OXYGEN CONSUMPTION AND HEMOLYMPH OSMOLALITY OF BROWN SHRIMP, *PENAEUS AZTECUS*

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ABSTRACT

Oxygen consumption and (or) osmoregulation of brown shrimp was measured under conditions applicable to their natural environment or culture. Shrimp were acclimated to test salinity and temperature a minimum of 1 week prior to any test and to the respirometer chamber for 1 hour prior to recording data. Time of day, effects of white-light illumination, and crowding were not found to influence significantly their mass (m) specific oxygen consumption rate (mg O_2 · g wet m^{-1} · h^{-1}); however, disturbed shrimp consumed oxygen nearly four times faster than shrimp at rest (0.56 vs. 0.13 mg O_2 · g wet m^{-1} · h^{-1}). The effects of size (3.7 and 6.7 g shrimp), salinity (10, 20, and 30‰), and temperature (18°, 23°, 28°, 33° C) on shrimp hemolymph concentrations and oxygen consumption rates showed that hemolymph osmolalities increased significantly with salinity and that oxygen consumption rates increased significantly with temperature. Mean hemolymph concentrations in 10, 20, and 30‰ salinity were 616, 696, and 774 milliosmoles, but differences among oxygen consumption rates in these salinities were negligible, supporting the hypothesis that relatively little energy is required for osmoregulation by euryhaline species. Mean hemolymph concentrations were significantly higher for 3.7 g shrimp (796 milliosmoles) than for 6.7 g shrimp (753 milliosmoles) only 30‰ salinity, indicating that the larger shrimp may be better hypoosmoregulators. At 18° C, oxygen consumption rates averaged 0.29 mg O_2 · g wet m^{-1} · h^{-1} and increased significantly at each test temperature to 0.55 mg O_2 · g wet m^{-1} · h^{-1} at 33° C. Indirect calorimetry calculations showed that juvenile shrimp (~5.2 g) in 10-30‰ salinity and 23°-28° C respired a daily equivalent approximating 3.4% of their energy content, that is, 105 calories.

Shrimp comprise the basis for the nation's most valuable seafood industry (Roedel 1973). Demand has surpassed domestic production, and in 1975 the United States imported about 37% of its annual consumption (National Marine Fisheries Service 1978). Demand and high pound value have made shrimp an attractive species for culture (Rose et al. 1975). Although shrimp (*Penaeus* spp.) culture is biologically possible, no operations have been economically successful in the United States. Reasons for this, in part, are that in spite of years of study, many basic aspects of shrimp behavior, biology, and physiology remain unknown. Fundamental to intensive husbandry of any animal is knowledge of its energy budget, i.e., its consumption and utilization of energy under specified conditions.

Energy budgets are usually depicted as flow schemes and diagrammatically trace energy derived from food to expenditures in various physiological processes (see Brody 1945; Harris 1966; Crampton and Harris 1969; Brett 1970). The amount of energy channelled through an organism and the compartmentalization of that energy depends upon environmental and physiological variables such as season, temperature, photoperiod, salinity, sex, size, age, food, crowding, stage of molt cycle, etc. (Zeuthen 1947; Waterman 1960; Prosser and Brown 1961; Crampton and Harris 1969; Brett 1970). Because metabolic demands of maintenance and feeding activity must be satisfied before growth can occur, knowledge of these demands under various conditions may be used advantageously to control or manipulate food conversion (Brett 1970). Most assimilated energy is expended in basal metabolism and maintenance (Brody 1945).

Internal respiration or intermediary metabolism is the sum of enzymatic reactions in which energy is made available for biological work (Prosser and Brown 1961), and the best measure of metabolism is caloric output (Fry 1957). Obtaining the caloric output for an experimental organism requires the determination of its oxygen consumption, carbon dioxide production, nitrogen excretion, and the caloric content of excreta (Fry

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1957). This difficult task has seldom been carried out completely and usually oxygen consumption alone is used to measure metabolism (Fry 1957).

To date, few researchers have studied any portion of the energy budget of penaeid shrimp. The most complete attempt was that of Qasim and Easterson (1974), who ascertained energy ingested, assimilated, and egested by *Metapenaeus monoceros*. Condrey et al. (1972) tested conversion efficiencies of selected diets of *P. aztecus* and *P. setiferus*, and Nose (1964) obtained protein digestibility for *P. japonicus*. Finally, assimilation efficiencies of *P. aztecus* feeding naturally were determined by Jones (1973).

A number of investigators have studied penaeid oxygen consumption (Rao 1958; Egusa 1961; Kader 1962; Subrahmanyam 1962, 1976; Zein-Eldin and Klima 1965; Weerasinghe and Arudpragasam 1967; Steed and Copeland 1967; Kutty 1969; Ikeda 1970; Kutty et al. 1971; Venkataramiah et al. 1975, see footnote 3; Green et al. 1976; Venkataramiah et al.[4]). Subrahmanyam (1962) has shown that one shrimp, *P. indicus*, is an oxygen conformer and that its oxygen-consumption rate depends upon the partial pressure of oxygen, even at saturation levels. Thus, as the ambient oxygen concentration in a closed chamber decreases from respiration, the shrimp's respiratory rate will also decrease. Because all previous investigators, except Egusa (1961), Subrahmanyam (1976), and Venkataramiah et al. (footnote 4) used static situations to measure oxygen consumption of shrimp, their results may not be representative of respiratory rates in natural or culture conditions.

Shrimp of the genus *Penaeus* in the Gulf of Mexico exhibit a complex life cycle that includes a distinct migration between deep offshore waters and shallow estuarine waters. Shrimp enter estuaries as postlarvae and may grow from an initial size of 12 mm to lengths >100 mm before returning offshore (Williams 1965; Pérez Farfante 1969). In estuaries, shrimp experience daily and seasonal changes in salinity and temperature and, prior to emigration, are one of the most abundant and important macroinvertebrates. In this paper we report the effects of selected environmental factors influencing the shrimp's metabolic rate and (or) osmoregulation. We also estimate energy budgets for animals under typical environmental conditions. Experimental conditions were selected to be applicable to the shrimp's natural environment, i.e., typical estuarine salinities and temperatures (St. Amant et al. 1966), or to provide knowledge relevant to their intensive culture.

METHODS

Experimental Procedure

Brown shrimp, *Penaeus aztecus* Ives, were captured in a 4.9 m otter trawl in Airplane Lake, Jefferson Parish, La., between 1 September 1973 and 30 June 1974 (from November 1973 to January 1974, some pink shrimp, *P. duorarum*, may have been included among the test animals). After capture shrimp were selected for size and transported to Louisiana State University (LSU) in Baton Rouge. One of two size classes, 3.7±0.6 g (73-82 mm total length, TL) and 6.7±0.9 g (90-100 mm TL), of shrimp were used in all tests. The 3.7 g shrimp are typical of estuarine shrimp populations (St. Amant et al. 1966), and 6.7 g shrimp are frequently among the size range emigrating from estuaries (Parker 1970).

In the laboratory, shrimp were placed in polyethylene holding tanks and acclimated to test salinity and temperature combinations for a minimum of 1 wk (Sick et al. 1973) prior to any experiment. Acclimation and test temperatures were maintained to within ±1.5° C. Salinity was maintained to within ±1.5‰ (refractometer readings) with artificial sea salt. Photoperiod was kept at 12 h light, 12 h dark (12:12 LD); the photophase began at 0630 and ended at 1830 h central standard time (c.s.t.). Shrimp were starved 24 h before testing but otherwise fed daily an excess amount of an extruded pellet (FST 21-5/72A).[5] Uneaten food was removed daily. Chopped fresh shrimp or Tetra Werke's TetraMin[6] was occasionally included in the diet.

[3]Venkataramiah, A., G. J. Lakshmi, and G. Gunter. 1974. Studies on the effects of salinity and temperature on the commercial shrimp, *Penaeus aztecus* Ives, with special regard to survival limits, growth, oxygen consumption, and ionic regulation. U.S. Army Engineer WES, Vicksburg, Miss., Contract No. DACW 39-71-C-008, 134 p.

[4]Venkataramiah, A., G. J. Lakshmi, P. Biesiot, J. D. Valleau, and G. Gunter. 1977. Studies on the time course of salinity and temperature adaptation in the commercial brown shrimp *Penaeus aztecus* Ives. U.S. Army Engineer WES, Vicksburg, Miss., Contract No. DACW 39-73-C-0115, 370 p.

[5]Obtained from S. P. Meyers, Professor, Department of Food Science and Technology, Louisiana State University, Baton Rouge, LA 70803.

[6]Reference to trade names does not imply endorsement of that product by the National Marine Fisheries Service, NOAA.

A closed, continuously flowing, differential respirometer was used to measure the oxygen consumption rates. Its basic design was modified from the apparatus employed by Keys (1930) and consisted of a test chamber positioned between two oxygen polarographs through which a known volume of water flowed from a supply to a catchment reservoir (Bishop 1976). Hourly flow rates varied between 1.934 and 2.519 l depending on salinity-temperature combinations.

Prior to a test, polarograph readings were checked for identical response, shrimp were placed in the chamber, the chamber voided of air and sealed, and the water switched to flow through the test chamber. At the end of a test, water flow was again shunted past the chamber, and probe readings were rechecked to ensure similar readings. Probes were read to the nearest 0.05 ppm. If probe drift occurred and exceeded 0.15 ppm the test was discontinued and disregarded. If drift occurred, but was <0.15 ppm, it was assumed to have occurred at a constant rate, and data were corrected accordingly. After a test the shrimp were measured, sexed, and weighed individually. Except for diurnal experiments, all tests lasted 2 h. Mean live mass (m) of test shrimp is used to denote the size class of shrimp being discussed. Hourly rates of oxygen consumption are expressed on a per gram live mass basis, i.e., mg $O_2 \cdot$ g wet $m^{-1} \cdot h^{-1}$. Statistical designs and arrangements were from Cochran and Cox (1957) and Steel and Torrie (1960), and significant differences were tested at $\alpha = 0.05$ or 0.01.

Experiments

Diurnal Effects

Five 6.7 g shrimp were tested individually for 24 h under a 12:12 LD photoperiod. Test salinity and temperature was 20‰ and 25° C, respectively. Shrimp were allowed to acclimate to the test chamber during the first 1.5 h. Except for the initial 1.5 h and 1 h following each probe check, oxygen consumption data were averaged for each 15-min period and grouped into eight 3-h intervals (0630-0930, 0930-1230, ..., 0330-0630 h). An analysis of variance (ANOVA) employing a randomized block design was computed on the average oxygen consumption for each shrimp (block) during the eight 3-h intervals (treatments).

Light; Reduced-Light Effects

Four 6.7 g shrimp were individually tested while exposed to laboratory light (193 lm m^{-2}). Test salinity and temperature were 20‰ and 25° C, and tests lasted 2 h. An inverted, bottomless, opaque plastic bucket was placed over the test chamber to preclude visual disturbances. The next day each shrimp was again tested in the same sequence, but the light was reduced (<10 lm m^{-2}) by placing an intact plastic bucket over the test chamber. Two days of similar tests were repeated with three different 6.7 g shrimp except that the shrimp were first tested in reduced light. An ANOVA in a crossover design was computed on the average oxygen consumption rates of the last two 15-min periods.

Disturbance Effects

Four 6.7 g shrimp were tested singly for oxygen consumption after disturbance. Test salinity and temperature were 20‰ and 25° C, and ambient oxygen concentration was 7.4 ppm. Shrimp were placed in the test chamber, and the chamber was shaken by hand for approximately 5 min. The highest oxygen consumption rate during the following 15 min was considered to approach that for active shrimp.

The lowest oxygen consumption rate of shrimp from four randomly selected diurnal experiments was obtained to estimate standard respiration. Because both disturbance and diurnal tests were conducted at the same salinity and temperature, oxygen consumption differences between these two test conditions should result primarily from increased metabolic activity. We used t-tests comparing two sample means to test for significant differences between the shrimp's resting and active oxygen consumption rates.

Crowding Effects

The effects of crowding on the oxygen consumption of 3.7 and 6.7 g shrimp were investigated. Area of the test-chamber floor was 103.9 cm^2, and chamber volume was 240 ml. Shrimp were tested at 20‰ S (salinity) and 25° C. Light was reduced to <10 lm m^{-2} during the tests by placing an inverted, opaque plastic bucket over the test chamber. Eight replicates were obtained for 3.7 g shrimp tested in groups of one and two, and a t-test involving two sample means was employed to test for significant differences. Eight replicates of 6.7 g

shrimp in groups of one, two, and three, and four replicates of 6.7 g shrimp in groups of four were also tested. An ANOVA in a completely randomized design was computed for the average oxygen consumption of the last two 15-min periods of each test.

Size, Salinity, and Temperature Effects

The influence of salinity and temperature was tested on the oxygen consumption and osmoregulation of two sizes of *P. aztecus*. Three test salinities (10, 20, 30‰) and four temperatures (18°, 23°, 28°, 33° C) were selected to represent ranges that shrimp may experience in estuaries.

Shrimp were caught and maintained in salinities approximating 20‰; after acclimation to room temperature (23°-25° C) in the laboratory, shrimp of each size class were distributed equally among tanks of 10, 20, and 30‰ S. Transferred shrimp experienced no difficulties adjusting to a 10‰ S change at 23°-25° C. Ambient laboratory temperature was lowered to 18° C and maintained for a week. After oxygen consumption or hemolymph data were obtained from acclimated shrimp, ambient temperature was gradually raised for the next test and the procedure repeated. Four to five days appeared to be necessary to raise the temperature from 28° to 33° C; shrimp mortality increased with faster acclimation rates.

Shrimp were tested in pairs because two shrimp of the smaller size were necessary to cause approximately a 1 ppm oxygen concentration difference between the probes at the tested flow rates. A 1 ppm difference minimized percentage error caused by translating data from the strip-chart recorder and permitted enough flow through the test chamber to avoid oxygen depletion and excreta buildup. An inverted plastic bucket was placed over the chamber during tests to preclude visual disturbances and to reduce light (<10 lm m^{-2}).

Each of the 24 treatment combinations (2 sizes $\times$ 3 salinities $\times$ 4 temperatures) was replicated seven or eight times, and each test lasted 2 h. Acclimated shrimp were selected completely at random without replacement for each test. Therefore the oxygen consumption of a minimum of seven pairs of different shrimp was obtained for each treatment combination. To allow shrimp time to acclimate to the test chamber, data obtained during the first hour were disregarded. Data collected during the second hour were divided into four 15-min periods and the average oxygen consumption for each period was calculated. An ANOVA employing a split plot in a completely randomized design with a 2 $\times$ 3 $\times$ 4 factorial arrangement as the whole plots and period as the subfactor was computed on the data. The effects of the treatments (size, salinity, temperature), the periods, and the interactions on the oxygen consumption rates were evaluated. If a significant difference was found, then orthogonal comparisons (Snedecor and Cochran 1967) were made to explain more specifically the differences among the treatments, periods, and their interactions. Data plotted in the graphs are the average oxygen consumption during the last ½ h (the third and fourth periods) only.

Shrimp for the osmoregulation studies were caught between 20 March and 20 April 1974 at Airplane Lake. After shrimp were acclimated in the laboratory, hemolymph samples were obtained by puncturing the dorsal arthroidal membrane (just anterior to the first abdominal segment) and bleeding no less than 0.2 ml directly into cuvettes. Cuvettes were sealed with Parafilm to prevent evaporation. The least amount of hemolymph necessary for accurate osmolality determination was 0.2 ml and was obtained from each 6.7 g shrimp; however, two 3.7 g shrimp were needed to collect the minimum volume. Osmolality was measured within 1.5 h with an Osmette. Five samples were tested for each treatment combination except for the following instances: 6.7 g shrimp at 18° C and 10‰ S—three samples; 3.7 g shrimp at 33° C and 10, 20, 30‰ S—four samples; and 6.7 g shrimp at 18° and 28° C and 30‰ S—four samples. Hemolymph was not centrifuged, and little difficulty was experienced in obtaining repeatable readings with the Osmette.

Data were analyzed by an ANOVA employing a 2 $\times$ 3 $\times$ 4 factorial arrangement in a completely randomized design, and orthogonal comparisons were made on treatment combinations with significant differences. Correlations between hemolymph concentration and oxygen consumption data at corresponding size, salinity, and temperature combinations were made.

RESULTS

Diurnal Effects

Mean oxygen consumption rates ranged from 0.18 to 0.30 mg $O_2 \cdot$ g wet $m^{-1} \cdot h^{-1}$ among the eight

3-h periods (Table 1), but were not found to be significantly different. The mean oxygen consumption rates for individual shrimp during the 24-h test varied from 0.20 to 0.38 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ and were significantly different (Table 1).

TABLE 1.—Mean diurnal oxygen consumption rates (mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$) of five *Penaeus aztecus*; m = mass.

Time	Size (g) of individual test shrimp					Mean O_2 consumption per period[1]
	6.1	7.3	6.3	5.9	6.7	
0630-0930	0.18	0.38	0.49	0.17	0.25	0.29
0930-1230	.48	.14	.39	.18	.13	.26
1230-1530	.32	.16	.41	.22	.14	.25
1530-1830	.18	.18	.26	.12	.16	.18
1830-2130	.37	.21	.30	.32	.25	.29
2130-0030	.34	.18	.34	.23	.29	.28
0030-0330	.32	.15	.40	.28	.28	.29
0330-0630	.33	.20	.41	.28	.28	.30
Mean O_2 consumption per 24 h[2]	.32	.20	.38	.23	.22	.27

[1] Differences among time periods not significant.
[2] Differences among shrimp highly significant ($P < 0.01$).

Light; Reduced Light Effects

Mean oxygen consumption rates and standard error for seven shrimp tested in light compared with reduced light were 0.25±0.09 and 0.17±0.09 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ and were not found to differ significantly.

Disturbance Effects

The mean oxygen consumption rate of 6.7 g shrimp after disturbance was 0.56±0.05 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$ and 4.3 times higher than that (0.13±0.01 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$) for resting shrimp. This difference was highly significant.

Crowding Effects

Mean oxygen consumption rates and standard error for 3.7 g *P. aztecus* tested singly and in pairs were 0.50±0.06 and 0.41±0.05 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$. These differences were not found to be significant. One or two 3.7 g shrimp in the test chamber resulted in an average of 0.035 or 0.071 g of shrimp cm^{-2} of chamber floor and 0.015 or 0.031 g of shrimp cm^{-3} of chamber volume.

Mean oxygen consumption rates and standard error of 6.7 g *P. aztecus* tested singly and in groups of two, three, and four were 0.30±0.04, 0.37±0.02, 0.35±0.03, and 0.29±0.02 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$, respectively. These differences were not statistically significant. One, two, three, or four 6.7 g shrimp in the test chamber represented 0.064, 0.126, 0.188, or 0.247 g of shrimp cm^{-2} and 0.028, 0.054, 0.081, or 0.107 g of shrimp cm^{-3}, respectively.

Size, Salinity, and Temperature Effects

In the factorial test, size and temperature were the only significant main effects, but salinity-size and salinity-temperature effects were significant interactions. (Figure 1, Table 2). The smaller

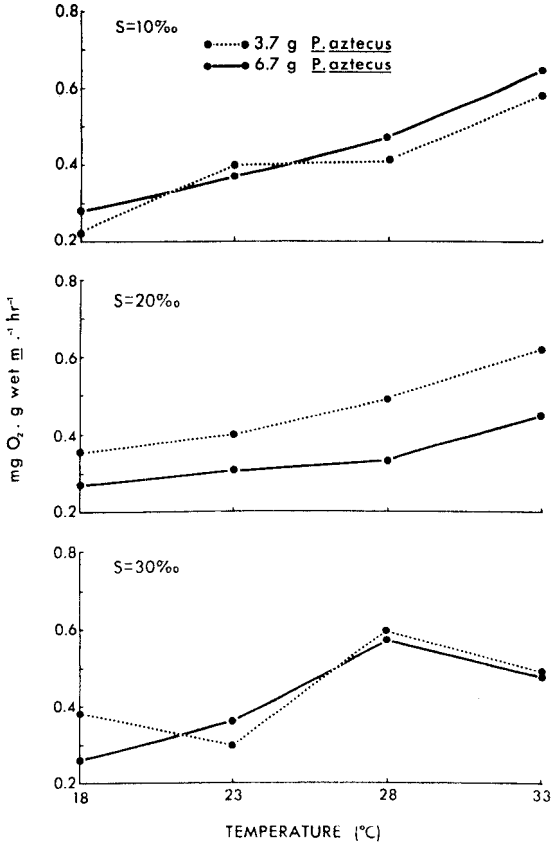

FIGURE 1.—Mean oxygen consumption rate of 3.7 and 6.7 g *Penaeus aztecus* vs. temperature at salinities of 10, 20, and 30‰.

shrimp consumed more oxygen per unit mass (0.44 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$) than did the larger shrimp (0.40 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$), but this difference was confined to salinities of 20‰ as shown by the salinity-size interaction (Figure 1, Tables 2, 3). In 20‰ S, the 3.7 g shrimp consumed an average of 0.46 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$, and the 6.7 g shrimp consumed about 0.34 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$.

TABLE 2.—Analysis of variance of the effects of size, salinity, temperature, and period on the mean oxygen consumption rates of *Penaeus aztecus*.

Source of variation	df	Mean square[1]
Size	1	0.3089*
Salinity	2	.0333
Salinity-size	2	.3922**
10‰:3.7 vs. 6.7 g shrimp	1	.0554
20‰:3.7 vs. 6.7 g shrimp	1	.9458**
30‰:3.7 vs. 6.7 g shrimp	1	.0480
Temperature	3	2.5200**
18°, 23° vs. 28°, 33° C	1	6.6970**
18° vs. 23° C	1	.3254*
28° vs. 33° C	1	.4532*
Temperature-size	3	.0172
Salinity-temperature[2]	6	.2744**
10‰:T_l	1	4.2317**
:T_q	1	.0100
:T_c	1	.0583
20‰:T_l	1	1.6643**
:T_q	1	.1327
:T_c	1	.0133
30‰:T_l	1	1.7817**
:T_q	1	.1393
:T_c	1	1.0509**
Size-salinity-temperature	6	.0636
Error (a)	161	.0597
Period:	3	.0838**
Periods 1, 2 vs. periods 3, 4	1	.2024**
Period 1 vs. period 2	1	.0266**
Period 3 vs. period 4	1	.0132**
Size period	3	.0023
Salinity period	6	.0005
Size-salinity period	6	.0001
Temperature period	9	.0048
Size-temperature period	9	.0019
Salinity-temperature period	18	.0031
Size-salinity-temperature period	18	.0007
Error (b)	481	.0017

[1]* = $P<0.05$; ** $P<0.01$.
[2]Subscripts: l = linear; q = quadratic; c = cubic.

TABLE 3.—Mean oxygen consumption rates of *Penaeus aztecus* for the salinity-size interactions; m = mass.

S (‰)	Size (g)	n	mg O_2 / g wet m·h	SE
10	3.7	127	0.411	0.022
10	6.7	120	.442	.022
20	3.7	127	.465	.022
20	6.7	116	.338	.023
30	3.7	124	.436	.022
30	6.7	124	.408	.022

The average oxygen consumption rate increased significantly with increasing temperature, from 0.29 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ at 18° C to 0.55 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ at 33° C (Table 4). At each salinity oxygen consumption increased linearly with temperature, except at 30‰, where oxygen consumption peaked at 28° C and decreased significantly at 33° C (Figure 1, Table 2).

Oxygen consumption rates differed significantly among periods (Table 2). Rates during the first 15-min period averaged 0.44 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ and decreased to an average of 0.40 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ during the fourth 15-min period (Table 5). Significant differences of oxygen consumption rates among period interactions were not found (Table 2).

TABLE 4.—Mean oxygen consumption rates of *Penaeus aztecus* for each test temperature; m = mass.[1]

T (°C)	n	mg O_2 / g wet m·h	SE
18	187	0.293	0.018
23	184	.352	.018
28	183	.479	.018
33	184	.549	.018

TABLE 5.—Mean oxygen consumption rate of *Penaeus aztecus* during four consecutive 15-min periods after 1 h acclimation in respirometer chamber; m = mass.

15-min period	n	mg O_2 / g wet m·h	SE
First	184	0.443	0.003
Second	184	.426	.003
Third	186	.407	.003
Fourth	184	.395	.003

When hemolymph osmolality was analyzed for shrimp acclimated to the same conditions as previously described, size and salinity were significant main effects; and salinity-size, temperature-size, and salinity-temperature effects were significant interactions (Figure 2, Table 6). The mean hemolymph osmolality of 3.7 g shrimp was significantly higher than that of 6.7 g shrimp (Tables 6, 7), but this difference was found only in combinations that included 30‰ S or 33° C. In 30‰ S the smaller shrimp's hemolymph osmolality averaged over all temperatures was 796 mOsm (milliosmoles) compared with 753 for the larger shrimp. At 33° C the same comparison averaged over all salinities was 734 and 678 mOsm (Figure 2).

The mean hemolymph osmolality increased with increasing salinity (616, 696, and 774 mOsm at 10, 20, and 30‰, respectively; Table 7). At each salinity, the effect of increasing temperature on the shrimp's hemolymph osmolality was tested. Significant linear responses were obtained at 10 and 30‰ (Table 6, Figure 3). Significant correlations were not found between hemolymph osmolality and oxygen consumption rates.

DISCUSSION

Sources of Variability

Many complicating variables must be considered in attempting to obtain the standard metabolism of penaeid shrimp. Physiological rhythms, stage of the molt cycle, and lunar phases

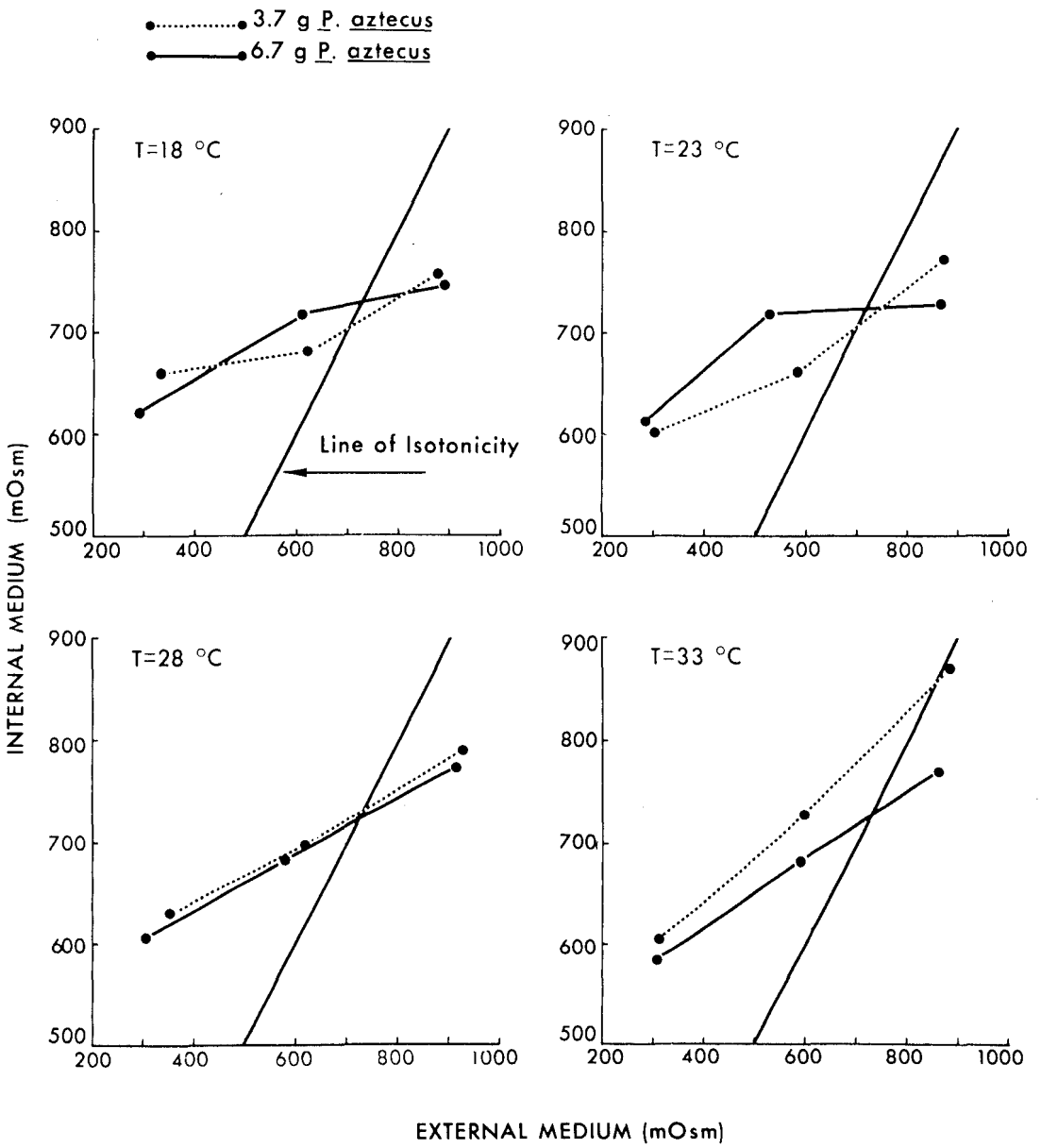

FIGURE 2.—Mean hemolymph osmolality (mOsm) of 3.7 and 6.7 g *Penaeus aztecus* vs. temperatures at 18°, 23°, 28°, and 33°C.

may complicate the ideal of testing uniform subjects under similar conditions. In addition, the effects of spontaneous activity often mask any differences of metabolism resulting from the effects of osmoregulation, size, temperature, etc. In the present study, attempts to eliminate molt-stage differences were made by testing a minimum of seven pairs of shrimp. Because integumental changes occur at least 70% of the time between successive molts for decapods (Passano 1960), the testing of only intermolt, acclimated animals would have been nearly impossible. Most of the shrimp tested, however, should have been in a stage other than immediate premolt, and newly molted shrimp were not tested. Therefore it is assumed that most of the test animals were at a molt stage that affected the total oxygen consumption relatively little.

TABLE 6.—Analysis of variance of the effects of size, salinity, and temperature on the osmolality of *Penaeus aztecus* hemolymph.

Source of variation	df	Mean square[1]
Size	1	9,343*
Salinity	2	231,198**
10, 20 vs. 30‰	1	332,414**
10 vs. 20‰	1	121,516**
Salinity-size	2	5,836*
10‰:3.7 vs. 6.7 g shrimp	1	4,076
20‰:3.7 vs. 6.7 g shrimp	1	624
30‰:3.7 vs. 6.7 g shrimp	1	16,781**
Temperature	3	2,734
Temperature-size	3	4,899*
18° C: 3.7 vs. 6.7 g shrimp	1	447
23° C: 3.7 vs. 6.7 g shrimp	1	367
28° C: 3.7 vs. 6.7 g shrimp	1	4,136
33° C: 3.7 vs. 6.7 g shrimp	1	20,449**
Salinity-temperature[2]	6	5,597**
10‰:T_l	1	8,959*
:T_q	1	231
:T_c	1	3,110
20‰:T_l	1	12
:T_q	1	1,523
:T_c	1	12
30‰:T_l	1	23,623**
:T_q	1	2,368
:T_c	1	1,065
Size-salinity-temperature	6	2,061
Error (a)	89	1,231

[1]* = $P<0.05$; ** = $P<0.01$.
[2]Subscripts: l = linear; q = quadratic; c = cubic.

TABLE 7.—Mean hemolymph osmolality of *Penaeus aztecus* in relation to size and salinity of acclimation water.

Variable	*n*	Hemolymph (mOsm)	SE	Osmolality of external medium (mOsm)
Size, g:				
3.7	56	703	4.7	606
6.7	57	688	4.6	584
Salinity, ‰:				
10	37	616	5.8	310
20	39	696	5.6	590
30	37	774	5.8	886

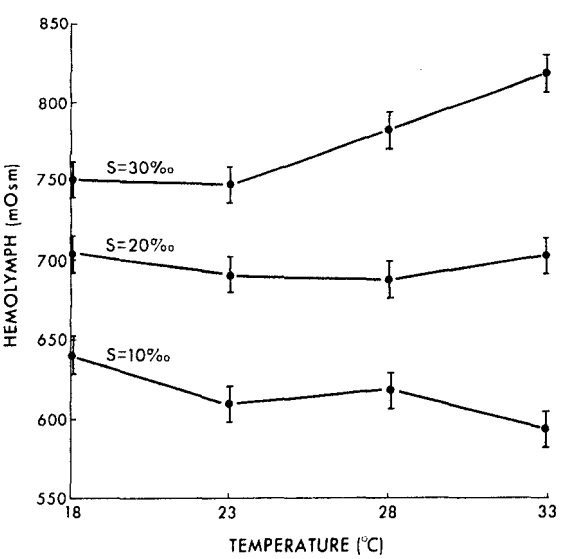

FIGURE 3.—Mean hemolymph osmolality of *Penaeus aztecus* vs. temperature at salinities of 10, 20, and 30‰.

Although no significant time-of-day differences were found (Table 1), efforts were made to test equal numbers of shrimp in the morning and afternoon at each treatment combination. Evidence indicates that shrimp are influenced by lunar cycles (Wheeler 1937; Racek 1959; Aaron and Wisby 1964; Wickham 1967; Hughes 1972; Bishop and Herrnkind 1976), but in the present studies, we assumed that lunar influences on the oxygen consumption were negligible because of acclimation periods. Subrahmanyam (1976) obtained results indicating the presence of an oxygen consumption rhythm in pink shrimp that coincided with the tidal cycle, but this rhythm waned after the shrimp were maintained for a week in captivity.

Because of the absence of standardized techniques for measuring routine oxygen consumption of poikilotherms, many of the previous studies on the oxygen consumption of penaeid shrimp are of limited usefulness. Frequently pertinent circumstances relating to acclimation time and (or) test conditions were not reported (Subrahmanyam 1962; Zein-Eldin and Klima 1965; Weerasinghe and Arudpragasam 1967; Steed and Copeland 1967), and closed chambers were used in most published studies. Consequently, test animals could not acclimate to test chamber conditions and probably exhibited increased activity.

In our studies, the shrimp's activity was minimized by several methods: first, the test animals were acclimated to a specific test salinity-temperature combination for at least a week prior to testing; second, the shrimp were allowed to acclimate to the test chamber for an hour before data were collected; and third, an inverted opaque plastic bucket was placed over the test chamber to reduce the light and to prevent disturbances from human activity in the laboratory.

Reducing the light to the test chamber reduced the mean oxygen consumption (0.25 vs. 0.17 mg $O_2 \cdot g$ wet $m^{-1} \cdot h^{-1}$) although the effect was not statistically significant. The hour acclimation prior to taking data was not enough time to allow the shrimp to adjust to the test chamber because the oxygen consumption rate for each 15-min period continued to decline throughout the second hour (Tables 2, 5). Although the average oxygen consumption rate decreased significantly during each subsequent 15-min period of the second hour of testing, the overall rate change was small, an 11% decrease between the first and last period. The rate change was consistent across all treatments and unrelated to the treatment effects because no

significant differences were found among any of the period interactions (Table 2); thus the effects of size, salinity, and temperature are independent of acclimation time. The average oxygen consumption data for each treatment combination in Table 3 and Figure 1 are slightly higher than would be expected for shrimp completely acclimated to the test chamber, however. Egusa (1961) found that the oxygen consumption rate of *P. japonicus* stabilized after about 3 h. Acclimation time to test conditions may have been reduced if fine-grained substrate had been included in the test chamber. Penaeid shrimp exhibit arrhythmic activity when they cannot bury in substrate (Racek 1959; Moller and Jones 1975).

Because shrimp may be both oxygen conformers and regulators, crowding could profoundly influence their oxygen consumption by increasing the extent of activity. We found no significant oxygen consumption rate differences between one and two 3.7 g *P. aztecus* or among one, two, three, and four 6.7 g *P. aztecus* when compared on a per gram wet mass basis, and believe that testing two shrimp simultaneously did not appreciably affect their oxygen consumption rates. Subrahmanyam (1976) noticed no differences in activity when testing pink shrimp singly or in pairs.

Salinity Effects on Oxygen Consumption and Osmoregulation

The influence of salinity on the life habits of penaeid shrimp has received considerable attention (Panikkar 1951, 1968; Gunter and Hildebrand 1954; Zein-Eldin 1963; Gunter et al. 1964; Parker 1970). Panikkar (1951) suggested that high salinity may be necessary for ovarian development, but its importance still remains unknown. Life cycles of the three penaeid shrimp important commercially in the Gulf are similar (Williams 1965), but juvenile white shrimp, *P. setiferus*, are reported to prefer salinities <10‰; juvenile brown shrimp, salinities between 10 and 20‰; and juvenile pink shrimp, salinities >18‰ (Gunter et al. 1964). Adaptation to low salinities is highly developed in young penaeids, and juveniles are more widely distributed in estuaries than are adults. Thus, osmoregulatory capabilities may influence emigration of subadults from estuaries (Panikkar 1968). Zein-Eldin (1963) obtained good growth and survival for postlarval *P. aztecus* at 2, 5, 10, 25, and 40‰, and concluded that salinity per se may not directly affect growth during the estuarine portion of their life cycle. These postlarvae were grown only to sizes <0.2 g (Zein-Eldin 1963), so the effects of low salinity on growth rate during a substantial portion of their life cycle remains uninvestigated.

Brown shrimp were hyperosmotic regulators in 10 and 20‰ S and hypoosmotic regulators in 30‰ S. Depending on salinity and temperature, hemolymph osmolality was maintained at concentrations approximating 600-900 mOsm (Figure 2). These results agree with those of Williams (1960) and McFarland and Lee (1963). Thus *P. aztecus* cannot be considered a perfect regulator, but it differs substantially from nonregulators. Panikkar (1968) considered homoiosmotic regulation to be one of the most advanced capabilities of marine invertebrates.

Oxygen consumption would be expected to increase for osmoregulators as the osmotic difference between the shrimp's hemolymph and its environment increased because metabolism would increase to maintain a constant hemolymph concentration. Energy expenditure for osmoregulation depends on the species and is related to temperature as well as other variables (see reviews by Kinne 1964, 1966, 1967).

There is conflicting evidence as to whether important energy expenditures are necessary to maintain homoiosmotic hemolymph (Schwabe 1933; Lofts 1956; Rao 1958; Dehnel 1960). In our tests hemolymph osmolalities of *P. aztecus* were significantly affected by salinity, but the energy expenditures for osmoregulation after acclimation were small in relation to total metabolic rate. Other studies on euryhaline decapods show that salinity does not have pronounced effects on oxygen consumption if the experimental animals are acclimated to the test salinities and if test salinities are not too extreme (Lofts 1956; Rao 1958; Kader 1962; Kutty et al. 1971).

Venkataramiah et al. (footnote 4) acclimated brown shrimp to 15‰ S at 25° C and measured oxygen consumption rates after salinity was changed to 2, 5, 10, 15, 25, and 36‰. Metabolic rates increased initially, but generally tended toward that of acclimation conditions after a day unless deviations from acclimation salinity were substantial, i.e., 2, 5, and 36‰. Salinity changes in the respirometer were made over a 1-h period, however, and may have been too rapid and (or) extreme for the shrimp's capacity to adjust. Venkataramiah et al. (footnote 4) found that blood hemolymph required 6 h to achieve osmotic stabil-

ity when shrimp were transferred from 15 to 2 or 36‰ S; osmotic stability was achieved in 2 h after transfer from 15 to 5, 10, 15, or 25‰ S.

Highest catch rates for brown shrimp were determined by Copeland and Bechtel (1974) to occur in salinities from <4 to >35‰. This lower limit is slightly less than the range of salinities (5-8‰) suggested by Khlebovich (1968) at which ion ratios change from typically freshwater to marine. Therefore it appears that if juvenile or subadult shrimp were acclimated to salinities that are typically marine (8-35‰), oxygen consumption rates will not reflect any significant increased energy demands necessary for osmoregulation. Table 8 summarizes oxygen consumption rates of penaeid shrimp that have been acclimated to and tested at various salinity-temperature combinations. Routine and standard rates vary from 0.14 to 0.75 mg $O_2 \cdot$ g wet $m^{-1} \cdot h^{-1}$.

Shrimp Size Effects on Oxygen Consumption and Osmoregulation

The effects of size on an animal's oxygen consumption are apparent for individuals ranging from 1 to 1,000 g (Zeuthen 1947). Generally, a large

TABLE 8.—Oxygen consumption of penaeid shrimps; some data converted to allow uniform reporting. Temperature (T) in degrees Celsius, salinity (S) in parts per thousand, and mass (m) of live shrimp in grams. Genera *Metapenaeus* and *Penaeus* abbreviated as *M.* and *P.*

Species	Acclimation T	Acclimation S	Acclimation Days	Test T	Test S	Size (g)	Metabolic state	mg O_2 g wet $m \cdot h$	Source
M. monoceros[1]	29	35	>3	29	30	0.53	Routine?	1.34	Kader (1962)
	31	33	1½	31	33	2-6	Routine	.75	Rao (1958)
	31	20	1½	31	17	2-6	Routine	.75	Rao (1958)
P. aztecus	—	—	Several	—	—	4-7	Routine?	.39	Zein-Eldin and Klima (1965)
	—	32	½	—	32	—	Routine?	.3	Steed and Copeland (1967)
	18	10	>7	18	10	3.7	Routine	.22	Bishop (1974)
	18	20	>7	18	20	3.7	Routine	.35	Bishop (1974)
	18	30	>7	18	30	3.7	Routine	.38	Bishop (1974)
	23	10	>7	23	10	3.7	Routine	.40	Bishop (1974)
	23	20	>7	23	20	3.7	Routine	.40	Bishop (1974)
	23	30	>7	23	30	3.7	Routine	.30	Bishop (1974)
	28	10	>7	28	10	3.7	Routine	.44	Bishop (1974)
	28	20	>7	28	20	3.7	Routine	.49	Bishop (1974)
	28	30	>7	28	30	3.7	Routine	.59	Bishop (1974)
	33	10	>7	33	10	3.7	Routine	.59	Bishop (1974)
	33	20	>7	33	20	3.7	Routine	.62	Bishop (1974)
	33	30	>7	33	30	3.7	Routine	.49	Bishop (1974)
	18	10	>7	18	10	6.7	Routine	.28	Bishop (1974)
	18	20	>7	18	20	6.7	Routine	.27	Bishop (1974)
	18	30	>7	18	30	6.7	Routine	.26	Bishop (1974)
	23	10	>7	23	10	6.7	Routine	.37	Bishop (1974)
	23	20	>7	23	20	6.7	Routine	.31	Bishop (1974)
	23	30	>7	23	30	6.7	Routine	.35	Bishop (1974)
	28	10	>7	28	10	6.7	Routine	.47	Bishop (1974)
	28	20	>7	28	20	6.7	Routine	.33	Bishop (1974)
	28	30	>7	28	30	6.7	Routine	.57	Bishop (1974)
	33	10	>7	33	10	6.7	Routine	.64	Bishop (1974)
	33	20	>7	33	20	6.7	Routine	.45	Bishop (1974)
	33	30	>7	33	30	6.7	Routine	.48	Bishop (1974)
	18	15	7	18	15	~6	Standard	.12	Venkataramiah et al. (text footnote 4)
	25	15	7	25	15	~6	Standard	.18	Venkataramiah et al. (text footnote 4)
	32	15	7	32	15	~6	Standard	.38	Venkataramiah et al. (text footnote 4)
P. duorarum	—	32	½	—	32	—	Routine	.14	Steed & Copeland (1967)
	25	20	1	25	20	0.44	Standard	.59	Subrahmanyam (1976)
	25	20	1	25	20	0.44	Active	1.19	Subrahmanyam (1976)
	25	20	1	25	20	0.52	Standard	.76	Subrahmanyam (1976)
	25	20	1	25	20	0.52	Active	1.54	Subrahmanyam (1976)
	25	20	1	25	20	1.68	Standard	.26	Subrahmanyam (1976)
	25	20	1	25	20	1.68	Active	.47	Subrahmanyam (1976)
	25	20	1	25	20	3.65	Standard	.47	Subrahmanyam (1976)
	25	20	1	25	20	3.65	Active	.57	Subrahmanyam (1976)
	25	20	1	25	20	9.66	Standard	.18	Subrahmanyam (1976)
	25	20	1	25	20	9.66	Active	.26	Subrahmanyam (1976)
	25	20	1	25	20	11.0	Standard	.26	Subrahmanyam (1976)
	25	20	1	25	20	11.0	Active	.30	Subrahmanyam (1976)
P. indicus	28	15	—	28	15	2.4-3.7	Routine	.57	Subrahmanyam (1962)
	28	15	—	28	15	5.1-7.8	Routine	.36	Subrahmanyam (1962)
	30	36	14	30	36	2.7	Routine	.7	Kutty (1969)
	28	21	5	28	21	0.1	Routine	.9	Kutty et al. (1971)
P. japonicus	23	28	7-14	23	28	2.4-3.7	Standard	.18	Egusa (1961)
	23	28	7-14	23	28	4.6-6.2	Standard	.15	Egusa (1961)
P. semisulcatus	30	36	14	30	36	17.3	Routine	.35	Kutty (1969)
P. setiferus	25	22	14	25	25	0.04	Routine?	1.60	Green et al. (1976)

[1] *Tested at 63% oxygen saturation.*

individual consumes more oxygen than a smaller one, but its rate of oxygen consumption per unit mass is less (Mill 1972). In our study this generalization was found for shrimp only at 20‰ S. Although it is not known why this difference was evident at only one salinity, it should be noted that among the six salinity-size treatment combinations, the lowest as well as the highest metabolic rates occurred at 20‰ S (Figure 4). It is possible that the 3.7 g shrimp were more active than "routine" in the test chamber and that the 6.7 g shrimp were less active than "routine." Tests for both sizes at each temperature were conducted within a few days of each other, and we believe that the time element was not responsible for the observed difference. Each salinity-size combination is the average of approximately 30 tests, and the possibility of obtaining the results by chance is small. The data in Table 8 indicate decreasing metabolic rate (per unit mass) with increasing size, although extreme variability exists.

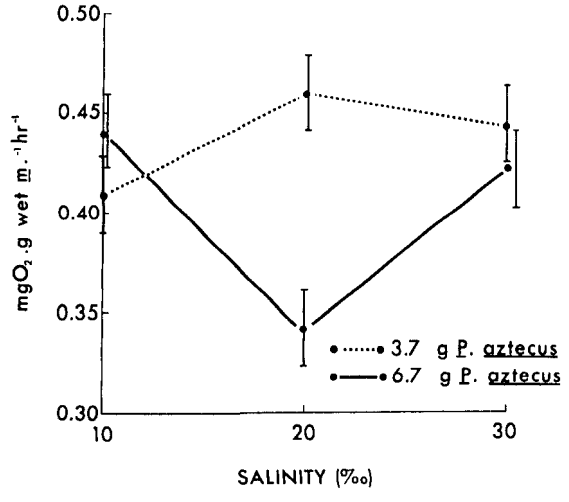

FIGURE 4.—Mean oxygen consumption rate (average for all test temperatures) of 3.7 and 6.7 g *Penaeus aztecus* at salinities of 10, 20, and 30‰.

As shrimp increase in size in the estuary, they move to higher, more stable salinities (Weymouth et al. 1933; Gunter 1945, 1950; Williams 1960; Bishop and Shealy[7]). This movement may be, in part, a response to a decrease in osmoregulatory ability with increasing size. Only two sizes of shrimp were tested, and both sizes were obtained from the same locality (often from the same trawl tow). Thus osmoregulation differences would not be anticipated to be large. The larger shrimp appear to be better regulators in hyperosmotic salinity and at high temperatures. The slopes of the hemolymph data over test salinities at 33° C for the 3.7 and 6.7 g shrimp were 0.47 and 0.33, indicating that the larger shrimp maintained homoiosmoticity to a better degree than did the smaller shrimp at a temperature approaching an environmental extreme (Figure 2).

Some of our test conditions and those of Williams (1960) are nearly identical, and hemolymph data from shrimp acclimated to similar conditions are comparable. Hemolymph data from both 3.7 and 6.7 g shrimp were averaged to be compatible with Williams' (1960) juvenile *P. aztecus* (42-100 mm TL). At 28° C and 10, 20, and 30‰ S, we obtained average hemolymph osmolalities of 619, 689, and 785 mOsm, respectively, whereas Williams obtained values approximating 657, 804, and 825 mOsm. Williams' values are somewhat higher than ours, but physiological differences in populations, analytical techniques, or acclimation history of test animals could be responsible.

Because small shrimp (3.7 g) may encounter highly variable salinities, they may be capable of tolerating relatively variable hemolymph osmolalities and their osmoregulatory processes may not be as capable of homoiosmoregulation as those of larger shrimp. This implies that varying salinities would be more expensive energetically for larger shrimp and partially responsible for their offshore movement prior to maturity.

Temperature Effects on Oxygen Consumption and Osmoregulation

Metabolic rate of most poikilotherms is related to temperature (Prosser 1973). The lowest test temperature that we used (18° C) approached as closely as our facilities permitted the 16° C at which *P. aztecus* is reported to exhibit little growth (St. Amant et al. 1966). The highest test temperature approaches the shrimp's lethal limit (Zein-Eldin and Griffith 1969) and is seldom experienced in Louisiana estuaries. The oxygen consumption rates of shrimp increased linearly as temperature increased, and rates for both sizes increased in a similar manner (Figure 1).

[7]Bishop, J. M., and M. H. Shealy, Jr. 1977. Biological observations on commercial penaeid shrimps caught by bottom trawl in South Carolina estuaries, February 1973 - January 1975. S.C. Wildl. Mar. Resour. Dep., Mar. Res. Div., Tech. Rep. 25, 97 p.

The Q_{10}'s [oxygen consumption at (T + 10) ° C/oxygen consumption at T° C] are presented in Table 9. Although there are minor differences at different temperature ranges, the average Q_{10}'s are nearly equal and very close to the average 1.7 obtained by Scholander et al. (1953) for *P. brasiliensis* tested at 25° and 30° C. Wolvekamp and Waterman (1960) stated that generally Q_{10} values increase as the temperature decreases, but an increase was not obvious in this study.

TABLE 9.—Q_{10}'s for two sizes of *Penaeus aztecus*; oxygen consumption data averaged over all test salinities.

Size (g)	Temperature (°C)	Q_{10}
3.7	18-28	1.59
3.7	23-33	1.63
6.7	18-28	1.71
6.7	23-33	1.63
Mean	18-28	1.65
Mean	23-33	1.63

Temperature effects at tested salinities were not uniform. In 10 and 20‰ S, oxygen consumption increased significantly as temperature increased (Figure 1, Table 2), but in 30‰ S, oxygen consumption peaked at 28° C and decreased at 33° C. This reduction indicates a possible detrimental effect on *P. aztecus* when both salinity and temperature are high. The osmoregulatory abilities of *P. aztecus* are reduced at 33° C (Figures 2, 3), and salinity effects appear to become increasingly important. Other studies have also indicated reduced responses of *P. aztecus* tested at high temperatures. Survival of juveniles (10-50 mm TL) was <80% at temperatures >28° C at 25‰ S (Zein-Eldin and Aldrich 1965; Zein-Eldin and Griffith 1969). Rates of growth (mass) of postlarvae in salinities >25‰ were less at 32° C than at 25° C (Zein-Eldin and Aldrich 1965). Brown shrimp acclimated to 32° C were more sensitive to temperature change than those acclimated to 18° or 25° C and showed reduced osmoregulatory abilities in salinities <10‰ (Venkataramiah et al. footnote 4).

The possibility exists that oxygen consumption rates at 33° C and 30‰ S are a reflection of reduced dissolved O_2 concentration. That is, at 33° C, oxygen is less soluble in 30‰ S than in 10 or 20‰ S, and the shrimp's oxygen consumption may be proportional to the oxygen concentration. To test this hypothesis, the difference between the average oxygen consumption in 20 and 30‰ S at 33° C was calculated and compared with the difference between the oxygen available in the test chamber at 20 and 30‰ at 33° C (Table 10). The decrease of

TABLE 10.—Calculation of oxygen available to *Penaeus aztecus* and consumed at 20 and 30‰ salinity (S) and 33° C; m = mass.

O_2 available (mg h^{-1}) at 20‰ S	15.62
O_2 available (mg h^{-1}) at 30‰ S	14.06
Difference (mg O_2 h^{-1})	1.56
Average O_2 consumption mg·g wet $m^{-1}\cdot h^{-1}$ for shrimp at 20‰S	0.54
Average mass (g) of shrimp	5.10
Average O_2 consumption (mg h^{-1}) per shrimp	2.75
Average O_2 consumption mg·g wet $m^{-1}\cdot h^{-1}$ for shrimp at 30‰ S	0.49
Average mass (g) of shrimp	5.47
Average O_2 consumption (mg h^{-1}) per shrimp	2.68
O_2 consumption difference between 20 and 30‰ S (mg O_2 h^{-1})	0.07

total oxygen consumption between 20 and 30‰ was <0.1 mg h^{-1} and is not of similar magnitude to the oxygen-available difference of 1.56 mg h^{-1}; the differences indicate that *P. aztecus* is an oxygen regulator. Also the saturated oxygen concentration at 30‰ S and 33° C is well above the stress level of 2 ppm obtained by Egusa (1961) for *P. japonicus*. Therefore the decrease in dissolved oxygen resulting from the increased salinity does not appear to be responsible for the reduced rate of oxygen consumption of brown shrimp in 30‰ S and 33° C.

As temperature increased to 33° C, hemolymph osmolality tended toward that of the external medium for shrimp tested in 10 and 30‰ S (Figure 3). Williams (1960) found the osmoregulatory abilities of *P. aztecus* were significantly less at 8.8° C than at 28° C. Thus it appears that as temperature approaches environmental extremes, osmoregulatory abilities are impaired, and shrimp tend toward osmoconformity. *Penaeus aztecus* was able to maintain homoiosmoticity at 20‰ over the tested temperatures (Figure 3), indicating that at high temperatures (33° C) and a moderate salinity, osmoregulatory processes are not adversely affected.

Energy Considerations

The metabolic energy expenditure of shrimp can be calculated from knowledge of their oxygen consumption rates and their metabolic substrate (indirect calorimetry). Because shrimp are omnivorous (Williams 1955; Mistakidis 1957; Eldred et al. 1961; Pérez Farfante 1969; Moriarty 1977), a combination of carbohydrate, lipid, and protein as the shrimp's metabolic substrate should give a reasonable estimate of the oxygen-consumption/energy-expenditure relationship. At standard conditions, combustion of 1 g of carbohydrate, lipid, or protein with 1 l of oxygen yields 5,007,

4,686, or 4,500 cal, respectively (Giese 1968). The caloric value of each of these sources varies <6% from the mean. Therefore, for every milligram of oxygen consumed, about 3.31 cal will be liberated. A 6.7 g *P. aztecus* utilizes 0.87 and 3.75 mg O_2 h^{-1} at rest and during activity at 25° C, which translates to 2.88 and 12.41 cal h^{-1}. (The caloric expenditure during activity is calculated from the maximum oxygen consumption over a 15-min period.) Other average energy expenditures of *P. aztecus* at selected conditions are presented in Table 11.

TABLE 11.—Mean rates of oxygen consumption and energy expenditures of *Penaeus aztecus* at each test temperature averaged over all test salinities; m = mass.

Size (g)	Temperature (°C)	mg O_2 / g wet $m \cdot h$	calories / g wet $m \cdot h$
3.7	18	0.32	1.06
3.7	23	0.36	1.19
3.7	28	0.51	1.69
3.7	33	0.57	1.89
6.7	18	0.27	0.89
6.7	23	0.34	1.13
6.7	28	0.45	1.49
6.7	33	0.53	1.75

About 80% of a penaeid shrimp's mass is water,[8] so the dry mass of a 3.7 and a 6.7 g shrimp approaches 0.74 and 1.34 g, respectively. A gram of dried whole *Metapenaeus monoceros* yields 3,066 cal upon combustion (Qasim and Easterson 1974); thus the energy content of a 3.7 g *P. aztecus* is about 2,269 cal and that of a 6.7 g shrimp, about 4,108.

If a 6.7 g shrimp maintains a resting state for 24 h at 25° C, then a minimum of 69 cal will be utilized just for maintenance. This is about 1.7% of its total caloric content or 0.11 g wet mass equivalent. Therefore, a 6.7 g shrimp must daily assimilate a minimum of 1.7% of its body wet mass of equal caloric value food to maintain itself at rest. If a maximum state of activity were continued for 24 h (oxygen consumption = 0.56 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$, then approximately 298 cal would be expended. This is more than 7.2% of the 6.7 g shrimp's total caloric content. Shrimp obviously do not maintain a continuous state of maximum activity, and their mean daily energy expenditure is probably 3-4% of body caloric content.

Oxygen consumption averaged over all test salinities and at 23° and 28° C during the fourth 15-min test period was 0.40 and 0.37 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ for 3.7 and 6.7 g shrimp (Bishop 1974). These two shrimp sizes and water temperatures are characteristic of Barataria Bay, La. during May (St. Amant et al. 1966), and an average oxygen consumption rate of 0.38 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ should be a conservative estimate of routine oxygen consumption for inshore shrimp during this time period. Because *P. aztecus* buries itself in the substrate during the day (Williams 1965), we calculated daily caloric expenditures based on a routine state of metabolism for 12 h and a resting state for 12 h. Using the average value of 0.38 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ for routine oxygen consumption and 0.13 mg $O_2 \cdot$g wet $m^{-1} \cdot h^{-1}$ for standard metabolism for 5.2 g *P. aztecus* (average of 3.7 and 6.7 g shrimp), a daily caloric expenditure of 105 cal is obtained. This is about 3.3% of a 5.2 g shrimp's caloric content and supports the assumption of a 3-4% expenditure of their body wet mass per 24 h.

St. Amant et al. (1966) estimated that *P. aztecus* grew an average of 1 mm d^{-1} while in the estuaries, which represents a daily gain in wet mass of 0.18 g (Fontaine and Neal 1971) or 110 cal in potential energy.

Because shrimp feed on a variety of materials in the estuary (Williams 1955; Dall 1968; George 1974), assimilation rates probably vary widely depending on the food ingested and its chemical composition. Assimilation efficiency calculated on a mass basis may differ from that based on calories, and a range of efficiencies would be expected in natural conditions. As assimilation efficiency decreases, maintenance energy increases, but the point of diminishing returns is not known. Condrey et al. (1972) determined from laboratory experiments that shrimp of the genus *Penaeus* assimilated 33-74% of the ingested food mass, and Jones (1973) reported 25-40% assimilation rates from shrimp feeding naturally in Airplane Lake. Using extremes of these percentages and assuming that assimilation rates for mass and calories are similar and that *P. aztecus* is primarily a detrital consumer in Louisiana estuaries, first order approximations are possible for daily ingestion rates (Table 12).

Assimilation (A) of food energy must equal the sum of that for respiration (R), stored energy (growth G), and excretion (E) (see Table 12). Assimilated food is derived from food ingested (I). If the energy assimilation efficiency ($A/I \times 100$) is assumed to be 34%, a 5.2 g shrimp must consume about 638 cal d^{-1} at observed growth rates [G +

[8]H. C. Loesch, marine biologist, 1232 Dahlia St., Baton Rouge, LA 70808, unpubl. data 13 November 1974.

$R + E = A$; 110 + 105 + 2 = 217 cal d^{-1}; $I = A/0.34$ = 638 cal d^{-1}]. This is equivalent to 1.10 g wet *Spartina alterniflora* detritus [assuming 3,760 cal/dry g (Gosselink and Kirby 1974) and 84.4% water[9]], or about 20.0% of the shrimp's body mass per day. Daily growth rates of brown shrimp have been reported as rapid as 3.3 mm (Ringo 1965). This is more than three times the rate used for our calculations and would substantially increase the amount of ingested food and consequently the percent of food mass intake relative to body mass.

TABLE 12.—Daily calorie values for energy ingested (I) and that utilized for growth (G), respiration (R), and excretion (E) based on assimilation rates of 25 and 74% for a 5.2 g (live mass) *Penaeus aztecus*.

Assimilation efficiency (%)	G	R	[1]E	I
25	110	105	2	868
74	110	105	2	293

[1]Calculated from Nelson et al. (1977) and Brafield and Solomon (1972).

Qasim and Easterson (1974) obtained caloric assimilation efficiencies as high as 96.84% for *M. monoceros*, but they fed shrimp small particle detritus, which they settled from estuarine waters. This detritus was composed of a substrate of "fine silt and sand" (Qasim and Sankaranarayanan 1972), and its caloric value was nearly an order of magnitude less than that of *S. alterniflora* detritus (Gosselink and Kirby 1974). The low caloric detritus used in Qasim and Easterson's experiments may be responsible for the high assimilation efficiencies (assimilation calculated on ingested mass would probably be less efficient). We believe that the wide range of assimilation efficiencies used in our calculations are representative of most wild shrimp even if efficiencies for ingested mass and calories differ considerably. Also, diets of shrimp are not readily ascertained and more refined estimates may not be practical. Shrimp grown in intensive culture situations and fed a prepared diet, however, exist in relatively stable conditions; energy budgets for these shrimp could be more accurately determined and used to reduce feeding costs and possibly to increase production.

The wide tolerance of *P. aztecus* to temperature and salinity allows it to make maximum use of estuaries. Although we obtained evidence indiciating that larger shrimp can regulate hypoosmotically to a better degree than smaller shrimp, smaller shrimp can readily grow and survive Gulf salinities (Hoese 1960; Zein-Eldin 1963). Thus during years when shrimp populations are unusually dense in estuaries, shrimp can emigrate from the estuaries to Gulf waters at a size less than that of shrimp during average population years. This may reduce competition for space and food in the nursery areas (Parker 1970) and result in greater estuarine shrimp production. The suitability of estuaries as nursery grounds for shrimp results from several important circumstances including food abundance (Zein-Eldin 1963; Copeland and Bechtel 1974), protection (Hoese 1960), cover (Williams 1955; Giles and Zamora 1973), substrate (Williams 1958), absence of competition between juveniles and adults, and to a lesser degree, the shrimp's osmoregulatory abilities.

[9]Unpublished data of senior author.

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