

The effect of temperature on physiological energetics of a fast-growing selective strain and a hatchery population of the Pacific oyster (*Crassostrea gigas*)

Jingxiao Zhang¹ | Qi Li^{1,2}  | Shikai Liu¹ | Hong Yu¹ | Lingfeng Kong¹

¹Key Laboratory of Mariculture, Ministry of Education, Ocean University of China, Qingdao, China

²Laboratory for Marine Fisheries Science and Food Production Processes, Qingdao National Laboratory for Marine Science and Technology, Qingdao, China

Correspondence

Qi Li, Key Laboratory of Mariculture, Ministry of Education, Ocean University of China, Qingdao, China.
Email: qili66@ouc.edu.cn

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Abstract

Growth is an important aquaculture trait, which has been one of the most important traits for genetic improvement in aquatic species. Numerous fast-growing domesticated aquaculture organisms are being cultured, but the physiological processes underlying growth remain largely unexplored. The Pacific oyster (*Crassostrea gigas*) is one of the most widely farmed bivalves. In order to improve the productivity traits, a fast-growing selective strain of *C. gigas* was established. In this study, we compared physiological energetics of the fast-growing selective strain and an unselected hatchery population of *C. gigas* under different conditions of temperature. Components of energy gain (clearance rates, ingestion rates, absorption efficiency and absorption rates), energy loss (metabolic rates) and resulting energy budget (scope for growth) were analysed at four temperatures (15, 20, 25 and 30°C). The results indicated that selective breeding oysters had a higher energy gain compared to unselected oysters, but the selected strain and hatchery population of oysters did not significantly differ in metabolic rates at all tested temperatures ($p > 0.05$). The enhanced energy gain resulted in almost two times higher scope for growth in selective breeding oysters compared with unselected oysters. Physiological characteristics of *C. gigas* were greatly affected by temperature and showed a fluctuation with the increase in temperatures. The selective breeding oysters outperformed those of hatchery population in growth performance by an increased energy gain along with a similar energy loss. This study provided insight into physiological energetics accounting for growth improvements in fast-growing selective strain of *C. gigas*.

KEYWORDS

energy budget, faster growth, Pacific oysters, physiological traits, selected strain

1 | INTRODUCTION

The Pacific oyster *Crassostrea gigas* naturally distributed in the Pacific coast of East Asia and has become a worldwide aquaculture species due to its strong environmental adaptability. *Crassostrea gigas* is cultured in 27 countries and has become the most highly produced bivalve species all around the world (FAO (Food and Agriculture Organization), 2016). China is the top oyster-producing country

worldwide with the total oyster production reached to 4,835 thousand metric tons in 2016 (BOF (Bureau of Fisheries), 2017). Nowadays, *C. gigas* is a major species for shellfish aquaculture in northern China, supporting the development of shellfish industry. However, with the rapid development of oyster aquaculture, serious problems with genetic deterioration have emerged due to inappropriate broodstock management and inbreeding. In order to genetically improve the productivity of *C. gigas*, a selective breeding program was

initiated in 2006 with the objective to produce fast-growing strain by mass selection (Li, Wang, Liu, & Kong, 2011). After nine generations of selection, remarkable genetic gains for growth rates were obtained in the selected strains (Wang, Li, Kong, & Yu, 2012).

Growth variation in bivalve molluscs can be attributed to many mechanisms, and the physiological processes that constitute growth are of fundamental interest (Bayne, Svensson, & Nell, 1999). The combinations of quantitative analysis of physiological components of growth with an energy budget have been reported to explain such growth variability. In clams *Ruditapes philippinarum*, sea cucumber *Apostichopus japonicus* and mussels *Mytilus galloprovincialis*, significant differences between fast and slow growers in energy acquisition rate (i.e. differences in clearance rates, in food ingestion and absorption rates), as well as in the rate of energy loss through metabolic costs have been reported (Bai et al., 2015; Fernandez-Reiriz, Irisarri, & Labarta, 2016; Tamayo, Ibarrola, Cigarria, & Navarro, 2015; Tamayo, Ibarrola, Urrutia, & Navarro, 2011). Bayne et al. (1999) demonstrated that Sydney rock oysters *Saccostrea commercialis* exhibited faster growth rate as a result of the increased energy acquisition and reduced metabolic costs of growth. Bivalve molluscs have a highly phenotypic flexibility and plastic growth physiology (Bayne, 2004). Although numerous studies have been conducted to reveal physiological basis underlying growth variation, the physiological processes are complex and vary among species and populations. So, there are concerns that successive artificial selection on growth performance may change physiological performance, which could be used as physiological markers for growth potentials. Moreover, analyses of differences in physiological energetics between the fast-growing selective strain and hatchery population of *C. gigas* could also provide a physiological interpretation for growth improvement in the selected strains.

Temperature is one of the most important abiotic factors in aquaculture, affecting physiological processes of intertidal marine invertebrates (Bayne & Newell, 1983). Molluscs living in subtropical waters are subject to strong temperature variations over seasonal cycles which influenced metabolic adaptation (Widdows, 1973). Besides, temperature is also one of the most important factors that impact bivalve growth rate (Laing, Utting, & Kilada, 1987). Thus, effects of temperature on the physiological components of growth have been profusely analysed in many species of bivalves, such as mussels (Van Erkom Schurink, & Griffiths, 1992), clams (Han, Lee, & Wang, 2008; Tamayo, Ibarrola, & Navarro, 2013) and oysters (Guzmán-Agüero, Nieves-Soto, Hurtado, Piña-Valde, & Garza-Aguirre, 2013; Haurea, Penissona, Bougrierb, & Bauda, 1998). However, the physiological responses of fast-growing selective strains of *C. gigas* to different temperature have not been documented.

In the present study, to understand physiological mechanisms responsible for the growth improvements in the selected strain, we examined the effect of temperature on physiological characteristics of a fast-growing selective strain and a hatchery population of *C. gigas*, and compared the differences of physiological energetics between them at different conditions of temperature.

2 | MATERIALS AND METHODS

2.1 | Oyster collection

One-year-old Pacific oysters were collected from a selected strain after nine generations of selection for fast growth and a hatchery population without artificial selection respectively. The unselected oysters were derived from natural seed collected on the coast and cultured on ropes suspended from rafts along the coastal regions. All oysters were grown in the same area located in Rushan Bay, Shandong Province, China. Oysters from the selected strain and hatchery population were further separated into two groups based on their shell height sizes, including large size (SL, 50.54 ± 4.08 mm) and small size (SS, 38.55 ± 4.37 mm) groups for selective breeding oysters, and large size (CL, 48.64 ± 3.39 mm) and small size (CS, 35.15 ± 4.73 mm) groups for the unselected oysters. The sizes (large and small) of oysters from the hatchery population were comparable to those of oysters from the selected strain (Table 1).

2.2 | Experimental design

Both groups of oysters were delivered in May 2016, and maintained in the laboratory for 1 week at natural water temperature (19°C) under identical feeding conditions, consisting of a mixture of *Isochrysis galbana* and *Nschia closterium* at a ratio of 1:1. Oysters were separated into 100 L tanks in which the ambient temperature was gradually changed (by 1°C per day) to four different temperatures including 15, 20, 25 and 30°C . Oysters were acclimated to these temperatures for over a week prior to start of the physiological experiments. A total of 80 chambers were used in the experiment (four temperature treatments \times four oyster groups \times five replicates). Samples in each group were intended to have a common live biomass and thus, comprised two individuals in large-sized groups (SL and CL groups) and four individuals in small-sized groups (SS and CS groups). Five replicates were set for each oyster group and temperature treatment, and one blank chamber with no oysters was used as the control for each temperature treatment. The experiment last for 3 hr; and closed-chamber respiration methods were employed to determine physiological measurements.

TABLE 1 Mean (\pm SD) shell heights and tissue dry weights of *Crassostrea gigas* in the four experimental categories

Category	n	Shell height (mm)	Tissue dry weight (g)
SL	40	50.54 ± 4.08^b	0.2640 ± 0.0459^c
CL	40	48.64 ± 3.39^b	0.2216 ± 0.0448^c
SS	80	38.55 ± 4.37^a	0.1004 ± 0.0231^b
CS	80	35.15 ± 4.73^a	0.0791 ± 0.0172^a

Note. CL: unselected oysters with large size; CS: unselected oysters with small size; SL: selective breeding oysters with large size; SS: selective breeding oysters with small size.

Values sharing different superscripted letters are significantly different ($p < 0.05$).

During the experiment, oysters were fed algae, *I. galbana*. To characterize the particulate components of the diet, samples of diets were filtered onto ashed, preweighted GF/C glass-fibre filters and processed for total particulate matter (TPM) and inorganic and organic particulate matter (PIM and POM) according to standard procedures as described by Tamayo et al. (2011). Samples of faeces collected from the bottom of the chambers were also filtered onto ashed preweighted GF/C glass-fibre filters and processed for total and organic matter as indicated for food samples. Organic content (OC) was estimated as POM/TPM.

2.3 | Physiological determinations

Clearance rate (CR) is a measure of the volume of water cleared of algal cells per hour (Bayne et al., 1999). The value of CR (L/hr) was estimated following the equation (Coughlan, 1969):

$$CR = \frac{V}{nt} \ln \frac{C_0}{C_t} - \ln \frac{C_0}{C_t}$$

where V is the volume (L) cleared, t is the duration of the measurement (hr), n is the number of individuals per chamber, C_0 and C_t are the concentrations of unicellular algae at start and end of an experiment respectively. C_0 and C_t are the concentrations at the start and end, respectively, in the blank chamber. Cell concentrations were measured by direct counting with haemocytometer. Recorded C_0 and C_t for oysters in each chamber was the average of five determinations on the concentrations of unicellular algae over time and reported values of CR are means of five these chamber measurements.

Absorption efficiency (AE) was used to measure the efficiency with which ingested organic material is absorbed by the animal. AE (decimal units) was determined following Conover (1966) as:

$$AE = (f - e)/(1 - e) * f$$

where f and e represent the OCs of food and faeces respectively.

Organic ingestion rate (OIR: mg/hr) is the rate of ingestion of organic matter. The value of OIR was computed as the product of CR (L/hr) and POM concentration in diets (mg/L).

Absorption rate (AR: mg/hr) of total organic matter was calculated as the product of OIR (mg/hr) and AE. For conversion of OIR and AR to energy units, an energy equivalent of 18.75 J mg POM⁻¹ was applied based on reported data for *I. galbana* (Whyte, 1987).

Oxygen consumption rate (OCR, mg/hr) was calculated following the equation as:

$$OCR = (DO_0 - DO_t)V/t$$

where DO_0 and DO_t represent the oxyty at the start and end of an experiment (mg/L), t is the duration of the measurement (hr), V is the volume of the chamber (L). Water samples were collected by siphoning, and dissolved oxygen was measured at the beginning and at the end of the experiment using the Winkler method respectively. Blank chambers were used to check the stability of oxygen concentration during the measurement period. DO_0 and DO_0 recorded for each chamber was the average of three determinations over time

and reported values of OCR are means of five of these chamber measurements.

The metabolic rate represents the heat losses in the process of aerobic metabolism, which is measured by oxygen consumption rate (Tamayo et al., 2011). Metabolic rates (R: J/hr) were derived from measurements of OCR using an oxycaloric coefficient of 20.08 J ml O₂⁻¹ (Gnaiger, 1983).

Scope for growth (SFG: J/hr) combines the physiological processes involved in the acquisition and the expenditure of energy, which determines the quantity of energy available for growth, thus being a good predictor of the growth rate (Guzmán-Agüero et al., 2013). The value of SFG was computed as the difference between AR and R (both in energy units form, J/hr).

Q_{10} (temperature coefficient), a parameter to describe the rate of change in a biological or chemical system as a consequence of increasing the temperature by 10°C, was calculated for *C. gigas* according to the Van't Hoff equation (Bayne & Newell, 1983; Tamayo et al., 2013).

$$Q_{10} = (R_2/R_1)^{(10/(t_2-t_1))}$$

where t_1 and t_2 represent the temperature of two group trials respectively. R_1 and R_2 represented corresponding metabolic rates (J/hr) under each temperature group.

Once physiological measurements were completed, soft tissues of oyster in each chamber were dissected and tissue dry weight (TDW: g) was individually determined after drying the tissues at 80°C for 48 hr. For comparison, physiological determinations were expressed as mass-specific rates in 1 g of TDW. Average values of TDW for oysters in each category are shown in Table 1.

2.4 | Data analyses

Statistical analyses were performed using the SPSS 23.0 statistical package (IBM Inc., Armonk, NY, USA). The differences in physiological measurements among different categories were analysed using one-way analysis of variance (ANOVA), followed by Duncan's multiple range tests for post hoc comparison of means. Normality and homogeneity of variances were tested by means of Kolmogorov–Smirnov and Levene tests, respectively, prior to performing parametric analyses. Arc-sine transformation of ratios was performed when necessary. Significant differences in shell height and tissue dry weight of oysters among different experimental categories were checked by means of t test comparisons.

3 | RESULTS

3.1 | Feeding components of the energy budget

Mass-specific clearance rates (CR) and organic ingestion rates (OIR) determined for oysters at four different temperatures are shown in Figure 1. It is clear that temperature had significant effects on feeding components of the energy budget: both CR and OIR increased when temperature changed from 15 to 25°C, but decreased when

temperature changed from 25 to 30°C. The highest CR and OIR were observed in the oysters acclimated to temperature at 25°C. Notably, the selective breeding oysters (SL and SS) had significantly ($p < 0.05$) higher CR and OIR than the unselected oysters (CL and CS) at the optimal temperatures of 20–25°C. No significant differences in CR and OIR between large and small oysters were observed in either selective breeding oysters or unselected oysters.

3.2 | Digestive components of the energy budget

Absorption efficiencies (AEs) varied among the oysters acclimated with different temperatures, reaching the highest value at 25°C

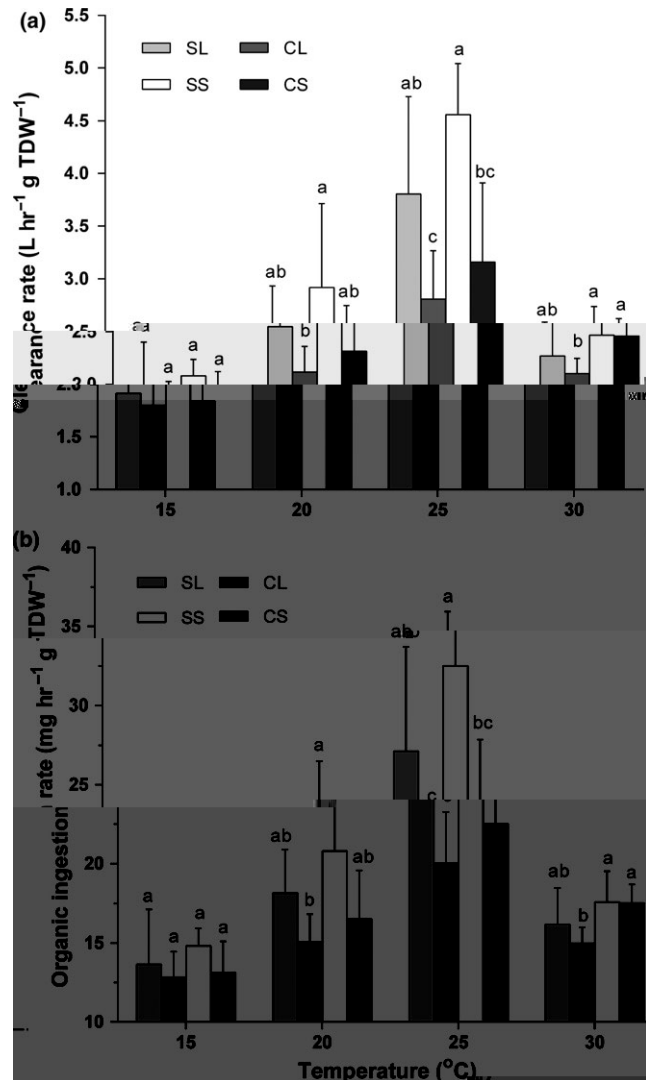


FIGURE 1 Comparison of clearance rates (a) and organic ingestion rates (b) between selective breeding oysters and unselected oysters with different sizes acclimated to different temperatures. Physiological rates were presented as mass-specific rates in gram of tissue dry weight (TDW). Bars denote standard deviation (five replicates of determinations). Different lowercase letters indicate significance ($p < 0.05$), while identical letters indicate nonsignificance ($p > 0.05$). SL, selective breeding oysters with large size; CL, unselected oysters with large size; SS, selective breeding oysters with small size; CS, unselected oysters with small size

(Figure 2). At all temperatures, the selective breeding oysters with both large and small sizes had significantly higher absorption efficiencies than the unselected oysters respectively ($p < 0.05$; Figure 2). The effects of size on absorption efficiency in selective breeding oysters were not significant at 15°C ($p > 0.05$), but the differences become significant while temperature increased from 20 to 30°C ($p < 0.05$). For the unselected oysters, significant differences in absorption efficiency between large- and small-sized oysters were observed only at 15 and 30°C, where AE was higher in small-sized oysters (Figure 2).

The observation of temperature effect on mass-specific absorption rate (AR) was consistent with observed variations in OIR and AE, which increased from low to medium temperature (15–25°C) but decreased from medium to high temperature (25–30°C) (Figure 3). The differences of AR between selective breeding oysters and unselected oysters were great, particularly at medium and high temperature (20–30°C), where the selective breeding oysters had significantly higher rates of absorption than unselected oysters ($p < 0.05$; Figure 3). However, the effects of size on mass-specific absorption rates of *C. gigas* were not significant at low and medium temperatures (15, 20 and 25°C) ($p > 0.05$). Only at high temperature (30°C), was there a significant difference in AR between large- and small-sized oysters ($p < 0.05$).

3.3 | Metabolic components of the energy budget

The metabolic components of the energy budget were evaluated by the oxygen consumption rate (OCR). In general, the mass-specific

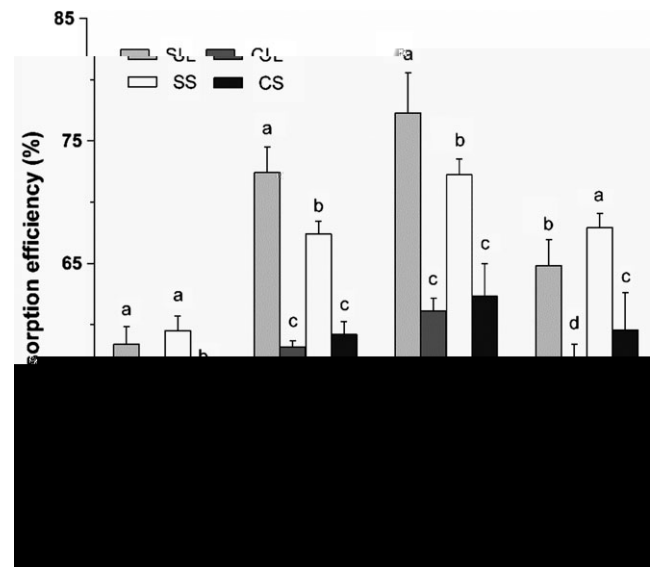


FIGURE 2 Comparison of absorption efficiencies between selective breeding oysters and unselected oysters with different sizes acclimated to different temperatures. Bars denote standard deviation (five replicates of determinations). Different lowercase letters indicate significance ($p < 0.05$), while identical letters indicate nonsignificance ($p > 0.05$). SL, selective breeding oysters with large size; CL, unselected oysters with large size; SS, selective breeding oysters with small size; CS, unselected oysters with small size

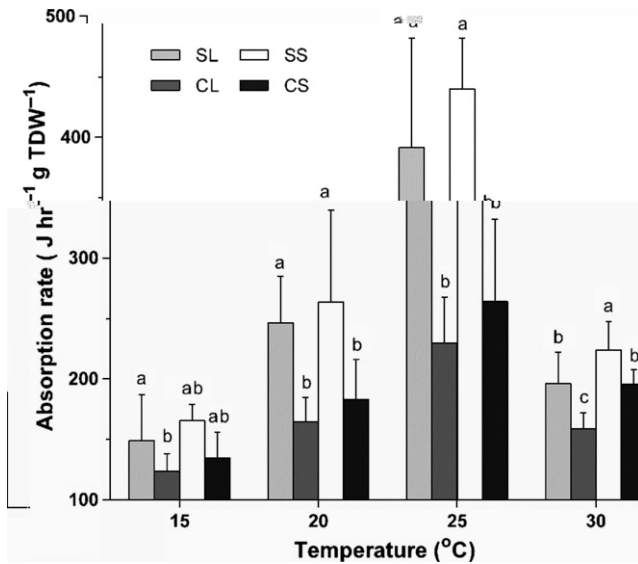


FIGURE 3 Comparison of absorption rates (energy units) between selective breeding oysters and unselected oysters with different sizes acclimated to different temperatures. Physiological determinations were presented as mass-specific values in gram of tissue dry weight (TDW). Bars denote standard deviation (five replicates of determinations). Different lowercase letters indicate significance ($p < 0.05$), while identical letters indicate nonsignificance ($p > 0.05$). SL, selective breeding oysters with large size; CL, unselected oysters with large size; SS, selective breeding oysters with small size; CS, unselected oysters with small size

oxygen consumption rates increased with the increase in temperature (Figure 4). Notably, significant differences in OCRs were observed between large- and small-sized oysters in both selected strains and hatchery population ($p < 0.05$), while no significant differences were observed between selective breeding oysters and unselected oysters at all tested temperatures ($p > 0.05$).

3.4 | Scope for growth

Mass-specific scope for growth (SFG) of oysters in both selected strain and hatchery population increased with temperature changed from 15 to 25°C, and decreased afterwards with the temperature changed from 25 to 30°C (Figure 5). The highest measurements of SFG were observed at 25°C (Figure 5). The selective breeding oysters had higher SFG than the unselected oysters at all tested temperatures, with significant differences being observed at medium temperatures (20–25°C, $p < 0.05$) (Figure 5). Overall, no significant differences in SFG were observed between large- and small-sized oysters, in both selected strain and hatchery population (Figure 5).

3.5 | Temperature coefficients

Calculated Q_{10} of metabolic rates at different temperature ranges are shown in Table 2. In both selected strain and hatchery population, large-sized oysters had higher Q_{10} values than small-sized oysters at different temperature intervals (15–20°C, 20–25°C and 25–30°C).

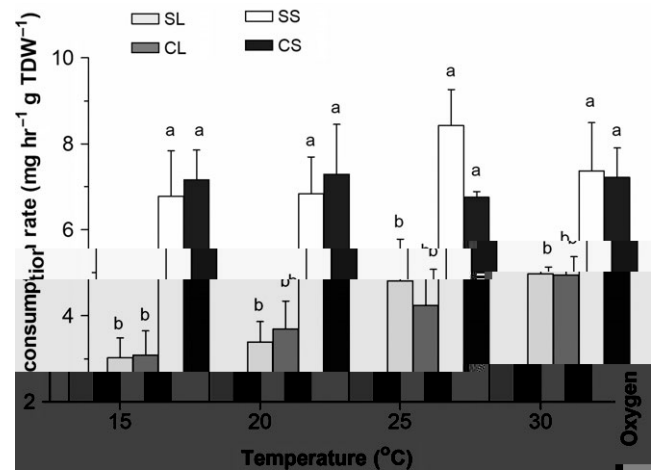


FIGURE 4 Comparison of oxygen consumption rates between selective breeding oysters and unselected oysters with different sizes acclimated to different temperatures. Results were presented as mass-specific values in gram of tissue dry weight (TDW). Bars denote standard deviation (five replicates of determinations). Different lowercase letters indicate significance ($p < 0.05$), while identical letters indicate nonsignificance ($p > 0.05$). SL, selective breeding oysters with large size; CL, unselected oysters with large size; SS, selective breeding oysters with small size; CS, unselected oysters with small size

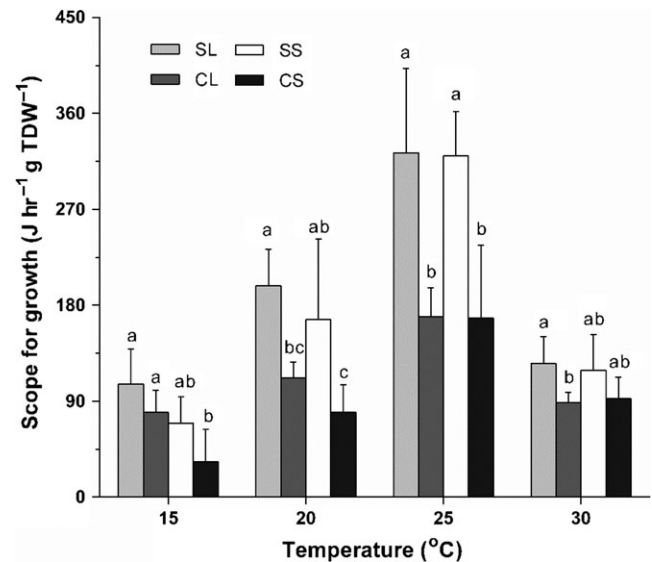


FIGURE 5 Comparison of scope for growth between selective breeding oysters and unselected oysters with different sizes acclimated to different temperatures. Physiological determinations were presented as mass-specific values in gram of tissue dry weight (TDW). Bars denote standard deviation (five replicates of determinations). Different lowercase letters indicate significance ($p < 0.05$), while identical letters indicate nonsignificance ($p > 0.05$). SL, selective breeding oysters with large size; CL, unselected oysters with large size; SS, selective breeding oysters with small size; CS, unselected oysters with small size

Compared with unselected oysters, lower values of Q_{10} were observed in selective breeding oysters when the temperature intervals at low and high levels (15–20°C and 25–30°C). Only at the medium level of

temperature interval (20–25°C), Q_{10} values for selective breeding oysters were higher than that for the unselected oysters.

4 | DISCUSSION

After nine generations of selection for rapid growth, oysters from the fast-growing selective strain outperformed those of hatchery population in growth performance. In this study, we detected differences in several underlying physiological parameters, and focused on identifying those factors contributing to the improved growth performance exhibited by the selective breeding oysters.

Differences in growth performance were reflected in differences in the feeding traits. The selective breeding oysters had a higher mass-specific CR and OIR than unselected oysters at all tested temperatures, indicating that selective breeding oysters had a higher energy acquisition compared to unselected oysters. Correlations between growth and feeding rates have been documented in other marine bivalves (Tamayo et al., 2015; Teixeira de Sousa, Matias, Joaquim, Ben Hamadou, & Leitão, 2011). Fernandez-Reiriz et al. (2016) studied the physiological traits underlying interindividual growth differences in mussels and found that interindividual differences in growth were achieved by higher CR and OIR in fast growers compared to slow-growing mussels. Bayne et al. (1999) also reported that faster growth in Sydney rock oyster was positively correlated with increased feed intake. The observation that feeding rates (CR and OIR) of selective breeding oysters outperformed that of unselected oysters suggests the potential presence of morphological-functional determinants of feeding rates, such as the higher feeding efficiency contributing to higher growth rates in clams and mussels was attributed to a larger gill area and gill efficiency (Fernandez-Reiriz et al., 2016; Tamayo et al., 2011). However, it is still uncertain whether this phenomenon reflects phenotypic differences have evolved as a consequence of the selection for fast growth, and potential presence of genes that are responsible for these physiological determined morpho-functional variation requires further investigation.

Digestive capability such as absorption efficiency is also closely related to growth performance (Stead, Thompson, & Jaramillo, 2003). In this study, fast-growing selective breeding oysters showed a significantly higher absorption efficiency and absorption rates than the

unselected oysters, indicating that selective breeding oysters could be able to process food more efficiently than the unselected oysters and exhibited an increased digestive and absorptive performance. Genetic causes of differences in digestive characteristics between selective breeding and unselected oysters are presently unknown. It is suggested that the successive selection on rapid growth may have positive impacts on hydrolytic activities of gland tissues and enzyme activities in digestive organs, which are closely linked to digestive capacities of bivalves (Ibarrola, Etxeberria, Iglesias, Urrutia, & Angulo, 2000; Ibarrola, Iglesias, & Navarro, 1996; Tamayo et al., 2015). Besides, a larger size of digestive glands which is associated with increased gut passage time of food could also contribute to the higher digestive efficiency of fast-growing individuals (Bayne, Hawkins, & Navarro, 1987; Bayne, Hawkins, Navarro, & Iglesias, 1989).

Metabolic expenditure as assessed by oxygen consumption rates was not significantly different between selective breeding oysters and unselected oysters in this study. Similarly, Bayne et al. (1999) observed no significant differences of metabolic rate between fast- and slow-growing in the Sydney rock oyster. However, in clams (Tamayo et al., 2011), mussels (Tamayo, Azpeitia, Markaide, Navarro, & Ibarrola, 2016) and rainbow trout (McCarthy, Houlihan, & Carter, 1994), a reduced metabolic rate was observed in fast-growing individuals. These processes generally appeared to be genotype dependent, and they were always attributed to reduced rates of protein turnover and high efficiency in protein deposition (Bayne, 2004; Hawkins, 1995; Hawkins & Day, 1996). Because oysters have a high degree of phenotypic plasticity, environment can play a large role in genotype expression (Bayne, 2004). The correlation between fast growth and reduced metabolic rates of *C. gigas* was not found in this study, also indicating both genetic and environmental factors (temperature) are implicated in variation in physiological processes.

As a consequence of increased rates of feeding (CR and IR) and digestion (AE and AR), rates of energy acquisition were consistently high in selective breeding oysters. Since no significant differences in metabolic energy expenditure were observed, the SFG (energy budget) in selected strain and hatchery population of oysters mainly reflected the differences in energy acquisition. The value of SFG is almost 2 times higher in selective breeding strain than in hatchery population of *C. gigas*, and a significant difference of SFG between the two populations of oysters was observed at 20 and 25°C, suggesting the potential for providing a high growth rate for shell and tissue in selective breeding oysters. Similarly, comparison of energy budget underlying interindividual growth differences in mussels highlighted that fast-growing mussels had significantly higher SFG than slow-growing mussels (Fernandez-Reiriz et al., 2016). The results obtained here were also in line with those of Tamayo et al. (2011), who compared the physiological energetics of fast- and slow-growing clams and found that fast growers exhibited about two to three times higher SFG than slow growers.

By experimenting with selective breeding and unselected oysters of different sizes, and standardizing the measurements according to the tissue dry weight of samples, we demonstrated that size was not a significant factor affecting most of the observed differences in

TABLE 2 Q_{10} coefficients of *Crassostrea gigas* in different experimental categories calculated from different temperature ranges

Temperature range (°C)	Q_{10} coefficients			
	SL	CL	SS	CS
15–20	1.083	1.426	1.017	1.018
20–25	2.013	1.317	1.522	0.927
25–30	1.067	1.363	0.765	1.068

Note. CL: unselected oysters with large size; CS: unselected oysters with small size; SL: selective breeding oysters with large size; SS: selective breeding oysters with small size.

physiological determinations (such as in clearance rates, ingestion rates, absorption rates and scope for growth) between the selected strain and hatchery population of *C. gigas*. Previous study on rock oyster also suggested that there were no effects of size on the differences in physiological determinations due to selection (Bayne et al., 1999). In this study, physiological characteristics of *C. gigas* were greatly affected by temperature and showed a fluctuation with the increase in temperatures. For most of the physiological determinations (CR, OIR, AE, AR and SFG) of *C. gigas*, values of measurements obtained in this study increase with temperature, up to a maximum or optimum limit beyond which they rapidly decrease. This trend was consistent with the results of previous studies for other bivalve species (Bayne & Newell, 1983).

The temperature coefficient is a parameter to describe the sensitivity of organisms to temperature increase, and the value of Q_{10} can reflect the adjustments related to the enzymatic and physiological requirements for energy when temperature increases within the natural range (Kim, Yoon, Kim, Gil, & Lee, 2005; Tamayo et al., 2013). Q_{10} values have been reported in many shellfish species, and the values of Q_{10} for metabolic rates were generally close to two in aquatic animals, suggesting that the metabolic increases twofold for a temperature change of 10°C (Saucedo, Ocampo, Monteforte, & Bervera, 2004; Zheng, Jin, Li, Bai, & Dong, 2008). In this study, the Q_{10} values ranged from 0.765 to 2.013 for selective breeding oysters and from 0.927 to 1.426 for unselected oysters, indicating both of the fast-growing selective strain and hatchery population of *C. gigas* will be well adapted to changes of temperature within the natural range. Besides, selective breeding oysters had a lower value of Q_{10} at 15–20°C and 25–30°C temperature intervals, indicating the respiration of selective breeding oysters reacted less sensitively than unselected oysters at these temperatures by increasing rapidly and the selective breeding oysters had a higher tolerance to high and lower temperature than unselected oysters.

In summary, oysters from the fast-growing selective strain had a faster rate of energy acquisition, food ingestion and food absorption compared to unselected oysters. No significant differences in metabolic rates between the selected strain and hatchery population of *C. gigas* were observed at all tested temperatures. The enhanced energy gain resulted in almost two times higher scope for growth in selective breeding oysters compared with unselected oysters at 20 and 25°C. The selective breeding oysters outperformed those of hatchery population in growth performance by an increased energy gain along with a similar energy loss. Further investigations are required to compare expression patterns of genes in contrasting physiological phenotypes in order to identify candidate genes for growth regulation.

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ORCID

Qi Li  <http://orcid.org/0000-0002-8180-729X>

REFERENCES

- Bai, Y., Zhang, L., Liu, S., Ru, X., Xing, L., Cao, X., ... Yang, H. (2015). The effect of salinity on the growth, energy budget and physiological performance of green, white and purple color morphs of sea cucumber, *Apostichopus japonicus*. *Aquaculture*, *437*, 297–303. <https://doi.org/10.1016/j.aquaculture.2014.12.020>
- Bayne, B. L. (2004). Phenotypic flexibility and physiological tradeoffs in the feeding and growth of marine bivalve molluscs. *Integrative and Comparative Biology*, *44*, 425–432. <https://doi.org/10.1093/icb/44.6.425>
- Bayne, B. L., Hawkins, A. J. S., & Navarro, E. (1987). Feeding and digestion by the mussel *Mytilus edulis* L. (Bivalvia: Mollusca) in mixtures of silt and algal cells at low concentrations. *Journal of Experimental Marine Biology and Ecology*, *111*, 1–22. [https://doi.org/10.1016/0022-0981\(87\)90017-7](https://doi.org/10.1016/0022-0981(87)90017-7)
- Bayne, B. L., Hawkins, A. J. S., Navarro, E., & Iglesias, I. P. (1989). Effects of seston concentration on feeding, digestion and growth in the mussel *Mytilus edulis*. *Marine Ecology Progress Series*, *55*, 47–54. <https://doi.org/10.3354/meps055047>
- Bayne, B. L., & Newell, R. C. (1983). Physiological energetics of marine mollusks. In A. S. M. Saleuddin, & K. M. Wilbur (Eds.), *The Mollusca* (pp. 407–515). New York, NY: Academic Press.
- Bayne, B. L., Svensson, S., & Nell, J. A. (1999). The physiological basis for faster growth in the Sydney rock oyster, *Saccostrea commercialis*. *Biology Bulletin*, *197*, 377–387. <https://doi.org/10.2307/1542792>
- BOF (Bureau of Fisheries) (2017). *China Fisheries Statistic Yearbook 2016*. Beijing, China: China Agriculture Press.
- Conover, R. J. (1966). Assimilation of organic matter by zooplankton. *Limnology and Oceanography*, *11*, 338–345. <https://doi.org/10.4319/lo.1966.11.3.0338>
- Coughlan, J. (1969). The estimation of filtering rate from the clearance of suspensions. *Marine Biology*, *2*, 356–358. <https://doi.org/10.1007/BF00355716>
- FAO (Food and Agriculture Organization) (2016). *Global aquaculture production 1950–2015*. Rome, Italy: Food and Agriculture Organization of the United Nations.
- Fernandez-Reiriz, M. J., Irisarri, J., & Labarta, U. (2016). Flexibility of physiological traits underlying inter-individual growth differences in intertidal and subtidal mussels *Mytilus galloprovincialis*. *PLoS ONE*, *11*, e0148245. <https://doi.org/10.1371/journal.pone.0148245>
- Gnaiger, E. (1983). Heat dissipation and energetic efficiency in animal anoxibiosis: Economy contra power. *Journal of Experimental Zoology*, *228*, 471–490. <https://doi.org/10.1002/jez.1402280308>
- Guzmán-Agüero, J. E., Nieves-Soto, M., Hurtado, M. Á., Piña-Valde, P., & Garza-Aguirre, M. C. (2013). Feeding physiology and scope for growth of the oyster *Crassostrea corteziensis* (Hertlein, 1951) acclimated to different conditions of temperature and salinity. *Aquaculture International*, *21*, 283–297. <https://doi.org/10.1007/s10499-012-9550-4>
- Han, K. N., Lee, S. W., & Wang, S. Y. (2008). The effect of temperature on the energy budget of the Manila clam, *Ruditapes philippinarum*. *Aquaculture International*, *16*, 143–152. <https://doi.org/10.1007/s10499-007-9133-y>
- Haurea, J., Penissona, C., Bougrierb, S., & Bauda, J. P. (1998). Influence of temperature on clearance and oxygen consumption rates of the flat oyster *Ostrea edulis*: Determination of allometric coefficients. *Aquaculture*, *169*, 211–224. [https://doi.org/10.1016/S0044-8486\(98\)00383-4](https://doi.org/10.1016/S0044-8486(98)00383-4)
- Hawkins, A. J. S. (1995). Effects of temperature change on ectotherm metabolism and evolution: Metabolic and physiological interrelations

- underlying the superiority of multi-locus heterozygotes in heterogeneous environments. *Journal of Thermal Biology*, 20, 23–33. [https://doi.org/10.1016/0306-4565\(94\)00023-c](https://doi.org/10.1016/0306-4565(94)00023-c)
- Hawkins, A. J. S., & Day, A. J. (1996). The metabolic basis of genetic differences in growth efficiency among marine animals. *Journal of Experimental Marine Biology and Ecology*, 203, 93–115. [https://doi.org/10.1016/0022-0981\(96\)02572-5](https://doi.org/10.1016/0022-0981(96)02572-5)
- Ibarrola, I., Etxeberria, M., Iglesias, J. I. P., Urrutia, M. B., & Angulo, E. (2000). Acute and acclimated digestive responses of the cockle *Cerastoderma edule* (L.) to changes in the food quality and quantity: II. Enzymatic, cellular and tissular responses of the digestive gland. *Journal of Experimental Marine Biology and Ecology*, 252, 199–219. [https://doi.org/10.1016/s0022-0981\(00\)00235-5](https://doi.org/10.1016/s0022-0981(00)00235-5)
- Ibarrola, I., Iglesias, J. I. P., & Navarro, E. (1996). Differential absorption of biochemical components in the diet of the cockle *Cerastoderma edule*: Enzymatic responses to variations in seston composition. *Canadian Journal of Zoology*, 74, 1887–1897. <https://doi.org/10.1139/z96-213>
- Kim, W. S., Yoon, S. J., Kim, J. M., Gil, J. W., & Lee, T. W. (2005). Effects of temperature changes on the endogenous rhythm of oxygen consumption in the Japanese flounder *Paralichthys olivaceus*. *Fisheries Science*, 71, 471–478. <https://doi.org/10.1111/j.1444-2906.2005.00990.x>
- Laing, I., Utting, S. D., & Kilada, R. W. S. (1987). Interactive effect of diet and temperature on the growth of juvenile clams. *Journal of Experimental Marine Biology and Ecology*, 113, 23–38. [https://doi.org/10.1016/0022-0981\(87\)90080-3](https://doi.org/10.1016/0022-0981(87)90080-3)
- Li, Q., Wang, Q., Liu, S., & Kong, L. (2011). Selection response and realized heritability for growth in three stocks of the Pacific oyster *Crassostrea gigas*. *Fisheries Science*, 77, 643–648. <https://doi.org/10.1007/s12562-011-0369-0>
- McCarthy, I. D., Houlihan, D. F., & Carter, C. G. (1994). Individual variation in protein turnover and growth efficiency in rainbow trout, *Oncorhynchus mykiss* (Walbaum). *Proceedings of the Royal Society B: Biological Sciences*, 257, 141–147. <https://doi.org/10.1098/rspb.1994.0107>
- Saucedo, P. E., Ocampo, L., Monteforte, M., & Bervera, H. (2004). Effect of temperature on oxygen consumption and ammonia excretion in the Calafia mother-of-pearl oyster, *Pinctada mazatlanica* (Hanley, 1856). *Aquaculture*, 229, 377–387. [https://doi.org/10.1016/s0044-8486\(03\)00327-2](https://doi.org/10.1016/s0044-8486(03)00327-2)
- Stead, R. A., Thompson, R. J., & Jaramillo, J. R. (2003). Absorption efficiency, ingestion rate, gut passage time and scope for growth in suspension- and deposit-feeding *Yoldia hyperborea*. *Marine Ecology Progress Series*, 252, 159–172. <https://doi.org/10.3354/meps252159>
- Tamayo, D., Azpeitia, K., Markaide, P., Navarro, E., & Ibarrola, I. (2016). Food regime modulates physiological processes underlying size differentiation in juvenile intertidal mussels *Mytilus galloprovincialis*. *Marine Biology*, 163, 131. <https://doi.org/10.1007/s00227-016-2905-z>
- Tamayo, D., Ibarrola, I., Cigarria, J., & Navarro, E. (2015). The effect of food conditioning on feeding and growth responses to variable rations in fast and slow growing spat of the Manila clam (*Ruditapes philippinarum*). *Journal of Experimental Marine Biology and Ecology*, 471, 92–103. <https://doi.org/10.1016/j.jembe.2015.05.017>
- Tamayo, D., Ibarrola, I., & Navarro, E. (2013). Thermal dependence of clearance and metabolic rates in slow- and fast-growing spats of manila clam *Ruditapes philippinarum*. *Journal of Comparative Physiology B*, 183, 893–904. <https://doi.org/10.1007/s00360-013-0764-1>
- Tamayo, D., Ibarrola, I., Urrutia, M. B., & Navarro, E. (2011). The physiological basis for inter-individual growth variability in the spat of clams (*Ruditapes philippinarum*). *Aquaculture*, 321, 113–120. <https://doi.org/10.1016/j.aquaculture.2011.08.024>
- Teixeira de Sousa, J., Matias, D., Joaquim, S., Ben Hamadou, R., & Leitão, A. (2011). Growth variation in bivalves: New insights into growth, physiology and somatic aneuploidy in the carpet shell *Ruditapes decussatus*. *Journal of Experimental Marine Biology and Ecology*, 406, 46–53. <https://doi.org/10.1016/j.jembe.2011.06.001>
- Van Erkom Schurink, C., & Griffiths, C. L. (1992). Physiological energetic of four South African mussel species in relation body size, ration and temperature. *Comparative Biochemistry and Physiology Part A: Physiology*, 101, 779–789. [https://doi.org/10.1016/0300-9629\(92\)90358-w](https://doi.org/10.1016/0300-9629(92)90358-w)
- Wang, Q., Li, Q., Kong, L., & Yu, R. (2012). Response to selection for fast growth in the second generation of Pacific oyster (*Crassostrea gigas*). *Journal of Ocean University of China*, 11, 413–418. <https://doi.org/10.1007/s11802-012-1909-7>
- Whyte, J. N. C. (1987). Biochemical composition and energy content of six species of phytoplankton used in mariculture of bivalves. *Aquaculture*, 60, 231–241. [https://doi.org/10.1016/0044-8486\(87\)90290-0](https://doi.org/10.1016/0044-8486(87)90290-0)
- Widdows, J. (1973). The effects of temperature on the metabolism and activity of *Mytilus edulis*. *Netherlands Journal of Sea Research*, 7, 387–398. [https://doi.org/10.1016/0077-7579\(73\)90060-4](https://doi.org/10.1016/0077-7579(73)90060-4)
- Zheng, Z., Jin, C., Li, M., Bai, P., & Dong, S. (2008). Effects of temperature and salinity on oxygen consumption and ammonia excretion of juvenile miiuy croaker, *Miichthys miiuy* (Basilewsky). *Aquaculture International*, 16, 581–589. <https://doi.org/10.1007/s10499-008-9169-7>

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