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Optimum temperature for growth of an invasive green mussel *Perna viridis* population from Venezuela, determined in an open-flow system

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ABSTRACT

Optimum temperature for growth of an invader population of green mussel *Perna viridis* (31.1 ± 1.9 mm SL; 0.8 ± 0.2 g DTW) from Guayacan Venezuela, was determined by means of scope for growth (SFG) at 22 − 34 °C with an open-flow system. The objective was to find the suitability of its cultivation in the Gulf of Cariaco Venezuela. Morphometric relationships of shell length vs. wet and dry weights were obtained to determine the condition index of experimental mussels. SFG was highest at 26 °C (64 ± 16 J g^{-1} h^{-1}), was positive at 22–30 °C (35 ± 3 and 20 ± 1 J g^{-1} h^{-1} respectively) and negative at 34 °C (-39 ± 11 J g^{-1} h^{-1}). Mussels employed were at good condition indicated by a positive allometry of shell length–total wet weight (*b*-value = 3.7394) (R^2 = 0.397) which was higher than in native populations. Condition index (2.01–13.49) indicated that the mussels studied were not active in reproduction. Based on SFG results and temperature published data from the Gulf of Cariaco, it is concluded that temperature-wise this site (20.1–29.1 °C) is appropriate for aquaculture of the population of *P. virids* studied. Further studies on the combined effect of temperature and seston concentrations over SFG are needed since a combination of high temperature and seston depletion frequently occurs in this site from September to January. The advantages of the new open-flow sytem for ecophysiological studies in aquatic organisms are discussed.

1. Introduction

The green mussel *Perna viridis* (L.) is native to the Indo-Pacific region extending from Japan to New Guinea and from the Persian Gulf to South Pacific Islands (Siddall, 1980). They generally inhabit marine intertidal, subtidal, and estuarine environments with high salinity (Rajagopal et al., 2006). This species is being cultivated in India, Malaysia, Philippines, Singapore and Thailand, reaching a production from aquaculture of 146,815 tons in 2016 and only 12,020 tons from fisheries (FAO, 2019). *P. viridis* is considered an invasive species, living in dense patches in many parts of the world (CABI, 2019) The population has extended geographically to the western hemisphere in waters surrounding the Caribbean island of Trinidad in 1990 (Agard et al., 1992; Rylander et al., 1996), Venezuela in 1993 (Segnini et al., 1998), and the U.S. in 1999 (Power et al., 2004). The invasive capacity of this species has been attributed to its remarkable settlement success, and its long larval stage (Malavé and Prieto, 2005; Rajagopal et al., 2006). It grows quickly, has high fecundity, matures early, has high secondary productivity, and can withstand extreme environmental conditions of temperature, salinity, and turbidity (Malavé and Prieto, 2005; Rajagopal et al., 2006; Segnini, 2003, 2009). Now it has become a valuable fishery resource in Venezuela (Lodeiros and Freites, 2008) and there is a growing interest in its cultivation in Gulf of Cariaco, Venezuela (Acosta et al., 2009; Tejera et al., 2000).

Selection of aquaculture sites must be based in the right match between environmental conditions and the optimum and extreme values for growth of the species. The environmental conditions of the Gulf of Cariaco have been described by Acosta et al. (2012), who found a temperature range of 22 − 32 °C, and a range of organic seston of 1 − 8 mg l^{-1} from July 2007 to February 2008. Calvo-Trujillo et al.

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(2018), evaluated the spatial and temporal distribution of phytoplankton and other water variables such as water transparency, salinity, chlorophyll a, phytoplankton abundance and temperature at the surface and at 10 m depth, in seven stations from February 2014 to January 2015. Segnini et al. (1998) determined the low and high lethal temperatures of *P. viridis* (6.0 and 37.5 °C respectively), but the optimum temperature for growth of this Venezuelan population is still unknown. Soon and Ransangan (2016) selected the optimum site for cultivation of *P. viridis* in Marudu Bay, Malaysia, using a quantitative method where a rated value was given to every environmental variable, and a weighed value was given to every potential station based on its effects on the growth or survival of the green mussel. The weighted value for temperature, was highest in sites with a temperature range of 26 – 32 °C. Weighed values were extracted from published literature, but because of optimum and extreme ranges of preference and tolerance of a given population could change as it is adapting to the new environment, it is necessary to study such particular population (Koch et al., 2015).

Scope for growth (SFG) is the surplus of energy available for growth beyond that required for maintenance. SFG is used to measure the energy balance as the difference between energy intake and metabolic output in bivalves (Rueda and Smaal, 2004; Widdows and Staff, 2006). It is used for estimating growth and reproductive potential of a species (Sobral and Widdows, 2000; Velasco and Navarro, 2002), to assess carrying capacity of coastal waters that are used for bivalve aquaculture (Sará and Mazzola, 2004; Sará and Pusceddu, 2008; Sará et al., 2008), to determine the energy balance of bivalves (Rueda and Smaal, 2004; Widdows and Staff, 2006) and the stress levels of animals growing under polluted conditions (Gibbs, 2007). Beiras et al. (1994) demonstrated that the SFG calculated from these physiological parameters agreed with the long-term growth performance, validating the physiological energetics method as a valuable tool for predicting long-term growth performance under constant environmental conditions. Methods to estimate SFG in molluscs have been described by Widdows and Staff (1997), but Beiras et al. (1993) developed a practical open-flow system to estimate SFG in oysters, incubating groups of individuals in a single chamber and using polarographic electrodes for respiration rate. This system could be improved by the use of micro-optodes that give precise and quick readings of O_2 concentrations.

SFG of a population can be modified by the condition of the organism during stress situations or during reproduction. Sexual maturity of *P. viridis* occurs at 15 – 30 mm shell length (FAO, 2019) and therefore, it is important to determine the reproductive state of the organisms under investigation. Allometry is a good tool to determine condition index, but also it may be a tool to understand the effect of environment where the mussels grow. Distinct forms of raft- and shore-grown mussels have been found and for instance, mussels grown intertidally are wider, less high and heavier than mussels of similar length grown in suspension (Hickman, 1979). According to Froese (2006), weight–length relationships (WLR) are used for estimating the weight corresponding to a given length, and condition factors are used for comparing the condition, fatness, or well-being of species, based on the assumption that heavier organisms of a given length are in better condition.

In the present work we determined the optimum temperature for growth of a population from the Caribbean Sea of Venezuela by means of the scope for growth determined with a new open-flow system. Morphometric relationships of shell length vs. wet and dry weights of shells and tissues of all individuals collected were obtained to determine the condition index of experimental mussels. Based on these results and published information, the feasibility of green mussel aquaculture in the Gulf of Cariaco is discussed, taking into account the environmental variables.

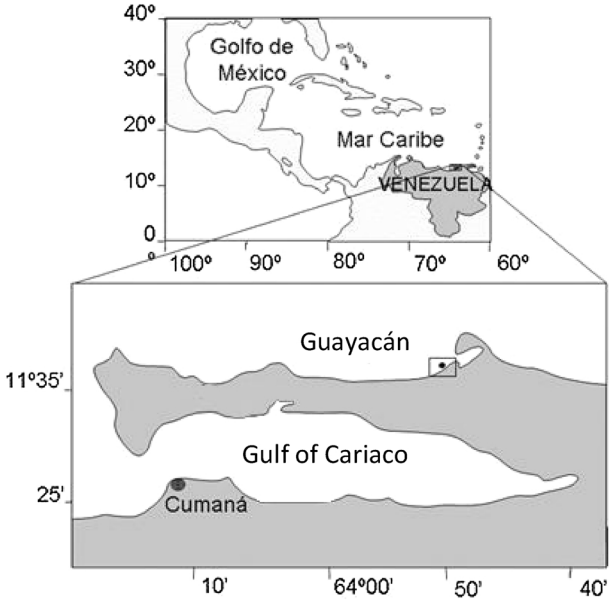

Fig. 1. Map showing the site of collection of *Perna viridis*, the Gulf of Cariaco, Venezuela.

2. Materials and methods

2.1. Experimental organisms

A total of 150 green mussels were collected in Guayacán, Venezuela (10°39'00.26 N; 63°49'53.94 W) (Fig. 1) (31.1 ± 1.9 mm shell length and 0.8 ± 0.2 g dry tissue weight). Four groups of 10 individuals each were acclimated in 60 l plastic tanks at 26 °C in aerated, 1 µm filtered seawater at 34 psu. The mussels were fed once a day with *Isochrysis galbana* at an initial concentration of 150 cell μl^{-1}. Temperature was increased or decreased at the rate of 1 °C d^{-1} until the experimental temperatures of 22, 26, 30, and 34 °C were reached. Water was exchanged daily (40 % volume) at the same treatment temperatures, and the microalgae concentration replenished. Once the experimental temperatures were reached, tanks were maintained at these temperatures for one week feeding the mussels as described previously. Temperature in the tanks was controlled with a multichannel temperature controller developed at a CIBNOR.

2.2. Experimental open-flow system

Experiments were conducted in the open-flow system as shown in Fig. 2. This system allows for precise determinations of oxygen uptake (respiration) rate, clearance (feeding) rate and food absorption efficiency, to subsequently calculate the Scope for Growth (SFG).

A storage tank of 500 l was filled with seawater at 34 psu salinity and at a temperature close to the experimental temperature (Fig. 2). A suspension of microalgae *I. galbana* was added to give a concentration of 150 cell μl^{-1}, which is equivalent to 3 mg l^{-1} of organic matter considering a dry organic weight of 20 pg $cell^{-1}$ (Helm and Bourne, 2004). This concentration falls within the range (1 – 8 mg l^{-1}) of organic seston concentration in the Gulf of Cariaco (Acosta et al., 2012). The mixture was constantly aerated and mixed with a submersible pump placed on the bottom of the tank. Four experimental glass chambers made of 1.5 l bale jars with airtight hinged lids and a leak proof gasket, were submerged up to the neck into the temperature-controlled 60 l tank. Three chambers held a group of 10 mussels each that were starved for 24 h prior to the experiments. One chamber without mussels served as control. The glass lids of the glass chambers were replaced with Nylamid© lids to which a lateral hole of 3.2 mm

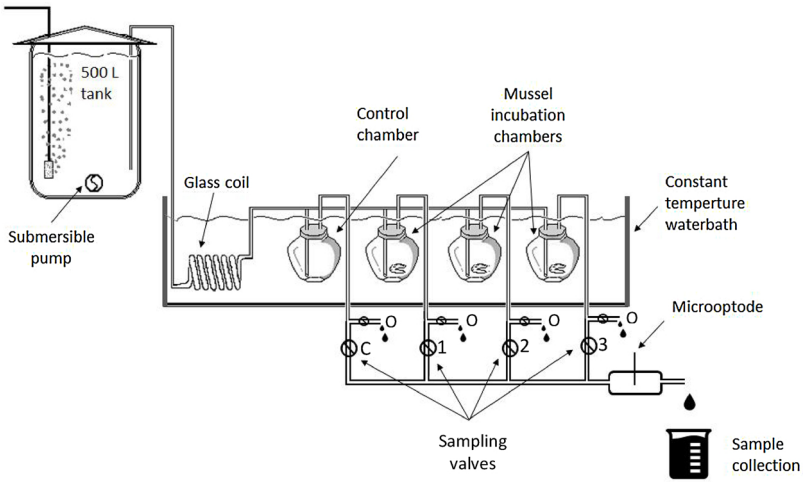

Fig. 2. Open-flow system developed for assessment of physiological parameters of aquatic organisms. O = continuous outflow.

was drilled to insert an inlet tube, long enough to reach the bottom of the chamber to allow effective mixing of the water inside the chambers. A central hole of the same diameter was drilled to insert an outlet tubing just to reach the inner surface of the lid. The inner side of the lids was conical to allow automatic expulsion of air bubbles that may get trapped inside the chambers. The mixture of sea water and microalgae was siphoned through plastic tubing of 10 mm diameter from the storage tank to a glass coil submerged in the water bath to ensure that the mixture was at the experimental temperature before entering the chambers. The coil was connected to the inlet tubes which reached the bottom of the chambers. The outlet tubes were connected to a plastic "T" connecting in one arm to a control valve for flow regulation through the chambers. Once the valves of each chamber were adjusted to 180 ml min^{-1}, they remained untouched during the whole experiment. At this flow, the water in the chambers was completely replaced every 8 min. In the other arm of the "T", an aquarium 4-channel manifold with four inlets controlled with plastic valves and only one outlet was connected to do the oxygen readings and the microalgae samplings. The outlet of the manifold was connected via Luer-Lock adapter to a flow-through cell housed oxygen micro-optode sensor FTCH-PSt1 (PreSens Precision Sensing GmbH) with a measurement range of 0–50 % oxygen, and a detection limit of 0.05 % oxygen. The oxygen micro-optode sensor with a tip size of 140 µm was optimized for a fast response time of 5 s. The sensor was connected to a Microx TX oxygen meter connected to a PC via USB interface. This included a software with which the transmitter can be controlled and data collected.

2.3. Scope for growth

Physiological responses of *P. viridis* at different temperatures were integrated by means of the energy balance equation and performance was assessed in terms of Scope for Growth (SFG);

$$SFG = (I \times AE) - R$$

where I = ingested energy, AE = absorption efficiency and R = respired energy (Beiras et al., 1994).

2.4. Respired energy

Respired energy (R) at different temperatures was determined from respiration (oxygen uptake) rates (RR). The RR were calculated by the differences between concentrations in the control chamber vs. experimental chambers containing the mussels (Fig. 2). Before starting, the mussels were left undisturbed with the water flowing in the chambers until all the organisms were pumping with the valves opened. O_2 data from control chamber were first read closing all valves but the control chamber. Once the readings were stable (Fig. 3), the valve of the control chamber was closed and that of chamber 1 was opened. A quick drop on concentration was observed to a certain level reflecting O_2 concentration of chamber 1. After approximately 30 s of readings every 5 s, the control chamber was read back again by closing chamber 1 valve and opening the valve of the control chamber. This procedure was repeated with chambers 2 and 3. Three replicates of each reading were obtained by doing the whole procedure three times. In this way, a fret-shaped graph was built of each experiment for later analyses. Precise flow of the water was determined at the end of each sampling with a 10 ml graduated cylinder (ml min^{-1}), taken at the outflow port (Fig. 2). The whole experiment at a single temperature lasted 30 min approximately, and was repeated for each temperature treatment.

Respiration rate (RR) was calculated with the formula:

$$RR = [(PO_2c - PO_2i) \times Q] \times Dw^{-1} \text{ mg } O_2\, g^{-1}\, h^{-1}$$

where, PO_2c and PO_2i were the oxygen concentrations in control and mussel chambers respectively, Q was the flow (ml h^{-1}) through the experimental chambers, and Dw dry tissue weight (mg) of incubated mussels. RR was converted to energy values using the conversion factor of 20.33 J mg^{-1} to obtain respired energy (R) *J* mg^{-1} h^{-1} (Widdows and Johnson, 1988).

2.5. Ingested energy

Ingested energy (J $mg^{-1}\, h^{-1}$) was calculated from the ingestion rate (IR) (cell $g^{-1}\, h^{-1}$) following the equation (Widdows and Bayne, 1971; Wilson, 1980): IR = [(Cc-Ci) x Q] x Dw, where Cc and Ci were the microalgal concentrations (cell ml^{-1}) in control and experimental chambers, Q was the flow (ml h^{-1}) through the experimental chambers, and Dw dry tissue weight of incubated mussels. Microalgal concentrations (cell ml^{-1}) of water samples taken from the outflow ports of the control and experimental chambers were determined by triplicate on a Multisizer 3, Beckman-Coulter, Fullerton, CA., equipped with a 100 µm pore size tube. IR was then transformed to ingested biomass considering an organic weight of 20 pg $cell^{-1}$ (Helm and Bourne, 2004) and finally converted to ingested energy (I) considering an energy equivalent of 23.5 J mg^{-1} for organic content of microalgae ingested (Widdows and Johnson, 1988).

2.6. Absorption efficiency

Absorption efficiency (%) was determined following the method by

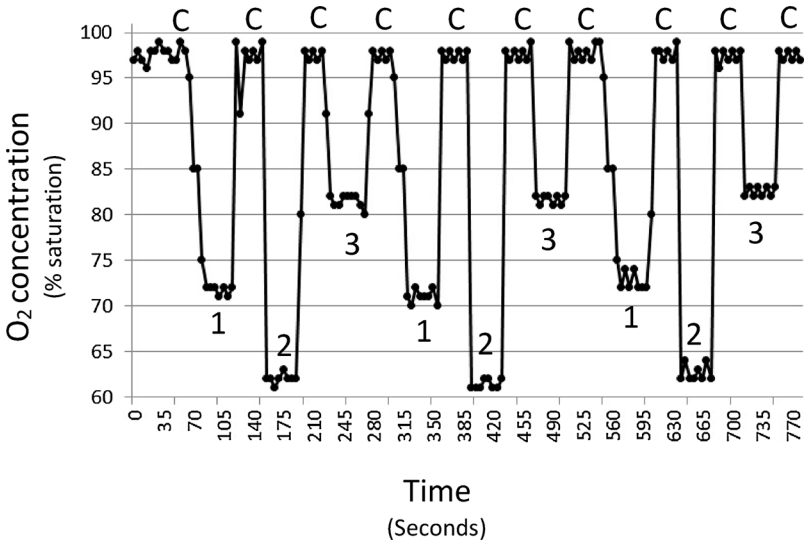

Fig. 3. Typical fret-shaped graph of a respiration experiment. Each dot is an O_2 measurement taken every 5 s with an oxygen micro-optode with a 140 µm sensor. C = control chamber. Numbers are chamber number.

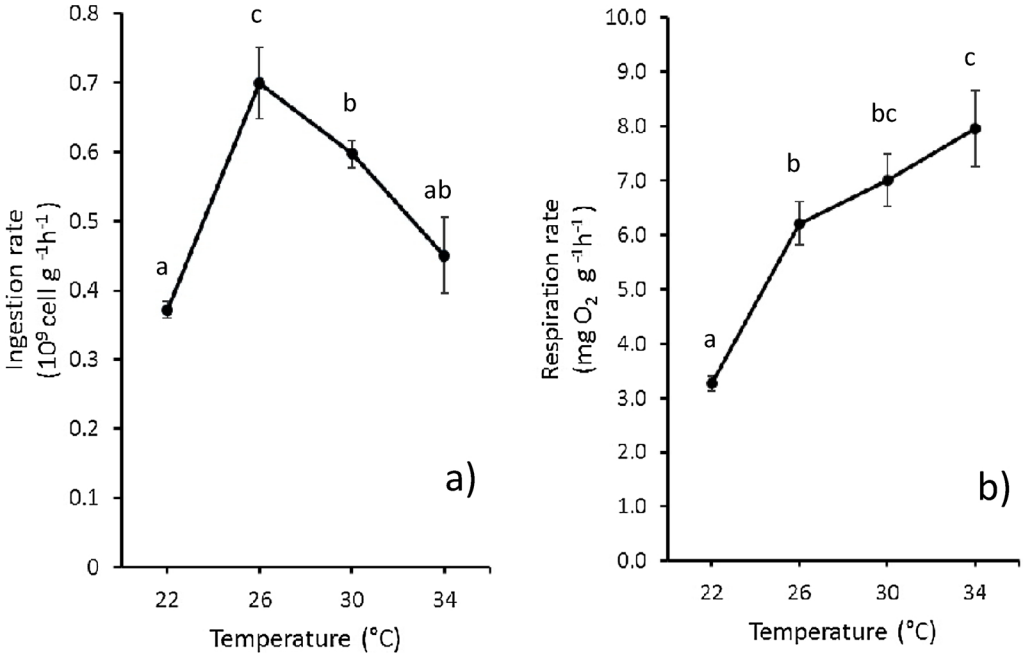

Fig. 4. Ingestion (a) and respiration (b) rates of green mussel *Perna viridis* (31.1 ± 1.9 mm shell length and 0.8 ± 0.2 g dry tissue weight) from Guayacan, Venezuela, at different temperatures. Different letters indicate significant differences between treatments at $p < 0.05$. n = 9. (For interpretation of the references to colour in the Figure, the reader is referred to the web version of this article).

Table 1
Scope for growth of green mussel *Perna viridis* of 31.1 ± 1.9 mm shell length and 0.8 ± 0.2 g dry tissue weight from Guayacán Venezuela population, at different temperatures. Numbers are the mean ± SDEV of 9 determinations. Different letters indicate statistical significant differences between treatments ($p < 0.05$).

Temperature	Ingested energy	Absorption efficiency	Absorbed energy	Respired energy	Scope for growth
°C	J g^{-1} h^{-1}	(%)	J g^{-1} h^{-1}	J g^{-1} h^{-1}	J g^{-1} h^{-1}
22	175 ± 6^{a}	58 ± 15^{a}	101 ± 3^{a}	66 ± 3^{a}	35 ± 3^{b}
26	328 ± 24^{c}	78 ± 5^{b}	190 ± 14^{d}	126 ± 8^{b}	64 ± 16^{a}
30	281 ± 9^{b}	80 ± 15^{b}	163 ± 5^{c}	142 ± 10^{bc}	20 ± 1^{c}
34	212 ± 26^{ab}	82 ± 10^{b}	123 ± 15^{b}	162 ± 14^{c}	−39 ± 11^{d}

Conover (1966). The inorganic and organic content of feces were determined gravimetrically in a similar manner as for the microalgae (Strickland and Parsons, 1968). Feces collected by triplicate at the end of the experiment at each temperature, were transferred to ashed preweighted Whatman GF/C filters under vacuum pressure. Filters were rinsed with isotonic 3 % ammonium formate, dried at 60 °C for 24 h, weighted to obtain the dry weight of feces, and burned in a muffle furnace at 450 °C for 5 h to determine ash-free dry weight of feces. The same procedure was followed for microalgae as previously indicated. Absorption efficiency (%) was calculated with the equation:

$$AE = 100 \times ([F - E] \times [F\,(1 - E)]^{-1})$$

where F and E were the organic content in the food (F) and feces (E) respectively.

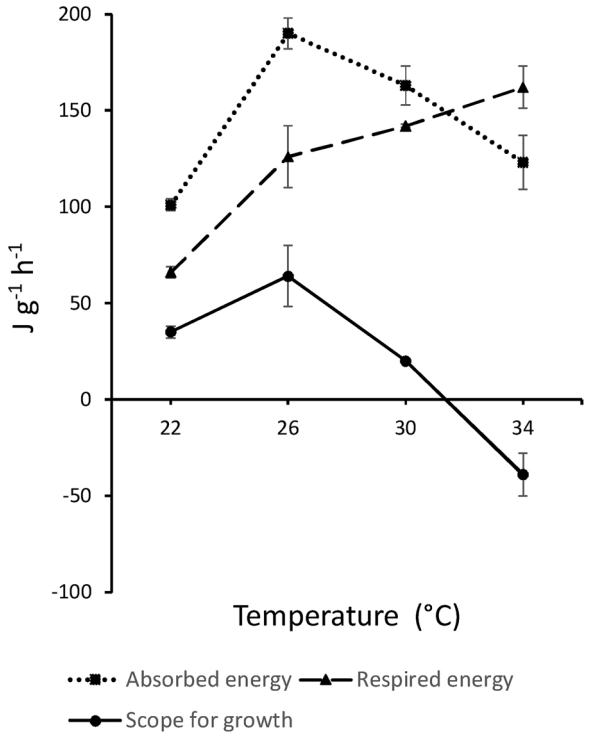

Fig. 5. Scope for growth and absorbed and respired energy of green mussel *Perna viridis* (31.1 ± 1.9 mm shell length and 0.8 ± 0.2 g dry tissue weight) from Guayacan, Venezuela, at different temperatures. (For interpretation of the references to colour in the Figure, the reader is referred to the web version of this article).

2.7. Absorbed energy

Absorbed energy was calculated multiplying ingested energy (I) by absorption efficiency (AE) (J $mg^{-1} h^{-1}$).

2.8. Morphometric relationships and condition index

Morphometric relationships were obtained from 110 mussels to compare the condition of the population studied with published information of other populations of *P. viridis* (Aban et al., 2017; Chatterji et al., 1984; Hemachandra and Thippeswamy, 2008; Hickman, 1979; Mamon et al., 2016; Thejasvi et al., 2013), and to calculate the condition index. Shell length of all the mussels collected for this study was measured with a caliper. Then were deshelled, blotted and weighted individually on an electronic balance with 0.01 g resolution to obtain total wet weight. The meat was separated from the shells and weighted separately in the same balance to obtain wet tissue weight and shell weight. The tissues of each mussel were placed in pre-weighted aluminum foil trays and were dried in an oven at 80 °C during 24 – 48 h until a constant dry tissue weight was obtained. The estimation of shell weight-length relationship was made by adjustment of a power curve to the data: $W = a L^b$ (Gaspar et al., 2001), where W = weight, L = shell length, a = intercept: initial growth coefficient, and b = slope: allometric value. Condition index was calculated by the relationship dry tissue weight/shell weight.

2.9. Statistics

Data from ingestion and respiration experiments were averaged (n = 9: three experimental chambers x 3 sampling times), and the standard deviation was calculated. The non-parametric Kruskall-Wallis analysis was used to find significant differences between treatments at $p < 0.05$. For the morphometric parameters the length-weight relationships were estimated by linear regression analysis (least squares method), and the association degree between variables was calculated by the determination coefficient R^2.

3. Results

3.1. Scope for growth

Results of ingestion and respiration rates of *P. viridis* at different temperatures are shown in Fig. 4. Ingestion rate was significantly ($p < 0.05$) highest at 26 °C with a value of 0.69 ± 0.05 × 10^9 cell $g^{-1} h^{-1}$, then declined at 30 and 34 °C to 0.59 ± 0.01 and 0.45 ± 0.05 × 10^9 cell $g^{-1} h^{-1}$ respectively. The lowest value recorded was obtained at 22 °C with 0.37 ± 0.01 × 10^9 cell $g^{-1} h^{-1}$. Respiration rate varied directly proportional with temperature. The lowest value was obtained at 22 °C with 3.3 ± 0.1 mg O_2 $g^{-1} h^{-1}$, which was significantly different ($p < 0.05$) to the rates at higher temperatures. Respiration rates increased to 6.2 ± 0.4 and 7.0 ± 0.5 mg O_2 $g^{-1} h^{-1}$ at 26 and 30 °C respectively and peaked at 34 °C with a value of 8.0 ± 0.7 mg O_2 $g^{-1} h^{-1}$. Table 1 shows these rates converted to energy equivalents (J $g^{-1} h^{-1}$). Significant differences were found between ingested energy at different temperatures ($p < 0.05$). Highest ingested energy was obtained at 26 °C (328 ± 24 J $g^{-1} h^{-1}$) and the lowest at 22 °C (175 ± 6 J $g^{-1} h^{-1}$). Absorption efficiency (Table 1) varied directly proportional with temperature from 58 ± 15 % at 22 °C to 82 ± 10 % at 34 °C. With these results, calculated absorbed energy was significantly ($p < 0.05$) highest at 26 °C (190 ± 14 J $g^{-1} h^{-1}$) and lowest at 22 °C (101 ± 3 J $g^{-1} h^{-1}$). Respired energy (Table 1) also varied directly proportional with temperature from 66 ± 3–162 ± 14 J $mg^{-1} h^{-1}$ at 22 and 34 °C respectively. With this results, calculated SFG (Table 1; Fig. 5) was significantly different ($p < 0.0.5$) among treatments, being from highest to lowest in the following order: 26 > 22 > 30 > 34 °C. The first three SFG values were positive with mean values of 64, 35 and 20 J $g^{-1} h^{-1}$ respectively, but at treatment 34 °C SFG was negative (−39 J $g^{-1} h^{-1}$).

3.2. Morphometric relationships and condition index

The size range of experimental organisms was 28.6–33.9 mm shell length. Positive allometry was obtained for all shell length (SL) – weight relationships except for SL-shell weight relationship. *b*-values of SL-total wet weight (TWW) was 3.7394, 6.1192 for SL-wet tissue weight (WTW), and 5.798 for SL-dry tissue weight (DTW). For SL-shell weight (SW) the b-value was 2.3958 (Fig. 6). Highest correlation value was obtained in the SL-TWW (R^2 = 0.397). The range of condition index (dry tissue weight/shell weight) was 2.01–13.49 (Fig. 6).

4. Discussion

Regardless *P. viridis* is a native species for the Indo-Pacific, it is invading quickly new areas of the world (CABI, 2019). Once established in a new area and because of its good market value, it becomes an attractive species for fisheries (Lodeiros and Freites, 2008; Malavé and Prieto, 2005), with high potential to be cultured. For instance, it meets most of the criteria as a good candidate for aquaculture in the Caribbean (Mann, 1984) and particularly in Venezuela (Acosta et al., 2009). It is fast growing and there is spat available for collection from the wild. Based on our results of SFG at different temperatures, the Gulf of Cariaco Venezuela is a good place for aquaculture of green mussel. The optimum temperature for growth of the population studied from Guayacan Venezuela was 26 °C, with positive SFG at 22–30 °C. The thermal range in the Gulf of Cariaco was 20.06–29.10 °C (Calvo-Trujillo et al., 2018) which agrees well with the range of positive SFG. Based on the literature, Soon and Ransangan (2016) suggested an optimum range for *P. viridis* at 26 – 32 °C, which appears to be high for the Venezuelan population, considering that SFG could be zero at 32 °C (Fig. 5). The

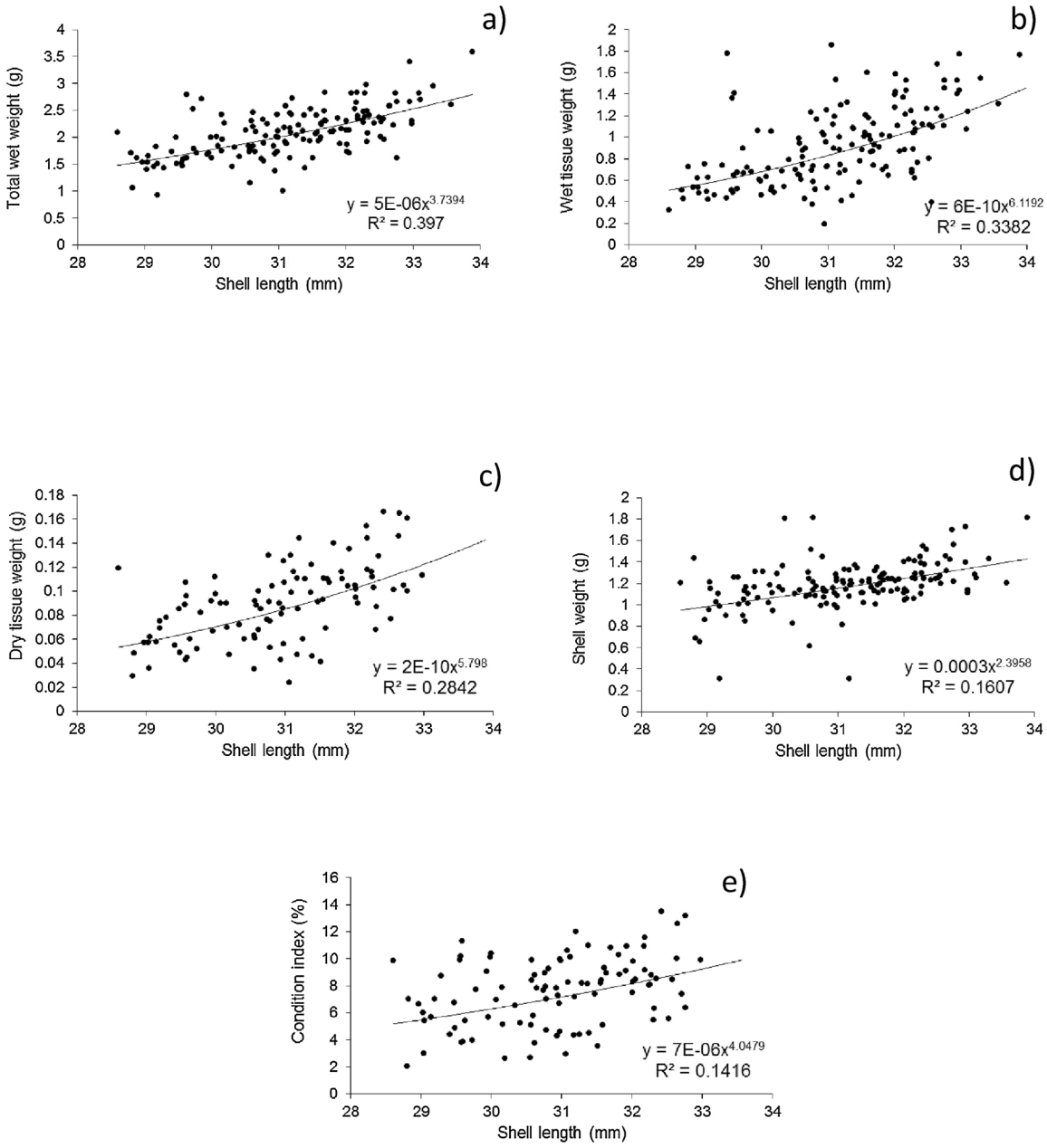

Fig. 6. Morphometric relationships (a–d) and condition index (e) of green mussel *Perna viridis* from Guayacan, Venezuela (n = 110). (For interpretation of the references to colour in the Figure, the reader is referred to the web version of this article).

range of temperature in Marudu Bay Malaysia is higher (27.2–32.3 °C) (Soon and Ransangan, 2016), than that recorded in Gulf of Cariaco (20.06–29.10 °C; Calvo-Trujillo et al., 2018), and therefore it appears that the species is adapting genetically to the new (colder) environment. Adaptations of this kind, have been reported in the scallop *Nodipecten subnodosus* by Koch et al. (2015) who found differences in performance of reciprocal transplants of from the Pacific coast (cold) vs. Gulf of California (warm) populations.

According to the morphometric parameters and the condition index, our mussels were in good condition and therefore our SFG results are representative of the population studied. Aban et al. (2017) indicates that shell length (SL) is the ideal weight growth estimator for the green mussel population in Bolinao Bay. They found highest correlation values in the SL-Total wet weight (R^2 = 0.82) and SL-wet tissue weight (R^2 = 0.85) relationships. In our work highest correlation was found in the SL-Total wet weight relationship (R^2 = 0.397). This value is lower than that found by Aban et al. (2017) probably as a result of the smaller range of size of the organisms employed (28.6–33.9 mm SL) and the fewer number of mussels measured (110). The *b*-values of morphometric relationships are used to compare between dimensional growth of related species or same species in varied habitats. Relationships of the morphometric parameters of shellfish is a measure of weight-growth. When the parameter "*b*" is equal to 3.0, the organisms show an isometric growth pattern and when the values are greater or lesser than the isometry situation, it is said to be that the sampled species is growing in a positive ($b > 3.0$) or negative ($b < 3.0$) way (Aban et al., 2017). Values reported of SL-Total wet weight relationship for *P. viridis* in two sites of India were negatively allometric 2.7411 and 2.9495 in Mukka, (Thejasvi et al., 2013) and St Mary´s Island (Hemachandra and Thippeswamy, 2008) respectively. Aban et al. (2017) also reported negative allometric growth with a *b* value of 2.299 in Bolinao Bay Phillipines. In our work *b* value was positively allometric (3.7394) indicating higher meat growth than shell, representing a good condition of the mussels. This result agrees with condition index (CI) values

obtained in our work (2.01–13.49). Hemachandra and Thippeswamy (2008) reported CI values of 5.51–7.76 of a *P. viridis* population from St Mary´s Island India and found a good correlation between CI values and the breeding season and they recorded a maximum value of 22-24. As *P. viridis* become sexually mature when they are 15–30 mm SL (FAO, 2019) and our size range was 28.6–33.9 mm shell length, it is unlikely that our mussels were on a gonad maturation stage, and therefore no interference with our physiological measurements was expected. In addition no spawning was observed during the study.

SFG is a good tool for quick and precise determination of optimum and extreme ranges of temperature. There are several papers dealing with SFG in *P. viridis* (Tateda et al., 2015; Wang et al., 2011; Wong and Cheung, 2001, 2003a; 2003b) and in all of them, they employ static methods for measurement of physiological parameters. Beiras et al. (1994) demonstrated a good agreement between SFG results vs. growth results in the field using an open-flow system developed earlier (Beiras et al., 1993). In this work we determined SFG with an open-flow system which allows precise determinations of respiration and ingestion rates. Our system produces a continuous flow of water inside the chambers at the same time that O_2 readings and water samples for microalgae counting are taken without interruption. Thus, oxygen and phytoplankton depletion and ammonia buildup during incubation are eliminated. In addition it ensures a good mixing of water, automatic expulsion of air bubbles and avoids water stratification and seston sedimentation inside the chambers. The use of temperature-compensated micro-optodes for the O_2 measurements, allowed building a fret-shaped graph while running the experiment, ensuring consistency of the readings and the detection of any problem with performance (pumping cessation) of any individual from the group of bivalves incubated. Indeed, our results are consistent despite the time elapsed from the first to the last reading (8 − 10 min) of a particular chamber (Fig. 3), with confidence limits (SDEV) lower than 10 % of the mean in O_2 uptake measurements (Fig. 4). In this work, the conditions recommended by (Widdows and Staff, 1997) of water flow (180 ml min^{-1}) and cell concentration in the outflow (>50 % and <80 %) of the inflow concentration water were met.

In this work SFG was highest at 26 °C with positive at 22–30 °C, and negative at 34 °C. The shape of the SFG curve at tested temperatures was governed by ingested energy. In mollusks high filtration rates are found in a range of temperatures, but pumping decrease or cease at temperatures out of such range. For instance, the Mediterranean mussel *Mytilus galloprovincialis* has a high filtration rate at temperatures between 15 °C and 25 °C but there is low or no filtration outside of this range (Schulte, 1975). In this work, ingestion of microalgae never ceased within the temperature range studied, but followed the pattern already described in Fig. 4. The negative SFG at 34 °C was produced by a high respiration energy and a diminished absorbed energy, despite ingested energy was higher at 34 °C (212 ± 26 J g^{-1} h^{-1}) than at 22 °C (175 ± 6 J g^{-1} h^{-1}). This is partly explained by the inverse relationship found between absorption efficiency (AE) and temperature. It is known that AE is affected not only by temperature but also by seston concentrations in mussels, oysters, and other bivalves (Navarro et al., 2000; Velasco, 2006). In *Ostrea edulis* Beiras et al. (1994) found an inverse relationship of AE vs. *Isochrysis galbana* concentrations, with values of 61 % at 200 cell µl-1, and 95 % at 10 cell $µl^{-1}$. In this work, AE values were never higher than 82 %, probably because of the high microalgae concentration (150 cell $µl^{-1}$) employed.

In conclussion, optimum temperature for growth of the population studied from Guayacán Venezuela was 26 °C, with positive SFG from 22–30 °C. Therefore considering the temperature range in the Gulf of Cariaco Venezuela, this is an appropriate place for aquaculture of *P. viridis* considering only temperature as the key variable. However, further studies have to be made testing the combined effect of temperature and seston concentrations on SFG of *P. viridis* to define its suitability of culture year round in Gulf of Cariaco. A reliable open-flow sytem was described for ecophysiological studies in aquatic organisms.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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