range was exceeded efficiency averaged from 60-97% over a wide range of oxygen tensions. The filtration efficiency in these size range over 3 μ was not a function of particle size or particle concentration naturally present in the York River. In general,

Figure 3

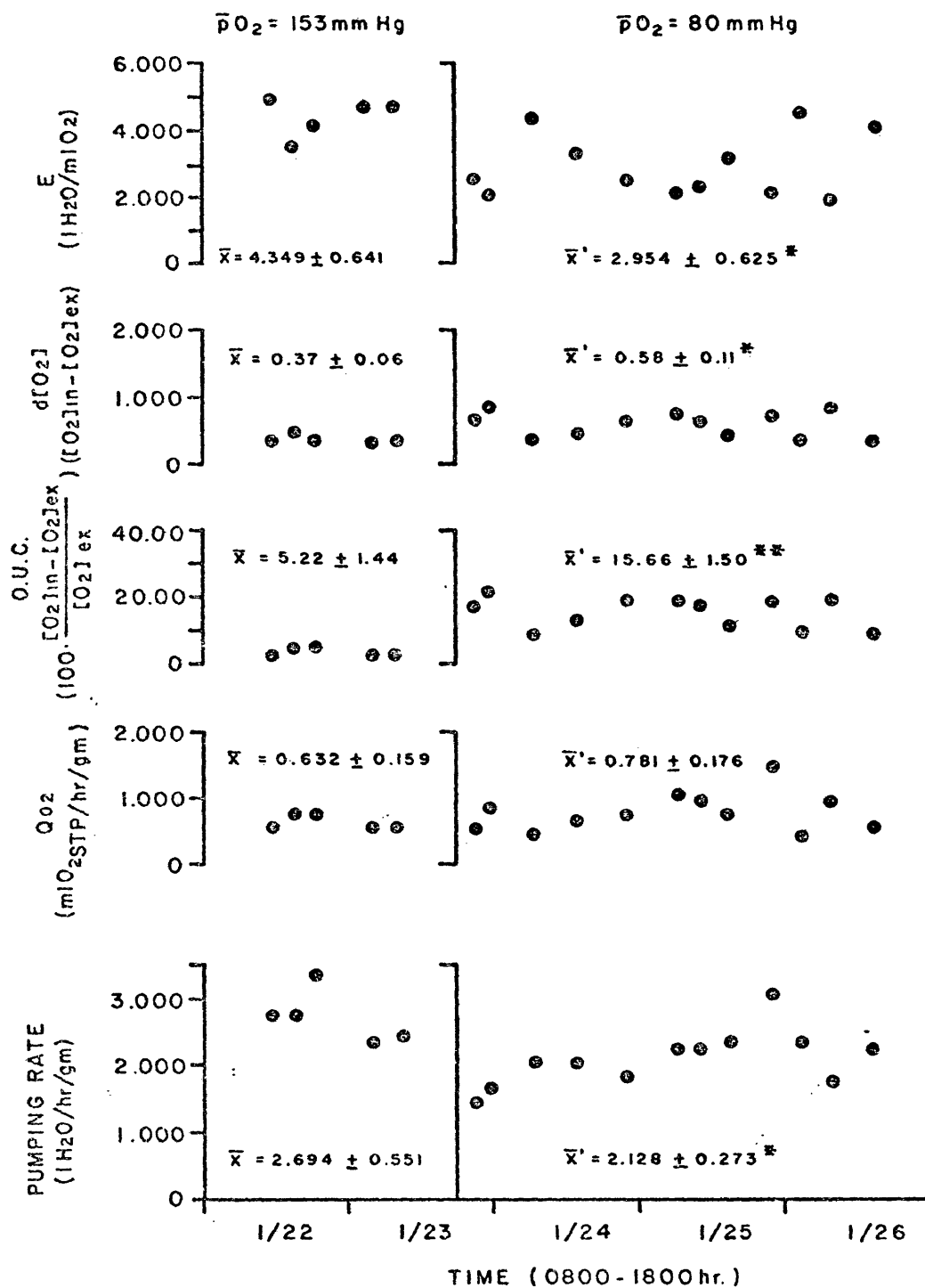
Male Mercenaria displaying the second mode of respiratory regulation while exposed to low oxygen levels (50% sat)

CLAM IB-I
SEX ♂

Length: 69.3 mm

Wet tissue wt. 12.43 gm

Dry tissue wt. 1.96 gm



the volume of particles removed decreased with increasing particle size (Figures 7 A-D).

In one series of experiments, the clam's filtration efficiency, pumping rate, filtering rate and oxygen consumption were measured at high oxygen tensions for two days (Figures 7A-B). The oxygen tension was then lowered below the critical oxygen tension for both male and female clams. After one hour and 24 hours exposure, the same four measurements were taken again (Figure 7 C-D). A surprising result of these experiments was that the filtration efficiency remained unchanged below the critical oxygen tension even though the pumping rate, filtration rate and oxygen consumption had declined precipitously.

A second series of experiments were performed on the same time schedule as those determining the critical oxygen tension. For example, a clam whose dry tissue weight was 2.20 g had an average pumping rate of 1.294 L/hr/g and a filtering efficiency of 84% during two days at high oxygen tensions (filtration rate: 1.036 L/hr/g). During 48 hours exposure to an oxygen tension of 40 mm Hg, the average pumping rate was 1.254 L/hr/g and the filtration efficiency was 85% (filtration rate: 1.066 L/hr/g).

Sex did not influence the filtration efficiency of the clam. For example, a male (2.86 g dry weight) showed a mean filtration efficiency of 91% at high oxygen tensions; at 80 mm Hg the mean filtration efficiency was 97%. This particular male closed between an oxygen tension of 80 mm Hg and 40 mm Hg. In the

same experiment a female (2.72 g dry weight) had a filtration efficiency of 88% at high oxygen tensions compared to 87% at 80 mm Hg and 40 mm Hg.

4. Influence of Environmental variables, body weight and oxygen utilization

In the multiple linear regression analysis the amount of variation of Y (pumping rate and oxygen consumption) explained by the four variables ($X_1 - X_4$) ranged from $R^2=0.098$ to $R^2=0.83$. Analysis by MLR revealed that the turbidity, food level (Chlorophyll "A"), temperature and salinity had little effect of Mercenaria's pumping rate or oxygen consumption (Tables 9,10). Initially, a seven factor MLR was run but the effect of turbidity and chlorophyll "A" were so insignificant that they were dropped from further analysis.

Increasing the temperature from 22.2 to 27 C caused a slight increase in oxygen consumption of males at high oxygen tensions. At low oxygen tensions only the combined effect of all four variables tested had a small effect on male oxygen consumption (Table 10). Female oxygen consumption increased with decreasing salinity at low oxygen tensions, but this effect was not evident at high oxygen tensions. The pumping rate of both sexes was not affected by the observed temperatures or salinities at either high or low oxygen tensions (Tables 9,10).

In contrast to the environmental variables, body weight and oxygen utilization usually displayed a highly significant partial

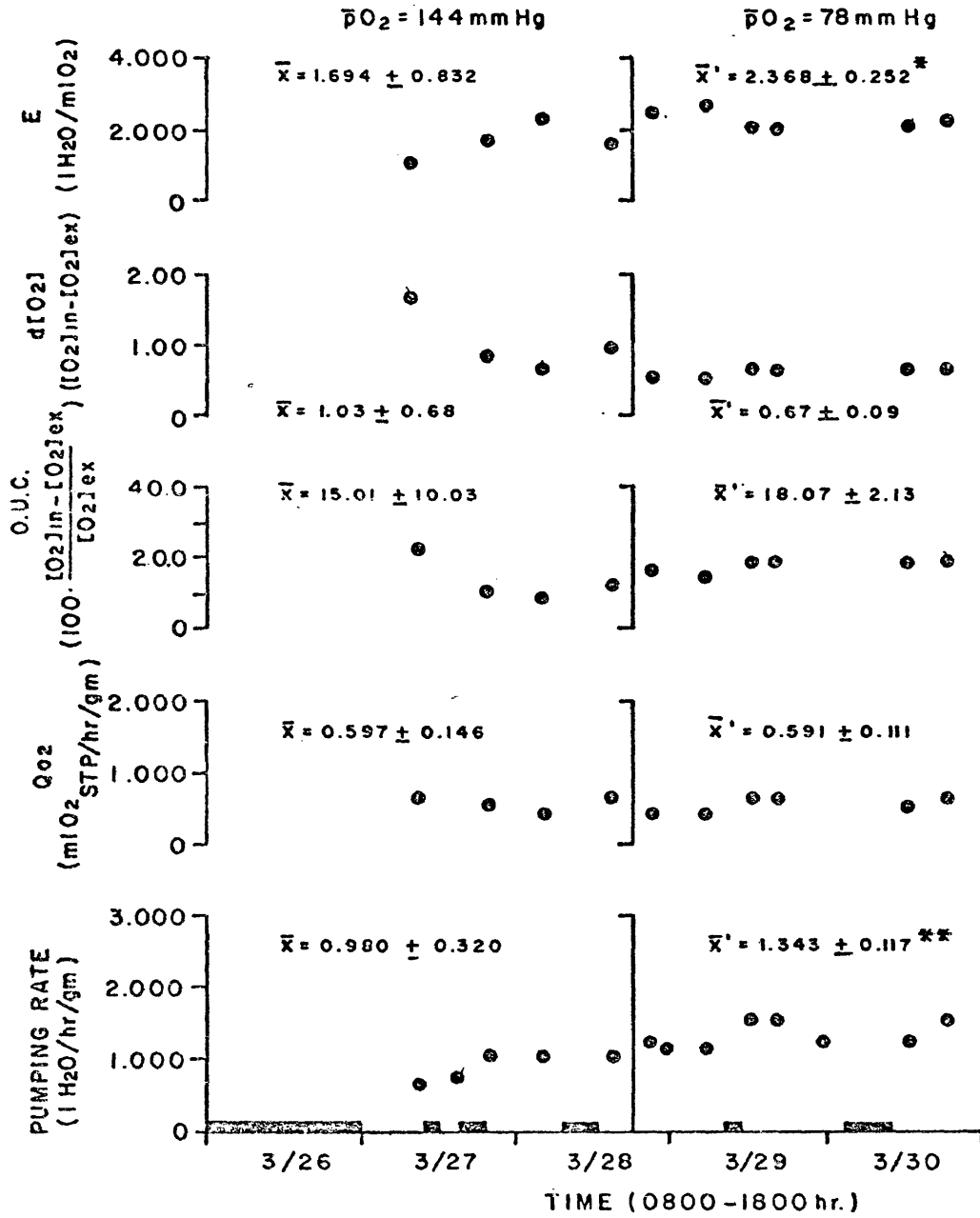
Figure 4

Female Mercenaria displaying the anomalous third mode of respiratory regulation while exposed to low oxygen levels (48% sat.)

CLAM IB - VIII

SEX: Q

Length: 68.3 mm Wet tissue wt. 16.28 gm Dry tissue wt. 2.28 gm



regression coefficient in the MLR analysis. Thus, both oxygen consumption and pumping rate increased in both sexes with increasing weight at high oxygen tensions.(Tables 9-10). This relationship continued to hold for females at 40 mm Hg oxygen tension (Table 9). However, male oxygen consumption and pumping rate showed no statistically significant dependence on weight at 40 mm Hg oxygen tension (Table 10).

Surprisingly, the largest partial regression coefficient was for the regression of pumping rate on oxygen utilization, indicating a highly significant ($P < 0.01$) relationship between these two factors. At high oxygen tensions both sexes required an approximately equal reduction of pumping rate to obtain an increase in the amount of oxygen extracted from the water passing over the gills. However, at the low oxygen tension of 40 mm Hg. a much greater reduction in the pumping rate of the female was required for a given increase in the oxygen utilization than was evident for the male.(Tables 9-10).

Discussion

A. Statistical Evaluation

The large biological variability associated with the parameters studied in this report caused difficulties when the data was subjected to statistical evaluation. Pooling the data produced two deleterious effects: first, it weakened the power of the F-test in the Analysis of Variance (ANOVA) for the weight class. The error mean square for the pooled data was larger than the error mean square calculated during ANOVA for individual clams. In only one case, however, did the ANOVA results for pooled data on oxygen consumption differ from ANOVA for individual clams of a given weight class. It involved the two experimental females in weight class 3.00-3.99 g. which were subjected to a low oxygen tension of 40 mm Hg. The pooled ANOVA for these two animals indicated a significant decline in oxygen consumption (Table 3). However, an ANOVA analyses of each individual animal revealed no significant decline in oxygen consumption.

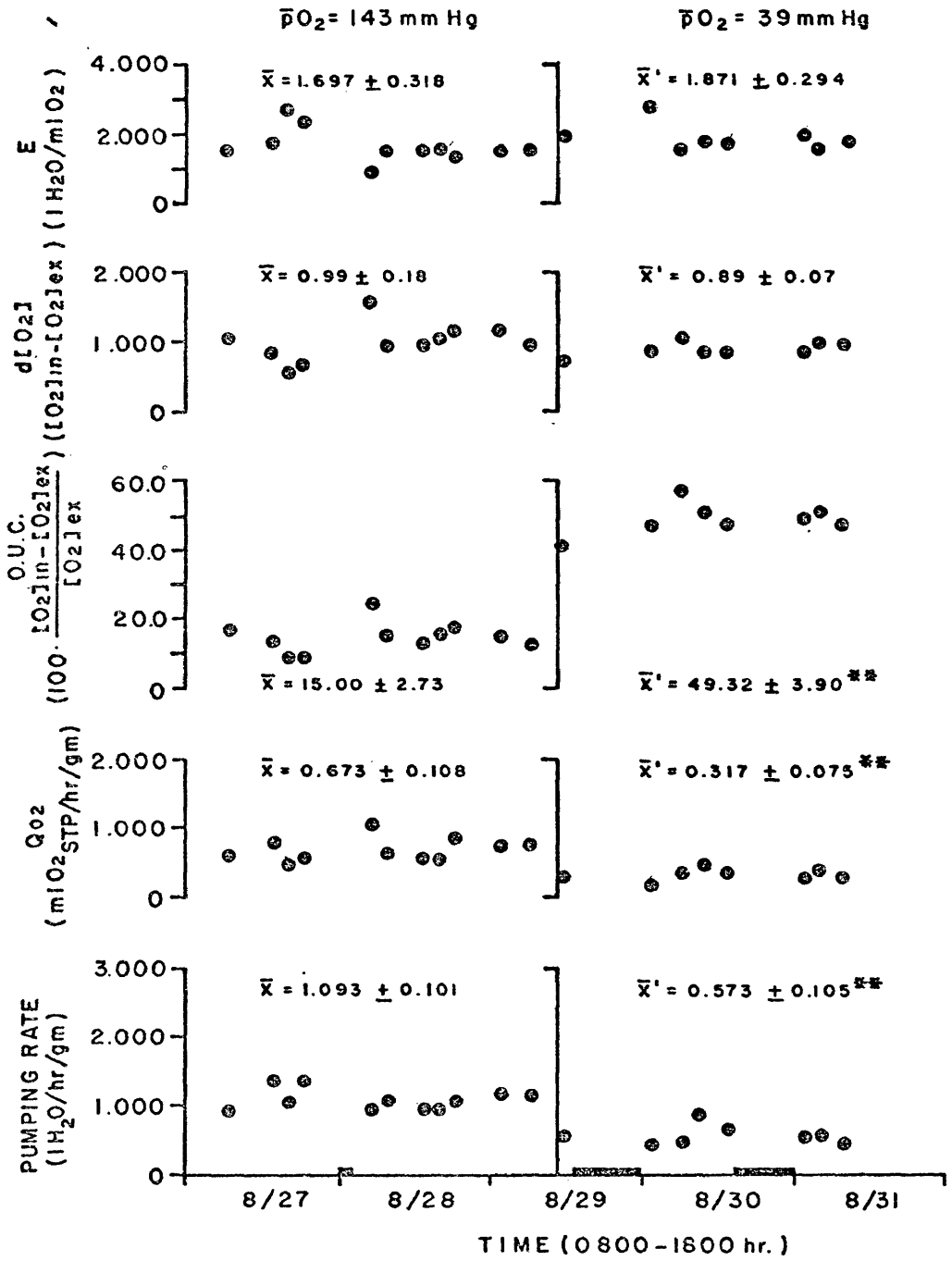
The second effect of pooling data was that the interaction between pumping rate and oxygen utilization was often obscured due to the wide range variability associated even with clams of the same weight class. The interaction between pumping rate and oxygen utilization was evident in the analysis of each individual clam. Thus individual clam data was used in evaluating modes of regulation, but both pooled and individual data were used in

Figure 5

Male Mercenaria displaying loss of respiratory regulation
at 39 mm Hg oxygen tension (24% sat.)

CLAM IA-~~XXI~~
SEX: ♂

Length: 70.8mm Wet tissue wt. 15.24gm Dry tissue wt. 2.81gm



determination of the critical oxygen tension.

B. Critical Oxygen Tension (P_c)

In the only other study of the effects of declining oxygen tension on Mercenaria, Hamwi (1969) found the P_c to be 104 mm Hg (65% sat.) at a temperature of $20^{\circ} \pm 1^{\circ}\text{C}$ and salinity 21.5-22.8 ppt. Indirect evidence indicated the seven clams tested in Hamwi's study had a dry tissue weight of 3.0-7.0 grams; sex was not determined. Using measurement techniques and a flow through system similar to Hamwi, the results of the present study differed significantly. I found females in the dry weight range of 1.21-5.03 gms. exhibited a P_c of around 40 mm Hg. (25% sat.). Some evidence is presented indicating large males might also have a P_c of 40 mm Hg. Males less than 3.0 grams dry weight had a P_c which fell between 80 mm Hg and 40 mm Hg.

The large difference between Hamwi's results and the present results may be due to the rapidity with which Hamwi's clams were subjected to declining oxygen tension and the short exposure time to low oxygen levels.

That is, Hamwi took measurements at ambient oxygen tension and made comparative measurements on the same clam at lower designated oxygen tensions. Hamwi apparently allowed the oxygen level to change rapidly in the flowing chamber ("under rapid fluctuations in oxygen level"). I found Mercenaria often decreased its pumping rate or even closed if the oxygen level was lowered too quickly. In contrast, when the oxygen tension

was lowered gradually over one hour, Mercenaria adjusted quickly; after one more hour at the designated oxygen level, the animal was almost completely acclimated, if the oxygen tension was not below P_c .

The dependence of P_c on size displayed by the male clams in the present study has been found for several bivalves. For example, the P_c of Mytilus perna (Bayne, 1967) and M. edulis and Laevicardium crassum (Bayne, 1971a) is size-dependent. Part of the reason for this size dependence of P_c is that small individuals have high metabolic rates and are less tolerant of low oxygen tensions than larger individuals with relatively low metabolic rates.

However, the mechanism for the size-independence of the P_c for female Mercenaria is unknown. No significant difference was found between male and female oxygen consumption at high oxygen tensions ($pO_2 = 120-160$ mm Hg), provided they were of the same size. As was to be expected, smaller male and female clams had higher weight specific oxygen consumption values than larger clams. Differences between the sexes appeared only below an oxygen tension of 80 mm Hg (50% sat.). Sexual differences in response to declining oxygen have been reported for other invertebrates. For example, Haefner (1970) found gravid female sand shrimp to be less tolerant of low oxygen than males.

Below P_c the oxygen consumption of males and females in all weight classes studied drops to very low values. Recent

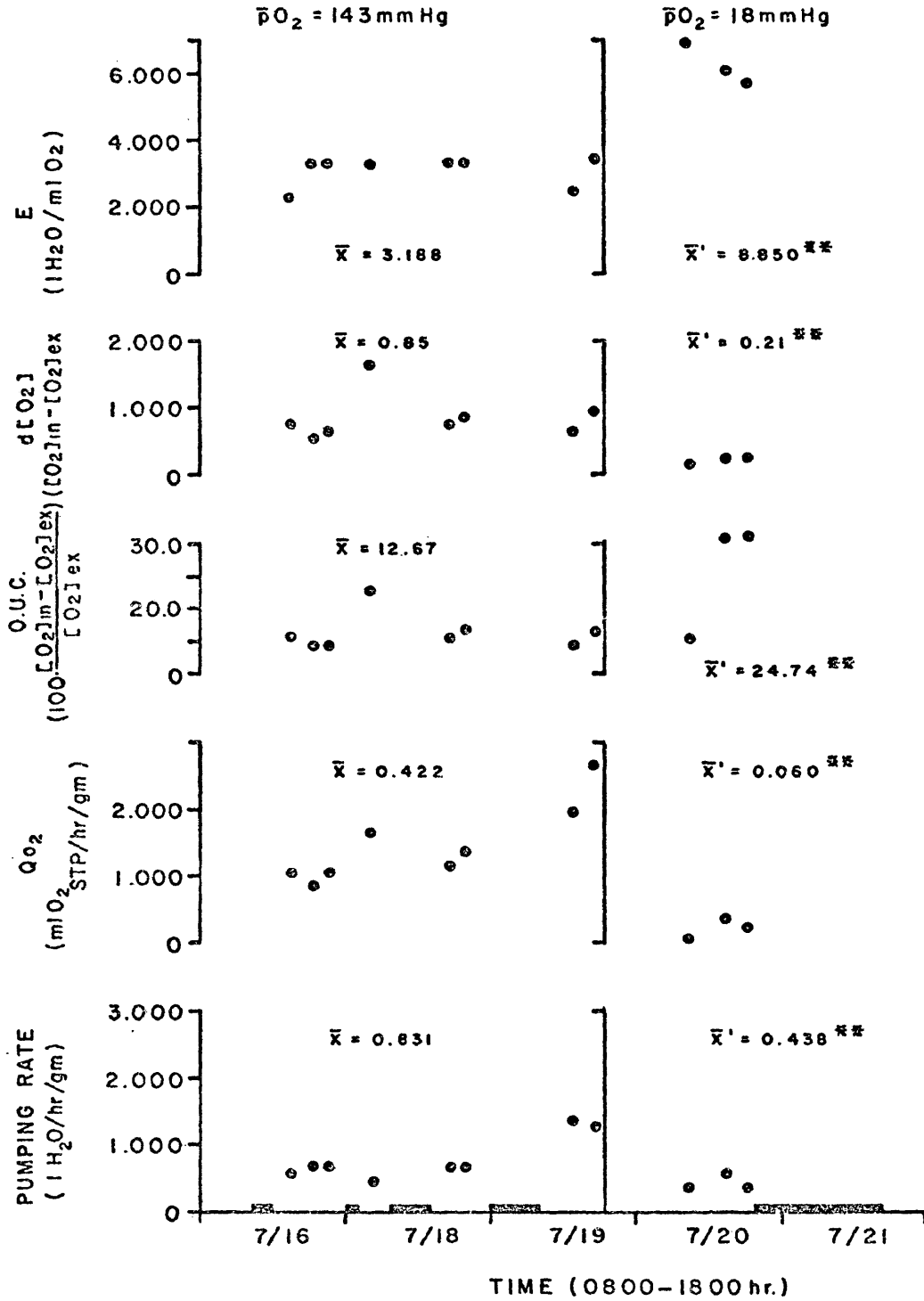
Figure 6

Female Mercenaria displaying loss of respiratory regulation at 18 mm Hg oxygen tension (11% sat)

CLAM 2B - XVIII

SEX : ♀

Length: 73.3 mm Wet tissue wt. 18.02 gm. Dry tissue wt. 3.17 gm.



work on bivalve facultative anaerobiosis (Hochachka, Fields and Mustufa, 1973; Simpson and Awapara, 1966) indicated bivalve respiration may continue to supply the animal with energy by a unique pattern of anaerobic carbohydrate metabolism. This may explain why in other investigations carried out in this laboratory, small male and female Mercenaria (< 1.0 g dry wt) were still alive after two weeks' exposure to oxygen tensions below 18 mm Hg (12% sat.).

C. Mode of Regulation

Oxygen consumption of Mercenaria remained constant at oxygen tensions above P_c . The first mode of regulation involves maintenance of both the pumping rate and oxygen utilization at a relatively constant value at oxygen tensions above P_c . In Hamwi's (1969) study, Mercenaria, subjected to rapid fluctuations in oxygen tension, had this mode of regulation. Crassostrea virginica also maintained a stable oxygen consumption down to 40-50 mm Hg. by this same mode of regulation (Galtsoff and Whipple, 1931). In addition, the present study found that Mercenaria also displayed a second mode of regulation involving a reduction in pumping rate coupled with an increase in the oxygen utilization. This mode of regulation has not been previously reported in the literature.

An anomalous third mode of regulation was also observed. Here the pumping rate increased, but the oxygen utilization showed no significant decline as would be predicted from the

theoretical model presented in the introduction of this paper. However, in all cases where this third mode was evident, the oxygen utilization was much more variable than in the other two modes. Furthermore, examination of the oxygen utilization data in these cases revealed that the trend was certainly toward a smaller value of oxygen utilization at lower oxygen tensions (Fig. 4). However, the trend was not significant during the time of exposure to low oxygen. Thus this particular mode of regulation might take more than 48 hours to establish itself. Mytilus perna L. displayed this third mode of regulation after a short exposure time at reduced oxygen tensions (Bayne, 1967). Bayne (1971b) suggested that regulation of oxygen consumption in Mytilus at reduced oxygen tension is based on the control of the ventilation: perfusion ratio, a ratio of the pumping rate to the frequency and amplitude of heart beat.

The percentage of oxygen removed from the water by the clam increased with decreasing oxygen tension in all three modes of regulation. However, this does not necessarily mean an increase in the "extraction efficiency" of the gill in removing oxygen from the water. Recall the oxygen utilization coefficient is the ratio of oxygen removed (ie. oxygen utilization) divided by the oxygen available ($[O_2]$ in) expressed as a percentage. In the first mode of regulation the amount of oxygen removed, the oxygen utilization, remains unchanged in declining oxygen tension,

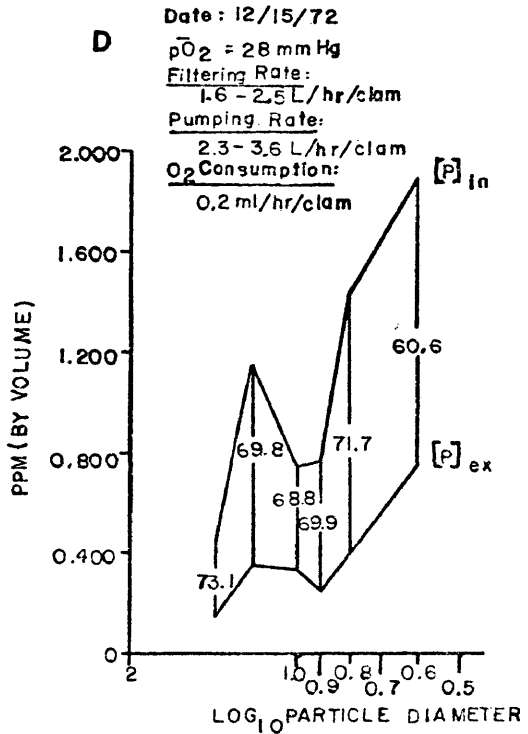
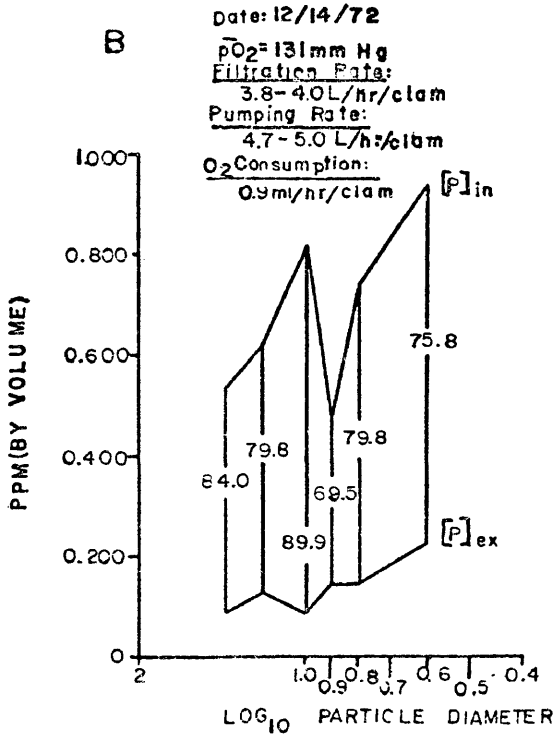
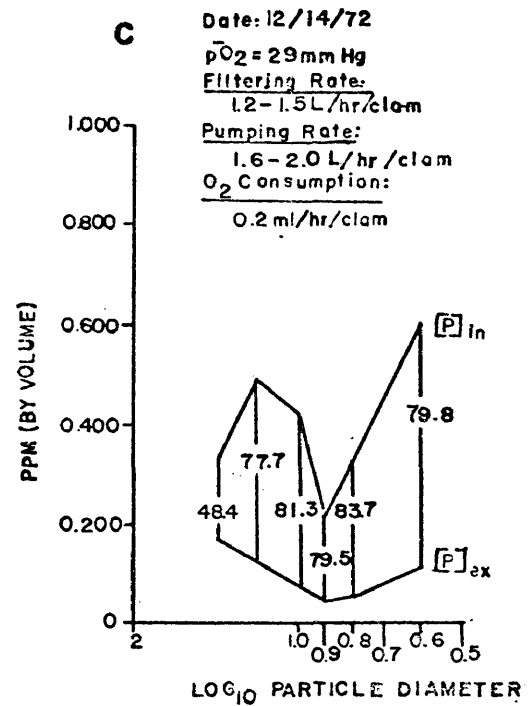
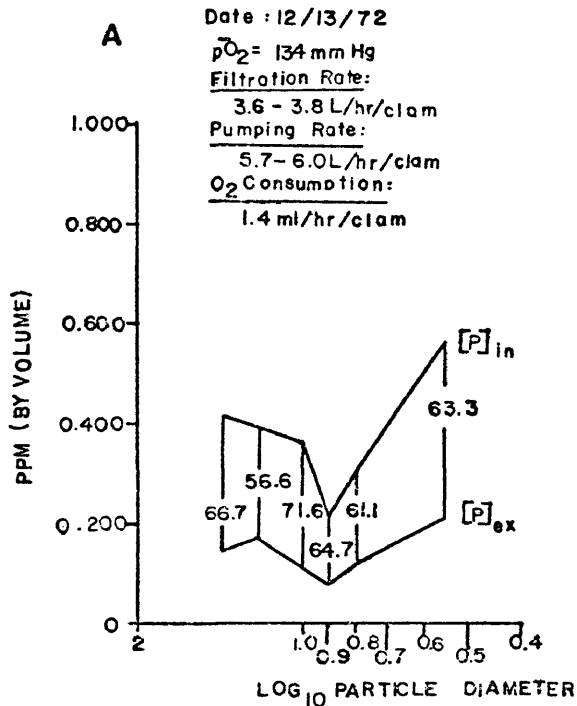
Figure 7 (A-D)

The effect of oxygen tension below P_c on the filtration efficiency of Mercenaria

P_{in} Concentration of particles (3-20 μ) entering the animal.

P_{ex} Concentration of particles (3-20 μ) after filtration by the gills.

The numbers between P_{in} and P_{ex} give the percent removal of a given particle size. The mean filtration efficiency is the average of these numbers.



but the oxygen available is less at low oxygen tensions; therefore, the O.U.C. increased in value as the oxygen level declined. In the second mode, the oxygen utilization increased as the oxygen available decreased resulting in an increase in the value of O.U.C. In the third mode, the oxygen utilization decreased, but the O.U.C. increased in declining oxygen tension because the oxygen utilization and oxygen available were not decreasing proportionately.

The point to be made is that the O.U.C. is not only a function of the bivalve's respiration in declining oxygen, expressed here as the oxygen utilization, but its value is also a function of the declining oxygen tension, the denominator in the O.U.C. ratio. Declining oxygen tension can be brought about by many other factors in addition to bivalve respiration. Interpretation of O.U.C. in declining oxygen tensions can thus lead to questionable conclusions. For example, several authors (Hazelhoff, 1938; Bayne, 1967, 1971b) have used the O.U.C. as a measure of the gill's "extraction efficiency" in declining oxygen tension. I believe, the parameter E (efficiency) which is the amount of water pumped to gain one milliliter of oxygen is more accurate indicator of the gill's oxygen "extraction efficiency". As an example, Bayne (1967) indicated the gill's "extraction efficiency" (O.U.C.) of Mytilus perna L. is unchanged over all oxygen tensions above the animal's P_c . In order for this to be true, the mussel's oxygen utilization must have decreased

proportionately with decreased oxygen tension. The decrease in oxygen utilization was compensated by an increase in the mussel's pumping rate to give a constant oxygen consumption. Recall this is the third mode of regulation available to bivalves. Now if the pumping rate is increased and the oxygen consumption remained unchanged then the amount of water pumped to gain one milliliter of oxygen increased, indicating a decrease in the efficiency of the gill to extract oxygen. Thus, in actuality, the capacity of Mytilus's gill to remove oxygen decreased in declining oxygen tension.

As can be seen in the preceding discussion, the efficiency in removing a milliliter of oxygen from solution depends on the magnitude of the pumping rate because the oxygen consumption, by definition, remains unchanged in all modes of regulation. Thus the efficiency in the second mode of regulation must increase because the pumping rate decreased. Efficiency in the first mode of regulation is unchanged because pumping rate remained unchanged at all oxygen tensions.

Two sources in the literature have reported the efficiency of Mercenaria in removing oxygen from the water is independent of pumping rate.

Hamwi and Haskin (1969) reported a linear relationship between pumping rate and oxygen consumption. Besides indicating a constant efficiency (E) regardless of pumping rate, these findings predict a decline in oxygen consumption whenever their

is a reduction in pumping rate. Hamwi and Haskin (1969) used linear regression analysis to describe this relationship between oxygen consumption and pumping rate. The graphs and equations of Hamwi and Haskin are invalid because they plotted a variable (pumping rate) against a function of that variable (oxygen consumption). They measured pumping rate and oxygen utilization, but they computed the oxygen consumption as a product of these two variables. Pumping rate and oxygen consumption must be independently determined before they can be analyzed by linear regression analysis.

At all oxygen tensions above P_c the clam's pumping rate and oxygen consumption did decrease together as the animal begins to close. Upon opening, the clams pumping rate and oxygen consumption would increase together. However, the relationship between oxygen consumption and pumping rate during opening and closing was not linear, but roughly hyperbolic: that is oxygen consumption increased rapidly with the initiation of the pumping apparatus, but soon reached a plateau. Thus, most of the time the clam was open and oxygen consumption remained stable despite fluctuations in the pumping rate. Similar stable oxygen consumption has been reported in resting specimens of Pecten irradians. (Van Dam, 1954) and Crassostrea virginica (Galtsoff, 1964).

Loveland and Chu (1969) derived a mathematical formula relating pumping rate to oxygen consumption:

$$m = \frac{1}{dp} \frac{Mdp}{dt} \frac{wt}{wt} = \frac{1}{dp} Q_{O_2} \text{ wt}$$

where m is pumping rate, M is volume pumped, dp is absolute oxygen utilization (ie., $d [O_2]$) and Q_{O_2} is weight (wt) - specific oxygen consumption. They obtained Mdp or total oxygen removed, gasometrically and dp polarographically. Knowing weight, they computed pumping rate from the above formula. Their results indicated that at constant oxygen concentration, temperature and salinity, the volume of water pumped to remove one milliliter of oxygen (E) was constant and independent of pumping rate. The experiments of Loveland and Chu (op. cit.) were performed at a constant O_2 concentration of 5.0 ml/l. The present study indicated a different pattern exist under fluctuating environmental conditions and declining oxygen tensions. The mean efficiency did remain constant, regardless of pumping rate, in the first mode of respiratory regulation because the average pumping rate did not change during the decline in oxygen tension. However, in the other two modes of regulation, the mean efficiency depended on the pumping rate in declining oxygen tension.

D. Filtration Efficiency

In this study Mercenaria showed a high (60-97%) filtration efficiency for particles above 3μ in diameter. This has also been recorded for Mercenaria by Smith (1957), Rice and Smith (1958) and Walne (1972), and for Crassostrea virginica by Haven

and Morales-Alamo (1970). Also, the present study verified that the filtration efficiency was independent of the pumping rate and filtration rate as reported by Smith (1957).

Contrary to this, Dral (1967) found Mytilus edulis filtered particles more efficiently at lower filtration rates. Jorgenson (1966) has attributed much of the differences in filtration efficiency and rates between bivalves to differences in technique. The differences in filtration efficiency among bivalves may, however, reflect true differences based on species morphology. For example, Tenore and Dunstan (1973) found the (filtering) rates of Mytilus was greater than Crassostrea and Mercenaria. The same measuring technique was used for all three bivalves. The results would indicate the gills of Mytilus are more efficient in retaining particles because the flow of water past all three animals was the same.

In the only other study of filtration rate as a function of declining oxygen tension, Mytilus edulis increased its filtration rate slightly down to a P_c of 80-100 mm Hg pO_2 (Bayne, 1971b). With the technique used, this would indicate the filtration efficiency increased slightly at the oxygen tension declined.

The observed independence of Mercenaria's filtration efficiency from its pumping rate can be explained in the following manner. Dral (1967) and Moore (1971) present conclusive evidence the lateral-frontal cilia control the filtration efficiency of the gill by forming a fine mesh over the gill ostia. Galtsoff (1964) has shown the synchronized beats of the lateral cilia are the major factor in producing the water flow

(pumping rate). Obviously, the size of the animal, temperature, salinity, turbidity, pH, etc, may influence the number and rate of beat of the lateral cilia. The lateral-frontal cilia, adductor mussel, gill muscles and ostia and the mantle all may contribute to the pumping rate, but under normal conditions their support is small. For example, the ciliary currents on the mantle are mainly used for cleansing and for rejection of deposited material (Hillman, 1964).

These findings indicate the pumping rate is a function of lateral cilia movement, but the filtration efficiency is a function of the structure of the lateral-frontal cilia. Therefore, no matter what the speed of water through the lateral-frontal cilia mesh, the mesh structure of these cilia is going to determine the particle retention efficiency. The amount of material swept from the water per unit time (filtration rate) will depend on both the amount of water pumped through the mesh (pumping rate) and the filtration efficiency.

Although the filtration efficiency for particles in the size range below 3 μ may be very low, this low percentage does represent a sizeable volume of potential food for the bivalve, because natural particles were numerically most abundant in this size range. In fact, even though the percentage removed in this size range is small, the volume this percentage represents may exceed the total volume removed over the size range 3-20 μ . For example, in Crassostrea virginica, the combined volume

removed between 1.0-4.0 μ represents 52% of the total removed between 1.0 and 12.0 μ . The 4-7 μ fraction represented 34.5% of the total (Haven and Morales-Alamo, 1970). However, the nutritional value of these size particles is uncertain. Marine bacteria are within the 1-3 μ size range, but Davis (1953) tested 13 species of marine bacteria and none were utilized by larvae of Crassostrea.

D. Environmental variables, body weight and oxygen utilization

The unexplained variation in R for the multiple linear regression is probably due to seasonal variation; diurnal cycles, influence of the tide and probably to a large degree, random variation.

1. Salinity

Castagna and Chanley, (1973) determined experimentally that the minimum salinity the Chesapeake Bay Mercenaria tolerate is 12.5‰. In the present study, a salinity above 14‰ did not affect the clam's capacity to regulate in declining oxygen tensions. The bivalves Geloina ceylonica, Anadara granosa and Mytilus edulis likewise did not lose their capacity to regulate in declining salinities until their salinity tolerance limit was appropriate (Bayne, 1973). However, as the salinity declined to Mercenaria's lower tolerance limit (12.5⁰/‰), the animals closed for much longer periods of time in low oxygen tension water compared to controls at high O₂ tension (Table 6).

2. Temperature

The results indicate oxygen consumption and pumping rate of Mercenaria were influenced little by the observed temperature variation over the range of oxygen tensions tested. At high oxygen tensions Hamwi (1969) found no change in the pumping rate of Mercenaria between 12-18°C. and optimum conditions between 20-25°C. Feng (1968) found with increase in temperature, the greatest increase in clam activity occurred between 4-8°C., with no further significant increase between 8-22°C. I believe the clams capacity to regulate at low oxygen tensions was not affected by the observed temperature variation range because this range was well within the temperature limits of Mercenaria. Hamwi (1969) found the temperature limits for the clam's pumping rate were 6° and 32°C. at favorable salinities; and high oxygen tensions, oxygen consumption did not decline until temperatures exceeded 26°C.

3. Turbidity and food level.

The observed levels of turbidity and food had no effect on the clam's pumping rate or oxygen consumption at either high or low oxygen tensions. Again, the observed levels were well within the clam's tolerance.

Mercenaria are highly tolerant of silt concentrations below 1000 mg/l. (Hamwi, 1969). The average turbidity in this study was below 100 mg/L. The natural food content of the water

was low and generally did not influence the clam. However, during the course of these experiments, a red tide (Cochladium hetrolabortum) occurred for several weeks in the late summer. This high level of algae seriously weakened the clam's capacity to regulate at low oxygen tensions. A possible reason for this loss of regulation is that the decay of the large concentrations of dead cells produced by-products which are more toxic at low oxygen tensions. Hydrogen sulfide could occasionally be smelled in the experimental trough, supporting this hypothesis: Another explanation might be that the heavy cell concentrations clogged the animal's gills.

4. Body weight and Oxygen utilization.

As previously indicated, the capacity of Mercenaria to regulate is dependent on size and sex. This was again indicated in the MLR analysis on the two sexes. This study confirmed Hamwi's (1969) report that male and female oxygen consumption and pumping rate increased with increasing weight at high O_2 tensions. I found this relationship continued to hold for females down to an oxygen tension of 40 mm Hg. Male oxygen consumption showed no dependence on weight at 40 mm Hg. oxygen tension. This breakdown in the relationship between oxygen consumption and weight is probably correlated with the disappearance of respiratory regulation in the male at oxygen tensions below the P_c of 40 mm Hg.

The negative partial regression coefficient for the regression of pumping rate on oxygen utilization indicates that slower the pumping rate, and thus the longer the water takes to pass over the gills, the greater will be the extraction of oxygen from the water. Sexual differences were again observed in this relationship between pumping rate and oxygen utilization at 40 mm Hg oxygen tension. In both sexes there was a clockwise rotation of the slope of the line to a more negative value; however, the female regression coefficient indicated a much greater rotation of the slope of the line than the male at 40 mm Hg. oxygen tension. This rotation of the slope of the line by both sexes indicates that at low oxygen tensions a greater reduction in pumping rate is necessary to gain an increase in the amount of oxygen extracted from the water than is the case at high oxygen tensions. This required reduction in pumping rate is greater for the female than the male at 40 mm Hg. oxygen tension. It is interesting to note that the majority of females tested the pumping rate either remained unchanged or increased when the oxygen was lowered to a level above P_c (Tables 1-5). The two exceptions were a female that had spawned (Table 1) and a large female (5.09g dry weight) exposed to a low oxygen tension of 80 mm Hg. (Table 5).

The male could get a greater amount of oxygen from the water per unit reduction in its pumping rate at low oxygen tensions, but apparently below P_c this increase in the oxygen

utilization was not enough to compensate for the reduced pumping rate. Consequently, below 80 mm Hg. oxygen tension the oxygen consumption, a product of the pumping rate and oxygen utilization, steadily declined and regulation was no longer evident.

Summary

1. In the laboratory Mercenaria mercenaria from the York River, Virginia were exposed to various low oxygen tensions under fluctuating environmental conditions of temperature, salinity, turbidity and food level. The effects of these low oxygen tensions on the clam's pumping rate, oxygen consumption and filtration efficiency were recorded and compared to similar measurements taken on the same clam at high oxygen tensions.
2. Gravid females, ranging in dry tissue weight from 1.20 - 5.03 g, regulated their oxygen consumption down to an oxygen tension of 40 mm Hg. Male clams, with gametes, whose dry tissue weight was below 3.0 g could regulate their oxygen consumption down to a critical oxygen tension of 80 mm Hg. Evidence from a single male weighing over 3.0 dry weight indicated large males had a critical oxygen tension of 40 mm Hg.
3. Regulation of oxygen consumption above the critical oxygen tension was accomplished by three different modes, involving the pumping rate and oxygen utilization. In the most consistent mode of regulation, the pumping rate and oxygen utilization remained constant such that the product of these two variables, the oxygen consumption, remained

unchanged. The other two modes of regulation involved an increase or decrease in the pumping rate compensated by a decrease or increase in the oxygen utilization, such that the oxygen consumption remained constant.

4. At oxygen tensions below the critical oxygen tensions, oxygen consumption, pumping rate and filtration rate declined to very low values, but the clam's capacity to filter particles from the water was not affected at least for 48 hours.
5. The efficiency with which the gill removes particles in the size range of 3-20 μ was consistently high (60-97% retention) and was found to be independent of the oxygen consumption, pumping rate and oxygen tensions tested. A review of the literature support the hypothesis that filtration efficiency is dependent only on the structure of the gill's lateral-frontal cilia.
6. Using multiple linear regression analysis, the observed values of temperature, salinity, turbidity and food level, were shown to have little effect on Mercenaria's pumping rate or oxygen consumption at oxygen tensions above 40 mm Hg.
7. Below a critical level of 80 mm Hg O_2 tension, male oxygen consumption and pumping rate did not increase with increasing

size of the clam. Female oxygen consumption and pumping rate did increase with size down to an oxygen tension of 40 mm Hg.

8. Multiple linear regression analysis indicated that female oxygen utilization could not be increased in large amounts by reduction in pumping rate at 40 mm Hg oxygen tension. This conclusion is supported by the observation that most females maintained or increased their pumping rate in declining oxygen. Males, however, could gain more oxygen by a reduction in pumping rate, but increase in oxygen utilization was not enough to maintain a constant oxygen consumption at 40 mm Hg.

Tables 1-8

The Effect of declining oxygen tensions on male and female
Mercenaria: pooled data.

- N, Total number of animals tested in a given weight class.
- n, Number of animals tested at each oxygen level.
- d.f. Degrees of freedom in the analysis of variance (ANOVA).
- Tb. Turbidity (milligrams particulate matter/liter).
- chl"A". A measure of the food content of the water (ug"A"/L.).
- SPR. Weight specific pumping rate
- Q_{O_2} . Weight specific Oxygen consumption
- O.U.C. Oxygen Utilization Coefficient
- $d[O_2]$ Oxygen utilization
- E. Efficiency of gill in removing oxygen
- * Significant differences between means (P 0.05)
- ** High significant differences between means (P 0.01)

Table 1

The effect of low oxygen levels on female Mercenaria
(dry tissue weight 1.00-1.99g): pooled data

Table 1

Weight class: 1.00-1.99 g (dry tissue wt.)

Sex: Female

N = 11

n = 3

Mean wt. 1.74 g

d.f. (1,52)

	$\overline{pO_2} = 149$	$\overline{pO_2} = 77$		Environmental Variables
	$\bar{x} \pm t .05 \frac{S}{\bar{x}}$	$\bar{x} \pm t .05 \frac{S}{\bar{x}}$	F	\bar{x} Range
SPR	2.046 \pm 0.389	1.749 \pm 0.366	0.84	15.27 12.19 - 18.84
QO ₂	0.835 \pm 0.143	0.804 \pm 0.037	0.09	25.2 22.9 - 27.5
O.b.c.	9.25 \pm 1.25	23.61 \pm 6.29	61.58**	32.3 3.5 - 50.5
d [O ₂]	0.648 \pm 0.082	0.820 \pm 0.118	4.86*	17.3 5.7 - 43.0
E	2.518 \pm 0.248	1.801 \pm 0.239	14.45**	

n = 1

Weight 1.21 g

d.f. (1,13)

	$\overline{pO_2} = 148$	$\overline{pO_2} = 38$		Environmental Variables
	$\bar{x} \pm t .05 \frac{S}{\bar{x}}$	$\bar{x} \pm t .05 \frac{S}{\bar{x}}$	F	\bar{x} Range
SPR	2.338 \pm 0.857	3.006 \pm 0.430	7.86*	15.06 13.93 - 16.94
QO ₂	1.110 \pm 0.391	0.905 \pm 0.211	1.35	24.2 23.0 - 26.0
O.b.c.	12.54 \pm 7.46	28.94 \pm 6.96	15.65**	34.2 26.5 - 48.0
d [O ₂]	0.887 \pm 0.531	0.511 \pm 0.128	3.20	13.54 5.6 - 18.0
E	2.389 \pm 1.163	3.476 \pm 0.818	3.14	

Table 1 (cont)

Experimental

n = 1 (spawned)
Weight 1.54
d.f. (1,11)

	$\overline{pO_2} = 141$	$\overline{pO_2} = 39$		Environmental Variables
	$\bar{x} \pm t .05 \frac{S}{x}$	$\bar{x} \pm t .05 \frac{S}{x}$	F	\bar{x} Range
SPR	1.595 \pm 0.391	0.561 \pm 0.127	68.42**	15.43 14.07 - 16.11
QO ₂	0.961 \pm 0.090	0.252 \pm 0.125	126.42**	24.6 23.8 - 25.8
O.U.C.	15.48 \pm 5.56	36.99 \pm 9.79	27.57**	30.8 18.0 - 47.5
d [O ₂]	1.03 \pm 0.38	0.68 \pm 0.21	2.99	9.4 1.5 - 12.5
E	1.654 \pm 0.341	2.366 \pm 0.667	7.39*	

Control

n=6
Mean Wt. 1.67 g
d.f. (1,48)

	$\overline{pO_2} = 146$	$\overline{pO_2} = 145$		Environmental Variables
	$\bar{x} \pm t .05 \frac{S}{x}$	$\bar{x} \pm t .05 \frac{S}{x}$	F	\bar{x} Range
SPR	2.371 \pm 0.336	2.254 \pm 0.406	0.21	15.16 12.5 - 18.84
QO ₂	1.083 \pm 0.141	0.810 \pm 0.156	6.71*	25.0 23.3 - 27.3
O.U.C.	10.86 \pm 1.15	8.53 \pm 1.77	6.26*	32.7 3.5 - 50.5
d [O ₂]	0.74 \pm 0.07	0.57 \pm 0.12	7.17*	12.6 2.2 - 32.3
E	2.222 \pm 0.276	3.098 \pm 0.646	8.71*	

Table 2

The effect of low oxygen levels on female Mercenaria
(dry tissue weight 2.00-2.99 g): pooled data

Table 2

Weight Class: 2.00-2.99 g (dry tissue wt.)
 Sex: Female
 N = 8

Experimental

n = 1
 Weight: 2.28 g
 d.f. (1,8)

$\overline{pO_2} = 144$
 $x \pm t .05 \frac{S}{x}$

SPR	0.980 ± 0.320
QO ₂	0.597 ± 0.146
O.U.C.	15.01 ± 10.03
d [O ₂]	1.030 ± 0.680
E	1.694 ± 0.832

$\overline{pO_2} = 78$
 $x \pm t .05 \frac{S}{x}$

	1.378 ± 0.144
	0.591 ± 0.111
	18.07 ± 1.72
	0.67 ± 0.07
	2.360 ± 0.350

Environmental Variables

	\bar{x}	Range
S ^o /oo	15.21	13.75 - 15.82
T ^o C	24.9	23.0 - 26.0
Tb.	32.8	18.5 - 55.0
chl. "A"	13.0	5.4 - 21.6

F

19.12**
0.01
1.70
4.57

n = 5
 Mean wt. 2.52g
 d.f. (1,36)

$\overline{pO_2} = 143$
 $x \pm t .05 \frac{S}{x}$

SPR	1.472 ± 0.169
QO ₂	0.644 ± 0.131
O.U.C.	10.17 ± 1.37
d [O ₂]	0.07 ± 0.11
E	2.603 ± 0.532

$\overline{pO_2} = 40$
 $x \pm t .05 \frac{S}{x}$

	1.451 ± 0.278
	0.491 ± 0.052
	29.54 ± 4.66
	0.55 ± 0.07
	2.987 ± 0.433

Environmental Variables

	\bar{x}	Range
S ^o /oo	15.60	12.50 - 19.42
T ^o C	24.3	22.0 - 25.9
Tb.	42.7	20.0 - 121.5
chl. "A"	9.71	1.5 - 20.2

F

0.02
2.74
92.66
3.70
1.00

Table 2 (cont)

Control

n = 2
 Mean Wt. 2.68 g
 d.f. (1,16)

	$\overline{pO_2} = 154$	$\overline{pO_2} = 138$			
	$\bar{x} \pm t .05 \frac{S}{\bar{x}}$	$\bar{x} \pm t .05 \frac{S}{\bar{x}}$	F	x	Range
SPR	0.268 ± 0.083	0.183 ± 0.011	5.16*	15.01	13.75 - 16.08
QO ₂	0.431 ± 0.212	0.329 ± 0.119	0.19	24.6	22.2 - 26.0
O ₂ C.	36.83 ± 10.39	41.16 ± 5.93	3.95	32.9	18.5 - 55.0
d [O ₂]	2.688 ± 0.772	2.068 ± 3.493	1.24	13.3	5.4 - 21.6
E	0.604 ± 0.171	0.572 ± 0.177	1.56		
				S ^o /oo	
				T ^o C	
				Tb.	
				chl. "A"	

Table 3

The effect of low oxygen levels on female Mercenaria
(dry tissue weight 3.00-3.99g): pooled data

Table 3

Weight class: 3.0-3.99 g (dry tissue wt)
 Sex: Female
 N = 8

n = 2
 Mean wt. 3.60g
 d.f. (1,28)

Experimental

	$\overline{pO_2} = 138$		$\overline{pO_2} = 79$		F	Environmental Variables
	$\bar{x} \pm t$	$.05 \frac{S}{\bar{x}}$	$\bar{x} \pm t$	$.05 \frac{S}{\bar{x}}$		
SPR	1.218	± 0.306	0.985	± 0.078	1.10	S ^o /oo
QO ₂	0.892	± 0.129	0.676	± 0.134	6.06*	T ^o C
O.U.C.	21.08	± 5.17	35.87	± 5.28	18.63**	Tb.
d [O ₂]	1.334	± 0.343	1.235	± 0.201	0.24	chl "A"
E	1.344	± 0.318	1.316	± 0.245	0.02	

n = 1
 Weight 3.90g
 d.f. (1,15)

	$\overline{pO_2} = 124$		$\overline{pO_2} = 37$		F	Environmental Variables
	$\bar{x} \pm t$	$.05 \frac{S}{\bar{x}}$	$\bar{x} \pm t$	$.05 \frac{S}{\bar{x}}$		
SPR	1.946	± 0.196	1.714	± 0.192	3.059	S ^o /oo
QO ₂	0.565	± 0.149	0.487	± 0.115	1.008	T ^o C
O.U.C.	7.24	± 1.55	24.53	± 4.28	83.56	Tb.
d [O ₂]	0.442	± 0.097	0.440	± 0.079	0.02	chl "A"
E	3.841	± 1.325	3.828	± 1.105	0.003	

Table 3 (cont)

Weight class: 3.0-3.99 g (dry tissue wt)
 Sex: Female
 N = 8

Experimental (cont)

n = 2 (red tide)
 Mean wt. 3.55 g
 d.f. (1,26)

	$\overline{pO_2} = 160$	$\overline{pO_2} = 42$			
	$\bar{x} \pm t .05 S_{\bar{x}}$	$\bar{x} \pm t .05 S_{\bar{x}}$	F	Environmental Variables	Range
SPR	0.833 \pm 0.166	0.927 \pm 0.155	0.79	S ^o /oo	19.60 - 20.25
QO ₂	0.601 \pm 0.074	0.426 \pm 0.061	14.78**	T ^o C	25.0 - 26.1
O.D.C.	17.56 \pm 3.66	41.15 \pm 4.71	82.88**	Tb.	6.5 - 77.5
d [O ₂]	1.228 \pm 0.240	0.756 \pm 0.074	16.39**	chl "A"	5.3 - 43.0
E	1.410 \pm 0.269	2.326 \pm 0.467	13.46**		

Control

n = 3
 Mean wt. 3.55 g
 d.f. (1,30)

	$\overline{pO_2} = 126$	$\overline{pO_2} = 129$			
	$\bar{x} \pm t .05 S_{\bar{x}}$	$\bar{x} \pm t .05 S_{\bar{x}}$	F	Environmental Variables	Range
SPR	2.134 \pm 0.342	2.280 \pm 0.352	0.399	S ^o /oo	14.53 - 19.42
QO ₂	0.506 \pm 0.065	0.612 \pm 0.134	2.480	T ^o C	19.0 - 24.9
O.D.C.	6.20 \pm 1.13	6.38 \pm 1.37	0.453	Tb.	31.0 - 121.5
d [O ₂]	0.379 \pm 0.051	0.421 \pm 0.079	0.953	chl "A"	3.7 - 14.0
E	4.220 \pm 0.620	3.757 \pm 0.547	1.389		

Table 4

The effect of low oxygen levels on female Mercenaria
(dry tissue weight 4.00-4.99 g): pooled data

Table 4

Weight class: 4.00-4.99g (dry tissue wt)
 Sex: Female
 N = 8

Experimental

n = 1
 Weight 4.68g.
 d.f. (1,13)

	$\overline{PO_2} = 137$	$\overline{PO_2} = 72$			Environmental Variables
	$\bar{x} \pm t .05 \frac{s}{\bar{x}}$	$\bar{x} \pm t .05 \frac{s}{\bar{x}}$	F		\bar{x} Range
SPR	1.310 \pm 0.247	1.143 \pm 0.286	1.095	S ^o /oo	19.74 19.31 - 20.21
QO ₂	0.506 \pm 0.138	0.604 \pm 0.125	1.654	T ^o C	25.6 24.9 - 26.1
O.D.C.	10.08 \pm 3.81	31.47 \pm 7.91	25.67**	Tb.	24.6 7.0 - 61.5
d [O ₂]	0.63 \pm 0.24	0.92 \pm 0.31	3.16	chl "A"	8.3 3.4 - 17.7
Z	2.844 \pm 1.094	2.145 \pm 1.155	1.086		

n = 4
 Mean wt. 4.55 g
 d.f. (1,70)

	$\overline{PO_2} = 124$	$\overline{PO_2} = 39$			Environmental Variables
	$\bar{x} \pm t .05 \frac{s}{\bar{x}}$	$\bar{x} \pm t .05 \frac{s}{\bar{x}}$	F		\bar{x} Range
SPR	1.823 \pm 0.144	1.859 \pm 0.140	0.13	S ^o /oo	16.66 14.53 - 19.38
QO ₂	0.504 \pm 0.070	0.517 \pm 0.050	0.09	T ^o C	21.3 19.0 - 24.2
O.D.C.	7.20 \pm 0.97	22.78 \pm 2.75	60.75**	Tb.	56.6 31.0 - 121.5
d [O ₂]	0.42 \pm 0.05	0.45 \pm 0.06	0.65	chl "A"	7.2 3.7 - 15.8
Z	3.830 \pm 0.474	3.730 \pm 0.460	0.09		

Table 4 (con't)

Control

n = 3
 Mean wt. 4.27g
 d.f. (1,58)

	$\overline{pO_2} = 143$		$\overline{pO_2} = 135$		F	Environmental Variables
	$\bar{x} \pm t .05 \frac{S}{\sqrt{x}}$	$\bar{x} \pm t .05 \frac{S}{\sqrt{x}}$	$\bar{x} \pm t .05 \frac{S}{\sqrt{x}}$	$\bar{x} \pm t .05 \frac{S}{\sqrt{x}}$		
SPR	0.956 ± 0.115	0.892 - 0.192	0.388	18.16	14.53 - 20.25	
QO ₂	0.520 ± 0.057	0.513 - 0.055	0.03	24.1	19.0 - 26.7	
O.D.C.	14.92 ± 2.506	17.32 - 3.17	0.250	33.25	7.0 - 87.0	
d [O ₂]	0.99 ± 0.16	1.08 - 0.19	0.55	10.64	3.4 - 43.0	
E	2.045 ± 0.398	1.652 - 0.311	2.085			

Table 5

The effect of low oxygen levels on female Mercenaria
(dry tissue weight 5.00-5.99 g): pooled data

Table 6

The effect of low oxygen levels on male Mercenaria
(dry tissue weight 1.00-1.99 g): pooled data

Table 6 (cont)

Control

n = 4
 Mean Wt. 1.58 g
 d.f. (1,46)

	$\overline{pO_2} = 153$	$\overline{pO_2} = 154$				
	$\bar{x} \pm t .05 \frac{S}{\sqrt{x}}$	$\bar{x} \pm t .05 \frac{S}{\sqrt{x}}$	F	\bar{x}	Range	Environmental Variables
SPR	2.065 \pm 0.358	1.638 \pm 0.440	2.4	14.23	12.31 - 15.83	
QO ₂	0.846 \pm 0.115	0.877 \pm 0.066	0.2	24.9	22.9 - 26.7	
O.U.C.	9.89 \pm 0.70	13.79 \pm 0.81	6.7*	34.8	19.5 - 52.0	
d [O ₂]	0.74 \pm 0.03	1.037 \pm 0.213	6.8*	10.9	1.5 - 24.0	
E	2.281 \pm 0.337	1.195 \pm 0.191	23.3**			
						S ^o /oo T ^o C Tb. chl. "A"

Table 7

The effect of low oxygen levels on male Mercenaria
(dry tissue weight 2.00-2.99g): pooled data

Table 7

Weight class: 2.00-2.99g (dry tissue wt)

Sex: Male

N = 10

Experimental.

n = 2

Mean wt. 2.39 g

d.f. (1,35)

$$\overline{pO_2} = 148$$

$$\bar{x} \pm t .05 \frac{S}{\bar{x}}$$

SPR	1.321 ± 0.561
QO ₂	0.658 ± 0.126
O.U.C.	15.17 ± 4.50
d [O ₂]	1.084 ± 0.325
E	1.915 ± 0.724

$$\overline{pO_2} = 77$$

$$\bar{x} \pm t .05 \frac{S}{\bar{x}}$$

	1.496 ± 0.503
	0.829 ± 0.154
	28.21 ± 6.16
	1.032 ± 0.229
	1.722 ± 0.416

Environmental Variables

	\bar{x}	Range
S ^o /oo	15.39	13.75 - 18.84
T ^o C	24.6	22.2 - 26.0
Tb.	34.2	18.5 - 55.0
chl. "A"	13.2	5.4 - 21.6

n = 5

Mean wt. 2.65g

d.f. (1,61)

$$\overline{pO_2} = 147$$

SPR	1.721 ± 0.266
QO ₂	0.829 ± 0.121
O.U.C.	11.55 ± 1.57
d [O ₂]	0.79 ± 0.10
E	2.227 ± 0.273

$$\overline{pO_2} = 40$$

	1.278 ± 0.253
	0.473 ± 0.079
	35.62 ± 3.76
	0.66 ± 0.07
	2.684 ± 0.318

	\bar{x}	Range
S ^o /oo	16.42	13.80 - 19.20
T ^o C	24.4	22.8 - 26.0
Tb.	39.2	14.5 - 115.5
chl. "A"	10.6	1.5 - 32.3

	6.44**
	23.73**
	57.46**
	4.86*
	5.06*

Table 7 (cont)

n = 3
 Mean wt. 2.38 g
 d.f. (1.36)

	$\overline{pO_2} = 133$		$\overline{pO_2} = 138$		F	Environmental Variables	
	$x \pm t$	$.05 \frac{S}{\bar{x}}$	$x \pm t$	$.05 \frac{S}{\bar{x}}$		\bar{x}	Range
SFR	1.895	± 0.308	1.643	± 0.348	1.58	S°/oo	14.95 - 19.38
QO ₂	0.727	± 0.110	0.615	± 0.100	2.41	T°C	22.2 - 27.0
d [O ₂]	0.70	± 0.18	0.72	± 0.10	0.04	Tb.	14.5 - 121.5
O.U.C.	11.16	± 2.96	11.36	± 3.24	0.01	chl. "A"	3.7 - 18.2
E	3.031	± 0.756	3.250	± 1.263	0.11		

Table 8

The effect of low oxygen levels on male Mercenaria
(dry tissue weight 4.00-4.99g): pooled data

Table 8

Weight class: 4.00-4.99g (dry tissue wt.)

Sex: Male

N = 3

Experimental

n = 1

Weight: 4.16 g

d.f. (1,12)

	$\overline{pO_2} = 124$	$\overline{pO_2} = 37$				
	$x \pm t .05 \frac{s}{x}$	$x \pm .05 \frac{s}{x}$	F	x	Range	Environmental Variables
SPR	1.712 ± 0.277	1.914 ± 0.119	4.84*	15.11	14.53- 16.08	
QO ₂	0.506 ± 0.107	0.580 ± 0.099	1.57	19.3	19.0 - 21.3	
O ₂ d.c.	6.18 ± 1.38	23.82 ± 5.54	76.52**	57.7	31.0 -101.0	
d[O ₂]	0.45 ± 0.09	0.46 ± 0.07	0.04	10.2	5.4 - 13.0	
E	3.278 ± 1.695	3.152 ± 0.440	0.14			

Table 8 (cont)

Control

n = 2
 Mean Weight: 4.11 g.
 d.f. (1,22)

	$\overline{pO_2} = 145$	$\overline{pO_2} = 134$				Environmental Variables
	$\bar{x} \pm t \cdot .05 \frac{S}{\sqrt{x}}$	$\bar{x} \pm t \cdot .05 \frac{S}{\sqrt{x}}$	F	x	Range	
SPR	1.000 \pm 0.154	0.583 \pm 0.136	16.12**	18.73	17.61 - 20.21	S ^o /oo
QO ₂	0.557 \pm 0.065	0.513 \pm 0.106	0.68	25.3	24.9 - 26.7	T ^o C
O ₂ .C.	14.36 \pm 1.96	23.22 \pm 4.18	20.61**	26.3	7.0 - 83.0	Tb.
d [O ₂]	0.92 \pm 0.12	1.42 \pm 0.25	12.76**	10.0	3.4 - 19.7	chl. "A"
E	1.792 \pm 0.261	1.113 \pm 0.138	16.93**			

Table 9

The effect of environmental variables, body weight and oxygen utilization on the oxygen consumption and pumping rate of female Mercenaria as analyzed by multiple linear regression with ANOVA

- R² Multiple correlation coefficient
- d.f. degrees of freedom in ANOVA
- b. partial regression coefficient
- * significant (P 0.05)
- ** high significant (P 0.01)

Table 9

Oxygen Consumption
(ml O₂/hr/clam)
Sex: female

$\overline{pO_2} = 142$ mm Hg

	Range	b	ANOVA
Oxygen Consumption	0.882 - 3.881		R ² 0.098
(X ₁) dry wt.	1.34 - 4.72	b ₁ 0.438**	d.f. (4,137)
(X ₂) T°C	18.7 - 27.3	b ₂ 0.151	F 3.71*
(X ₃) S°/oo	13.34 - 20.03	b ₃ -0.107	
(X ₄) pO ₂	111 - 163	b ₄ -0.009	

$\overline{pO_2} = 38$ mm Hg

	Range	b	ANOVA
O ₂ Consumption	0.832 - 4.501		R ² 0.52
(X ₁) dry wt.	1.21 - 5.03	b ₁ 0.574**	d.f. (4,58)
(X ₂) T°C	18.7 - 26.0	b ₂ 0.050	F 15.67**
(X ₃) S°/oo	13.93 - 18.50	b ₃ -0.205*	
(X ₄) pO ₂	33 - 46	b ₄ 0.008	

Table 9 (cont)

Pumping Rate
($l_{H_2O}/hr/clam$)

Sex: Female

$\overline{pO_2} = 142$ mm Hg

Range

ANOVA

b

Pumping rate	Range	b	F	d.f.	R ²
(X ₁) dry wt.	0.480 - 12.421				0.59
(X ₂) T°C	1.34 - 4.72	b ₁	0.690**	(4,130)	
(X ₃) S°/oo	18.7 - 27.3	b ₂	-0.295		
(X ₄) d [O ₂]	13.34 - 20.03	b ₃	-0.150		
	0.25 - 3.37	b ₄	-2.084**		

$\overline{pO_2} = 38$ mm Hg

Range

Pumping rate	Range	b	F	d.f.	R ²
(X ₁) dry wt.	2.071 - 12.630				0.74
(X ₂) T°C	1.21 - 5.03	b ₁	1.966**	(4,58)	
(X ₃) S°/oo	18.7 - 26.0	b ₂	0.265		
(X ₄) d [O ₂]	13.93 - 18.50	b ₃	-0.578		
	0.21 - 0.79	b ₄	-7.855**		

Table 10

The effect of environmental variables, body weight and oxygen utilization on the oxygen consumption and pumping rate of male Mercenaria as analyzed by multiple linear regression with ANOVA

- R² Multiple correlation coefficient
- d.f. degrees of freedom in ANOVA
- b. partial regression coefficient
- ** high significant (P 0.01)

Table 10 (cont)

Pumping Rate
($l_{H_2O}/hr/clam$)

Sex: Male

$\overline{pO_2}$
Range

	Range	b	ANOVA
Pumping rate	1.440 - 11.999		R^2 0.62
(X_1) dry wt.	1.34 - 5.20	b_1 1.237**	d.f. (4,143)
(X_2) $T^\circ C$	22.2 - 27.0	b_2 -0.005	F 58.13*
(X_3) S°/oo	12.06 - 20.14	b_3 -0.274	
(X_4) d [O_2]	0.15 - 2.91	b_4 -2.928**	

$\overline{pO_2}$ = 39 mm Hg

Range

	Range	b	ANOVA
Pumping rate	1.400 - 8.400		R^2 0.83
(X_1) dry wt.	1.34 - 4.16	b_1 0.524	d.f. (4,33)
(X_2) $T^\circ C$	19.2 - 26.0	b_2 -0.464	F 39.42
(X_3) S°/oo	13.07 - 18.98	b_3 -0.389	
(X_4) d [O_2]	0.37 - 1.05	b_4 -3.395**	

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