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IMPACT OF HIGH FEEDING ON THE LOCOMOTIVE CAPACITY OF THE JUVENILE PERUVIAN SCALLOP *ARGOPECTEN PURPURATUS* AFTER EXPOSURE TO HYPOXIA

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ABSTRACT The scallop *Argopecten purpuratus* is a species of high commercial interest in northern Chile and Peru. Both natural and cultured populations are located in shallow bays which are periodically subjected to decreases in the levels of dissolved oxygen and to variations in the availability of food, due to upwelling events or large-scale oscillations such as El Niño–Southern Oscillation. The aim of the present study was to evaluate how the nutritional status of *A. purpuratus* juveniles affects their escape capacity (as a measure of their vitality) after exposure to hypoxia cycles such as those encountered in their natural environment. For this, three feeding levels were applied for 15 days: scallops fed with a mixture of microalgae equivalent to (1) 6% or (2) 3% of their body mass and (3) unfed scallops. Subsequently, half of the individuals in each treatment underwent daily hypoxia cycles for 7 days and the other half was maintained under normoxia. After this period, using their predator, the sea star *Meyenaster gelatinosus*, the scallops were induced to escape, and several escape response indicators were evaluated. In general, scallops fed with the highest microalgal ration (6% of scallop mass) showed the best escape performance in terms of the reaction time to the predator, total number of claps, and clapping time and rate, closely followed by scallops fed 3% of their mass. Unfed scallops showed the poorest performance in each of these escape parameters. These results were closely related with the carbohydrate content of the adductor muscle, with unfed scallops showing the lowest content. Hypoxia exposure resulted in a decrease in escape response, and unfed scallops were the most affected. Among unfed scallops, 40% of the individuals maintained under normoxia showed an escape response, whereas only 15% of those exposed to hypoxia escaped the predator. By contrast, and regardless of environmental oxygenation, more than 90% of individuals fed with either 3% or 6% rations escaped the predator. In conclusion, when scallops are under reduced nutritional state (due to low food availability), the cyclical hypoxic periods that they encounter in the natural environment can have profound effects on their vitality, making them more vulnerable against predators.

KEY WORDS: hypoxia, escape capacity, feeding level, nutrition, scallop culture, *Argopecten purpuratus*

INTRODUCTION

Both natural and cultured populations of the scallop *Argopecten purpuratus* located on the north coast of Chile and Peru are increasingly exposed to coastal upwelling processes during spring and summer (Wolff 1987, Uribe & Blanco 2001). The upwelling causes intrusion of water masses characterized by low oxygen content, low temperatures, and low food concentrations in the bays where this scallop is typically present (Diaz & Rosenberg 1995, Zhang et al. 2010).

Depending on the oceanographic dynamics, these water masses may remain in the bays from days to weeks, meaning that organisms present in these areas, as it is the case of *Argopecten purpuratus*, will be exposed to relatively long periods of hypoxia and reduced food concentrations.

Many species of bivalve molluscs can withstand conditions of environmental or functional hypoxia using anaerobic metabolic pathways (Livingstone et al. 1981, Rivera-Ingraham et al. 2013), and scallops in particular may survive long periods under such conditions (Livingstone et al. 1981, Chih & Ellington 1983). The intense swimming behavior often shown by scallops may also lead to (functional) hypoxia in their tissues, in which case anaerobic metabolism supplies the energy needs for adductor muscle contractions during the escape response (Chih &

Ellington 1983). Adductor muscle contraction is energetically supported mainly by the ATP generated from the phosphagen arginine phosphate (Bailey et al. 2003, Pérez et al. 2008a), and its recovery initially relies on anaerobic glycolysis with octopine accumulation (Grieshaber 1978, Livingstone et al. 1981). Full recovery of scallops from exhaustive swimming activity requires aerobic metabolism, which is likely more efficient under normoxic environmental conditions.

Scallops such as *Placopecten magellanicus*, *Argopecten irradians concentricus*, and *Patinopecten yessoensis* also use arginine phosphate and anaerobic metabolism as the source of ATP during environmental hypoxia (Livingstone et al. 1981, Chih & Ellington 1983), with octopine accumulation reaching levels of 12.8 $\mu\text{mol/g}$ wet mass (Enomoto et al. 2000). Similarly, during an escape response, the glycolytic rate is increased by about 10 times, resulting in octopine concentrations of about 8 $\mu\text{mol/g}$ wet mass (Chih & Ellington 1983). Thus, the metabolic pathways used to provide energy during both environmental and functional hypoxia are similar in scallops.

To escape from predators, scallops use their phasic adductor muscle for jet-powered swimming (Barbeau & Scheibling 1994). As escape responses require a good physiological status, the swimming capacity of scallops can be used as an indicator of vitality and general physiological condition (Brokordt et al. 2000a, 2000b, Brokordt et al. 2006, Pérez et al. 2008b).

Scallop escape capacity has been shown to be affected by the reproductive status (Brokordt et al. 2000a, 2000b, Brokordt

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et al. 2006, Perez et al. 2011), stress due to manipulation under culture conditions (Pérez et al. 2008b), seasonal temperature variations (Guderley et al. 2008), and hypoxia (Brokordt et al. 2013). Brokordt et al. (2013) demonstrated that environmental hypoxia reduces the escape capacity of both adult and juvenile *Argopecten purpuratus*. In addition, these authors observed that after 7 days of daily hypoxia cycles, adductor muscle carbohydrate content decreased by 65% in juvenile individuals, indicating that this substrate supports metabolism during chronic hypoxia.

A decrease in food availability, as it occurs during upwelling processes, could reduce carbohydrate storages in scallops, affecting in turn their metabolic capacity and, hence, their tolerance to prolonged environmental hypoxia. Brokordt et al. (2013) proposed that the hypoxia-induced decrease in escape response capacity reflects an energetic compromise between locomotion and the ability to withstand conditions of low oxygen environment. From the aforementioned evidence, the question that arises is how feeding affects the escape response of scallops under hypoxic conditions. To answer this question, in the present study, the effects of food availability on the nutritional status of *Argopecten purpuratus* juveniles, and how this affected the ability to escape after exposure to environmental hypoxia cycles were evaluated.

MATERIALS AND METHODS

Scallops Obtaining and Feeding Treatments

Juvenile *Argopecten purpuratus* scallops (20–30 mm height; $n = 120$) were obtained from the Culture Center of the Universidad Católica del Norte, located at Tongoy Bay, Coquimbo (30° 16' S, 71° 35' W). The scallops were transported to the marine culture laboratory of the Universidad Católica del Norte at Coquimbo, where they were allowed to acclimate to laboratory conditions for 15 days, in 25 L aquaria with filtered (50 μ m) and circulating seawater (flow ~ 1.8 L/min), with constant aeration, and at a temperature of approximately $\sim 16^\circ\text{C}$. Scallops from two aquaria ($n = 40$) were fed with a mixture of microalgae (50% *Isochrysis galbana* and 50% *Chaetoceros calcitrans*) in an amount of food equivalent to 6% of the average dry mass of the scallops (i.e., high feeding treatment, according to Martínez et al. 2000). Scallops in another two aquaria ($n = 40$) were fed the same diet but using a quantity equivalent to 3% of their average dry mass (i.e., intermediate feeding treatment). Scallops of the last two aquaria ($n = 40$) did not receive external food, but some phytoplankton was likely present in the filtered seawater. Animals were fed twice a day, and the water in the aquarium was changed before the first feeding. The treatments with the different feeding levels were maintained for 15 days before the application of the hypoxia cycles.

To determine the amount organic matter that the scallops received from each feeding treatment, three 1-L samples were obtained from each aquarium. Samples were filtered (using 11- μ m Watmann filters) and the resulting material was washed with 3% ammonium formate solution to dissolve salts. Samples were then oven-dried at 70°C until achieving constant mass, and the mass of organic matter per treatment was determined (Fig. 1).

Hypoxia Treatments

After the 15 days of applying the different feedings, for each treatment, one of the two aquariums ($n = 20$ scallops) was

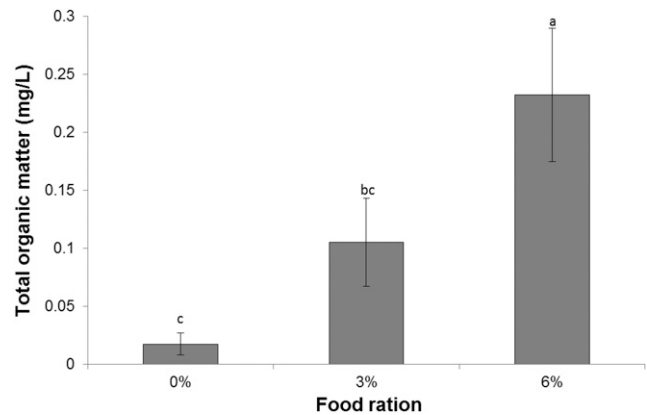


Figure 1. Total organic matter registered for each of the food ration treatments (food rations equivalent to 0%, 3%, or 6% of scallop average dry mass) applied to *Argopecten purpuratus* juveniles. Values represent the mean \pm SE ($n = 3$ samples per treatment). Values sharing the same letter are not significantly different ($P \geq 0.05$) as indicated by an *a posteriori* comparison test.

maintained under normoxia (serving as control), whereas the second was subjected to 7 days of daily hypoxia cycles. To achieve this, water in the corresponding aquaria was pumped with gaseous nitrogen to decrease dissolved oxygen at a rate of ~ 1 mg $\text{O}_2/\text{L h}^{-1}$ until reaching a concentration of ~ 2 mg O_2/L (i.e., hypoxia).

Hypoxic conditions were maintained for 3 h, after which air-saturated water was slowly added until normoxic oxygen levels (~ 8 mg O_2/L) were achieved. Scallops were then allowed to recover for a period of approximately 2 h. Counting the time required to change oxygenation levels in addition to the 3-h hypoxia exposure, scallops were exposed to reduced oxygen conditions for ~ 6 h per day. Scallops were fed according to their respective treatments throughout the duration of the experiment.

Evaluation of the Escape Response

Once the period of hypoxia cycles was complete, the escape response capacity of scallops from each feeding treatment was individually evaluated using 25 L plastic containers with circulating seawater at approximately 16°C . After the start of the escape response test, scallops were allowed to settle for 2 min. The test began by carefully approaching the natural predator, the sea star *Meyenaster gelatinosus* (Ortiz et al. 2003), to the scallop to stimulate the escape response. Six indicators of the escape response capacity were measured for each scallop (Brokordt et al. 2006): (1) reaction time, measured as the time passing until the scallop makes the first clap; (2) total number of claps made until exhaustion (i.e., no response during 1 min of stimulation); (3) total response time from the stimulus until exhaustion; (4) clapping rate (i.e., number of claps per minute); (5) proportion of recovered claps after 10 min of recovery; and (6) proportion of recovered clapping rate after 10 min of recovery.

Once the behavioral experiments were completed, scallops were killed and their adductor muscles were weighed and frozen at -80°C for the determination of their carbohydrate content.

Adductor Muscle Carbohydrate Content

To measure muscle carbohydrate content, carbohydrates were extracted and quantified according to Dubois et al. (1956).

Statistical Analysis

To evaluate if feeding treatment and oxygenation conditions influence the escape response in scallops, two-way analyses of variance (ANOVA) were carried out, after ensuring that the assumptions of normality and homoscedasticity of variances were met. When assumptions were not met, data were either transformed or nonparametric statistical analyses were applied. For muscle carbohydrate content, the same two-way ANOVA was performed. After each ANOVA, *a posteriori* Tukey tests were applied for specific comparisons.

RESULTS

Effect of Feeding Levels and Hypoxia Exposure on Escape Capacity

Feeding and oxygenation levels, as well as the interaction between these factors, significantly affected each of the escape response parameters (Table 1). In general, regardless of the feeding level, scallops maintained under normoxia performed better than those subjected to the hypoxia cycles (Fig. 2). Specifically, juveniles fed the highest food ration (6% of their mass) had the best performance, whereas unfed scallops showed the poorest, regardless of whether they were maintained under normoxia or hypoxia (Fig. 2A). The maximal number of claps

performed until exhaustion was highest in scallops fed 6% of their mass, but exposure to hypoxia cycles caused this value to decrease to levels similar to those shown by scallops fed 3% of their mass (Fig. 2B). The shortest clapping time (total time of response until exhaustion) was observed in unfed scallops subjected to hypoxia cycles, but unfed scallops maintained under normoxia had higher levels (Fig. 2C). Scallops fed 3% and 6% of their mass showed similar times of clapping, but exposure to hypoxia decreased this significantly in scallops fed 3% of their mass. The clapping rate was the slowest in unfed scallops after hypoxia, although values ameliorated when maintained in normoxia; but still clapping rates were very slow compared with that in fed juveniles (Fig. 2D). The fastest clapping rate was registered in scallops fed 6% of their mass and maintained under normoxia. Regardless of the oxygen level under which scallops were maintained, both the capacity to recover the initial number of claps and the clapping rate were lowest in unfed juveniles and highest in fed scallops (3% or 6% of their mass) (Fig. 2E, F).

Carbohydrate Content

In general, only adductor muscle carbohydrate content was significantly affected by feeding level ($F = 54$, $P < 0.0001$), with unfed scallops showing the lowest levels (Fig. 3). Although carbohydrate content tended to be lower after scallops were exposed to the 7 days of hypoxia cycles, in each feeding treatment, this effect was not statistically significant ($F = 1.9$, $P < 0.173$).

TABLE 1.

Two-way ANOVA for escape responses of *Argopecten purpuratus* juvenile scallops, after having been exposed to different feeding and oxygenation levels.

Source of variation	DF	F	P value
Reaction time			
Food	2	33	0.00000
Oxygen (ox)	1	10	0.002
Food*ox	2	7	0.002
Error	87	–	–
Clap number			
Food	2	154	0.00000
Oxygen (ox)	1	23	0.000004
Food*ox	2	4.4	0.0252804
Error	114	–	–
Clapping time			
Food	2	38	0.000000
Oxygen (ox)	1	15	0.000188
Food*ox	2	3.6	0.03
Error	114	–	–
Clapping rate			
Food	2	156	0.00000
Oxygen (ox)	1	18	0.0001
Food*ox	2	4.9	0.009
Error	114	–	–
Recovered claps			
Food	2	3.82	0.014
Oxygen (ox)	1	6.06	0.008
Food*ox	2	3.77	0.017
Error	114	–	–
Recovered clapping rate			
Food	2	47.11	0.00000
Oxygen (ox)	1	5.9	0.02
Food*ox	2	3.77	0.017
Error	114	–	–

DISCUSSION

Escape responses are an effective behavioral indicator of the physiological condition and vitality of several species of scallops (Brokordt et al. 2000a, 2000b, Fleury et al. 2005, Brokordt et al. 2006, Pérez et al. 2008b, Guderley et al. 2011). This study demonstrates that feeding level affected the escape response capacity of juvenile *Argopecten purpuratus* scallops. In general, scallops fed with the highest microalgal ration (6% of their mass) showed the best escape performance in terms of reaction time to the predator stimuli, total number of claps, and clapping time and rate, closely followed by scallops fed 3% of their mass. Unfed scallops showed the poorest performance in each of these escape parameters. These results were closely related to the carbohydrate content present in the adductor muscle, where unfed scallops showed the lowest content.

Carbohydrates are the main substrate fueling many scallop activities and play an especially important role in muscle contraction during the escape response and swimming, given that it is mainly supported by glycolytic pathways (de Zwaan et al. 1980, Livingstone et al. 1981). Arginine phosphate is the main source of ATP for the escape activity of scallops, and the glycolytic pathway not only provides energy for muscle contraction but also allows the rapid recovery of arginine phosphate levels in muscles (de Zwaan et al. 1980, Livingstone et al. 1981, Bailey et al. 2003). Therefore, adequate feeding directly affects the escape capacity of *Argopecten purpuratus*, in both the initial response and the recovery for subsequent escape responses. In this regard, results of this study showed that unfed juvenile scallops had the lowest recovery rates in terms of number of claps and clapping rate.

The observed deterioration of the escape response of juvenile scallops caused by the cyclic periods of hypoxia agrees with

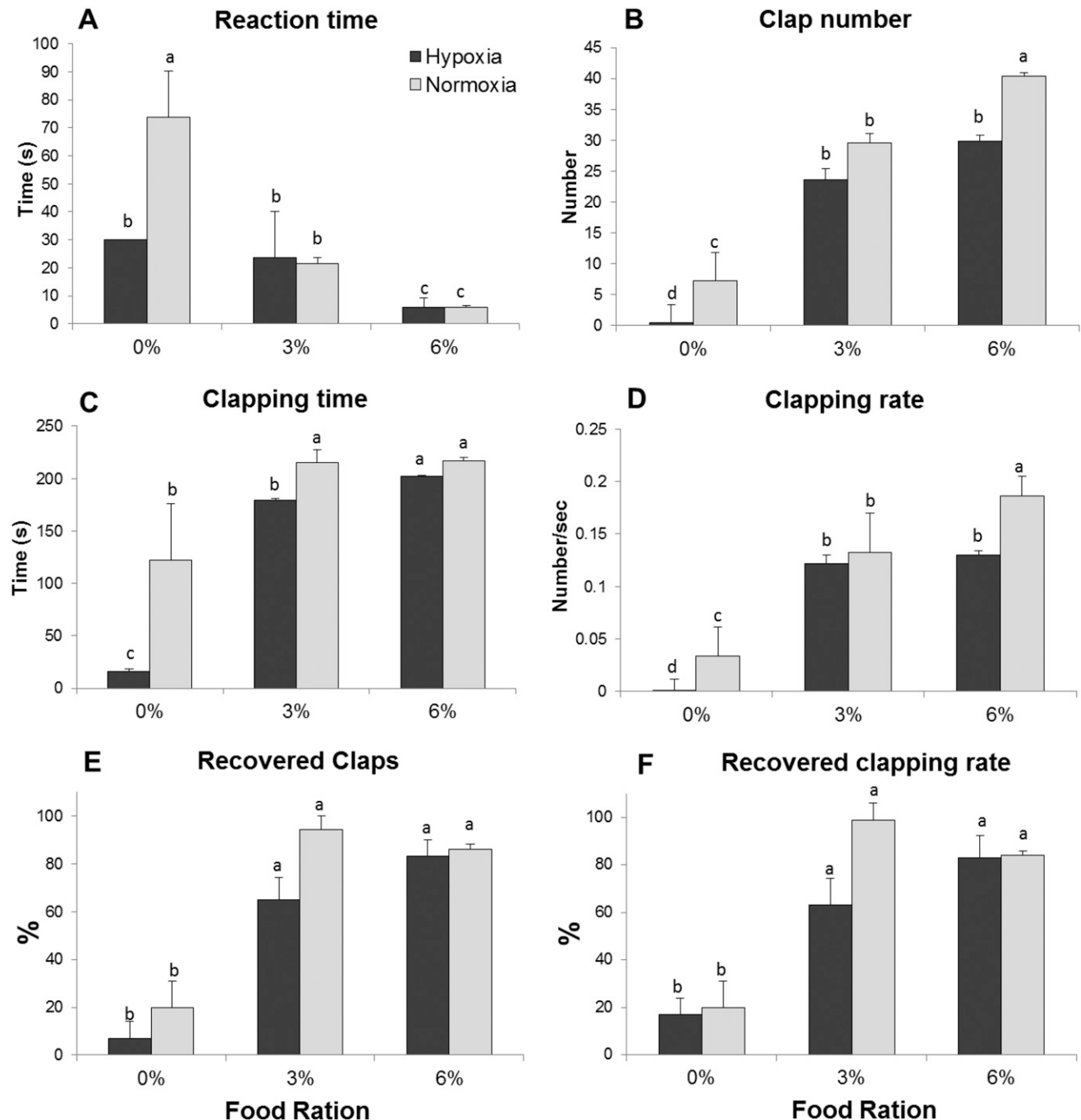


Figure 2. Escape response parameters of *Argopecten purpuratus* juveniles subjected to different feeding treatments (food rations equivalent to 0%, 3%, or 6% of scallop average dry mass) and oxygenation levels (normoxia: ~ 8 mg O₂/L; or hypoxia: ~ 2 mg O₂/L). The escape response parameters are (A) reaction time, (B) clap number, (C) clapping time, (D) clapping rate, (E) recovered claps, and (F) recovered clapping rate after 10 min of recovery. Values represent the mean \pm SE ($n = 20$ individuals per treatment). Values sharing the same letter are not significantly different ($P \geq 0.05$) as indicated by *a posteriori* comparison tests.

Brokordt et al. (2013), who demonstrated that exposure to single or multiple daily cycles of hypoxia decreases the capacity of *Argopecten purpuratus* juveniles and adults to escape by 15%–20%. Results of this study showed that scallops fed the highest microalgal ration had the best escape performance in terms of clap number and clapping rate, but after exposure to hypoxia cycles, these responses were reduced to similar levels as

those observed in scallops fed rations equivalent to 3% of their mass. The latter did not see their escape parameters reduced (with the exception of the clapping time) after hypoxia, suggesting that the highest feeding level may have increased metabolic costs associated with digestion. Other parameters affecting metabolic rates have also been described to impact escape performance. For example, Schalkhauser et al. (2014)

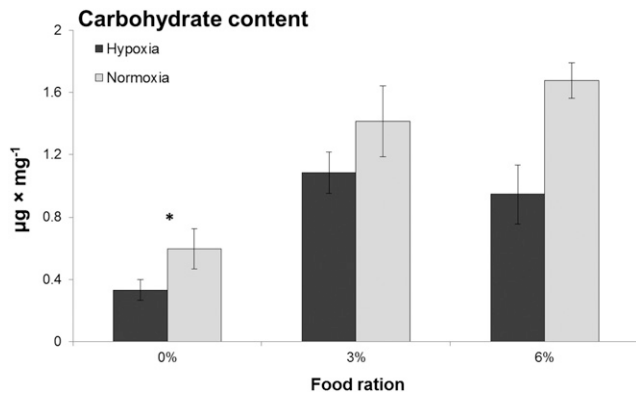


Figure 3. Carbohydrate content in the adductor muscle of *Argopecten purpuratus* juveniles subjected to different feeding treatments (food rations equivalent to 0%, 3%, or 6% of scallop average dry mass) and oxygenation levels (normoxia: $\sim 8 \text{ mg O}_2/\text{L}$; or hypoxia: $\sim 2 \text{ mg O}_2/\text{L}$). Values represent the mean \pm SE ($n = 20$ individuals per treatment). Values sharing the same letter are not significantly different ($P \geq 0.05$) as indicated by an *a posteriori* comparison test.

observed that by increasing water temperature to 20°C , the mean phasic force during escape performance is decreased, whereas the recovery time after fatigue is increased. This deterioration of the escape response in warm acclimated scallops might be a consequence of elevated metabolic costs at reduced oxygen availability under high temperatures.

Brokordt et al. (2013) observed that scallops exposed to daily cycles of hypoxia for 7 days had decreased muscle carbohydrate contents. In this study, carbohydrate content was strongly influenced by feeding levels but not hypoxia.

Most of the *Argopecten purpuratus* populations, both natural and cultivated, normally inhabit semienclosed bays, close to sources of upwelling systems (Wolff 1987, Uribe & Blanco 2001). The subsurface waters that normally emerge from these events are cold water masses, with low concentrations of dissolved oxygen (Guillen et al. 1977, Olivares 1988, Mendo et al. 1989, Olivares 1989, Uribe & Blanco 2001). These variations may last several days during the spring–summer periods (Zhang

et al. 2010, Brokordt et al. 2013). These periods with highly variable environmental conditions have been associated with high mortalities of bivalve molluscs (Xiao et al. 2005, Burdon et al. 2014). Wolff (1987) recorded massive mortalities of *A. purpuratus* experiencing dissolved oxygen concentrations lower than 40% saturation. Increased mortality rates have also been reported for Chilean–Peruvian *A. purpuratus* beds (Cabello et al. 2002).

Productive activities, enhancing stress due to handling and transportation of cultured scallops, usually increase, coinciding with periods of high abiotic variation, which include increasing the frequency of hypoxic events (Christophersen 2000). Thus, the synergic effects of abiotic and handling stress can generate a physiological imbalance, potentially leading to increased mortality rates or decreased ability to respond to additional (stressful) environmental changes (Brokordt et al. 2013). The results here presented suggest that an increased availability of food for juvenile scallops can mitigate the stressful effects of a variable environment, in particular during periods of high frequency of hypoxic events. This study shows that an increased amount of food enhances the tolerance of *Argopecten purpuratus* juveniles to hypoxia, which have a faster reaction time and a prolonged time of response when facing a predator. The interaction of two or more factors can generate positive or negative synergies on the physiological condition of the organisms (Perdue et al. 1981, Samain et al. 2007). In this case, cyclical periods of hypoxia, such as those experienced by *A. purpuratus* in its natural environment, would affect juvenile vitality mainly under conditions of low food availability; however, high availability of food can compensate for the negative effects of hypoxia on scallop vitality.

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