



Combined effects of warming and freshening on the physiological energetics of the edible whelk *Trophon geversianus*

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ABSTRACT

The interacting effects of climate change pressures and human use of natural resources are increasingly affecting marine biodiversity. Variations in key abiotic factors such as temperature and salinity may therefore negatively influence marine organisms that are already threatened by intensive fisheries. Herein, we tested the hypothesis that future ocean warming and freshening will affect the fitness and survival of the overexploited snail *Trophon geversianus* in Southern Patagonia. To test this hypothesis, we investigated the effect of a 50 day incubation period of five temperatures (1, 5, 9, 12 and 15 °C) and two salinities (25 and 30 psu), (which correspond to current and projected conditions for Antarctic and Sub-Antarctic regions), on the physiological energetics (ingestion rate, absorption efficiency, oxygen uptake and scope for growth (SFG)) of the edible whelk *T. geversianus*. Our results showed no significant effects for salinity or the combination of temperature and salinity on *T. geversianus* bioenergetics. On the contrary, incubation at low temperatures (1 and 5 °C) was shown to affect the ingestion rate, absorption efficiency, oxygen uptake and SFG for *T. geversianus*, whereas for specimens incubated at 12 and 15 °C, physiological rates remained similar to control. Our data suggests that *T. geversianus* might be robust to warming and future variations of salinity, but longer term experiments are needed to ensure that no reduction of performance will occur after an extended incubation time from an increase in temperature.

1. Introduction

Global climate change is threatening biodiversity and will increasingly do so into the future. In the ocean, the variation of key abiotic factors such as temperature, pH and salinity are altering the physiology and phenology of a large diversity of organisms (Deutsch et al., 2015; Peck et al., 2009; Thomas et al., 2004). The oceans are heating up 40% faster than expected with recent studies suggesting a global increase of sea surface temperature of 1.5 °C by the end of the century (IPCC, 2014; Cheng et al., 2019; Zanna et al., 2019). Temperature is one of the most studied physical factors and plays a key role in both the performance and fitness of ectotherms, as their body temperature changes with the temperature of the surrounding environment (Sokolova and Lannig, 2008). In a warming ocean, the internal temperature of ectothermic organisms increases, in turn altering biochemical and metabolic rates. Hence, the resilience of marine ectotherms to global warming is mainly determined by their thermal tolerance, phenotypic plasticity, and in the longer term, their adaptive capacity (Huey et al., 2012).

High latitudes are particularly sensitive to global warming and the pattern of increasing temperature is expecting to have a large impact in ice-covered regions (Constable et al., 2014; Shadwick et al., 2013; Swart et al., 2018). Recently, substantial increases in melting ice has led to an

increase of freshwater inputs into the North Atlantic Ocean (Dickson et al., 2002), diminishing total alkalinity in seawater and contributing to carbonate under saturation (Manno et al., 2012). Changes in seawater salinity and carbonate saturation also affects the biological composition of marine invertebrates, especially marine ectotherms, which are stenohaline, and therefore exhibit a restricted salinity tolerance (Smyth and Elliott, 2016). Hence, ice-melt in high latitudes could affect marine ectotherms' biological features such as growth, reproduction, larval recruitment and dispersal.

The freshening in polar regions perfectly exemplifies how climate change encompasses a wide range of physical and chemical changes, that are likely to interact in a complex non-linear way (Kinne, 1964; Kroeker et al., 2017; Sokolova, 2013). To successfully assess the vulnerability of marine organisms to climate change and predict changes in species distribution, it is imperative to take into account the multiplicity of climate change-induced pressures (Williams et al., 2008). For example, the combination of both increasing temperature and low salinity has been shown to decrease the oxygen saturation of the environment, impacting the survival and settlement of barnacle larvae of *Balanus improvisus* in the Baltic sea (Nasrolahi et al., 2016). More, when studying the effects of low salinity and warming on the invasive mussel *Brachidontes pharaonis*, Sarà et al. (2008) observed a reduced scope for

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growth (energy available for growth and reproduction) at higher temperature but no effect of low salinity. Conversely, Wang et al. (2011) described a decrease in scope for growth of the green-lipped mussel *Perna viridis*, with decreasing salinity and dissolved oxygen concentration.

Within the glacier-fjord system of Southern Chilean Patagonia, the Strait of Magellan (53°S) separates the American continent from the Tierra del Fuego Island, and connects the Pacific and Atlantic oceans (Pantoja et al., 2011). In this region, freshwater from glacier melting and river mixes with Sub-Antarctic water, resulting in large decreases in salinity that could affect benthic stenohaline organisms, which are abundant in the Pacific side of the Strait of Magellan (Iriarte, 2018; McCulloch and Davies, 2001).

The muricid gastropod *Trophon geversianus*, is an endemic gastropod of southern South America (Patagonia) where it is abundant and widely distributed. *Trophon geversianus* has been described in the entire Magellan region, along the Pacific coast, from Chiloe Island (42°S) to Cape Horn (56°S), and along the Atlantic coast from the Cape Horn to Buenos Aires (36°S) (Castellanos et al., 1988; Griffin and Pastorino, 2005). Inhabiting the low intertidal or shallow subtidal zones *T. geversianus* preys almost exclusively on the mussel *Mytilus chilensis*, where it takes a long period of time (7–10 days) to catch and consume its prey (Andrade et al., 2009; Curelovich et al., 2016). In the Strait of Magellan, the over exploitation of *T. geversianus* in the 1990's led to a drastic diminution of its population and was followed by the establishment of a fisheries closure in order to replenish the stock (González et al., 2007). However, due to its extended growth, long life cycle, low productivity, and its selectivity for only one prey (Andrade et al., 2009), *T. geversianus* is particularly vulnerable and the population in the Magellan Strait is currently in recovery phase.

In this study, we test the hypothesis that warming, low salinity, or the combination of both will affect the physiological energetics of the gastropod *T. geversianus*. To test this hypothesis, we investigated the effect of five temperatures (1, 5, 9, 12 and 15 °C) and two salinities (25 and 30 psu), that correspond to current and projected conditions for the Antarctic and Sub-Antarctic region (IPPC AR5 RCP8.5, 2014), on the feeding metabolism and growth of *T. geversianus*. Since the fishery closure will end in 2020, it is essential to predict the effect of a future climate change scenario to prevent a further reduction of *T. geversianus*' stocks, or worse, an extinction of the species in the Strait of Magellan.

2. Materials and methods

2.1. Animal collection

Sixty adult *T. geversianus* were collected in June 2016 from the subtidal zone (a depth of 18 m) at the San Isidro Lighthouse (53°47'S, 70°58'W), which is in close proximity to the city of Punta Arenas. This site is characterized by minor variations in temperature between summer and winter of 6–9 °C, and a salinity range of 28–30 psu. After collection, animals were transported in chilled conditions to our laboratory and transferred to 50 L tanks. Snails with an average shell length of 6.6 ± 0.5 cm and a dry tissue weight of 10.4 ± 0.5 g were selected and acclimatized to laboratory conditions (filtered sea water 1 µm, T = 9 °C ± 0.2 °C, salinity = 30) during a 3 months period, before the commencement of experiments.

2.2. Experimental design

After acclimation, to investigate the combined effects of salinity and temperature on *T. geversianus*' physiology, whelks were placed in individual aquariums (4 L) and were randomly distributed into 5 groups corresponding to five experimental temperatures (1, 5, 9, 12 and 15 °C) (n = 8 whelks/temperature treatment). Then, for each temperature treatment, animals were divided into two sub-groups corresponding to the experimental salinities (25 and 30 psu) (n = 4 whelks/treatment of

temperature and salinity). After animal allocation, the temperature was increased (for treatments of 12 and 15 °C) or decreased (for treatments of 1 and 5 °C) by 0.5 °C/day until reaching the target temperature corresponding to day 0 of the experiment. Simultaneously, 4 individuals per temperature treatment were submitted to a salinity of 25 psu, while the other 4 remained at 30 psu. The treatment of 9 °C and 30 psu was used as a control for the experiment. Experiments were carried out for 50 days and every ten days whelks were fed with the mussel *Mytilus chilensis* (ca. 1500 mg dry weight/10 days/gastropod, corresponding to ca. 150 mg/day/gastropod). Every three days, seawater was partially changed. Similar experimental designs have been described in other species from high latitude exposed to different combinations of temperature and salinity (Vargas-Chacoff et al., 2019; Navarro et al., 2019).

2.3. Physiological parameters

2.3.1. Ingestion rate

Values of ingestion rate were standardized to an equivalent of 10 g dry weight according to Bayne et al. (1987). Consumed prey mass was measured every ten days by collecting all the empty shells and the remaining tissue in the bivalves. The length of the empty shells was measured and the unconsumed soft tissues were dried to a constant weight. To evaluate the daily ingested ration, regressions between the shell lengths of 40 individuals of each prey (L = cm) versus dry tissue weight (W = g) were carried out using the allometric equation $W = aL^b$.

2.3.2. Absorption efficiency

The percentage of absorption efficiency was assessed using the method developed by Conover (1966), as follows: $[(F-E)/(1-E) \cdot F] \cdot 100$, with F corresponding to the fraction of organic content of the food (total dry weight of mussels ingested), and E to the organic content of the faeces produced by the gastropod. For each individual, faeces were collected using a Pasteur pipette, filtered on pre-ashed, pre-weighed Whatman GF/C filters (1.2 µm) rinsed with ammonium formate (3%), and dried to a constant weight (100 °C). Filters were then weighed, reduced to ashes (combusted at 450 °C for 3 h), and weighed again to estimate the organic and inorganic fraction of the faeces. A similar approach was used to determine the organic fraction of the mussels supplied as food for the gastropods. Representative samples (n = 5) of *Mytilus chilensis* were dried (100 °C) to a constant weight and ashed at 450 °C for 16 h to determine the organic content of the food.

2.3.3. Oxygen uptake

Oxygen uptake was measured every 10 days. Gastropods were incubated individually in 810 mL sealed glass chambers filled with seawater at the corresponding temperature and oxygen uptake was measured using a Fiber Optic Oxygen Transmitter (FIBOX 3, PreSens) and oxygen sensor spots (PreSens GmbH, Regensburg, Germany), that were attached to the inner wall of the chambers. This process ensures a high temporal resolution and measurement; without drift, oxygen consumption, or gas exchange between the incubation chamber, and the environment (Warkentin et al., 2007). During each measurement, two chambers of similar volume without specimens were used as controls. Data were recorded using OxyView 3.51 software (PreSens GmbH). The measurement system was calibrated with a two-point calibration before each experiment. The 0% oxygen saturation was obtained by adding sodium dithionite to distilled water. The calibration to 100% oxygen saturation was carried out using filtered seawater, which was aerated for 20 min. In the same way as for ingestion rate, values of oxygen uptake were standardized to an equivalent of 10 g dry tissue weight.

2.3.4. Scope for growth

Scope for growth (SFG) gives an insight on the energy status of organisms and was calculated according to Winberg (1960). Accordingly, oxygen uptake and absorption rates were converted to energy equivalents: 1 mL of O₂ corresponds to 19.9 J (Elliott and Davison, 1975) and

1 mg of organic food material corresponds to 21 J (McLusky, 1989). In this study, energy lost in ammonia excretion was not measured as it was considered a negligible energy loss (Bayne et al., 1985; Fuentes-Santos et al., 2018).

2.4. Statistical analysis

Ingestion rate, absorption efficiency, oxygen consumption and SFG were measured every 10 days for the same individuals over the 50 day-experiment. Statistical differences between treatments were calculated using a four-way permutational multivariate analysis of variance (PERMANOVA) (Anderson, 2001), based upon Euclidean distance (analogous to traditional ANOVA with univariate data) with 4,999 permutations. In addition to multivariate analyses, pairwise tests were used when corresponding. Factors used in statistical analyses were time (fixed, 5 levels), temperature (fixed, 5 levels), salinity (fixed, 2 levels) and individual snails (random, nested within all combinations of temperature \times salinity). PERMANOVAs and pairwise test were performed using PRIMER 7 (Clarke and Warwick, 2001).

3. Results

We found no significant effects for time, salinity or the interaction between time, temperature and salinity, on any of the physiological measurements (Table 1). However, temperature significantly affected ingestion rate, absorption efficiency, oxygen uptake and SFG (Table 1).

The ingestion rate of individuals exposed to 9, 12 and 15 °C were significantly higher ($p < 0.001$) than at 5 °C (Table 1, Fig. 1). No food was ingested by *T. geversianus* at 1 °C (Fig. 1).

Absorption efficiency was relatively high in all treatments (60–85%) regardless of the temperature or salinity. Absorption efficiency (%) was significantly higher at 5 °C compared to the control temperature (9 °C) (Fig. 2). Although not statistically significant, absorption efficiency was slightly higher at 12 and 15 °C than for the control temperature.

Regardless of the level of salinity, oxygen uptake was greatest at the

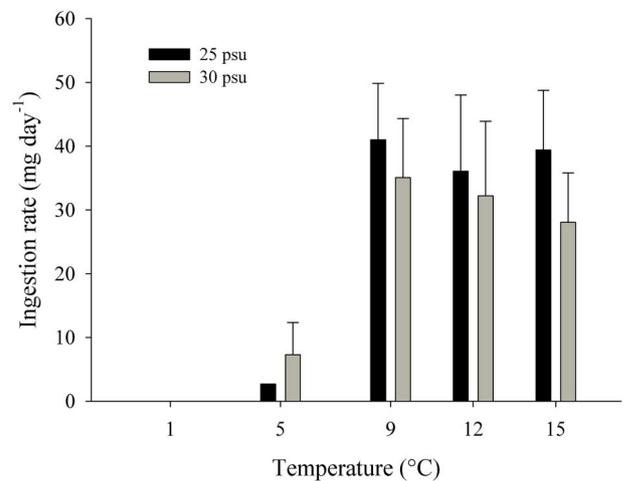


Fig. 1. Ingestion rate in *Trophon geversianus* exposed to experimental temperatures (1, 5, 9, 12, 15 °C) and salinities (25 and 30 psu). Values were standardized to 10 g dry weight and represent mean \pm standard error.

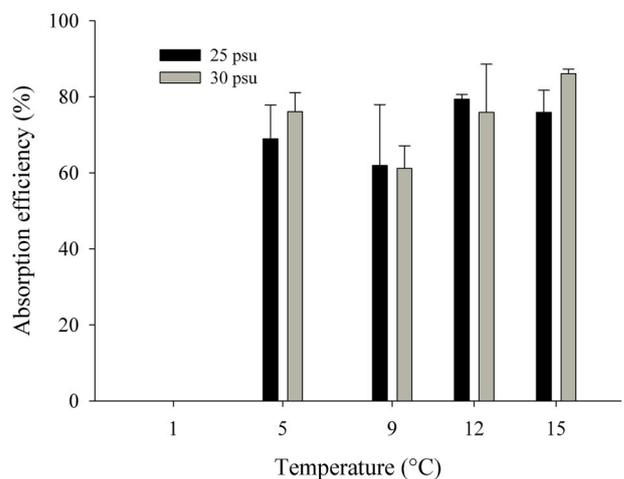


Fig. 2. Absorption efficiency (%) in *Trophon geversianus* under experimental temperatures (1, 5, 9, 12, 15 °C) and salinities (25 and 30 psu). Values represent mean \pm standard error.

Table 1

Analysis were carried out on four physiological variables in the muricid *T. geversianus* exposed to 5 levels of temperature (1, 5, 9, 12 and 15 °C) and two levels of salinity (25 and 30 psu) at five different times. For each F-ratio, variable and residual degrees of freedom are provided. Significant effects are highlighted in bold. Pair-wise tests are shown when corresponded.

	Absorption efficiency	Oxygen uptake	Ingestion rate	Scope for growth
Time	F _{5, 200} = 0.14 P = 0.97	F _{5, 200} = 0.66 P = 0.67	F _{4, 160} = 1.75 P = 0.34	F _{4, 160} = 1.04 P = 0.18
Temperature	F_{4, 200} = 2.58 P = 0.04	F_{4, 200} = 9.77 P < 0.001	F_{4, 160} = 10.4 P < 0.001	F_{4, 160} = 2.6 P = 0.04
Salinity	F _{1, 239} = 0.02 P = 0.94	F _{1, 200} = 0.81 P = 0.37	F _{1, 160} = 0.57 P = 0.45	F _{1, 160} = 3.9 P = 0.95
Time x Temp	F _{20, 200} = 1.22 P = 0.24	F _{20, 200} = 1.38 P = 0.14	F _{16, 160} = 1.55 P = 0.28	F _{16, 160} = 1.14 P = 0.18
Temp x Salinity	F _{4, 200} = 0.58 P = 0.69	F _{4, 200} = 0.08 P = 0.98	F _{4, 160} = 0.04 P = 0.99	F _{4, 160} = 0.99 P = 0.43
Time x Salinity	F _{5, 200} = 1.00 P = 0.42	F _{5, 200} = 1.18 P = 0.32	F _{4, 160} = 0.815 P = 0.53	F _{16, 160} = 1.55 P = 0.28
Individuals (Temp x Salinity)	F _{30, 200} = 1.34 P = 0.20	F _{30, 200} = 1.09 P = 0.35	F _{30, 160} = 1.37 P = 0.11	F _{30, 160} = 1.08 P = 0.35
Time x Temp x Salinity	F _{19, 200} = 0.60 P = 0.89	F _{19, 200} = 0.95 P = 0.52	F _{15, 160} = 1.17 P = 0.27	F _{15, 160} = 0.735 P = 0.79
Pair-wise test	9 < 1 = 5	1 = 5 < 9, 12, 15	1 = 5 < 9, 12, 15	1 = 5 < 9, 12

highest temperature of 15 °C (reaching almost 40 mL day⁻¹), with significant differences between the cold (1 and 5 °C) and warm (9 and 15 °C) treatments (Fig. 3, Table 1).

Finally, SFG was dependent on temperature with a similar separation between the cold and warm treatments. SFG was found to be statistically lower (negative) for the cold temperature treatments (1 and 5 °C) (at salinity 30, -427 and -370 J day⁻¹, respectively) than for the warm treatments (9, 12 and 15 °C) (at salinity 30, 570, 820 and 560 J day⁻¹, respectively) (Fig. 4, Table 1).

4. Discussion

4.1. Bioenergetics

This study describes the first attempt to investigate the effect of climate change pressures such as ocean freshening and global warming on the physiology of the overexploited Patagonian whelk *T. geversianus*. The investigation of an organism physiological energetics in response to environmental factors is a powerful approximation to reflect and predict the fitness and survival of marine organisms (Sokolova, 2013). Scope for growth which corresponds to the energy remaining after all metabolic demands are met (energy available for growth and reproduction), is a

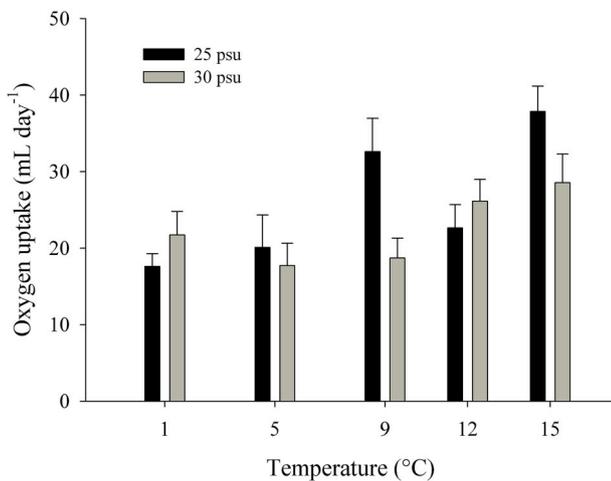


Fig. 3. Oxygen consumption in *Trophon geversianus* exposed to experimental temperatures (1, 5, 9, 12, 15 °C) and salinities (25 and 30 psu). Values were standardized to 10 g dry weight and represent mean \pm standard error.

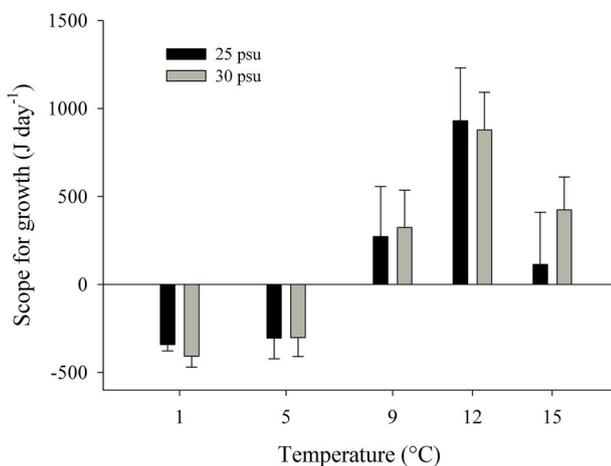


Fig. 4. Scope for growth in *Trophon geversianus* exposed to experimental temperatures (1, 5, 9, 12, 15 °C) and salinities (25 and 30 psu). Values were standardized to 10 g dry weight and represent mean \pm standard error.

particularly good indicator of longer term acclimation capacity (Bayne and Newell, 1983; Stickle and Bayne, 1987).

After 50 days of exposure to five levels of temperature and two levels of salinity, there was no effect of salinity or the combination of temperature and salinity, on the physiological energetics of the whelk *T. geversianus*. At low salinity, the slightly reduced SFG (mostly for the temperature control) could have been caused by the extra energy required for osmotic regulation in freshening conditions, which would diminish the energy allocated for drilling and foraging; and in turn may reduce the energy required for feeding (Pörtner, 2012). Exposure to out of range salinity is often associated with reduced performance in marine gastropods (Chaparro et al., 2008; Deschaseaux et al., 2011; Montory et al., 2014; Zhang et al., 2015). For instance, hyposalinity has been shown to cause hypoosmotic stress in some intertidal gastropods (*Littorina saxatilis* and *Littorina obtusata*) in which incubation at low salinity (<20) led to the expression of stressed proteins (e.g. heat shock proteins, glutathione S-transferase), reducing the energy available for growth or reproduction (Muraeva et al., 2017). However, resilience of *T. geversianus* to variations of salinity is not surprising, as detrimental effects of hyposalinity in numerous marine molluscs were generally observed when exposed to salinities of less than 20 psu (Navarro, 1988; Navarro and Gonzalez, 1998). Nevertheless, the combination of both

salinity and temperature has been shown to negatively affect the hatching time in three marine gastropods (*Bembicium nanum*, *Siphonaria denticulata* and *Dolabrifera brazueri*) (Deschaseaux et al., 2011), and the feeding of the scavenging gastropod *Nassarius festivus* (Zhang et al., 2015). In contrast, the present study revealed a significant effect of temperature on the gastropod's ingestion rate, absorption efficiency, oxygen uptake and SFG. In numerous marine ectotherms, rising temperatures induce increasing energetic demands that in turn may exceed energy supply and overcome the capacity of the cellular machinery to produce enough adenosine triphosphate (ATP) (Lannig et al., 2010). To compensate this high energy demand, one strategy is to increase energy intake, and/or to elevate metabolism (Lannig et al., 2010). Following the 50 days exposure to five temperatures, *T. geversianus* did not show any alteration of its feeding physiology at higher temperatures (i.e. 12 and 15 °C), compared to the control. The 12 and 15 °C treatments simulate the predicted scenario of climate change (an increase of 2 and 4 °C, respectively) for the Magellan region according to IPCC's prediction (IPCC, 2014). Thus, the positive SFG observed for individuals of *T. geversianus* acclimated to 9, 12 and 15 °C, and the very small difference in SFG between the control and the treatments that correspond to a climate change scenario, suggest that *T. geversianus* in the Strait of Magellan might be better adapted to warmer water temperatures (9–15 °C). The plasticity of *T. geversianus* from cold to warmer temperatures can be correlated with its wide distribution in Patagonia (sea surface temperature ranging from 6 to 18 °C) and vertical distribution along the shore, where juveniles occur at the mid intertidal level and facing periods of desiccations, and adults living almost exclusively at subtidal level (Andrade et al., 2009; Curelovich et al., 2016; González et al., 2007). Although an increase in temperature has been shown to affect the feeding physiology of other gastropods e.g. the subtidal gastropod *Thalotia conica*; (Leung et al., 2017), distributional range has been shown to affect organisms vulnerability toward changes in temperature (Somero, 2005). In the broadly distributed gastropod, *Tegula funebralis*, activity and consumption rates were shown to be less affected by temperature than those of the narrowly distributed *Tegula aureoincta* (Yee and Murray, 2004). The assumption that *T. geversianus* might be adapted to higher temperature (up to 15 °C) is consistent with the negative SFG observed in individuals acclimated to 1 and 5 °C and with the absence of correlation between drilling frequency and temperature in specimens of *T. geversianus* along its Atlantic distribution (Martinelli et al., 2013).

4.2. Implication on *T. geversianus* vulnerability

This study has shown that the Patagonian whelk *T. geversianus* relatively robust to the effects of moderate freshening. Temperature had a greater effect on the physiological energetics of *T. geversianus* than low salinity levels, and no interactive effect of temperature and salinity was observed. Furthermore, the current study has shown that the SFG of *T. geversianus* is affected at 1 and 5 °C, which are lower temperatures than those experienced by this gastropod inhabiting the Strait of Magellan. On the contrary, after incubation at 12 and 15 °C, the SFG of *T. geversianus* was positive and similar to the SFG observed in individuals that were incubated at the control temperature. These results suggest that *T. geversianus* adults from the Strait of Magellan might be resilient to future scenarios of ocean warming and moderate freshening. However, these results should be interpreted with caution as recent studies on marine ectotherms from high latitudes, have indicated that acclimation may require longer time periods (Form and Riebesell, 2012). Some ectotherms might be able to cope perfectly with the exposure to short term stressors, however exposure to the same stressor for an extended period of time might result in a reduction of performance (Morley et al., 2016). Further, warm-adapted species inhabiting the intertidal zone have been shown to be more threatened by increasing temperatures than subtidal individuals (Somero, 2005). Therefore, long-term studies combining multiple environmental effects (e.g. temperature, salinity, ocean

acidification and hypoxia) should be performed on juvenile *T. geversianus* that occur at the intertidal zone.

In conclusion, this study shows that in the Magellan region, subtidal *T. geversianus* are quite robust to the predicted global climate change scenario of an increase in temperature and decrease in salinity; provided they are able to recuperate from overexploitation that has drastically affected Magellan populations.

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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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2019.104840>.

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