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Temperature effects on growing, feeding, and swimming energetics in the Patagonian blennie *Eleginops maclovinus* (Pisces: Perciformes)

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Abstract The Patagonian blennie *Eleginops maclovinus* is a coastal and estuarine species, important in recreational and commercial fisheries, and with aquaculture potential. This study assessed the effect of temperature on feeding and the allocation of energy in growth and swimming in a sub-Antarctic population. For growth experiments, two groups of 8 juveniles were reared at 4 and 10 °C (corresponding to winter and summer habitat temperatures, respectively) for 3 months. Swimming experiments were conducted at 5 and 10 °C, measuring the oxygen consumption before and after forced swimming for 1 min at a speed of 10 total lengths (TL)/s. Temperature affects growth. TL increased 0.09 cm at 4 °C versus 0.30 cm at 10 °C. Body mass grew 0.49 g at 4 °C versus 1.65 g at 10 °C, whereas the Fulton's condition factor increased 0.021 at 4 °C versus 0.080 at 10 °C. The ingested food was more than twofold higher at 10 than at 4 °C, while the feces produced at 4 °C was about twofold higher. The scope between baseline and peak oxygen consumption after forced swimming was affected by temperature, being 4.51 at 5 °C and 3.03 at 10 °C. The percentage energy expenditure until the return of baseline oxygen consumption values showed a marked temperature effect, being higher at 5 °C. We propose the existence of a trade-off in the allocation of energy between swimming activity and growth, with proportionally more energy being consumed at low temperatures for swimming than for other physiological functions like growth.

Keywords Assimilation efficiency · *Eleginops maclovinus* · Forced swimming · Growth · Temperature

Introduction

The coastal fish *Eleginops maclovinus* (Cuvier 1830; Eleginopidae, Notohenioidei; Spanish v. n. *róbalo*) is the only species of the family Eleginopidae (Order Perciformes; Suborder Notothenioidei). This euryhaline and eurythermic fish (Pequeño 1989; Pavés et al. 2005) is present in the sub-Antarctic coastal waters of South America (Norman 1937). The southernmost point of its distribution is the Beagle Channel, with a range from Valparaíso in the Pacific (Chile, 33°S) to the San Matías Gulf (Argentina, 40°S) in the Atlantic Ocean, respectively (Pequeño 1989; Cousseau and Perrota 2000). This species is exposed to a wide thermal range, from ~4 °C (winter, Beagle Channel; Vanella et al. 2007) to ~18 °C (summer, San Matías Gulf; Piola and Falabella 2009). The róbalo present an extended bioceanic distribution, and genetic population studies using mitochondrial DNA do not show a marked structure or patterns of isolation by distance (Ceballos et al. 2011). However, studies conducted with nuclear DNA reveal a low, but significant, genetic structure (Ceballos 2011) linking the Beagle Channel populations with the Pacific ones. This species has a generalist diet, with predominant carnivorous feeding habits (Isla and San Román 1995; Huergo et al. 1996; Martin and Bastida 2008; Pequeño

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et al. 2010). The reproductive strategy of this fish is protandric hermaphroditism (Calvo et al. 1992; Brickle et al. 2005b). The growth rate of *E. maclovinus* has been reported to be about 110 mm/year (Gosztonyi 1980) and 102 mm/year (Brickle et al. 2005a) in two different Atlantic populations (Puerto Deseado and Islas Malvinas, respectively). However, in studies performed on Pacific populations, the average growth rate is approximately 60 mm/year (Licandeo et al. 2006). According to some authors, *E. maclovinus* seems to be one of the most r-selected strategists among notothenioids, showing relatively high growth rates and short longevity (Brickle et al. 2005a, b).

Energy and nutrients must be regulated among other metabolic functions in an organism, and when resources are limited, an increase in allocation for one function will result in a decrease in allocation for another (Arendt 1997). In juvenile fishes, intrinsic growth rates are rarely viewed as maximized, and in several species, a trade-off between growth and swimming capacity has been documented at different temperatures and levels of food availability (Billerbeck et al. 2000; Arnott et al. 2006). Of course, growth is not only controlled internally, with temperature and food being two of the more important exogenous factors involved in the control of growth rates (Mommsen 1998).

Fish swim to escape from predators, to capture prey, and for migratory and reproductive reasons. Therefore, since swimming is so strongly related to survival, it is reasonable to expect natural selection to exert pressure on swimming capacities (Videler 1993). Three main fiber types exist in fish skeletal muscles involved in swimming: slow oxidative, fast glycolytic, and intermediate fibers. These names indicate the swimming speeds for which they are used and the aerobic or anaerobic metabolism involved in their operation (Videler 1993; Rome 1998; Webb 1998). The distribution and abundance of the different fiber types are related to the swimming capacity of fish species. Over 95 % of axial musculature of *E. maclovinus* is composed of fast glycolytic fibers (Fernández personal communication). It is known that temperature affects the fast-start performance of *E. maclovinus*. Fernández et al. (2002) measured the swimming performance by the velocity, acceleration, and power output in this species at 2, 4, 6, 8, and 10 °C. Lower temperatures (2, 4, and 6 °C) were found to provoke a reduction in swimming performance and an increase in the curvature of the spine during swimming. Maximum velocity was registered at about 8 °C, with a slight decrease at 10 °C.

The aim of this work was to study the effect of environmental temperature on feeding and the allocation of energy in growth and swimming of the sub-Antarctic notothenioid *E. maclovinus*. The results have allowed us to test the hypothesis that there is a trade-off in energy allocation between growth and swimming that varies with temperature.

Materials and methods

In March 2006, young of the year *Eleginops maclovinus* were captured at Bahía Cambaceres (54°52′ S, 67°16′ W; Beagle Channel, Tierra del Fuego) using a seine net (10 m long, 1 m high, 2.5 cm mesh size) at a 0–1 m depths, in the vicinity of a stream outlet. We worked with this life stage because their small size makes them suitable for working in aquariums and respirometric chambers and for their elevated growth rate (Brickle et al. 2005a). Furthermore, since *E. maclovinus* shows protandry as reproductive strategy (Calvo et al. 1992), we were sure all specimens used were males.

Growth and feeding

Holding conditions

The experiments started 7 weeks after capture to provide the fish a proper accustoming to captivity conditions. One month before initiating the experiment, fish were acclimated in common 65-l aquaria at 10 °C, under a photoperiod of 13:11-h light/darkness, similar to natural light condition in the moment of capture. The salinity of the water was maintained at 30 before and during the experiment. The standard length and body mass of the fish used in the experiment were 10.61 ± 0.32 cm and 7.51 ± 0.85 g, respectively (mean ± SD). Fish were fed twice a week with chopped hake filet meat until satiation.

Experimental design

Sixteen fishes were accommodated in individual experimental aquaria, transferring them from the acclimation tanks. No visual signs of stress were observed. The aquaria were made of fiberglass and were designed to minimize leaching of food and feces, and also to facilitate its collection (Online Resource 1; Fig. 1). The aquaria were divided into two parts: the upper section and the collector funnel. These compartments were separated by a grill. The available volume of water for the fish in the upper section of the aquaria was 3 l. The volume of the collector funnel was 1.9 l, adding up to a total volume of 4.9 l. Each aquarium had soft aeration installed over the grill and a surface area of 600 cm^2 (20 × 30 cm). A trough, constructed with a thin narrow transparent plastic plate (20 × 5 cm), was placed in one of the short sides of the grill that was installed between the upper section and the

collector funnel. Feces and unconsumed food were collected from the funnel section by a flexible pipe, which was fixed to a lower connection, through a filter. The collected material was then separated manually from the filter using a magnifier. Each aquarium was covered with a black net, to minimize any visual stimulation of the fish and/or the possibility of escape.

Groups of four experimental aquaria containing individual fish were placed in four container tanks (of 65 l each). Each container tank was provided with filtered seawater at a controlled temperature. Two containers tanks, with four individual aquaria each one, were maintained at 4 °C (±1 °C; low temperature group). The other two containers tanks were maintained at 10 °C (±1 °C; high temperature group). These temperatures were selected as being near the average temperatures of summer and winter in waters of the Beagle Channel and were therefore not expected to be stressful for the fish. There was no connection or mixing of water between individual aquaria or with container tanks, in order to avoid pseudoreplication. The water of each container, thermally stabilized, was used to replace any water that was lost from the individual experimental aquaria, after the collection of feces and unconsumed food. The general photoperiod of the experiment was 12:12-h light/darkness, following the photoperiod used in the previous works (Vanella and Calvo 2005; Vanella et al. 2010).

Growth measurements

The experiment was carried out over a 12-week period. Each fish was measured at the beginning of the experiment (T0), then after 4 (T1), 8 (T2), and 12 (T3) weeks. During measurements, fish were anesthetized using MS-222. Measured variables were the following: total length (TL, cm); body mass (BM, g); Fulton's Condition Index (K), which was calculated as:

$$K = \left(\mathrm{BM}/\mathrm{TL}^3\right) \times 100,$$

and thermal unit growth coefficient (TGC; Cho 1992), which was calculated as:

$$\mathrm{TGC} = \left(\mathrm{BM}_{(\mathrm{T3})}^{1/3} - \mathrm{BM}_{(\mathrm{T0})}^{1/3}\right) / \sum \text{degree days}.$$

Feeding and digestibility analysis

Both groups (high and low temperatures) were fed twice a week with known quantities of chopped hake filet meat until satiation during the 12-week experimental period. In the previous work, we established that gut evacuation occurs 3 and 4 days after feeding at 10 and 4 °C, respectively (Vanella 2005). The excess of food was removed after 2 h from aquaria, dried in an oven at 80 °C, and weighed. The original fresh weight was calculated using a curve of the relationship between frozen hake meat and dried hake meat after 2 h in salt water.

The biochemical proximate composition of hake filet was determined using standard techniques: percentage of water (by drying in an oven at 80 °C), ash (by burning at 450 °C), protein (by the Anthrona method; Seifter et al. 1949), glycogen (by the Lowry method; Lowry et al. 1951), and lipid (by the subtraction of the other components). The energy density (kJ/g dry mass and kj/g dry mass ash free) was also obtained using a Parr 1425 micro-calorimeter bomb.

Feces were collected daily and separated from unfed food. The calculated variables were the following: ingested food (dry mass): g/fish; feces (dry mass): g/fish; digestibility (dry mass): ((dry mass food − dry mass feces)/dry mass food) × 100; feeding efficiency: body mass gain/ingested food (dry mass); and voracity, determined by the total number of animals that attacked the food within 30 s of introduction to the aquaria.

Since the biological functions studied (growth and swimming) are composed of many steps, the magnitude of the temperature effect was estimated using the Q_{10}, following the criteria of Willmer et al. (2000). The formula used was (Jobling 1994) the following:

$$Q_{10} = \left(\mathrm{Variable}_{10\,^\circ\mathrm{C}}/\mathrm{Variable}_{4 \text{ or } 5\,^\circ\mathrm{C}}\right)^{10/10\,^\circ\mathrm{C}-4 \text{ or } 5\,^\circ\mathrm{C}}.$$

Recovery after forced swimming

Two groups containing five individuals of *E. maclovinus* (TL = 8.99 ± 1.11 cm; BM = 5.24 ± 1.61 g) each were acclimated at temperatures of 5 and 10 °C for 15 days, respectively, following the protocol used in the previous respirometric work (Vanella and Calvo 2005; Vanella et al. 2010). The lower temperature was set at 5 °C because in previous trials it was very difficult to achieve a sustained swimming at 4 °C. Fish were not fed for 1 week before the experiments. This time was enough to avoid the effects of specific dynamic action on oxygen consumption, and to allow the emptying of the digestive system, even at low temperature (Vanella 2005). Then, each animal was individually accommodated inside the forced swimming respirometric chamber (Online Resource 1; Fig. 2).

Measurements were not made for the first 12 h, and the animals were not fed or forced to swim. The forced swimming respirometric chamber was submerged in oxygen-saturated seawater (salinity, 30). The oxygen concentration was maintained near saturation inside the respirometric chamber by using the re-saturation pump. To measure oxygen consumption, the chamber was closed for 1–4 h. O_2 saturation never declined below 80 % at any given temperature during these time periods. The same protocol was followed in the previous works (Vanella and

Calvo 2005; Vanella et al. 2010) with no conspicuous effects on oxygen consumption rates. Water samples (5 ml) were collected through a rubber diaphragm with a syringe. Oxygen concentration was measured using a Rank Brothers (model U 10) Clark-Type polarographic electrode (resolution, 0.1 % saturation). The oxygen consumption baseline was established at 0 speed, by closing the chamber and measuring the drop in oxygen concentration. Subsequently, the chamber was refilled with water saturated in oxygen.

Once the baseline was established, the chamber was opened and the fish was forced to swim for 1 min at a speed of 10 TL/s, which compels the fish to use principally the caudal peduncle for swimming, consisting mostly of anaerobic white muscles, generating a measurable oxygen debt, sensu (Jobling 1995). TL was used to fix the forced swimming speed in order to follow the same criteria used in the previous work for this species (Fernández et al. 2002). Subsequently, the chamber was closed at the entrance and exit floodgate (Online Resource 1; Fig. 2), and the decline in O_2 concentrations was measured. Then, the chamber was refilled with O_2-saturated water using the secondary pump. This process was repeated several times until O_2 consumption returned to baseline values.

A number of variables were determined. Baseline oxygen consumption (mg O_2 h^{-1} g^{-1}) was the metabolic rate of post-absorptive individuals at 0 speed. Peak oxygen consumption (mg O_2 h^{-1} g^{-1}) was determined as the post-forced swimming peak in metabolism. The scope was the peak/baseline O_2 consumption ratio. The time to peak (h) was calculated as the time period between the start of forced swimming and the time at peak oxygen consumption. The recovery time was determined from the time period (h) between the time at the cessation of forced swimming and the time when the metabolic rate was no longer greater than baseline oxygen consumption values. The absolute recovery energy (kJ) was the energy expenditure during the recovery time, which was calculated from oxygen consumption values using the caloric equivalent (1 mg O_2 is equivalent of 14.06 J; Johnston and Battram 1993). The relative recovery energy (%) was the energy expenditure above the baseline during the recovery time, which was expressed as a percentage of the total energy expenditure for the same time.

Statistics

Growth and feeding

To test initial differences between groups, one-way ANOVA was conducted for each variable measured at T0, which comprised TL and BM.

To test variations within each group across the experiment, a repeated measures ANOVA was carried out for each variable. To test differences in growth between high and low temperature groups, one-way ANOVA was carried out for the total difference between variables at the beginning and at the end of the experiment.

To test differences between high and low temperatures groups, one-way ANOVA was carried out.

Data transformations were made when necessary. In cases of violation of ANOVA assumptions, a nonparametric Mann–Whitney test was carried out.

Recovery after forced swimming

A repeated measures design was applied (Friedman test) to test differences between baseline and peak oxygen consumption. A Mann–Whitney test was used to compare groups of *E. maclovinus* forced to swim at different temperatures.

In all cases, $\alpha = 0.05$.

Results

Growth and feeding

No significant differences were observed for any variable between the groups of fishes maintained at 4 °C and 10 °C at the onset of the growth and feeding experiment (T0; one-way ANOVA: $P > 0.05$ in all cases; Table 1). TL was 10.71 ± 0.23 cm for animals in the low temperature group, and 10.52 ± 0.38 cm for fish in the high temperature group. The initial BM was 7.68 g ± 0.49 and 7.35 ± 1.13 g for animals reared at 4 and 10 °C, respectively. K was the same for both groups: 0.63 ± 0.04. During the experiment, two animals died in each temperature group and were removed from the analysis.

Growth in length (TL) was significant at both 10 and 4 °C after the 12-week experiment (repeated measures ANOVA; $P < 0.05$). Nevertheless, growth was significantly higher at 10 °C than at 4 °C (3.3-fold; Table 1). Growth in BM was significant at 10 °C (repeated measures ANOVA; $P < 0.05$) but not at 4 °C (repeated measures ANOVA; $P > 0.05$), with a higher total difference between T0 and T3 at 10 °C (3.4-fold; Table 1).

K changed significantly at 10 °C but not at 4 °C. Despite this, even though K was higher at 10 °C than at 4 °C at the end of the experiment, the difference was not significant ($P = 0.064$; Table 2). TGC was not significantly different at 10 °C compared to 4 °C (Table 2).

Q_{10} values were high for all measured growth variables (Tables 1 and 2, calculated for variables with statistically significant differences).

The proximate composition of hake filet was obtained: percentage of water, 82.28 ± 1.48; percentage of ash,

Table 1 Growth performance I

Temperature (°C)	TL (cm)			BM (g)		
	T0	T3	T3 − T0	T0	T3	T3 − T0
4	10.71 ± 0.23	10.52 ± 0.38	0.09 ± 0.07	7.68 ± 0.49	8.17 ± 0.86	0.49 ± 0.88
10	10.52 ± 0.38	10.81 ± 0.35	0.30 ± 0.12	7.35 ± 1.13	8.99 ± 1.27	1.65 ± 0.30
Test	1-W	1-W	1-W	1-W	1-W	Mann–Whitney
	ANOVA	ANOVA	ANOVA	ANOVA	ANOVA	$P = 0.017$*
	$P = 0.32^{ns}$	$P = 0.96^{ns}$	$P = 0.0062$*	$P = 0.56^{ns}$	$P = 0.20^{ns}$	
Q_{10}	–	–	7.47	–	–	7.60

Comparison in T0, T3 and total difference between T0 and T3 of each variable for groups at 4 and 10 °C (*TL* total length, *BM* body mass). Test for comparisons and *P* values are provided (*ns* not significant, * significant). Q_{10} values were calculated for variables with a significant difference between treatments

Table 2 Growth performance II

Temperature (°C)	*K*			TGC
	T0	T3	T3 − T0	
4	0.63 ± 0.04	0.65 ± 0.04	0.021 ± 0.061	$1.14 \times 10^{-4} \pm 2.12 \times 10^{-4}$
10	0.63 ± 0.04	0.71 ± 0.04	0.080 ± 0.035	$1.55 \times 10^{-4} \pm 1.55 \times 10^{-4}$
Test	1-W	1-W	1-W	Mann–Whitney
	ANOVA	ANOVA	ANOVA	$P = 0.70^{ns}$
	$P = 0.92^{ns}$	$P = 0.019^{ns}$	$P = 0.064^{ns}$	
Q_{10}	–	–	9.34	–

Comparison in T0, T3 and total difference between T0 and T3 of *K* (Fulton's Condition Index) for groups at 4 and 10 °C and TGC (thermal unit growth coefficient). Test for comparisons and *P* values are provided (*ns* not significant, * significant). Q_{10} values were calculated for variables with a significant difference between temperatures and for *K* T3 − T0

5.5 ± 1.08; percentage of proteins, 78.24 ± 6.16; and percentage of lipids, 9.07 ± 5.15. The proportion of glycogen was negligible. The energy density was 22.44 ± 4.89 kJ/g dry mass and 25.11 ± 5.31 kJ/g ash free dry mass.

After the 12-week experiment, ingested food, digestibility, and voracity were significantly higher at 10 °C than at 4 °C (2.2-fold, 3.2-fold, and 1.09-fold, respectively; Table 3). In contrast, the amount of feces accumulated during the experiment was significantly higher in fish that were acclimated and reared at 4 °C than at 10 °C (2.2-fold; Table 3).

Feeding efficiency was not significantly different between temperatures. The Q_{10} values were highly different for feeding parameters. Voracity and ingested food had the largest Q_{10} values, with the former reaching a Q_{10} of 8.1, which was more than twice the value of the latter (3.72). Digestibility showed Q_{10} values near to 1, while the Q_{10} value of feces was 0.28 (Table 3).

Recovery after forced swimming

Baseline values were significantly higher at 10 °C than at 5 °C (Table 4). Peak values were higher at 10 °C than at 5 °C, but the difference was not significant (Table 4). The scope and the relative recovery energy (%) were significantly greater at 5 °C than at 10 °C. The time to peak, recovery time, and absolute recovery energy did not show significant differences (Table 4).

Discussion

The amount of food eaten by the fish on a daily basis was significantly greater at 10 °C than at 4 °C (~45 % more; $Q_{10} = 3.72$). This may be partially explained by a significant difference in voracity ($Q_{10} = 8.1$), since fish were fed to satiation, therefore indicating there was a difference in appetite. Moreover, both energy acquisition and digestibility were significantly higher at 10 °C than at 4 °C. These differences were strongly reflected in the growth performance of fish. Two of the variables that were used for measuring growth (TL and BM) showed significantly higher values at 10 °C than at 4 °C. As a consequence of the difference in the food ingested, energy intake was noticeably higher at 10 °C. In contrast, feces production was lower at 10 °C than at 4 °C. Therefore, the energy budget of *E. maclovinus* at 10° C was much larger than at 4 °C. These parameters are, as expected, in agreement with an increment in the routine metabolic rate with

Table 3 Feeding performance

Temperature (°C)	Ingested food (g/fish^{-1})	Feces (g/fish^{-1})	Digestibility (%)	Feeding efficiency	Voracity
4	1.32 ± 0.46	0.019 ± 0.009	98.32 ± 0.93	0.14 ± 0.98	16
10	2.90 ± 0.43	0.0088 ± 0.0064	99.68 ± 0.28	0.57 ± 0.10	56
Test	1-W	1-W	Mann–Whitney	Mann–Whitney	Mann–Whitney
	ANOVA	ANOVA	$P = 0.0043$*	$P = 0.39^{ns}$	$P \ll 0.01$*
	$P \ll 0.01$*	$P = 0.039$*			
Q_{10}	3.72	0.28	1.02	–	8.1

Total change from T0 to T3 of each variable for groups at 4 and 10 °C. Ingested food: g fish^{-1}; feces: g fish^{-1}; digestibility (%): ((dry mass food − dry mass feces)/dry mass food) × 100; feeding efficiency: ratio of body dry mass gain to ingested food mass; voracity: determined by the total number of animals that attacked the food within 30 s of introduction to the aquaria. Means ± standard deviations, test used for comparisons, and *P* value are provided (*ns* not significant, * significant). Q_{10} values were calculated for variables with a significant difference between temperatures

temperature, something that we have previously measured for this species (Vanella and Calvo 2005).

Digestibility was also significantly higher at 10 °C than at 4 °C, even though both values were very close to 99 % with hake meat–like food. In contrast, while the TGC was greater at 10 °C than at 4 °C, it was not significantly higher. These results support existing published literature. Ingestion rates are usually positively correlated with temperature, with an absorption efficiency of around 80–97 % for carnivorous fishes (Jobling 1994). These values are comparable with the values obtained here for generalist and predominant carnivorous *E. maclovinus* (Isla and San Román 1995; Pequeño et al. 2010), fed with fish meat. Azevedo et al. (1998), working with *Oncorhynchus mykiss*, found that a large increment in the ingested food (∼3.75 times) was related to a rise in temperature (from 6 to 15 °C, $Q_{10} = 4.35$; calculated from Azevedo et al. (1998)). Furthermore, as temperature rose, there were a decrease in the quantity of total solid wastes (∼1.62 times; $Q_{10} = 0.58$) and a considerable increase in energy and nutrient gains. These findings were similar to the outcomes of the current study, even in the magnitude of the temperature effect analyzed through Q_{10}.

The growth rates recorded by us were substantially lower than those measured in wild populations of *E. maclovinus.* Brickle et al. (2005a) and Gosztonyi (1980) reported a growth rate of 102 and 110 mm/year in Malvinas Is. and Puerto Deseado, respectively, and also Licandeo et al. (2006) reported a substantially lower value (60 mm/year), but still much higher than the one presented in this work, in a Pacific population. Our results showed a much lower growth, at a rate of 13 and 3.9 mm/year for groups reared at 10 and 4 °C, respectively. For *Galaxias maculatus*, another sub-Antarctic teleost, a growth rate of about 2 mm/month was observed under summer conditions (∼10 °C), even in nature or laboratory environment (Boy, personal communication). In addition, TGC was also much lower than the values obtained for other teleosts (Kaushik 1998; Azevedo et al. 1998). The disparity observed between this study and observations in the wild for this species may indicate differences in natural and artificial environmental conditions, such as the salinity used in the experimental aquaria. Faster growth rate is usually observed in juveniles when salinity is intermediate (i.e., estuarine conditions), which correlates well with lower standard metabolic rates (for review see Jobling 1994; Boeuf and Payan 2001). Because *E. maclovinus* is a marine fish, the present work was conducted at a salinity of 30, which is the standard salinity used in the previous work with this species (Fernández et al. 2002; Vanella and Calvo 2005), and it is very close to average salinity values found in the Beagle Channel. However, juvenile Patagonian blennies of the proximate year can be found in waters of intermediate salinity. Nevertheless, *K* values indicate the fish were healthy during the current experiments.

Routine oxygen consumption measured before swimming showed a very good adjustment to the general allometric scaling equation that has been previously published for *E. maclovinus* (Vanella and Calvo 2005), at 5 and 10 °C. This variable was significantly higher at 10 °C, but even though the peak after swimming was higher at 10 °C than at 5 °C, it was not significantly different. Nevertheless, the scope of activity, which is the measure of the capacity of exercise at different temperatures, was significantly higher at 5 °C. The energy that was required by the fish to recover routine oxygen consumption (recovery energy, %) was also significantly greater at 5 °C. Rome et al. (1992) suggested a mechanism termed "compression of the recruitment order theory" to explain how fish maintain similar kinematics of locomotion, regardless of changes in muscle properties with temperature. At a given speed of locomotion, more motor units are recruited at lower temperatures to compensate for reduced power output. In our experiment, the recruitment of more motor units at 5 °C may explain the significantly higher proportion of energy required to recover at low temperatures. In our previous work (Fernández et al. 2002), we demonstrated

Table 4 Forced swimming

Temperature (°C)	Baseline O_2 consumption (mg $O_2/h^{-1}/g^{-1}$)	Peak O_2 consumption (mg O_2 h^{-1} g^{-1})	Scope	Time to peak (h)	Recovery time (h)	Absolute recovery energy (kJ)	Relative recovery energy (%) (kJ)
10	0.04 ± 0.01	0.13 ± 0.06	3.03 ± 0.70	1.73 ± 0.93	4.1 ± 2.08	0.018 ± 0.009	38.71 ± 8.32
5	0.01 ± 0.005	0.05 ± 0.03	4.51 ± 0.90	3.2 ± 2.98	5.76 ± 2.81	0.012 ± 0.008	65.31 ± 9.97
Test	Mann–Whitney	Mann–Whitney	Mann–Whitney	Mann–Whitney	Mann–Whitney	Mann–Whitney	Mann–Whitney
	$P = 0.021$*	$P = 0.083$ ^{ns}	$P = 0.043$*	$P = 0.56^{ns}$	$P = 0.39^{ns}$	$P = 0.49^{ns}$	$P = 0.021$*
Q_{10}	9.00	–	0.45	–	–	–	0.35

Scope: ratio of peak O_2 consumption to baseline O_2 consumption. Measured variables for groups at 4 and 10 °C. Means ± standard deviations, test used for comparisons, and P value are provided (*ns* not significant, * significant). Q_{10} values were calculated for variables with a significant difference between temperatures

that escape responses of *E. maclovinus* show an overall dependence on temperature and a direct relationship with a Q_{10} (calculated from data taken at 10 and 4 °C) of more than 1 for three measured variables: velocity ($Q_{10} = 2.23$), acceleration ($Q_{10} = 3.93$), and power ($Q_{10} = 6.18$). Following the same trend, the velocity of the wave along the spine showed a $Q_{10} = 0.45$. However, there was an increase in the curvature of the spine at low temperatures ($Q_{10} = 0.43$), showing a Q_{10} between 4 and 10 °C that was similar to that found for scope and recovery energy (%) in the present work (Table 4). Scope and recovery energy (%) at low temperatures should theoretically reflect the constraints for swimming at low temperatures, resulting in a greater curvature of the spine. It is interesting to note that the difficulty in obtaining sustained swimming at temperatures below 5 °C could highlight a threshold in swimming capacities of this species. Although the fast start could be studied at temperatures below 5 °C in our previous study, the analysis of data from Fernández et al. (2002) shows an abrupt fall in the total power invested in fast start of *E. maclovinus*, between 4 and 6 °C, coincident with the rise in the curvature of the spine.

Fernández et al. (2002) raised the necessity of further studies to determine whether *E. maclovinus* shows changes in locomotory performance with seasonal acclimatization. We can offer an integrative response from the analysis of our experiments. Combining the information provided for both, swimming and growth experiments, we can affirm energy allocation was significantly changed by temperature, with a higher proportion being directed to growth at high temperature and, on the contrary, being directed to swimming at low temperature. Therefore, this trade-off in the allocation of energy for physiological functions is affected by temperature. For this reason, *E. maclovinus* could be considered a good model to study this effect in a natural environment, due to the wide latitudinal range and the eurythermicity of this species. We belive this trade-off may be explained by biomechanical constraints for swimming, related to the "compression of the recruitment order theory" at low temperatures that generate proportionally higher energy requirements.

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References

Arendt JD (1997) Adaptive intrinsic growth rates: an integration across taxa. Q Rev Biol 72:149–177

Arnott SA, Chiba S, Conover DO (2006) Evolution of intrinsic growth rate: metabolic costs drive trade-offs between growth and

swimming performance in *Menidia menidia*. Evolution 60:1269–1278
Azevedo PA, Cho CY, Leeson S, Bureau DP (1998) Effects of feeding level and water temperature on growth, nutrient and energy utilization and waste outputs of rainbow trout (*Oncorhynchus mykiss*). Aquat Living Resour 11:227–238
Billerbeck JM, Schultz ET, Conover DO (2000) Adaptive variation in energy acquisition and allocation among latitudinal populations of the Atlantic silverside. Oecologia 122:210–219
Boeuf G, Payan P (2001) How should salinity influence fish growth? Comp Biochem Physiol C 130:411–423
Brickle P, Arkhipkin AI, Shcherbich ZN (2005a) Age and growth in a temperate euryhaline notothenioid, *Eleginops maclovinus* from the Falkland Islands. J Mar Biol Assoc UK 85:1217–1221
Brickle P, Laptikhovsky V, Arkhipkin A (2005b) Reproductive strategy of a primitive temperate notothenioid *Eleginops maclovinus*. J Fish Biol 66:1044–1059
Calvo J, Morriconi E, Rae G, San Román N (1992) Evidence of protandry in a sub-Antarctic nototheniid *Eleginops maclovinus* (Cuv. & Val. 1830) from the Beagle Channel. Argentine. J Fish Biol 40:157–162
Ceballos SG (2011) Estructura genética poblacional, historia demográfica y variación fenotípica del róbalo, *Eleginops maclovinus* (Perciformes). Doctoral Thesis, Universidad de Buenos Aires, Buenos Aires
Ceballos SG, Lessa EP, Victorio MF, Fernández DA (2011) Phylogeography of the sub-Antarctic notothenioid fish *Eleginops maclovinus*: evidence of population expansion. Mar Biol. doi: 10.1007/s00227-011-1830-4
Cho CY (1992) Feeding systems for rainbow trout and other salmonids with reference to current estimates of energy and protein requirements. Aquaculture 100:107–123
Cousseau MB, Perrota RG (2000) Peces Marinos de Argentina. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata
Fernández DA, Calvo J, Wakeling M, Vanella FA, Johnston IA (2002) Escape performance in the sub-Antarctic notothenioid fish *Eleginops maclovinus*. Pol Biol 25:914–920
Gosztonyi A (1980) Biología del róbalo (*Eleginops maclovinus* Cuv. & Val., 1830). Doctoral Thesis. Universidad Nacional de La Plata, La Plata
Huergo MA, San Román NA, Isla MS (1996) Estudio biológico pesquero sobre el recurso íctico "Róbalo" *Eleginops maclovinus* (Pisces, Nototheniidae) en la provincia de Tierra del Fuego, Antártida e Islas del Atántico Sur. Technical report, Tierra del Fuego, Antártida e Islas del Atántico Sur goverment, Ushuaia
Isla MS, San Román NA (1995) Feeding of *Eleginops maclovinus* (Pisces, Nototheniidae) in the Beagle Channel, Argentina. Naturalia Patagónica 3:107–127
Jobling M (1994) Fish bioenergetics. Chapman & Hall, London
Jobling M (1995) Environmental biology of fishes. Chapman & Hall, London
Johnston IA, Battram J (1993) Feeding energetics and metabolism in demersal fish species from Antarctic, temperate and tropical environments. Mar Biol 115:7–14
Kaushik SJ (1998) Nutritional bioenergetics and estimation of waste production in non-salmonids. Aquat Living Resour 11:211–217
Licandeo RR, Barrientos CA, Gonzáles MT (2006) Age, growth rates, sex change and feeding habits of notothenioid fish *Eleginops maclovinus* from the central-southern Chilean coast. Environ Biol Fish 77:51–61
Lowry OH, Rosebrough NJ, Farr AL, Randall RJ (1951) Protein measurement with the folin-phenol reagent. J Biol Chem 193(1): 265–275
Martin JP, Bastida R (2008) Contribución de las comunidades bentónicas en la dieta del róbalo (*Eleginops maclovinus*) en la ría Deseado (Santa Cruz, Argentina). Lat Am J Aquat Res 36:1–13
Mommsen TP (1998) Growth and metabolism. In: Evans DH (ed) The physiology of fishes. Boca Raton, Florida, pp 65–97
Norman JR (1937) Nototheniidae. Coast Fishes—Discovery Reports Part II Patagonian Region 16:1–150
Pavés H, Pequeño G, Bertrán C, Vargas L (2005) Limnetic feeding in *Eleginops maclovinus* (Valenciennes, 1830) in the Valdivia River, Chile. Interciencia 30:120–125
Pequeño G (1989) The geographical distribution and taxonomic arrangement of South American nototheniid fishes (Osteichthyes, Nototheniidae). Bol Soc Biol Concepción 60:183–200
Pequeño G, Pavés H, Bertrán C, Vargas-Chacoff L (2010) Seasonal limnetic feeding regime of the "robalo" *Eleginops maclovinus* (Valenciennes 1830), in the Valdivia river, Chile. Gayana 74:47–56
Piola AR, Falabella V (2009) El mar patagónico. Atlas del mar patagónico. Especies y espacios. Widlife Conservation Society and Birdlife International, Buenos Aires, pp 55–75
Rome LC (1998) Some advances in integrative muscle physiology. Comp Biochem Physiol B 120:51–72
Rome LC, Choi IH, Lutz G, Sosnicki A (1992) The influence of temperature on muscle function in the fast swimming scup. I. Shortening velocity and muscle recruitment during swimming. J Exp Biol 163:259–279
Seifter S, Dayton S, Novic B, Muntwyler E (1949) The estimation of glycogen with the anthrone reagent. Arch Biochem 25:191–200
Vanella FA (2005) Efectos de la temperatura en el metabolismo durante el reposo, natación y alimentación. Investigación sobre la Adaptación Metabólica al Frío en Teleósteos Subantárticos. Doctoral Thesis, Universidad Nacional de Córdoba, Córdoba
Vanella FA, Calvo J (2005) Influence of temperature habitat and body mass on routine rates of Subantarctic teleosts. Sci Mar 69(S2): 317–323
Vanella FA, Fernández DA, Romero MC, Calvo J (2007) Changes in the fish fauna associated with a sub-Antarctic Macrocystis pyrifera kelp forest in response to canopy removal. Pol Biol 30:449–457
Vanella FA, Boy CC, Lattuca ME, Calvo J (2010) Temperature influence on post-prandial metabolic rate of sub-Antarctic teleost fish. Comp Biochem Physiol A 156:247–254
Videler JJ (1993) Fish swimming. Chapman & Hall, London
Webb PW (1998) Swimming. In: Evans DH (ed) The physiology of fishes. Boca Raton, Florida, pp 3–24
Willmer P, Stone G, Johnston I (2000) Evironmental physiology of animals. Blackwell Science Ltd, Oxford