

The pond's shape matters: differential growth, physiological condition and survival of epibenthic *Farfantepenaeus aztecus* postlarvae

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Abstract

As a function of the water quality provided by square, circular and oval experimental ponds, the growth, survival and oxygen requirements in epibenthic postlarvae of *Farfantepenaeus aztecus* were analysed in relation to their routine metabolism and apparent heat increment. Temperature, oxygen concentration, pH and salinity were measured daily in two experimental ponds of each shape. The postlarvae oxygen consumption during two 24-h cycles, their growth, physiological condition and survival and the productivity in the ponds were estimated. Low values of pH, oxygen concentration and phyto-benthos productivity, and reduced postlarvae relative growth and survival were observed in the square ponds. We suggest that the latter results from a deficient water circulation related to the effect of the pond's shape on dissolved oxygen levels and, consequently, on growth and survival. The postlarvae routine metabolism, including feeding, varied between 1.91 and 2.25 mg O₂ h⁻¹g⁻¹ wet weight, whereas the minimum oxygen concentration needed in the ponds is approximately 4.25 mg O₂ L⁻¹. These conditions were achieved in the oval ponds concurrent with higher survival and growth values, in which individuals distributed randomly, for which we suggest that oval-shaped ponds could be the most adequate for the culture of this and other penaeid species.

Keywords: aquaculture, experimental culture, Gulf of México, marine invertebrates, Penaeidae

Introduction

The necessity of exploiting new protein sources for humans nutrition has led to the development of culture of marine invertebrates. Among these, the penaeid shrimp culture has represented an important option because of their high growth rate and high economic value (Gaudy & Sloane 1981; Orbe & Arias 1987). In México, shrimp culture is concentrated largely on the Northwest (Gulf of California) and the Pacific coast, and is based fundamentally on *Litopenaeus vannamei* (Boone 1931) (Vázquez-Domínguez, González-Cano & Arenas 1998; Páez-Osuna & Ruiz-Fernández 2005; González-Ocampo, Morales, Cáceres-Martínez, Ramírez-Aguirre, Hernández-Vázquez, Troyo-Dieguez & Ortega-Rubio 2006). In the Gulf of México, the white shrimp, *Litopenaeus setiferus* (Linnaeus 1767), and the brown shrimp, *Farfantepenaeus aztecus* (Ives 1891), represent important resources for shrimp culture (Orbe & Arias 1987; Casillas-Hernández, Magallón-Barajas, Portillo-Clarck & Páez-Osuna 2006; Casillas-Hernández, Nolasco-Soria, García-Galano, Carrillo-Farnes & Páez-Osuna 2007); *F. aztecus* is also considered to be a major component of the Gulf of México shrimp fishery (Saoud & Davis 2003). However, for a comprehensive shrimp culture development, it is critical that we understand its environmental requirements, and also that we increase the knowledge about shrimp biology, behaviour and physiology (Saoud & Davis 2003; Casillas-Hernández *et al.* 2006, 2007).

One of the basic problems for shrimp culture is the maintenance of suitable water and substrate

conditions in the culture tanks or ponds, which depend mainly on factors such as dissolved oxygen concentrations, temperature, pH and salinity (Bardach, Ryther & McLaren 1982; Samocha, Burkott, Lawrence, Juan, Jones & McKee 1998). These factors largely depend on the water source, water replacement rate, kind and frequency of food used, productivity and pond shape (Davidson & Summerfelt 2004; Lemonnier, Bernard, Boglio, Goarant & Cochard 2004; Casillas-Hernández *et al.* 2006, 2007).

The more frequently used ponds in semi-intensive shrimp culture are rectangular in shape, while circular ponds are more common for intensive culture (Larmoyeux & Pippet 1973; Davidson & Summerfelt 2004). Although ponds with an oval shape are not commonly used for aquaculture, it is suggested that they provide better water conditions because of improved water circulation (Baluyut 1989; Naessens, Lavens, Gómez, Browdy, McGovern-Hopkins, Spencer, Kawahigashi & Sorgeloos 1997). According to Wheaton (1982), these improved conditions are generated by an increase in the oxygen concentration and a decrease in the ammonia level, as well as a more efficient cleaning of waste products. The effects produced by these different kinds of ponds can be determined through changes in the organisms' physiological state and, consequently, in their growth and survival.

For culture, it is fundamental to know the animal's energetic metabolism, that is, the acquisition and utilization of energy under specific conditions (Bishop, Gosselink & Stone 1980; Taylor & Spicer 1991). Respiratory metabolism is considered to be a good indicator of an animal's general physiological activity; hence, it is appropriate for quantifying its energetic expenditure (Gaudy & Sloane 1981; Díaz, Espina, Rosas, Sánchez, Venegas & Díaz-Iglesia 1989; Hervant, Mathieu, Garin & Fréminet 1995). Accordingly, it is possible to estimate the energy requirements at routine levels of activity by measuring the organisms' oxygen consumption; this also allows an adequate control of the culture conditions in order to satisfy these requirements (Bishop *et al.* 1980; Díaz *et al.* 1989). Although different studies have been conducted on shrimp oxygen consumption in culture (Bishop *et al.* 1980; Gaudy & Sloane 1981; Ramos & Oliva 1984; Dall 1986; Dall & Smith 1986), the minimum dissolved oxygen requirements for optimal growth and survival, particularly in relation to the organisms' routine metabolism and feeding activity, have been scarcely studied (McGraw, Teichert-Coddington, Rouse & Boyd 2001).

Considering the importance of assessing and developing technology for shrimp aquaculture in the

Gulf of México, the aim of the present study was to evaluate the adequate oxygen concentration required for metabolic activity and its relation to growth, physiological condition and survival of epibenthic postlarvae of *F. aztecus*, as a function of the environmental conditions provided by ponds of three different shapes: square, circular and oval.

Material and methods

Capture and maintenance

The brown shrimp epibenthic postlarvae, *F. aztecus* Ives, were captured by trawling (Pullen, Mock & Ringo 1968) at the south zone of the Tamiahua Lagoon, which is located in the state of Veracruz, México (21°06'–22°06' N y 97°23'–97°46' W). The postlarvae were transported to the laboratory, which was located directly along the lagoon, and identified using the Williams (1959) and Ringo and Zamora (1968) identification keys. Fifty-four postlarvae were selected, encompassing a total length range from 1.5 to 2.5 cm, weighed to the nearest 0.05 g and placed in the experimental ponds. The weight of the selected individuals ranged from 0.3 to 1.4 g wet weight (ww).

We used six fibreglass ponds of square, circular and oval shapes (two of each), provided with water entrances and drain pipes (Fig. 1). They were filled with water provided directly from the lagoon. The water flow was regulated with plastic keys located at the water entrances, which maintained a constant 1.5 L h^{-1} flow, in order to guarantee a daily water replacement between 25% and 40% of the total water volume. The ponds were located outdoors and were provided with a partial shadow to avoid excessive solar radiation and to maintain similar environmental conditions for all ponds. The bottom of the ponds was covered with a 2-cm sand layer to provide a substratum for the organisms. The postlarvae were placed in the ponds as follows: 10 in the square, nine in the circular and eight in the oval ponds, to maintain a density of 10–12 postlarvae m^{-2} (Wyban, Lee, Sato, Sweeney & Richards Jr 1987).

During 24 days, including 5 days for acclimation, four water parameters were measured in the ponds: temperature, oxygen concentration [both with a polarographic sensor YSI 54 (YSI, Yellow Spring, OH, USA) ARC; $\pm 1 \text{ }^\circ\text{C}$], salinity ($\pm \text{‰}$) and pH (with a Corning potentiometer; ± 0.1); the latter was also recorded in the substratum. The ponds were superficially divided into quadrants (Fig. 1) to conduct measurements homogeneously, that is, the parameters were measured in every quadrant, daily at 09:00 and 19:00 hours. Also,

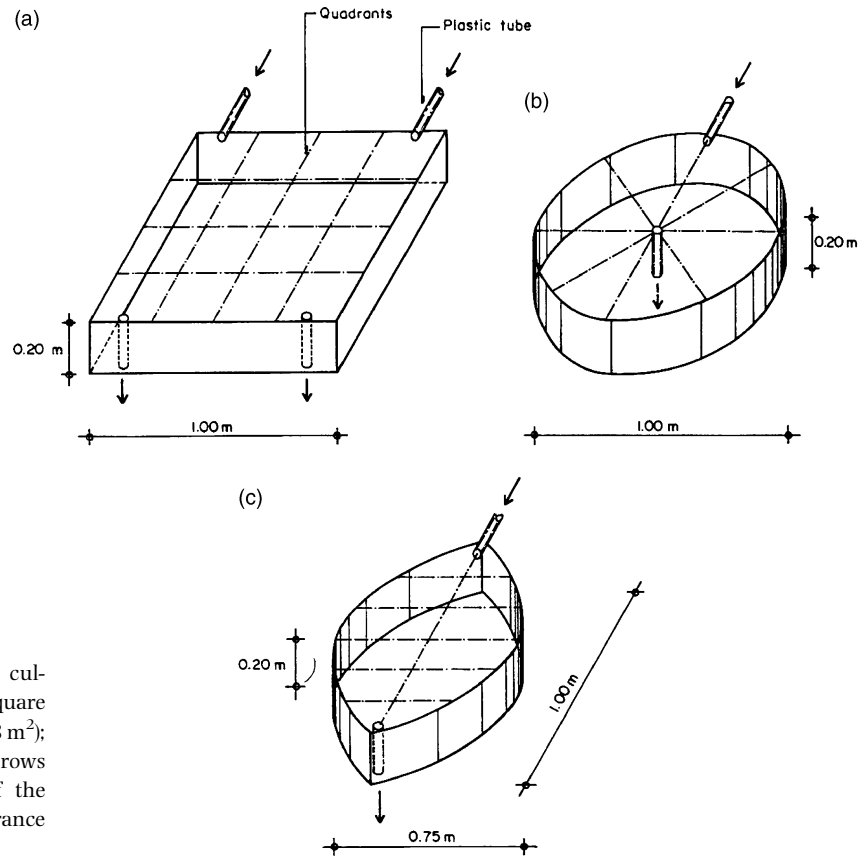


Figure 1 Experimental culture ponds used: a = square (1 m^2); b = circular (0.78 m^2); c = oval (0.39 m^2). The arrows indicate the direction of the water flow from the entrance to the drain pipe.

the postlarvae were fed twice a day with powder-balanced food at a rate of 10% of their weight on each occasion. This food contained 44% protein, 27% carbohydrates and 8% lipids.

Oxygen consumption

The shrimp's routine metabolic rate was estimated by measuring the oxygen consumption of the postlarvae during two 24-h cycles. A total of 18 dark bottles supplied with water from the main source were used as closed respirometers and one individual was placed inside each respirometer (three from each pond, total of 18 dark bottles). The bottles were maintained immersed in the ponds during cycles. Each cycle was initiated at approximately 16:00 hours: firstly, the initial oxygen concentration was recorded in each respirometer and they were immediately sealed; 90 min later, they were opened, a second measurement was taken, the water was completely replaced and the respirometers were sealed again. This procedure was performed every 90 min during the 24 h and the temperature was recorded during every mea-

surement. Individuals in the respirometers fasted during 29 h and were fed just once, at 14:00 hours, before the last cycle measurement. Finally, each animal was weighed to obtain ww measurements.

The oxygen consumption values were estimated by the difference between the dissolved oxygen concentration measured before and after the respirometers were sealed, i.e. after 90 min. These results were corrected with data derived from a control bottle with no shrimp. The metabolic amplitude, expressed as $\text{mg O}_2\text{ h}^{-1}\text{ g}^{-1}$ of ww, was obtained by the difference between the highest and the lowest oxygen consumption values, without considering the oxygen consumption from fed organisms. Finally, the difference between the postlarvae oxygen consumption after being fed and the highest consumption value from the unfed organisms was considered to be the apparent heat increment (Beamish & Trippel 1990).

Productivity

Net productivity in each pond was determined using the white and dark bottle system (Brower & Zar 1977),

in order to know the relationship between oxygen consumption and dissolved oxygen concentration variability in the ponds produced by photosynthesis. Thus, productivity was calculated as the difference in oxygen concentration between bottles at each 90-min lapse during both 24-h cycles mentioned above. Oxygen concentration was measured using a polarographic sensor YSI 54 ARC (0.01 mg L^{-1}), previously calibrated with oxygen-saturated seawater at 26°C .

Specifically, photosynthetic productivity (PP; $\text{mg O}_2 \text{ h}^{-1}$) was estimated as (Brower & Zar 1977):

$$\text{PP} = C_1 - C_2/\text{DT}$$

where C_1 and C_2 are the final oxygen concentrations in the light and dark bottle respectively; DT is the time between the initial and the final oxygen concentration measurements.

Net productivity (NP) was calculated as:

$$\text{NP} = \text{PP} - R$$

R being respiration ($\text{mg O}_2 \text{ h}^{-1}$) and estimated as:

$$R = C_i - C_2/\text{DT}$$

where C_i is the initial oxygen concentration in the water (environment) and C_2 is the final oxygen concentration in the dark bottle.

Growth, survival and distribution

Shrimp survival in each pond was determined by registering the number of postlarvae that died during the experimental period. The growth of the surviving postlarvae, at the end of the experiment, was estimated by the difference between the initial and the final weight. Also, in order to determine the energetic balance, the assimilation (As ; $\text{J week}^{-1} \text{ g}^{-1}$) was calculated using data from growth rate (biomass production: P) and oxygen consumption (routine metabolic budget: R)

$$R = \text{metabolic amplitude} \\ + \text{apparent heat increment.}$$

Assimilation was calculated using the equation (Lucas 1993):

$$As = R + P$$

Respiration values were obtained transforming oxygen consumption values to Joules using an oxygen coefficient factor of 14.3 J mg^{-1} oxygen consumed and expressed as $\text{J week}^{-1} \text{ g}^{-1}$ taking into account biomass in each treatment. Biomass production was transformed using a value of 26.32 J g^{-1} living weight and expressed as $\text{J week}^{-1} \text{ g}^{-1}$ (Rosas, Sán-

chez, Soto, Escobar & Bolongaro-Crevenna 1992; Rosas, Sánchez, Díaz, Soto, Gaxiola, Brito, Baes & Pedroza 1995).

Finally, the distribution of individuals in each pond was recorded daily, in the morning and afternoon, in order to observe whether the animals had a preference for any particular zone.

Statistical analyses

Differences between and within ponds for the four parameters measured (temperature, oxygen, pH and salinity) and the postlarvae oxygen consumption were tested using a Kruskal–Wallis test (Zar 1998). For a more detailed analysis of the temporal and spatial differences in these parameters and also for the productivity results, a two-factor analysis of variance without replication was used (Tabachnick & Fidell 1989). Finally, the mean-variance coefficient statistical test and the Blackman significance test (Ghent & Zucker 1990) were used to analyse the distribution pattern of organisms in the ponds.

Results

Physicochemical variables

No significant differences were found in water temperature and salinity among ponds ($P > 0.05$), likely because the water supply came from the same lagoon site. Nevertheless, it was observed that these two parameters did change within the ponds during the experimental period (between weeks), with ranges from 20 to 27.5°C and from 17% to 22% respectively ($P < 0.05$) (Fig. 2).

When comparing the dissolved oxygen and pH values inside each pond in relation to experimental time, no statistical differences were found ($P > 0.05$). For this reason, values for oxygen and pH concentrations were pooled to compare each pond and were analysed in relation to weekly changes (Table 1, Fig. 3). Pooled dissolved oxygen values were significantly different between ponds during the second and third weeks (Fig. 3): oval ponds were significantly different from both square and circular ponds but not from each other. Despite the observed variations between ponds of the same shape, particularly for the third week, the two square ponds showed no significant differences and these were different in relation to the circular ponds. The highest value was

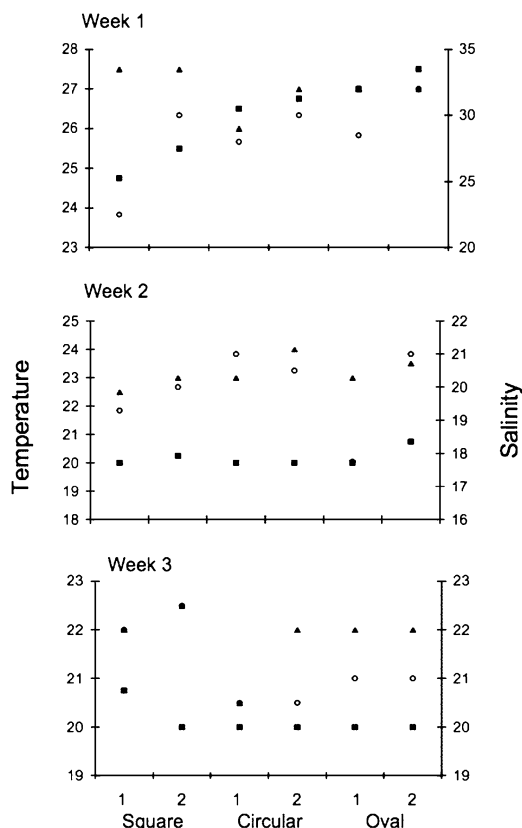


Figure 2 Temperature and salinity median values, the former in the morning and afternoon, the latter measured only once, during 3 weeks in the experimental ponds. Squares: temperature in the morning; triangles: temperature in the afternoon; circles: salinity.

observed in the oval pond ($7.1 \text{ mg O}_2 \text{ L}^{-1}$) and the lowest in the square pond ($2.7 \text{ mg O}_2 \text{ L}^{-1}$; $P < 0.05$).

Water pH values fluctuated from 8.46 to 9.68 and were significantly different between the morning and afternoon and among the different ponds ($P < 0.05$) (Table 1). For the substratum pH, significant differences were observed only during the second week, in which values fluctuated from 8.1 to 8.62 ($P < 0.05$), with lower values in the square ponds and higher values in the oval ponds.

Oxygen consumption

No significant differences were found for the postlarvae oxygen consumption values among ponds ($P > 0.05$); thus, values were pooled for each experimental cycle (Table 2). However, these values were

Table 1 Variation of superficial and substratum pH (median values), in the morning and afternoon, during 3 weeks in the experimental ponds

Ponds	Square		Circular		Oval	
	1	2	1	2	1	2
Week 1						
pH sup morning	8.65	8.77	8.79	8.73	8.71	8.71
pH sup afternoon	8.63	8.53	8.62	8.46	8.49	8.54
pH sub morning	8.38	8.42	8.58	8.57	8.48	8.54
pH sub afternoon	8.24	8.26	8.19	8.36	8.22	8.22
Week 2						
pH sup morning	8.72	8.88	9.31	9.68	9.55	9.55
pH sup afternoon	8.59	8.53	8.70	8.97	8.96	8.99
pH sub morning	8.26	8.25	8.47	8.50	8.43	8.62
pH sub afternoon	8.28	8.10	8.25	8.51	8.27	8.37
Week 3						
pH sup morning	9.12	9.79	9.79	9.98	9.79	9.69
pH sup afternoon	8.79	8.81	8.91	9.13	9.07	8.94
pH sub morning	8.46	8.41	8.67	8.60	8.19	8.45
pH sub afternoon	8.50	8.48	8.54	8.56	8.50	8.79

pH sup, superficial; pH sub, substratum.

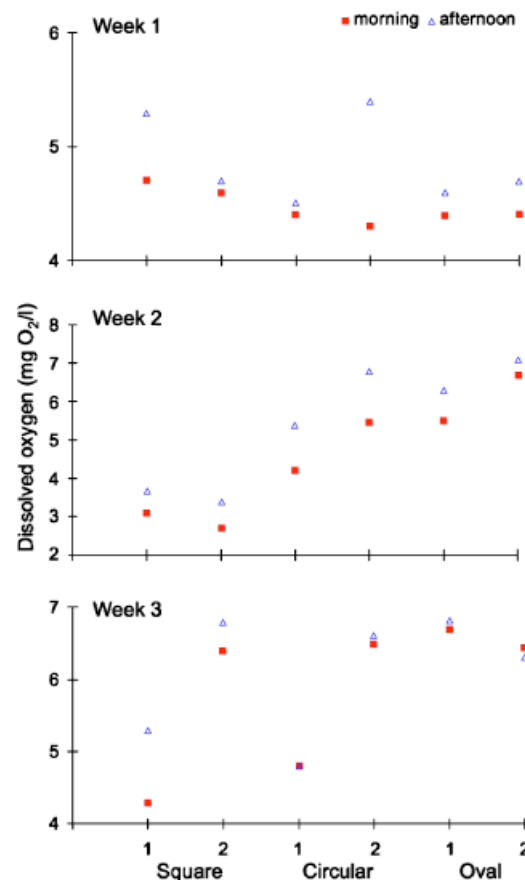


Figure 3 Dissolved oxygen variation (median values), in the morning and afternoon, during 3 weeks in the experimental ponds.

Table 2 Oxygen consumption of *Farfantepenaeus aztecus* (Ives 1891) postlarvae ($\text{mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$) in the experimental ponds during two 24-h cycles

Oxygen consumption			
Hour	Cycle 1	Hour	Cycle 2
1600	1.29 ± 0.42	1800	1.26 ± 0.54
1730	1.41 ± 0.56	1900	0.80 ± 0.57
1900	1.32 ± 0.56	2000	1.50 ± 0.74
2030	1.34 ± 0.49	2100	1.47 ± 0.35
2200	1.29 ± 0.33	2300	1.36 ± 0.54
2330	1.33 ± 0.53	2430	1.34 ± 0.53
0100	1.32 ± 0.52	0200	1.38 ± 0.30
0300	1.07 ± 0.25	0400	1.25 ± 0.39
0500	0.52 ± 0.14	0600	1.01 ± 0.29
0900	1.00 ± 0.28	0900	1.32 ± 0.44
1030	1.06 ± 0.38	1100	2.05 ± 0.77
1200	1.57 ± 0.33	1300	1.68 ± 0.57
1400	1.57 ± 0.35	1500	1.86 ± 0.64
1530	1.91 ± 0.73		

Median and 95% confidence interval are shown. $N = 18$ shrimps h^{-1} .

also not significantly different between cycles ($P > 0.05$).

Oxygen consumption values during the 24 h were significantly different among hours during each cycle ($P < 0.05$; Fig. 4). The maximum value for the first cycle was recorded at 15:30 hours ($1.91 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$) and the minimum towards 05:00 hours ($0.52 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$). For the second cycle, the highest value was at 11:00 hours and the lowest at 19:00 hours (2.05 and $0.8 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$, respectively, Table 2, Fig. 4).

The temperature changes during both 24-h cycles corresponded to the natural temperature oscillation between day and night, being less in the second cycle ($16\text{--}23^\circ\text{C}$) than in the first ($21\text{--}27^\circ\text{C}$; $P < 0.05$). The postlarvae oxygen consumption variation coincided with the temperature oscillation recorded, in which the greatest oxygen consumption was found during the highest temperature values, in both the first and the second cycles. Nevertheless, the temperature difference recorded between the first and second cycles showed no significant effects on the postlarvae oxygen consumption (Fig. 4).

Respiratory metabolism, growth and energetic balance

No significant differences were observed for the estimated metabolic amplitude between cycles (1.05 and

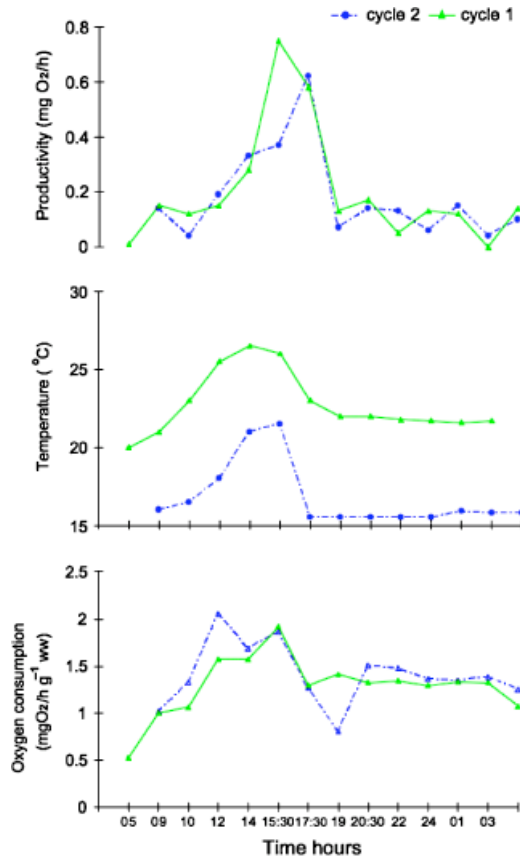


Figure 4 Net productivity, temperature and *Farfantepenaeus aztecus* (Ives 1891) postlarvae oxygen consumption in the experimental ponds during two 24-h cycles.

$1.06 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$, first and second cycles respectively; $P > 0.05$; Table 3), neither for the observed metabolic rate increment after feeding, which showed values from 1.91 to $2.25 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$ and from 2.05 to $2.24 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$, first and second cycles respectively ($P > 0.05$; Table 3). As a result, the apparent heat increment observed varied between 0.34 (first cycle) and $0.19 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$ (second cycle), which were significantly different ($P < 0.05$; Table 3).

The postlarvae routine metabolic budget (R) was estimated by adding the metabolic amplitude and the apparent heat increment of each cycle; no significant differences were observed between the first and second cycles (1.39 and $1.25 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$ respectively; $P > 0.05$). However, a tendency towards lower routine metabolic values during colder days (second cycle) was observed (Table 3).

Postlarvae relative growth was higher in the oval ponds (50% and 20% , first and second pond) and the

Table 3 Bioenergetic balance of *Farfantepenaeus aztecus* (Ives 1891) in non-fed and fed postlarvae. Oxygen consumption is expressed as metabolic amplitude (non-fed) and as apparent heat increment and routine metabolic budget (fed). Median and 95% confidence interval are shown

	Oxygen consumption					
	Cycle 1		Cycle 2			
	Square		Circular		Oval	
	1	2	1	2	1	2
Metabolic amplitude*	1.05 ± 0.23		1.06 ± 0.28			
Fed shrimps	1.91–2.25 ± 0.52		2.05–2.24 ± 0.42			
Apparent heat increment	0.34 ± 0.02		0.19 ± 0.01			
Routine metabolic budget†	1.39 ± 0.41		1.25 ± 0.28		1.39 ± 0.41	
mg O ₂ h ⁻¹ g ⁻¹ ww	1.39 ± 0.41		1.25 ± 0.28		1.39 ± 0.41	
R = J week ⁻¹ g ⁻¹	834.8 ± 100 ^b		1001 ± 89 ^b		667.9 ± 60 ^b	
Biomass production	60 ± 9		30 ± 4		729 ± 66	
g week ⁻¹	60 ± 9		30 ± 4		729 ± 66	
P = J week ⁻¹ g ⁻¹	582 ± 70 ^a		537 ± 60 ^a		3494 ± 454 ^c	
As‡ = R + P J week ⁻¹ g ⁻¹	1417		1538		1164 ± 151 ^c	
R/As (%)	59		52		16	
P/As (%)	41		48		84	

Different letters mean statistical differences at $P < 0.05$ level.

*Metabolic amplitude = maximum oxygen consumption – minimum oxygen consumption in a 24 h cycle.

†Routine metabolic budget = metabolic amplitude + apparent heat increment.

‡Assimilated energy.

lowest corresponded to the square ponds (9% and 8.3%; Fig. 4). Concerning survival, the higher percentage was observed in ponds 4, 5 and 6 (circular and oval) with 66.6%, 62.5% and 87.5%, respectively, and the lowest survival in square pond 1 (20%) and 2 (30%; Fig. 4).

Respiratory metabolism (J week⁻¹ g⁻¹) showed differences between ponds (Table 3). Respiration (R) values obtained in circular and oval ponds were significantly lower than that observed in the other treatments. Also, biomass production was higher in animals maintained in oval ponds compared with the rest (Table 3). As a consequence, energy channelled to production (P) was higher in animals cultured in oval ponds, followed by animals maintained in circular ones (Table 3), while small values were obtained from animals maintained in square tanks ($P < 0.05$; Table 3). Moreover, energy channelled to R also changed with the type of experimental pond, showing high values (59% to 65%) in animals maintained in square ponds and low values in those from oval ponds (16% to 27%) in relation to the assimilated energy (R/As) (Table 3); intermediate values were recorded in animals in circular ponds (34% to 52%). An inverse relation was observed in P as a proportion of

the assimilated energy (P/As), where higher values were observed in animals from oval ponds (Table 3).

Net productivity and distribution

Regarding net productivity, significant differences were found among hours during each cycle ($P < 0.05$; Fig. 4). However, when comparing this productivity among ponds and between cycles, no significant differences were observed ($P > 0.05$; Table 4).

Maximum net productivity in the first cycle was 0.75 mg O₂ h⁻¹, which coincides with the hour at which the maximum oxygen consumption was recorded (15:30 hours). For the second cycle, the maximum value was 0.62 mg O₂ h⁻¹, which was recorded 3 h after maximum oxygen consumption of postlarvae (Table 4, Fig. 4).

In relation to distribution, the organisms aggregated on both sides of the square ponds, between the water entrance and the drain pipe; in the circular ponds, the distribution was more homogeneous, although a higher number of organisms near the ponds' borders and the area adjacent to the drain pipe were observed. Inside the oval ponds, the animals

Table 4 Net productivity in the experimental ponds ($\text{mg O}_2 \text{ h}^{-1}$) during the 24-h cycles

Hours	Net productivity		
	Cycle 1	Cycle 2	
16:00	0.58	18:00	0.62
17:30	0.13	19:00	0.07
19:00	0.17	20:00	0.14
20:30	0.05	21:00	0.13
22:00	0.13	23:00	0.06
24:00	0.12	24:30	0.15
01:00	0.00	02:00	0.04
03:00	0.14	04:00	0.10
05:00	0.01	06:00	0.14
09:00	0.15	09:00	0.04
10:00	0.12	11:00	0.19
12:00	0.15	13:00	0.33
14:00	0.28	15:00	0.37
15:30	0.75		
<i>F</i> -test (ponds) 0.38427		<i>F</i> -test (ponds) 0.60101	
<i>F</i> -test (hours) 22.576*		<i>F</i> -test (hours) 12.698*	
<i>F</i> -test (cycles) 0.01308			
<i>F</i> -test (hours) 35.254*			

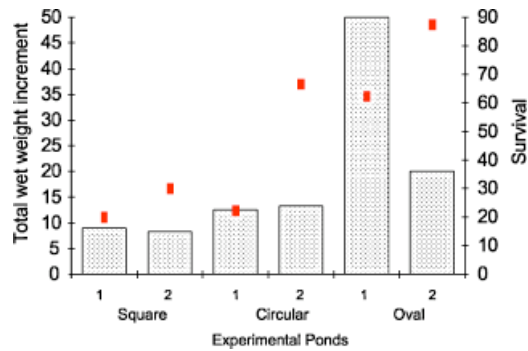
* $P < 0.05$.

showed no preference for a particular quadrant ($P > 0.05$). The results showed that the distribution of postlarvae was statistically different among ponds: contagious, i.e. in patches, in the square ponds (> 1) while, in the circular and oval shapes, it was a random distribution (< 1) (Blackman 1942; Ghent & Zucker 1990).

Discussion

The oxygen consumption rate of crustaceans can be modified by several environmental factors, among which temperature, salinity, pH, dissolved oxygen concentrations, size and feeding are the most important (Kulkarni & Joshi 1980; Gaudy & Sloane 1981; Dall & Smith 1986; Taylor & Spicer 1991; Lemonnier *et al.* 2004). Furthermore, regarding oxygen consumption rhythmicity, penaeid shrimps and other crustaceans tend to be, throughout their life cycle, more active at night than during the day, i.e. they exhibit an endogenous circadian rhythm influenced by photoperiod and tide cycles (Dall 1986; Du Preez, Chen & Hsien 1992; Rosas *et al.* 1992; Pontes, Arruda, Menezes & de Lima 2006; Aguzzi, Ramírez-Llodra, Telesnicki & Camps 2007) (Fig. 5).

This oxygen consumption variation dependent on the day–night cycle was not reflected in the present results, because the higher postlarvae oxygen consumption in both cycles was observed during day

**Figure 5** *Farfantepenaeus aztecus* (Ives 1891) postlarvae growth (% wet weight increment) and survival (%) in the culture ponds during the experimental period. Bars indicate weight increment and squares are survival values.

hours. The postlarvae acclimation to the culture conditions could have concealed the influence of these factors on the oxygen consumption, considering that individuals were neither exposed to tide cycles nor fed at night (Bishop & Herrnkind 1976; Bishop *et al.* 1980; Pontes *et al.* 2006). Also, given that postlarvae were fed only during day hours, results would suggest that their circadian rhythm was influenced by an opportunistic feeding conduct (Reynolds & Casterlin 1979; Nunes, Goddard & Gesteira 1996).

Accordingly, Hughes (1968) reported a reduction in the nocturnal activity in *Farfantepenaeus duorarum* shrimps when they were administered food during the day, with which the circadian activity rhythm was broken. Also, some organisms are more active during the day despite the inhibitive factor of high light intensity; for example, *L. vannamei* reared in aquaria showed substrate exploration, which characterizes the search for food, in both dark and light phases, with a most intense peak 7 h after the light phase onset (Pontes *et al.* 2006). Consequently, these results suggest that shrimps' rhythmicity, under culture conditions, can be manipulated by means of feeding. This can be used to improve culture results by feeding the animals when pond conditions are better, that is, when adequate oxygen concentrations and higher productivity exist.

Many crustaceans, because of their poikilothermic nature, are able to change their metabolic rate as a function of temperature; this can be appreciated as an increment in the animals' oxygen consumption at higher temperatures and a decrease at lower temperatures (Bishop *et al.* 1980; Ramos & Oliva 1984; Allan, Froneman & Hodgson 2006; Daoud, Chabot, Audet & Lambert 2007). The latter agrees with our results regarding temperature and postlarvae oxygen consumption changes during both 24-h cycles, in

which the highest oxygen consumption was observed at higher temperatures, and vice versa. Moreover, our results indicate that routine metabolism may be affected when measured in animals recently fed, because the processes of absorption, digestion and transportation of food materials induce an increment in oxygen consumption. As a consequence, it is possible to associate routine metabolism and feeding activity with the requirements of dissolved oxygen levels necessary to guarantee the organisms' growth and survival.

Broom (1970) and Dall (1986) reported that *E. aztecus* and *Penaeus esculentus* can tolerate oxygen levels of 2 ppm, although with some stress index, and that 4 ppm levels or above are the most indicated. McGraw *et al.* (2001) found higher survival rates in *L. vannamei* and *L. stylirostris* postlarvae at an oxygen level of $4.6 \text{ mg O}_2 \text{ L}^{-1}$. Accordingly, our results for the routine metabolism, including feeding, indicated that the minimum oxygen concentration required by the postlarvae fluctuates between 1.91 and $2.25 \text{ mg O}_2 \text{ h}^{-1} \text{ g}^{-1} \text{ ww}$. Thus, the dissolved oxygen level in the culture ponds should be above $4.25 \text{ mg O}_2 \text{ L}^{-1}$, considering that a concentration below $2 \text{ mg O}_2 \text{ L}^{-1}$ may induce stress (Du Preez *et al.* 1992; McGraw *et al.* 2001).

The dissolved oxygen concentration in a culture pond depends on the productivity and water replacement rate. In relation to this, the net productivity values, expressed as produced oxygen, were lower than the requirements of the shrimp's metabolic routine budget. For this reason, we examined the phytobenthos productivity, which is crucial in shallow systems like the ponds used in the present study (Spotts 1984). The phytobenthos productivity (Ppb) was estimated in each pond (expressed as $\text{mg O}_2 \text{ L}^{-1}$) considering the oxygen concentration in the ponds ($[\text{O}_2]$) at higher phytoplankton productivity hours (Ppp) as follows:

$$\text{Ppb} = [\text{O}_2] - \text{Ppp}$$

Because the phytoplankton productivity was not distinct in the three different ponds, it is possible to infer that the observed oxygen concentration differences may be associated with the phytobenthos. The phytobenthos productivity estimated was statistically distinct among ponds with higher values in the oval ($6.18 \text{ mg O}_2 \text{ h}^{-1}$) and lower in circular ($5.22 \text{ mg O}_2 \text{ h}^{-1}$) and square ponds ($3.28 \text{ mg O}_2 \text{ h}^{-1}$; $P < 0.05$).

The phytobenthos may be a good indicator of the conditions of a culture pond because it will only develop under adequate sediment conditions (Spotts 1984). Likewise, the physicochemical characteristics of the sediment are related to water circulation

patterns, because an efficient rechange of waste and non-consumed food materials depends on these patterns. Consequently, a deficient water replacement generally promotes the growth of micro-organisms that degrade waste material, which produce anaerobic microhabitats that tend towards acidification (low pH values) and inhibit phytobenthos development (Spotts 1984; Lemonnier *et al.* 2004).

The results of the present study suggest that the pond's shape, because of different water circulation patterns, may modify the dissolved oxygen levels, pH and productivity as well as the postlarvae growth and survival. Furthermore, the fact that the phytobenthos productivity values, correlated with the observed pH and dissolved oxygen values, were higher in oval ponds suggests a greater phytobenthos establishment in these ponds. On the other hand, the square ponds showed low pH values (i.e. a tendency towards acidification) and low dissolved oxygen levels.

The presence of 'dead zones' within culture ponds creates preferential areas for the organisms' establishment (Spotts 1984; Lemonnier *et al.* 2004), which is supported by our results regarding postlarvae distribution patterns in the different ponds. Although no significant differences were observed among quadrants within ponds for the physicochemical factors measured, postlarvae distribution was different inside each pond, which suggests that the organisms are capable of detecting subtle differences not registered by the measuring instruments. Also, these dead zones decrease the real amount of accessible area or space for organisms; this increases the density and induces physiological stress that negatively impacts the animals' growth and survival. Accordingly, we observed that both physiological state indicators (the postlarvae energetic balance and survival) were higher in the oval ponds. A higher proportion of assimilated energy was channelled to biomass production by shrimp maintained in the oval ponds, confirming that in such ponds the animals can be energetically more efficient, because they are able to waste less energy in their response to environmental stress.

Furthermore, the amount of dissolved oxygen in the water is an important condition to guarantee an adequate postlarvae growth and is basically determined by the water productivity (Bardach *et al.* 1982; Wyban *et al.* 1987). Hence, it is likely that the differences observed in postlarvae growth and survival are related to the oxygen concentration variations produced by the different circulation patterns in each experimental pond.

Conclusion

From the present study, we can conclude that the lowest pH levels and low oxygen concentrations observed in the square ponds may be directly related to a deficient water circulation, which also produced a decrease in the phytobenthos productivity. This was also appreciated as a reduced postlarvae relative growth, which was higher in the circular and oval ponds, likely as a result of their better water quality.

The minimum requirements of dissolved oxygen for the postlarvae spontaneous activity and for their adequate performance in culture found in the experimental ponds suggest that an oxygen concentration of approximately $4.25 \text{ mg O}_2 \text{ L}^{-1}$ should be sufficient. Also, the present results indicate that the phytoplankton as well as the phytobenthos productivity may be considered to be essential elements for the promotion of these requirements.

The ponds' circulation patterns influenced dissolved oxygen levels, growth and survival; additionally, the minimum oxygen requirements for spontaneous activity established by the routine metabolic budget measurement of *F. aztecus* postlarvae were found in the oval ponds. Hence, our results suggest that oval-shaped ponds could be the most adequate for the culture of this and other penaeid species.

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References

Aguzzi J., Ramírez-Llodra E., Telesnicki G. & Camps M. (2007) Day-night activity rhythm of the cold seep shrimp *Alvinocaris stactophila* (Caridea: Alvinocarididae) from the Gulf of Mexico. *Journal of the Marine Biological Association of the United Kingdom* **8**, 1175–1180.

Allan E.L., Froneman P.W. & Hodgson A.N. (2006) Effects of temperature and salinity on the standard metabolic rate (SMR) of the caridean shrimp *Palaemon peringueyi*.

Journal of Experimental Marine Biology and Ecology **337**, 103–108.

Baluyut E.A. (1989) *Aquaculture systems and practices: a selected review*. United Nations Development Programme. Publications Division, Food and Agriculture Organization of the United Nations (FAO). Project reports ADCP/REP/89/43. Rome, Italy.

Bardach J.E., Ryther J.H. & McLaren W.O. (1982) *Acuicultura: Crianza y Cultivo de Organismos Marinos y de Agua Dulce*. Wiley-Interscience, New York, NY, USA.

Beamish F.W. & Trippel E.A. (1990) Heat increment: a static or dynamic dimension in bioenergetic models? *American Fisheries Society* **119**, 649–661.

Bishop J.M. & Herrnkind W.F. (1976) Burying and molting of pink shrimp, *Penaeus duorarum* (Crustacea: Penaeidae) under selected photoperiods of white light and UV-light. *The Biological Bulletin* **150**, 163–182.

Bishop J.M., Gosselink J.G. & Stone J.H. (1980) Oxygen consumption and hemolymph osmolality of Brown shrimp, *Penaeus aztecus*. *Fishery Bulletin* **78**, 741–757.

Blackman G.E. (1942) Statistical and ecological studies in the distribution of species in plant communities. I. Dispersion as a factor in the study of changes in plant populations. *Annals of Botany London, n.s.* **6**, 351–370.

Broom J.G. (1970) *Shrimp culture*. Proceedings of the First Annual Workshop of the World Mariculture Society, February 9–10, Louisiana State University, Louisiana, USA, pp. 63–68.

Brower J. & Zar J. (1977) Aquatic productivity. In: *Field and Laboratory Methods for General Ecology* (ed. by J.E. Brower), pp. 156–160. Brown Company Publishers, Iowa, USA.

Casillas-Hernández R., Magallón-Barajas F., Portillo-Clarck G. & Páez-Osuna E. (2006) Nutrient mass balances in semi-intensive shrimp ponds from Sonora, Mexico using two feeding strategies: trays and mechanical dispersal. *Aquaculture* **258**, 289–298.

Casillas-Hernández R., Nolasco-Soria H., García-Galano T., Carrillo-Farnes O. & Páez-Osuna E. (2007) Water quality, chemical fluxes and production in semi-intensive Pacific white shrimp (*Litopenaeus vannamei*) culture ponds utilizing two different feeding strategies. *Aquaculture Engineering* **36**, 105–114.

Dall W. (1986) Estimation of routine metabolic rate in a penaeid prawn, *Penaeus esculentus* Haswell. *Journal of Experimental Marine Biology and Ecology* **96**, 57–73.

Dall W. & Smith D.M. (1986) Oxygen consumption and ammonia-n excretion in fed and starved tiger prawns, *Penaeus esculentus* Haswell. *Aquaculture* **55**, 23–33.

Daoud D., Chabot D., Audet C. & Lambert Y. (2007) Temperature induced variation in oxygen consumption of juvenile and adult stages of the northern shrimp, *Pandalus borealis*. *Journal of Experimental Marine Biology and Ecology* **347**, 30–40.

Davidson J. & Summerfelt S. (2004) Solids flushing, mixing, and water velocity profiles within large (10 and 150 m³)

- circular 'Cornell-type' dual-drain tanks. *Aquacultural Engineering* **32**, 245–271.
- Díaz F., Espina S., Rosas C., Sánchez A., Venegas C. & Díaz-Iglesia E. (1989) Ritmo respiratorio y amplitud metabólica del camarón café *Penaeus aztecus* (Tamiagua, México) con ablación de los pedúnculos oculares. *Revista de Investigaciones Marinas* **10**, 27–39.
- Du Preez H.H., Chen H.-Y. & Hsien C.-S. (1992) Apparent specific dynamic action of food in grass shrimp, *Penaeus monodon* Fabricius. *Comparative Biochemistry and Physiology* **103A**, 173–178.
- Gaudy R. & Sloane L. (1981) Effect of salinity on oxygen consumption in postlarvae of the penaeid shrimps *Penaeus monodon* and *P. stylirostris* without and with acclimation. *Marine Biology* **65**, 297–301.
- Ghent A.W. & Zucker N. (1990) A readily interpreted index of dispersion, based on nearest-neighbor analyses. *American Midland Naturalist* **124**, 184–187.
- González-Ocampo H.A., Morales L.F.B., Cáceres-Martínez C., Ramírez-Aguirre H., Hernández-Vázquez S., Troyo-Díez E. & Ortega-Rubio A. (2006) Shrimp aquaculture environmental diagnosis in the semiarid coastal zone in Mexico. *Fresenius Environmental Bulletin* **15**, 659–669.
- Hervant F., Mathieu J., Garin D. & Fréminet A. (1995) Behavioral, ventilatory, and metabolic responses to severe hypoxia and subsequent recovery of the hypogean *Niphargus rhenorhodanensis* and the epigeal *Gammarus fossarum* (Crustacea: Amphipoda). *Physiological Zoology* **68**, 223–244.
- Hughes D.A. (1968) Factors controlling emergence of pink shrimp (*Penaeus duorarum*) from the substrate. *The Biological Bulletin* **34**, 48–59.
- Kulkarni G.K. & Joshi P.K. (1980) Some aspects of respiratory metabolism of a penaeid prawn, *Penaeus japonicus* (Bate) (Crustacea, Decapoda, Penaeidae). *Hydrobiologia* **75**, 27–32.
- Larmoyeux J.D. & Pipper R.G. (1973) Evaluation of circular tanks for Salmonid production. *Progressive Fish-Culturist* **35**, 122–131.
- Lemonnier H., Bernard E., Boglio E., Goarant C. & Cochard J.C. (2004) Influence of sediment characteristics on shrimp physiology: pH as principal effect. *Aquaculture* **240**, 297–312.
- Lucas A. (1993) *Bioénergétique des Animaux Aquatiques*. Masson, Paris, France.
- McGraw W., Teichert-Coddington D.R., Rouse D.B. & Boyd C.E. (2001) Higher minimum dissolved oxygen concentrations increase penaeid shrimp yields in earthen ponds. *Aquaculture* **199**, 311–321.
- Naessens E., Lavens P., Gómez L., Browdy C.L., McGovern-Hopkins K., Spencer A.W., Kawahigashi D. & Sorgeloos P. (1997) Maturation performance of *Penaeus vannamei* co-fed *Artemia* biomass preparations. *Aquaculture* **155**, 87–101.
- Nunes A.J.P., Goddard S. & Gesteira T.C.V. (1996) Feeding activity patterns of the Southern brown shrimp *Penaeus subtilis* under semi-intensive culture in NE Brazil. *Aquaculture* **144**, 371–386.
- Orbe A. & Arias A. (1987) *Métodos de Cultivo del Camarón en México*. Secretaría de Pesca. Segunda edición, Mexico.
- Páez-Osuna F. & Ruiz-Fernández A.C. (2005) Environmental load of nitrogen and phosphorus from extensive, semi-intensive, and intensive shrimp farms in the Gulf of California ecoregion. *Bulletin of Environmental Contamination and Toxicology* **74**, 681–688.
- Pontes C.S., Arruda M.D., Menezes A.A.D. & de Lima P.P. (2006) Daily activity pattern of the marine shrimp *Litopenaeus vannamei* (Boone 1931) juveniles under laboratory conditions. *Aquaculture Research* **37**, 1001–1006.
- Pullen E.J., Mock C.P. & Ringo R.D. (1968) A net for sampling the intertidal zone of an estuary. *Limnology and Oceanography* **13**, 200–202.
- Ramos T.L. & Oliva M. (1984) Metabolismo energético en juveniles del camarón rosado *Penaeus notialis* (Pérez-Farfante, 1967). *Revista de Investigaciones Marinas* **5**, 35–55.
- Reynolds W.W. & Casterlin M.E. (1979) Diel activity of the pink shrimp *Penaeus duorarum*. *Hydrobiologia* **66**, 223–226.
- Ringo R. & Zamora G. (1968) A penaeid postlarval character of taxonomic value. *Bulletin of Marine Science* **18**, 471–476.
- Rosas C., Sánchez A., Soto L., Escobar E. & Bolongaro-Crevenna A. (1992) Oxygen consumption and metabolic amplitude of Decapod crustaceans from the northwest continental shelf of the Gulf of Mexico. *Comparative Biochemistry and Physiology* **101A**, 491–496.
- Rosas C., Sánchez A., Díaz E., Soto L., Gaxiola G., Brito R., Baes M.I. & Pedroza R. (1995) Oxygen consumption and ammonia excretion of *Penaeus setiferus*, *P. schmitti*, *P. duorarum* and *P. notialis* postlarvae fed purified test diets: effects of protein level on substrate metabolism. *Aquatic Living Resources* **8**, 161–169.
- Samocha T.M., Burkott B.J., Lawrence A.L., Juan Y.S., Jones E.R. & McKee D.A. (1998) Management strategies for production of the Atlantic white shrimp *Penaeus setiferus* as bait shrimp in outdoor ponds. *Journal of the World Aquaculture Society* **29**, 211–220.
- Saoud I.P. & Davis D.A. (2003) Salinity tolerance of brown shrimp *Farfantepenaeus aztecus* as it relates to postlarval and juvenile survival, distribution, and growth in estuaries. *Estuaries* **26**, 970–974.
- Spotts D. (1984) The development of Shigueno-Style shrimp culture in Southern Japan. *Aquaculture Magazine* **10**, 26–28.
- Tabachnick B.G. & Fidell L.S. (1989) *Using Multivariate Statistics*, 2nd edn. Harper Collins Publishers, New York, NY, USA.
- Taylor A.C. & Spicer J.I. (1991) Acid-base disturbances in the hemolymph of the prawns, *Palaemon elegans* and *Palaemon serratus* (Crustacea: Decapoda) during exposure to hypoxia. *Comparative Biochemistry and Physiology* **98A**, 445–452.

- Vázquez-Domínguez E., González-Cano J. & Arenas V. (1998) Áreas prioritarias marinas de uso de recursos. In: *Regiones Prioritarias Marinas de México* (ed. by L. Arriaga-Cabrera, E. Vázquez-Domínguez, J. González-Cano, R. Jiménez Rosenberg, E. Muñoz López & V. Aguilar Sierra), pp. 127–150. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, Mexico.
- Wheaton FW. (1982) *Acuicultura. Diseño y construcción de sistemas* Agt, S.A., México.
- Williams A.B. (1959) Spotted on brown shrimp postlarvae *Penaeus* in North Carolina. *Bulletin of Marine Science* **9**, 281–290.
- Wyban J.A., Lee C., Sato V.T., Sweeney J.N. & Richards W.K. Jr (1987) Effect of stocking density on shrimp growth rates in manure-fertilized ponds. *Aquaculture* **61**, 23–32.
- Zar J.H. (1998) *Biostatistical Analysis*, 4th edn. Prentice-Hall, Englewood Cliffs, NJ, USA.