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Research Article

Energetic Physiology of the Caribbean Estuarine Clam *Polymesoda arctata* (Deshayes, 1854) Exposed to Different Environmental Conditions under Laboratory

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The estuarine clam *Polymesoda arctata* is one of the commercially important bivalves of the Caribbean, which is currently considered endangered by overexploitation and habitat loss. With the purpose of gain knowledge about its environmental requirements for aquaculture and restocking purposes, its energetic physiology performance was evaluated under laboratory conditions in response to the variation of food concentration and water quality registered in their natural habitat. Different physiological variables, including the rates of filtration (FR), pseudofeces production (RR), ingestion (IR), absorption (AR), oxygen consumption (OCR), and ammonium excretion (UR), as well as absorption efficiency (AE) and scope for growth (SFG), were estimated in five successive experiments, where different concentration levels of food or particulate organic matter (1.8, 4.0, 7.3, and 13.0 mg L^{-1} equivalent to 2.3, 5.0, 9.3, and 16.6 mg of the microalgae *Isochrysis galbana* L^{-1}), salinity (5, 15, and 25‰), temperature (27, 29, and 32°C), ammonia concentration (7, 48 and 77 μg NH_3-N L^{-1}), and dissolved oxygen saturation (24, 48, and 93%) were tested. Intermediate conditions of food concentration, salinity, and temperature resulted in higher values for most of the physiological variables measured, except for the higher values of OCR and UR obtained at low salinity, as well as the higher values of AE, AR, and SFG measured at low temperatures. Most of the physiological variables increased under conditions of lower ammonia concentrations and higher dissolved oxygen saturation in the water. Although this species exhibited physiological plasticity, tolerance, and enough energy for growth and reproduction under the environmental variations of its habitat, it also showed a high sensitivity to its environment, having the highest SFG values under intermediate conditions of particulate organic matter (7.2 mg L^{-1} or 9.3 mg of *I. galbana* L^{-1}), salinity (15‰), and temperature (27–29°C), as well as at low ammonia concentration (7 μg NH_3-N L^{-1}) and high dissolved oxygen saturation (93%). Based on our results, we recommended the use of this values for reproductive conditioning of broodstock and juvenile culture in laboratory, and also as an input for selecting areas for aquaculture farming and restocking experiments.

1. Introduction

Polymesoda arctata (Deshayes, 1854) is a clam of the Cyrenidae family, with a geographic distribution that extends across the estuaries of the Caribbean, between Costa Rica and the Gulf of Venezuela [1, 2]. This species can reach 50 mm in length, and lives either buried in soft bottoms (up to 3 cm) or over grave bottoms below the tide line [1, 3, 4], at depths of 2.4 m or less, at densities as high as 150–700 ind m^{-2} [3–5]. The environments where this species is found are characterized by media values of seston concentrations between 20 and 250 mg L^{-1} (equivalent to between 2 and 13 mg L^{-1} of particulate organic matter), water temperatures between 27 and 32°C, salinities between 5 and 30‰, pH values between 7.0 and 8.5, dissolved oxygen concentrations between 1.6 and 7.3 mg O_2 L^{-1} (equivalent to 25 and 95% saturation, respectively), and ammonium concentrations between 100 and 500 μg N-NH_4^+ L^{-1} (equivalent to ammonia concentrations of 9 and 43 μg NH_3-N L^{-1}, respectively) [3, 5, 6]. This species has been reported to be

gonocoric in populations present in Venezuela, and sequential hermaphrodite in populations present in Colombia, with a first maturity size of 15–29 mm in shell length, and a continuous reproductive cycle, with the highest spawning rates associated with salinity changes [4]. The natural populations of this species have been historically exploited for human consumption at local and regional levels, thus being an important resource for artisanal fisheries in the estuarine areas of the Caribbean [5]. In recent decades, however, a decrease of the average densities of its natural populations has been observed, which can be attributed to overexploitation and habitat loss [4, 5]. Therefore, *P. arctata* is currently considered as an endangered species [7].

Some of the tools used to date for conservation purposes and sustainable use of threatened mollusk species are aquaculture and restocking of natural populations with hatchery-produced juveniles [8–10]. In order to accomplish this, gaining knowledge about the food and water quality requirements of the species under laboratory conditions remains critical. An approach to determine such requirements is the estimation of the scope for growth (SFG) or energetic balance, which is a physiological index that represents the amount of energy that is available in an organism to grow and reproduce. This is considered a good predictor of the rates of growth and reproduction, as well as an indicator of the state of condition, i.e., the fitness of an organism [11–13]. In addition, this index is very precise and sensitive to environmental variations [13], which makes it suitable to be used in the determination of optimal environmental conditions, even within narrow ranges of variation, such as temperature in tropical species.

Growth, gonadal development, survival, and/or SFG in bivalves are mainly affected by factors such as food availability (type and concentration) and water quality (salinity, temperature, concentration of oxygen and ammonia). In general, better results have been found feeding with live microalgae, especially *Isochrysis galbana* compared to other microalgal species [14–21]. For the other factors, the greatest performances can be very variable and dependent on the clam species and the environmental conditions of its habitat. That is the case of food concentration, with optimum results between 0.65 and 30 mg L^{-1} of particulate organic matter [22–28], salinities between 7 and 42‰ [29–33], temperatures between 5 and 32°C [28, 29, 34–39], ammonia concentrations lower than between 20 and 400 μg NH_3-N L^{-1} [40–42], and oxygen saturation levels of 50% and above [31, 43–48].

In order to establish the main appropriate environmental conditions for the maintenance of the Caribbean estuarine clam, and thus laying the foundations for aquaculture and population restocking, the present study evaluated the energetic physiology of this species in response to the variations of the food concentration, as well as the levels of salinity, temperature, ammonia concentration, and dissolved oxygen between the values registered in its habitat.

2. Materials and Methods

2.1. Obtaining and Acclimatizing Bivalves. A total of 292 specimens of *P. arctata* (21–46 mm in shell length, and 0.09–0.78 g in dry weight) were manually captured in the Lagoon Complex of Ciénaga Grande de Santa Marta (CGSM) (10° 43' N and 74° 27' W). The individuals captured were transferred in wet and cold conditions (18°C) to the Mollusks and Microalgae Laboratory of the Universidad del Magdalena, located in Taganga, Santa Marta, Colombia (11° 16' N, 74° 11' W). Once in the laboratory, the individuals were cleaned of epibionts and sediment debris using a brush, and then were individually tagged. They were kept for at least 2 weeks in plastic baskets suspended in rectangular tanks (300 L), at a density of 30% or less of bottom coverage. The tanks were supplied with microfiltered UV-treated water (1 μm), with aeration and maintained at a temperature of 27.0 ± 0.5°C, salinity of 5.0 ± 1.0‰, dissolved oxygen of 5.02 ± 0.1 mg O_2 L^{-1} (96 ± 1% saturation), pH of 8.1 ± 0.1, and ammonia concentration of 7.3 ± 0.4 μg NH_3-N L^{-1}. The microalgae *I. galbana* was supplied as feed by drip (1.083×10^6 cells hr^{-1} $animal^{-1}$), in order to maintain a constant concentration of 1.0×10^5 cells mL^{-1} (5 mg L^{-1}) in the tank, taking into account that the clearance rate at this concentration of microalgae is 0.26 L hr^{-1} $animal^{-1}$. The water in the tanks was fully replaced daily, cleaning the walls and bottom of the tanks with a sponge.

2.2. Experimental Design. A total of five consecutive experiments were performed with adult *P. arctata* individuals acclimatized to laboratory conditions (31 ± 2 mm in length, and 0.3 ± 0.01 g in dry weight), testing different levels of microalgae concentration (2.3, 5.0, 9.3, and 16.6 mg L^{-1} of *I. galbana*, equivalent to 1.8, 4.0, 7.3, and 13.0 mg L^{-1} of particulate organic matter), salinity (5, 15, and 25‰), temperature (27, 29, and 32°C), ammonia concentration (7, 48 and 77 μg NH_3-N L^{-1}), and oxygen saturation (24, 48 and 93%). Each treatment was applied to at least 30 individuals for 8 days, keeping them in the same culture system, with similar food and water quality conditions than those used during acclimatization, but with slight variations for each experiment, applying the same experimental conditions in which the highest values of SFG were observed in previous experiments (Table 1). In order to obtain the desired levels of ammonia and oxygen concentration in the water, appropriate amounts of ammonia (NH_3) (25%, PanReac AppliChem) and nitrogen gas (N_2) were added to the stocking tanks containing the water for each treatment, which were maintained under constant homogenization (using a recirculation pump and aeration) and physicochemical monitoring. During the last day of the experiments, physiological measurements were performed in 12 animals randomly chosen between those that showed feeding activity (open valves and extended siphons). For measuring the feeding rates, the animals were individually placed in rectangular acrylic chambers (0.8 L), following the design of Riisgård [49], in order to minimize water recirculation and sedimentation of microalgae. The chambers were maintained with a continuous water flow (120 mL min^{-1}), and under the same experimental condition of food and water quality. Additionally, there was also a control chamber with a pair of empty valves, from where reference water samples were collected to measure microalgae concentrations and, thus, correct the effect of food retention and sedimentation.

Table 1: Food conditions and water quality parameters applied in successive experiments to evaluate the energetic physiology of *P. arctata*.

Experiment	Treatments	*I. galbana* concentration ($mg\,L^{-1}$)	Salinity (‰)	Temperature (°C)	Ammonia concentration ($\mu g\ NH_3\text{-}N\ L^{-1}$)	Oxygen saturation (%)
I. galbana concentration	2.3	2.3 ± 0.2	5.0 ± 0.5	27.0 ± 0.5	7.3 ± 0.4	97 ± 1.0
	5.0	5.0 ± 0.8	5.0 ± 1.0	27.0 ± 1.0	2.8 ± 0.4	97 ± 1.0
	9.3	9.3 ± 1.5	5.0 ± 0.5	27.0 ± 0.3	3.0 ± 0.6	96 ± 1.0
	16.6	16.6 ± 0.6	6.0 ± 0.5	26.0 ± 0.5	5.8 ± 0.7	96 ± 1.0
Salinity	5	9.3 ± 1.5	5.0 ± 0.5	27.0 ± 0.3	3.0 ± 0.6	96 ± 1.0
	15	10.0 ± 0.4	15.0 ± 1.0	27.0 ± 0.1	7.1 ± 1.1	95 ± 1.0
	25	10.3 ± 1.9	25.0 ± 0.5	27.0 ± 0.2	7.0 ± 0.3	90 ± 1.0
Temperature	27	10.0 ± 0.4	15.0 ± 1.0	27.0 ± 0.3	7.1 ± 1.0	95 ± 1.0
	29	9.1 ± 0.9	15.0 ± 1.0	29.0 ± 0.3	7.1 ± 1.1	93 ± 1.0
	32	10.9 ± 0.3	15.0 ± 0.5	32.0 ± 0.1	7.3 ± 0.8	91 ± 1.0
Ammonia concentration	7	9.1 ± 0.9	15.0 ± 1.0	29.0 ± 0.3	7.1 ± 1.1	93 ± 1.0
	48	9.1 ± 1.6	15.0 ± 1.0	29.0 ± 0.1	47.7 ± 3.1	91 ± 1.0
	77	9.1 ± 0.9	15.0 ± 1.0	29.0 ± 0.1	77.0 ± 5.0	90 ± 1.0
Oxygen saturation	24	9.0 ± 0.6	15.0 ± 1.0	29.0 ± 0.1	12.0 ± 2.1	24 ± 1.0
	48	9.3 ± 0.9	15.0 ± 0.5	29.0 ± 0.5	11.0 ± 2.2	48 ± 1.0
	93	9.1 ± 0.9	15.0 ± 1.0	29.0 ± 0.3	7.1 ± 1.1	93 ± 1.0

2.3. Characterization of Microalgae. The microalgae *I. galbana* supplied as food came from the collection of marine microalgae of the Universidad del Magdalena (UMC-MA), and was cultured in batch systems using the F/2 medium of Guillard [50]. The average number of cells present in 1 mg dry weight ($27{,}838 \pm 695\ mg^{-1}$ cells) and the organic content ($79 \pm 10\%$) were determined from the characterization of triplicate culture samples (500 mL), which were homogenized and analyzed simultaneously in different terms. Cell concentration (mL^{-1} cells) was estimated using a Z2 Counter-BECKMAN particle counter. Dry weight of total particulate matter (TPM) ($mg\ L^{-1}$), particulate organic matter (POM) ($mg\,L^{-1}$), and particulate inorganic matter (PIM) ($mg\,L^{-1}$) was also determined, following the gravimetric methodology of Strickland and Parsons [51], using Whatman GF/F fiberglass filters with a pore diameter of 1 μm. In addition, the average energy content of *I. galbana* ($14.40 \pm 0.17\ J\,mg^{-1}$) was determined from triplicate algal samples (1 g), which were extracted by washing the microalgae with ammonium formate, followed by centrifugation and drying (70°C for 24 hr), and subsequent analysis in a microheater (IKA® C 200 and precision of $1\ J\,mg^{-1}$).

2.4. Determination of Physiological Variables. The feeding physiological variables were estimated following the biodeposition method described by Iglesias et al. [52], and validated by Navarro and Velasco [53]. Samples of water with microalgae flowing through the control chamber were collected every 2 hr (1 L). The total amount of feces (material ejected by the animal after being ingested but not absorbed) and pseudofeces (material embedded in mucus, which was filtered and rejected by the animal but not ingested) produced by each animal were differentiated and estimated over a period of 4 hr. The dry weight of total, organic, and inorganic contents in the samples was estimated following the same gravimetric methodology used for the characterization of the microalgae. With these data, the POM and PIM of each experimental diet were estimated, as well as the rates of biodeposits production of each experimental animal, which were total (RR) ($mg\,hr^{-1}$), organic (ORR) ($mg\,hr^{-1}$), and inorganic (IRR) ($mg\,hr^{-1}$) pseudofeces production, as well as total (ER) ($mg\,hr^{-1}$), organic (OER) ($mg\,hr^{-1}$), and inorganic (IER) ($mg\,hr^{-1}$) feces production.

The feeding variables were estimated following the equations proposed by Iglesias et al. [52]. The filtration rate (FR) or amount of particulate matter that was retained in the gills per unit of time was calculated as follows:

$$\mathrm{FR}\,(mg\,hr^{-1}\,g^{-1}) = \mathrm{IFR} + \mathrm{OFR}, \quad (1)$$

$$\mathrm{IFR}\,(mg\,hr^{-1}\,g^{-1}) = \mathrm{IRR} + \mathrm{IER}, \quad (2)$$

$$\mathrm{OFR}\,(mg\,hr^{-1}\,g^{-1}) = \mathrm{IFR} \times (\mathrm{POM}/\mathrm{PIM}), \quad (3)$$

where IFR = inorganic filtration rate ($mg\,hr^{-1}\,g^{-1}$) and OFR = organic filtration rate ($mg\,hr^{-1}\,g^{-1}$).

The rate of ingestion (IR) or amount of particulate matter consumed per unit of time was calculated using the following equation:

$$\mathrm{IR}\,(mg\,hr^{-1}\,g^{-1}) = \mathrm{FR} - \mathrm{RR}. \quad (4)$$

The absorption efficiency (AE) and the absorption rate (AR), which represent the ability and the speed to transfer the ingested organic matter from the digestive tract into the body's circulation, respectively, were calculated according to the Conover method [54] following the equations of Iglesias et al. [52]:

$$AE\,(\%) = AR/OIR \times 100, \quad (5)$$

$$OIR\,(mg\,hr^{-1}\,g^{-1}) = OFR - ORR, \quad (6)$$

$$AR\,(mg\,hr^{-1}) = OIR - OER, \quad (7)$$

where OIR = organic ingestion rate ($mg\,hr^{-1}$).

After the estimation of the feeding physiological variables, the animals were individually incubated for 2 hr in hermetic acrylic chambers (0.28–0.80 L), previously washed with diluted hydrochloric acid and filled with seawater of the same quality used in each experiment but without the feed supply. There were two control chambers, in which no animals were placed. After incubation, duplicate water samples were collected from each chamber using BOD bottles (120 mL) to determine the dissolved oxygen concentrations using the Winkler method modified by Carritt and Carpenter [51]. Duplicate water samples were also collected using test tubes (5 mL) to determine the ammonium concentration by the phenol–hypochlorite method of Solorzano [55]. The ammonia concentration in the control samples was estimated following Bower and Bidwell [56]. The oxygen consumption rate (OCR) and the ammonium excretion rate (UR) were estimated based on the difference between oxygen and ammonium concentrations in experimental chambers and control chambers, respectively [57].

After finishing the experiments, the experimental individuals were euthanized by freezing and dissected for shell separation. Their soft tissues were dried at 70°C for 48 hr, and individually weighed, to standardize the physiological rates to 1 g of dry weight, using the formula of Bayne et al. [58]:

$$Yts = (1g/DW)^b \times Ye, \quad (8)$$

$$WW = LW - SW, \quad (9)$$

where Y_{ts} = physiological rate standardized to a dry weight of 1 g, Ye = nonstandardized rate, DW = dry weight of the experimental animal, WW = wet weight of the soft parts of the experimental animal, b = dependence of physiological rates on the size of the animals (Table 2), LW = live wet weight of the experimental animal, and SW = shell weight of the experimental animal. To find the values of b, the physiological variables described above were estimated in 41 animals of different sizes (21–46 mm in length, and 0.09–0.78 g in dry weight), keeping them under the same conditions used during the acclimatization of the animals to laboratory conditions.

Finally, the scope for growth (SFG) was estimated from the Widdows et al. [57] energetic balance equation, after converting standardized physiological rates to energetic equivalents:

$$SFG\,(J\,hr^{-1}\,g^{-1}) = A - (R + U), \quad (10)$$

where A = absorbed energy ($J\,hr^{-1}$) = AR ($mg\,hr^{-1}\,g^{-1}$) *energy from dietary organic matter (18.2 $J\,mg^{-1}$), R = energy expenses ($J\,hr^{-1}$) = OCR (mL O_2 $hr^{-1}\,g^{-1}$) *20.08 (J mL O_2) [59] and U = energy losses ($J\,hr^{-1}$) = UR (μg NH_4-N $hr^{-1}\,g^{-1}$) *24.8 (J μg NH_4-N) [60].

Table 2: Regression analysis between the morphological and physiological variables of *P. arctata*.

Physiological variable	Equation	*P*	R^2
WW	$1.20\ e^{0.078\ SL}$	<0.0001	97.2
DW	0.73 ln (SL)–2.14	<0.0001	90.5
SL	$4.35\ e^{3.14\ DW}$	<0.0001	91.3
FR	$3.28\ DW^{0.36}$	0.0317	15.9
IR	$2.42\ DW^{0.33}$	0.0394	9.43
AE	–	0.0898	–
AR	–	0.6864	–
RR	$0.78\ DW^{0.53}$	0.0051	25.6
OCR	$0.38\ DW^{0.52}$	<0.0001	58.6
UR	$41.32\ DW^{0.49}$	0.0120	21.2
SFG	–	0.7567	–

WW, wet weight; DW, dry weight; SL, shell length; FR, filtration rate; RR, pseudofeces production rate; IR, ingestion rate; AE, absorption efficiency; AR, absorption rate; OCR, oxygen consumption rate; UR, ammonium excretion rate; SFG, scope for growth.

2.5. Statistical Analysis. In order to establish the existence of significant differences between the media values of the physiological rates measured at different levels of microalgae concentration and water quality, a one-way analysis of variance was applied, followed by Bonferroni multirange tests. Prior to these analyses, compliance with the assumptions of homogeneity of variances (Bartlett's test) and normality (Shapiro–Wilk test) of the physiological variables was verified, and the necessary data transformations were performed for several of the rates to comply with these assumptions. In the food concentration experiment, the square root transformation was applied to the RR, and the arcsine transformation to the AE. In the salinity experiment, the logarithmic transformation was applied to the RR, while the square root was used for the FR, IR, AR, UR, and SFG. For the temperature experiment, the logarithmic transformation was applied for the FR and IR, the arcsine for the EA, and the square root for the AR and SFG. As for the ammonia concentration experiments, the logarithmic transformation was applied for the FR, RR, IR, and AR, while the rank transformation was used for the SFG. Finally, in the oxygen saturation experiment, the square root transformation was used for the AR, logarithm for the FR and IR, arcsine for the EA, and the rank transformation for the SFG. On the other hand, regression analyses were conducted between the wet and dry weight of the animals, as well as between the different physiological rates measured and dry weight, in order to find equations that better describe the interdependence of these variables, and also to obtain a better estimation of the b value to be used in the standardization of the physiological variables measured in the different experiments. Statistical analyses were performed using the software Statgraphics Centurion XVII X64, considering an alpha value of 0.05 for all significance decisions.

Table 3: Media ± standard error of the physiological variables of *P. arctata* adults feed different *I. galbana* concentrations.

Physiological variable	*Isochrysis galbana* concentration ($mg\,L^{-1}$)			
	2.3	5.0	9.3	16.6
FR ($mg\,hr^{-1}\,g^{-1}$)	3.02 ± 0.19^{b}	4.66 ± 0.56^{b}	9.27 ± 0.87^{a}	5.31 ± 0.57^{b}
RR ($mg\,hr^{-1}\,g^{-1}$)	0.62 ± 0.05^{b}	0.92 ± 0.29^{b}	1.93 ± 0.18^{a}	1.76 ± 0.14^{ab}
IR ($mg\,hr^{-1}\,g^{-1}$)	2.40 ± 0.14^{b}	3.74 ± 0.64^{b}	7.34 ± 0.84^{a}	3.56 ± 0.54^{b}
AE (%)	58 ± 8	60 ± 14	74 ± 4	63 ± 3
AR ($mg\,hr^{-1}\,g^{-1}$)	1.16 ± 0.13^{b}	2.14 ± 0.67^{b}	5.13 ± 0.71^{a}	2.34 ± 0.50^{b}
OCR ($mL\ O_2\,hr^{-1}\,g^{-1}$)	0.30 ± 0.02^{c}	0.36 ± 0.02^{bc}	0.59 ± 0.05^{a}	0.41 ± 0.03^{ab}
UR ($\mu g\ NH_4\text{-}N\,hr^{-1}\,g^{-1}$)	23.66 ± 5.03^{b}	79.87 ± 7.28^{a}	91.26 ± 6.81^{a}	55.90 ± 4.08^{b}
SFG ($J\,hr^{-1}\,g^{-1}$)	14.62 ± 2.15^{b}	29.76 ± 12.25^{b}	79.41 ± 12.16^{a}	32.88 ± 8.96^{b}

FR, filtration rate; RR, pseudofeces production rate; IR, ingestion rate; AE, absorption efficiency; AR, absorption rate; OCR, oxygen consumption rate; UR, ammonium excretion rate; SFG, scope for growth. ^{a,b,c,ab,bc}Different superscript letters indicate significant differences ($P<0.05$).

Table 4: Media ± standard error of the physiological variables of *P. arctata* adults at different salinities.

Physiological variable	Salinity (‰)		
	5	15	25
FR ($mg\,hr^{-1}\,g^{-1}$)	8.76 ± 0.82^{b}	19.75 ± 2.64^{a}	8.28 ± 0.74^{b}
RR ($mg\,hr^{-1}\,g^{-1}$)	1.93 ± 0.18^{ab}	2.54 ± 0.33^{a}	1.29 ± 0.11^{b}
IR ($mg\,hr^{-1}\,g^{-1}$)	6.83 ± 0.79^{b}	17.21 ± 2.46^{a}	7.49 ± 0.67^{b}
AE (%)	72 ± 5^{b}	90 ± 2^{a}	86 ± 2^{a}
AR ($mg\,hr^{-1}\,g^{-1}$)	4.62 ± 0.66^{b}	14.30 ± 2.30^{a}	5.88 ± 0.64^{b}
OCR ($mL\ O_2\,hr^{-1}\,g^{-1}$)	0.59 ± 0.05^{a}	0.45 ± 0.03^{b}	0.35 ± 0.02^{b}
UR ($\mu g\ NH_4\text{-}N\,hr^{-1}\,g^{-1}$)	91.26 ± 6.81^{a}	55.80 ± 8.43^{b}	18.82 ± 2.98^{c}
SFG ($J\,hr^{-1}\,g^{-1}$)	70.09 ± 11.32^{b}	249.81 ± 41.75^{a}	99.51 ± 11.65^{b}

FR, filtration rate; RR, pseudofeces production rate; IR, ingestion rate; AE, absorption efficiency; AR, absorption rate; OCR, oxygen consumption rate; UR, ammonium excretion rate; SFG, scope for growth. ^{a,b,c,ab}Different superscript letters indicate significant differences ($P<0.05$).

3. Results

3.1. Effect of Food Concentration. Most of the physiological variables, such as FR, IR, RA, OCR, UR, and SFG, presented the highest media values at an intermediate microalgal concentration of $9.3\,mg\,L^{-1}$ compared to the rest of the concentrations tested (Table 3; $P<0.05$). RR increased with increasing feed concentrations, from the lowest concentration tested ($2.3\,mg\,L^{-1}$) up to $9.3\,mg\,L^{-1}$, reaching values that remained stable even at the highest food concentrations (Table 3; $df=3$, $F=5.71$, $P=0.0025$). Conversely, AE did not vary with food concentration (Table 3; $df=3$, $F=1.19$, $P=0.3254$).

3.2. Effect of Salinity. In the treatment with the highest salinity, the animals were frequently observed with their valves closed. Several physiological variables (FR, RR, IR, RA, and SFG) exhibited higher media values at the intermediate salinity of 15‰ compared to those obtained at 5 and 25‰ (Table 4; $P<0.0001$). However, RR values in the treatment of 5‰ were intermediate, and similar to those obtained at 15 and 25‰ (Table 4; $df=2$, $F=6.32$, $P=0.0060$). The values of AE were higher at intermediate and high salinities (15 and 25‰, respectively) compared to those at 5‰ (Table 4; $df=2$, $F=7.66$, $P=0.0019$). Regarding the OCR and UR, both decreased with increasing salinity (Table 4; $P<0.0001$).

3.3. Effect of Temperature. The FR, RR, and IR media values were similar at all temperatures tested (Table 5; $df=2$, $P\geq 0.0588$), while those of the AE, AR, UR, and SFG measured in animals maintained at temperatures between 27 and 29°C were higher than that obtained at 32°C (Table 5; $P\leq 0.0143$). Respect to OCR, higher media values were presented at 29°C compared to the other temperatures tested (Table 5; $df=2$, $P\leq 0.0006$).

3.4. Effect of Ammonia Concentration. Most of the media values of the physiological variables of the clam (FR, RR, IR, AE, RA, OCR, and SFG) decreased significantly with increasing ammonia concentration in the water (Table 6; $df=2$, $P\leq 0.0007$). At the highest ammonia concentrations ($77\,\mu g\ NH_3\text{-}N\ L^{-1}$), the animals were frequently observed with their valves closed. Conversely, no significant differences in the UR were found for clams maintained at the different ammonia concentrations tested (Table 6; $df=2$, $F=2.37$, $P=0.1103$).

3.5. Effect of Oxygen Concentration. Most of the media values of the physiological variables of *P. arctata* (FR, IR, AE, AR, OCR, UR, and SFG) presented the highest values at the maximal oxygen saturation level tested (93%) when compared to those found at intermediate and low oxygenation levels (Table 7; $P\leq 0.0240$). No significant differences were

Table 5: Media ± standard error of the physiological variables of *P. arctata* adults at different water temperatures.

Physiological variable	Temperature (°C)		
	27	29	32
FR ($mg\,hr^{-1}\,g^{-1}$)	19.75 ± 2.64	21.16 ± 3.99	12.12 ± 1.27
RR ($mg\,hr^{-1}\,g^{-1}$)	2.54 ± 0.33	2.81 ± 0.49	2.85 ± 0.31
IR ($mg\,hr^{-1}\,g^{-1}$)	17.21 ± 2.46	18.63 ± 3.59	9.99 ± 1.04
AE (%)	90 ± 2^{a}	90 ± 3^{a}	73 ± 4^{b}
AR ($mg\,hr^{-1}\,g^{-1}$)	14.30 ± 2.30^{a}	15.56 ± 3.20^{a}	6.72 ± 0.98^{b}
OCR ($mL\ O_2\,hr^{-1}\,g^{-1}$)	0.45 ± 0.03^{c}	0.90 ± 0.03^{a}	0.56 ± 0.03^{b}
UR ($\mu g\ NH_4\text{-}N\,hr^{-1}\,g^{-1}$)	55.80 ± 8.43^{ab}	80.74 ± 6.36^{a}	38.88 ± 5.71^{b}
SFG ($J\,hr^{-1}\,g^{-1}$)	249.81 ± 41.75^{a}	263.20 ± 57.97^{a}	109.95 ± 17.51^{b}

FR, filtration rate; RR, pseudofeces production rate; IR, ingestion rate; AE, absorption efficiency; AR, absorption rate; OCR, oxygen consumption rate; UR, ammonium excretion rate; SFG, scope for growth. [a,b,c,ab]Different superscript letters indicate significant differences ($P<0.05$).

Table 6: Media ± standard error of the physiological variables of *P. arctata* adults at different ammonium concentration.

Physiological variable	Ammonia concentration ($\mu g\ NH_3\text{-}N\,L^{-1}$)		
	7	48	77
FR ($mg\,hr^{-1}\,g^{-1}$)	21.16 ± 3.99^{a}	6.47 ± 0.78^{b}	2.24 ± 0.36^{c}
RR ($mg\,hr^{-1}\,g^{-1}$)	2.81 ± 0.49^{a}	1.04 ± 0.11^{b}	1.01 ± 0.07^{b}
IR ($mg\,hr^{-1}\,g^{-1}$)	18.63 ± 3.59^{a}	5.60 ± 0.70^{b}	1.99 ± 0.29^{c}
AE (%)	90 ± 3^{a}	66 ± 5^{b}	52 ± 5^{b}
AR ($mg\,hr^{-1}\,g^{-1}$)	15.56 ± 3.20^{a}	3.55 ± 0.62^{b}	1.01 ± 0.22^{c}
OCR ($mL\ O_2\,hr^{-1}\,g^{-1}$)	0.90 ± 0.03^{a}	0.60 ± 0.02^{b}	0.57 ± 0.01^{b}
UR ($\mu g\ NH_4\text{-}N\,hr^{-1}\,g^{-1}$)	80.74 ± 6.36	60.62 ± 7.15	60.65 ± 7.92
SFG ($J\,hr^{-1}\,g^{-1}$)	263.20 ± 57.97^{a}	51.11 ± 11.39^{b}	5.39 ± 3.91^{c}

FR, filtration rate; RR, pseudofeces production rate; IR, ingestion rate; AE, absorption efficiency; AR, absorption rate; OCR, oxygen consumption rate; UR, ammonium excretion rate; SFG, scope for growth. [a,b,c]Different superscript letters indicate significant differences ($P<0.05$).

Table 7: Media ± standard error of the physiological variables of *P. arctata* adults at different oxygen concentration.

Physiological variable	Oxygen saturation (%)		
	24	58	93
FR ($mg\,hr^{-1}\,g^{-1}$)	6.79 ± 1.18^{b}	8.10 ± 1.07^{b}	21.16 ± 3.99^{a}
RR ($mg\,hr^{-1}\,g^{-1}$)	2.68 ± 0.47	2.31 ± 0.47	2.81 ± 0.49
IR ($mg\,hr^{-1}\,g^{-1}$)	4.11 ± 0.86^{b}	5.79 ± 0.94^{b}	18.63 ± 3.59^{a}
AE (%)	65 ± 10^{b}	64 ± 5^{b}	90 ± 3^{a}
AR ($mg\,hr^{-1}\,g^{-1}$)	2.90 ± 0.78^{b}	3.55 ± 0.72^{b}	15.56 ± 3.20^{a}
OCR ($mL\ O_2\,hr^{-1}\,g^{-1}$)	0.62 ± 0.02^{b}	0.61 ± 0.01^{b}	0.90 ± 0.03^{a}
UR ($\mu g\ NH_4\text{-}N\,hr^{-1}\,g^{-1}$)	60.29 ± 3.92^{b}	60.38 ± 5.84^{b}	80.74 ± 6.36^{a}
SFG ($J\,hr^{-1}\,g^{-1}$)	38.81 ± 14.14^{b}	50.81 ± 13.14^{b}	263.20 ± 57.97^{a}

FR, filtration rate; RR, pseudofeces production rate; IR, ingestion rate; AE, absorption efficiency; AR, absorption rate; OCR, oxygen consumption rate; UR, ammonium excretion rate; SFG, scope for growth. [a,b]Different superscript letters indicate significant differences ($P<0.05$).

found for the RR at the different oxygen concentration tested (Table 7; $df = 2$, $F = 0.43$, $P = 0.6545$).

4. Discussion

4.1. Effect of Food Concentration. The higher feeding rates of *P. arctata* with increasing food concentration in the water and the decrease of these variables at the highest concentration are similar to previous reports for other bivalve species [16, 23, 27, 28, 61–65]. According to these authors, increasing food concentrations results in a larger amount of particulate matter that is filtrated in the gills, which in part is rejected as pseudofeces and the rest is ingested. When the concentration of suspended particulate matter is too high, there is a saturation of the gills and/or the digestive system of bivalves, and the ingestion rate must be regulated. This regulation is made by the reduction of the filtration rate and/or by the increase in the pseudofeces production [64]. In this study, *P. arctata* exhibited mainly the first control mechanism at a particulate concentration around $9.3\ mg\,L^{-1}$

(7.2 mg POM L^{-1}). This umbral concentration of feeding system saturation is higher than those reported for other clam species such as *Meretrix meretrix* (6 mg POM L^{-1}; [65]) and *Ruditapes philippinarum* (0.65 mg POM L^{-1}; [27]), but it is lower than those reported for *Cerastoderma edule* (45 mg POM L^{-1}, [66]) and *Mytilus edulis* (20 mg POM L^{-1}; [64]). It is possible that such interspecific discrepancies are due to differences in the concentrations of seston that are normally found in their habitats, which confers a differential capacity of their digestive systems to process food. The intermittent pseudofeces production observed in *P. arctata* from the lowest microalgae concentrations tested has also been reported in other clams [64, 67]. Apparently, these species accumulate the material in excess in the pallial cavity, and from time to time, the suspend the pumping of incoming water by the inhalant siphon and reverse the direction to expel the stored pseudofeces by pulses.

The lack of effect of the food concentration on the absorption efficiency observed in *P. arctata* has also been reported in other bivalves fed with microalgae [22, 26, 27, 63, 65]. This response suggests that the activity of the digestive enzymes was high and independent of the variations in the ingestion rate and the time of gut residence.

The higher the rates of oxygen consumption and ammonium excretion of *P. arctata* at intermediate values of food concentration can be explained by the direct relationship between feeding activity, metabolic expenditure, and the use of food proteins as an energy source, as it has been observed in other bivalves [13, 22, 28].

The increase in the scope for growth of *P. arctata* with increasing availability of food, and its decrease in response to food concentrations higher than 9.3 mg L^{-1} (7.2 mg POM L^{-1}), is in agreement with results previously reported for other bivalves [22, 26–28, 68]. The highest SFG of *P. arctata* at intermediate concentrations of microalgae in the water was due to a higher food intake at these microalgae concentrations, as well as to the relatively low metabolic costs associated to the feeding activity in all of the treatments (<18% of the energy ingested). In the Ciénaga Grande de Santa Marta, the seston concentrations for most part of the year and sectors are higher than that found optimal for this clam, mainly due to the strong levels of sedimentation of the Magdalena River and to the lagoon system eutrophication [6]. So, these environmental conditions can be limiting the energy acquisition of the natural populations of estuarine clams, contributing to threaten its conservation status. Therefore, it is recommended to maintain an intermediate and stable food concentration in the culture tanks in the laboratory, suppling microalgae using a drip system. When choosing a site for either aquaculture or restocking, it is desirable to find a location without much influence direct of runoff, with moderated productivity and low levels of turbidity and sedimentation.

4.2. Effect of Salinity. The reduced feeding rates of *P. arctata* under extreme salinities, as well as the frequent closure of valves at the highest salinity tested, are in agreement to previous reports [30, 61, 69–73]. These responses seem to be strategies for minimize the contact with the surrounding water and the consequent osmotic interchange. Extreme salinities can cause oxidative stress and cell damage mainly in the gills and digestive gland [74, 75]. The reduced absorption efficiency of the estuarine clam under hypotonic condition could be the result of a functional deficiency derived from the oxidative stress effects on the digestive gland cells. On the contrary, the relatively high absorption efficiency of the clam at a hypertonic medium could be attributed to an increase in the time of gut residence associated to its frequent isolating behavior, as this has been observed in other species [31, 33, 70]. These results suggest that the feeding function of the clam under extreme salinities is reduced.

The increase in the rates of oxygen consumption and ammonium excretion of *P. arctata* with decreasing salinity is similar to previous findings in other marine and estuarine bivalves [33, 71, 76, 77]. Under hypotonic conditions, bivalves can avoid the dilution and swelling of the cells increasing the protein catabolism as a source of free amino acids that act as intracellular osmolytes, allowing to maintain osmotic concentration and cell volume appropriates for their functions [31, 33, 75–78]. The increase in the oxygen consumption of *P. arctata* at low salinity condition, despite its low feeding activity, suggests that the increased protein catabolism corresponds to a hypo-osmoregulation mechanism, metabolically costly.

The highest scope for growth of *P. artacta* observed at intermediate salinity (15‰) is similar to previous findings in other estuarine or invasive bivalves within the salinity range of their habitat, both for the SFG and the growth rate [71, 78–80]. This response was due to higher food ingestion and absorption capabilities under conditions of intermediate salinity (90% of the ingested energy) and to the relatively low values of energy expenditure and loss (10% of the total ingested energy). Results suggest that under a salt diluted media, *P. arctata* is able to produce intracellular osmolytes as osmoregulation mechanism, but under hypertonic conditions, there was no evidence of any energy consuming action, instead it minimized the energetic interchange adopting an isolation behavior inside the valves. Both situations derived in a decrease of the scope for growth and reproduction. The extreme values of salinity tested in this study are very common in the habitat of the estuarine clam [6], and this study results indicate that can be negatively affecting the ability for energy obtaining of its natural populations. On the other hand, the selection of a site for farming or restocking this species must require the absence of a direct influence of rivers and the ocean in order to avoid extreme levels of salinity.

4.3. Effect of Temperature. The lack of effect of water temperature on the rates of filtration, pseudofeces production, and ingestion of *P. arctata* indicates a high acclimation capability of the feeding rates to the small temperature variations registered in its natural habitat (5°C). This response differs from the increasing rates found in other bivalves exposed to the wider rising temperatures of their natural habitats [15, 28, 34–37, 69, 79, 81]. On the contrary, the reduction in the rates and efficiency of absorption of *P. artacta* at the

highest temperature tested (32°C) could be related with a denaturation of the digestive enzymes, as this has been previously reported in *Ruditapes decussatus* and *Venerupis pullastra* [82].

The highest rates of oxygen consumption and ammonium excretion of *P. arctata* at the intermediate temperature of 29°C have also been described for other bivalves [26, 39, 79, 83, 84]. These authors have explained that response by the variation of two opposing processes that occur simultaneously as the temperature increases: on one hand, there is an acceleration of the kinetics of metabolic chemical reactions, and on the other hand, there is a higher denaturation rate of the enzymes that catalyze these reactions [85].

The higher values of scope for growth obtained at low and intermediate temperatures (between 27 and 29°C) compared to that obtained at 32°C are in agreement with that found in other bivalves [26, 34–37, 69, 79, 81, 86]. Although the Caribbean estuarine clam was able to maintain high feeding rates independent of temperature values, there was a reduction of the absorption capacity under high temperature conditions (in around 20%), showing a greatest energy availability for growth and reproduction at low and intermediate temperatures (27 and 29°C). In the short term, this species is not able to acclimatize its energetic functions to temperatures higher or similar than 32°C, which are frequent in its habitat, especially during the rainy season (between April and October) [6]. Then, the high water temperature can be considered as an stressing agent for the natural populations, contributing in part to its current vulnerable ecological status. When selecting a site for farming or restocking purposes, it is recommended to avoid sites closed or locations with very shallow waters, given the potential exposure to evaporation and rising temperatures.

4.4. Effect of Ammonia Concentration. Ammonia is considered as one of the main pollutants in natural environments and limiting factors in aquaculture [87]. It can enter to aquatic animals by simple diffusion mainly through their gills due to the greater permeability and constant water pumping action through this tissue [88–90]. The decrease observed in almost all of the physiological variables of *P. arctata* at ammonia concentrations greater or similar than $48\,\mu g\,L^{-1}$, as well as the tendency of individuals to keep their valves closed at the higher concentration tested ($77\,NH_3\text{-}N\,\mu g\,L^{-1}$), is similar to previous reports in other mollusks species [41, 91, 92]. These responses can be explained as a strategy that contributes to minimize the contact of soft tissue with this toxic substance, as well as to reduce the metabolism and then, the extra ammonia production in their own wastes [88]. Additionally, the decline of the feeding rates could be related to functional damages in the gills and digestive gland derived from the oxidative stress, as this has been reported for *Corbicula fluminea* exposed to ammonia [87].

The lack of effect of the ammonia water concentration on the ammonium excretion rate of *P. arctata* is similar to previous findings in *R. decussatus* [41]. The relatively high rates of ammonium excretion of *P. arctata* under intermedia and high ammonia concentration in the water, while the feeding rates decreased, can be attributed to an actively elimination of the ammonia diffused from the medium, as this has been reported in crabs and fishes [89]. This response suggests an ammonia detoxification capability of the estuarine clam.

The reduction of the scope for growth in *P. arctata* at ammonia concentrations higher or equal than $48\,\mu g\ NH_3\text{-}N\,L^{-1}$ is consistent with what has been reported in other mollusks [40, 41, 91, 92]. At high ammonia concentration, this species reduced its energy obtaining from food in around 80% causing energetic deficiencies in the animals. The ammonia concentration in the *P. arctata* habitat is over this critical value in several sectors, especially those near human settlements and river outlets [6]. So, this factor can be affecting negatively the capacity of energy acquisition of its natural populations. Then, it is important to maintain low culture densities and an adequate water renewal in the laboratory tanks, as well as to select farming and restocking areas far from the sectors indicated above and those used for fish aquaculture, in order to prevent additional sources of this toxic substance.

4.5. Effect of Oxygen Concentration. The reduction of most of the physiological variables measured in *P. arctata* at intermedia and low concentrations of dissolved oxygen in the water (≤48%) is in agreement with previous findings in other bivalves [31, 43–47, 93]. According to these authors, the high concentrations of dissolved oxygen in the surrounding water and hemolymph permit an efficient mitochondria functioning, increasing all of the functional process energy dependents, as the feeding rates. However, the lack of reduction of this variables under the lowest oxygen saturation tested suggests that this species is able to maintain a moderated energy obtaining process even under very hypoxic conditions. The reduction in the production of pseudofeces of *P. arctata* under hyperoxic conditions permitted the great increase of the ingestion rate verified at this condition.

The rates of oxygen consumption and ammonia excretion of the estuarine clam were directly related with most of the feeding rates, showing an interdependence of the nutrient catabolism process and the feeding activity, as this has been found in other bivalves [31, 43, 44, 47]. However, the similarity of the rate of pseudofeces production at the different oxygen concentrations, as well as the lack of relationship of this variable with the other physiological variables measured, suggests that this activity did not had a significant energetic demand and was performed independently of the availability of dissolved oxygen in the water. These results are consistent with those reported in *Unio douglasiae* [94].

The reduction in the scope for growth of *P. arctata* at dissolved oxygen concentration similar or lower than 48% coincides with results previously reported for this variable and for growth in other mollusks [31, 43–45, 47, 48, 93]. Under reduced dissolved oxygen saturation, there was an abrupt decrease in the capacity for energy obtaining from food (77%), and although the energy outputs also decreased, these represented only 10% of the energy ingested. Results suggest that this species requires hyperoxic conditions (≥93%) for its optimal physiological performance. The

hypoxic conditions (<48%) commonly found in the eutrophicated natural environment it inhabits, especially at night [6], seem be limiting the energy obtaining of the natural populations, contributing to its current ecological risk. Therefore, it is recommended to maintain enough aeration or water renewal in the culture tanks in laboratory, as well as to choose a site for farming or restocking without signs of strong eutrophication, where oxygen depletion at night is frequent.

5. Conclusions

P. arctata exhibited a great physiological plasticity, allowing positive energetic balances along the water quality variations occurring in its habitat. Under conditions of extreme salinity values, low oxygen levels, as well as high concentrations of particulate organic matter and ammonia in the water, clams regulated the food intake and metabolism reducing filtering activity, increasing pseudofeces production, and/or closing the valves. The highest amount of energy available for growth and reproduction of this species was found at intermediate values of food concentration (9.3 mg of *I. galbana* L^{-1} or 7.2 L^{-1} of particulate organic matter), salinity (15‰), and temperature (between 27 and 29°C), as well as at low ammonia concentrations ($\leq 7\,\mu g$ NH_3-N L^{-1}) and high dissolved oxygen saturation in the water (≥93%). Therefore, these are the water quality conditions recommended to be used for reproductive conditioning and juvenile culture of this species under hatchery conditions and for the natural places selection for farming and restocking purposes. Additional research about such topics is needed in order to validate and refine this study findings, as well as to determine the interaction effects of environmental factors under uncontrolled natural conditions.

Abbreviations

A : Absorbed energy
AE: Absorption efficiency
AR: Absorption rate
b: Dependence of physiological rates on the size of the animals
DW: Dry weight of the experimental animal
ER: Rate of feces production or ejection rate
FR: Filtration rate
IER: Rate of inorganic feces production or inorganic ejection rate
IFR: Inorganic filtration rate
IR: Ingestion rate
IRR: Rate of inorganic pseudofeces production or inorganic rejection rate
OCR: Oxygen consumption rate
OER: Rate of organic feces production or ejection rate
OFR: Organic filtration rate
OIR: Organic ingestion rate
ORC: Oxygen consumption rate
ORR: Oate of organic pseudofeces production or organic rejection rate
LW: Live wet weight of the experimental animal
PIM: Particulate inorganic matter
POM: Particulate organic matter
R: Energy expenses
RR: Rate of pseudofeces production or rejection rate
SFG: Scope for growth
SL: Shell length
SW: Shell weight of the experimental animal
TPM: Total particulate matter
U: Energy losses
UR: Ammonium excretion rate
WW: Wet weight of the soft parts of the experimental animal
Ye: Nonstandardized physiological rate
Y_{ts}: Physiological rate standardized to a dry weight of 1 g.

Data Availability

Data used to support the findings of this study are available from the corresponding author upon request.

Conflicts of Interest

The authors declare do not have any conflicts of interest related with this manuscript.

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