

*Effects of changes in salinity on oxygen and food consumption of the young sub-Antarctic notothenioid Eleginops maclovinus: possible implications of their use of an estuarine habitat*

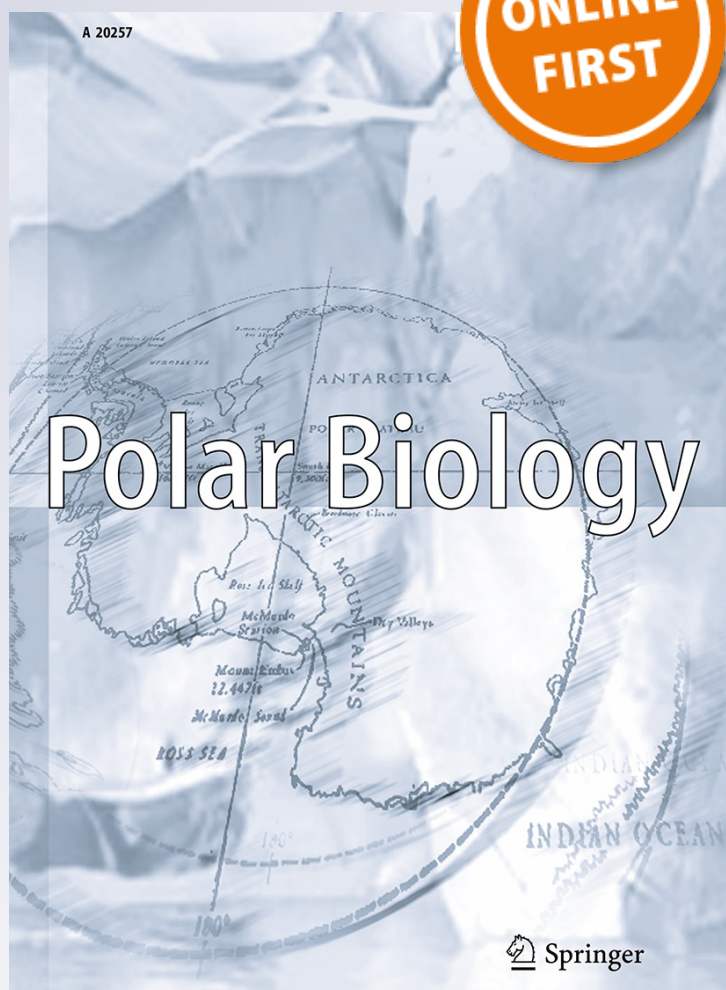
**Fabián Alberto Vanella, Claudia Alejandra Duarte, María Eugenia Lattuca, Daniel Alfredo Fernández & Claudia Clementina Boy**

**Polar Biology**

ISSN 0722-4060

Polar Biol

DOI 10.1007/s00300-016-1986-y



**Your article is protected by copyright and all rights are held exclusively by Springer-Verlag Berlin Heidelberg. This e-offprint is for personal use only and shall not be self-archived in electronic repositories. If you wish to self-archive your article, please use the accepted manuscript version for posting on your own website. You may further deposit the accepted manuscript version in any repository, provided it is only made publicly available 12 months after official publication or later and provided acknowledgement is given to the original source of publication and a link is inserted to the published article on Springer's website. The link must be accompanied by the following text: "The final publication is available at [link.springer.com](http://link.springer.com)".**

# Effects of changes in salinity on oxygen and food consumption of the young sub-Antarctic notothenioid *Eleginops maclovinus*: possible implications of their use of an estuarine habitat

Fabián Alberto Vanella<sup>1</sup> · Claudia Alejandra Duarte<sup>2</sup> · María Eugenia Lattuca<sup>1</sup> · Daniel Alfredo Fernández<sup>1,2</sup> · Claudia Clementina Boy<sup>1</sup>

Received: 10 June 2015 / Revised: 24 May 2016 / Accepted: 25 May 2016  
© Springer-Verlag Berlin Heidelberg 2016

**Abstract** Salinity is one of the most important structuring factors in the distribution and bioenergetics of estuarine fishes. The aims of this work were to study the distribution of the sub-Antarctic, eurythermic, euryhaline and coastal notothenioid *Eleginops maclovinus* in Lapataia estuary (Tierra del Fuego National Park), in relation to salinity conditions, and the effect of salinity on the oxygen consumption of this species. The spread of the mixing zone of Lapataia was studied and physicochemical properties (conductivity, pH, temperature and salinity) were measured. Distribution of *E. maclovinus* juveniles was investigated principally by electrofishing in the field. Oxygen consumption of absorptive and post-absorptive young-of-the-year individuals (8–10 cm total length) was analyzed by stop-flow respirometry measurements, performed at three salinities (1, 12 and 30 psu). The intermediate mixing zone is relatively small in this system, showing an extension of ~1.5 km upstream from Lapataia Bay. It was found that there was a strong relationship between the mixing zone and the distribution of juveniles of *E. maclovinus*. No differences were found in the metabolic baseline at different salinities. A punctual feeding

provoked a typical SDA response, with a significant higher ingested food and metabolic scope at intermediate salinity (12 psu). An increased scope was reached by increasing the energy intake and not through a decrease in the standard metabolic rate. Under an available food condition, this capacity could result in an increased growth rate at intermediate salinity.

**Keywords** *Eleginops maclovinus* · Metabolism · Respirometry · Salinity · Estuarial zone · Lapataia Bay

## Introduction

The coastal fish *Eleginops maclovinus* (Cuvier 1830; Eleginopidae, Notothenioidei; Spanish c. n. *róbalo*) belongs to the monospecific family Eleginopidae (Order Perciformes; Suborder Notothenioidei). *Eleginops maclovinus* inhabits the sub-Antarctic coastal waters of South America, the southernmost point of its distribution being 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). *Eleginops maclovinus* is considered eurythermic and euryhaline (Pequeño 1989; Pavés et al. 2005), and it is exposed in nature 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). This species inhabits mainly marine and estuarine environments, although it has been captured in limnetic areas, where they also feed (Pavés et al. 2005; Pequeño et al. 2010).

A difference in osmotic concentration of internal fluids of fishes and their environment must be covered by energy expenditure (Jobling 1994; Boeuf and Payan 2001). This

✉ Fabián Alberto Vanella  
fvanella@gmail.com

<sup>1</sup> Laboratorio de Ecología, Fisiología y Evolución de Organismos Acuáticos, Centro Austral de Investigaciones Científicas (CADIC-CONICET), Ushuaia, Tierra del Fuego, Argentina

<sup>2</sup> Instituto de Ciencias Polares, Recursos Naturales y Ambientes, Universidad Nacional de Tierra Del Fuego, Ushuaia, Argentina

process may involve the alteration of the energy metabolism of osmoregulatory and non-osmoregulatory organs (Sangiao-Alvarellos et al. 2003) and influences the habitat selection and the growth performance of fishes (Cardona 2000, 2006). Jobling (1994) highlights that some experimental studies indicate that when euryhaline species are held in media that are isosmotic or nearly isosmotic with their body fluids, their metabolic rates are lower than those of fishes held in either fresh water or seawater. According to this author, these studies would seem to provide evidence that the energetic costs of ion and osmoregulation are lower in environments where the gradient between blood and water is minimal. In this regard, Herrera et al. (2012) described a lower oxygen consumption rate in individuals of *Solea senegalensis* that were acclimated and maintained at sea water salinity (37.5 psu) than animals which were acutely changed to low salinity (5 psu) and high salinity water (55 psu). Boeuf and Payan (2001) conclude that in fishes, a better growth is often observed in an intermediate salinity condition, i.e. brackish water, and this is frequently correlated with a lower standard of metabolic rate. There is little information about how the metabolic rate is affected by salinity, even in routine post-absorptive and absorptive conditions. Vargas-Chacoff et al. (2014) describe that in *E. maclovinus*, acclimation to different salinities induced changes in plasma metabolites (glucose, lactate and proteins), cortisol and  $\text{Na}^+\text{K}^+$ -ATPase activity in different organs. Some parameters show a direct and positive relationship with salinity, while others show a U-shaped relationship. Moreover, Vargas-Chacoff et al. (2015) demonstrated a better growth rate for *E. maclovinus* chronically exposed for salinities near to the iso-osmotic point (15 psu) than to the hyper-osmotic environment (31 psu). These changes are related to an allostatic energy response, and they likely impact on oxygen consumption. On the other hand, salinity has been mentioned as one of the factors that could affect the site-specific value in such as nurseries of intermediate salinity environments (Beck et al. 2001). For this reason, these authors suggest that a better understanding of the relationship between metabolic rate and habitat selection is necessary.

The complex formed by Lapataia Bay, Lapataia River and Ovando River (Fig. 1), under the Pritchard (1967) definition, constitutes an estuary, being “a semi-enclosed coastal body of water which has a free connection with open sea and within which seawater is measurably diluted with fresh water derived from land drainage”. The physics of this system was studied previously by Isla et al. (1999), who described a limited water exchange with the Beagle Channel due to a submerged frontal moraine and the existence of a mixing area located in the Cormoran Archipelago zone (Fig. 1). But, the measurements

performed by Isla et al. were made punctually in time, the tide influence was not studied and the limits of the mixing zone and its influence on aquatic species distribution were not known. In addition to *E. maclovinus*, the Lapataia estuarine zone is inhabited by other euryhaline fishes such as *Galaxias maculatus* (Boy et al. 2007), *Odontestes* sp. (Lattuca, pers. comm.) and introduced salmonids like *Oncorhynchus tshawytscha* (Fernández et al. 2010; Riva Rossi et al. 2012). The presence of numerous juveniles of *E. maclovinus* in the Lapataia estuarine zone highlights the importance of this area for this species, which is probably used as a nursery. A possible reason, besides refuge and food, could be some kind of energetic advantage provided by the intermediate salinity zone.

The aims of this work were to study the presence of the sub-Antarctic notothenioid *E. maclovinus* in the Tierra del Fuego National Park (TDFNP), Argentina, in relation to salinity conditions and the effect of salinity on the oxygen consumption in postabsorptive and absorptive individuals. Physicochemical parameters of Lapataia Bay and its vicinities were studied in order to know the extension of the mixed zone and its influence on the distribution of juveniles of this species. The results have allowed us to test the hypothesis that there is an energy saving related to lower metabolic cost at intermediate salinities, and to relate this to the distribution of *E. maclovinus* in Lapataia estuarine complex.

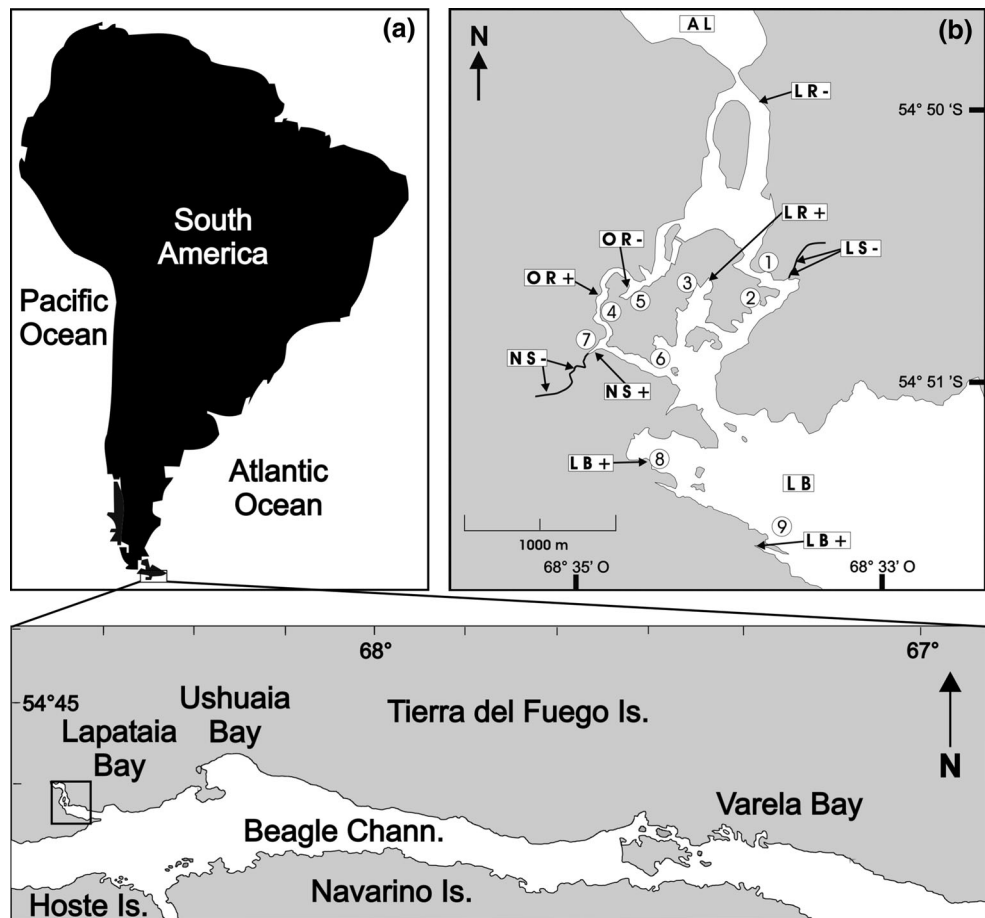
## Materials and methods

### Physicochemical analysis of the estuarine zone and distribution of *E. maclovinus* juveniles

Physicochemical properties of Lapataia estuary in the Beagle Channel were studied, in order to know the spread of the mixing zone between fresh and marine water and its relation with the distribution of juveniles of *E. maclovinus*. This information was also used to obtain more realistic parameters with which to conduct the experiments. Each variable (conductivity, pH, temperature and salinity) was measured with a Horiba U-10 in nine sites along the estuary at high and low tide for each season, totaling eight values per site (Fig. 1).

To study the distribution of juveniles of *E. maclovinus*, individuals were captured by electrofishing, with LR-24 backpack unit (Smith-Root Inc.) or with a seine net (10 m long, 1 m deep, 5 mm mesh size) whenever water conductivity or flow rate prevented the use of the electrofishing device. On each sampling site (Fig. 1), captured individuals were counted and measured at 5 mm total length (TL) intervals to avoid handling stress and then immediately returned to the water.

**Fig. 1** **a** Geographic location of Beagle Channel; **b** estuarine complex of Lapataia Bay. Lapataia Bay (**L B**), Lapataia River (**L R**), Ovando River (**O R**), Negro Stream (**N S**), Lapataia Stream (**L S**) and Acigami Lake (**A L**). Physicochemical measurement sites, numbered from 1 to 9. Arrows indicate fishing points (+ positive *Eleginops maclovinus* fishing; - negative *Eleginops maclovinus* fishing)



## Oxygen consumption of juvenile *E. maclovinus*

### General information and techniques

Young-of-the-year *E. maclovinus* (8–10 cm TL) for the respirometric experiment were captured using a seine net (10 m long, 1 m high, 5 mm distance between two knots) at Varela Bay, Beagle Channel (54°52'21.13"S; 67°16'30.52"W; 70 km west to Lapataia Bay). Experimental animals were preferred to be captured outside of the National Park in order to diminish local disturbance. *Eleginops maclovinus* show a low level of genetic differentiation, even throughout thousands of kilometers, along Atlantic and Pacific Patagonian coasts (Ceballos et al. 2015). This added to the high dispersal capacity and vagility proposed for this species (Ceballos et al. 2012), making predictable a high homogeneity in the Beagle Channel population and as a consequence no experimental effects due to the location of capture. The current authors worked with this life stage because their small size makes them suitable for working in aquaria and respirometric system. Furthermore, since *E. maclovinus* shows protandry as reproductive strategy (Calvo et al. 1992), the current authors were certain that all specimens used were immature males. Animals

were transported to the Centro Austral de Investigaciones Científicas (CADIC, Ushuaia, Tierra del Fuego, Argentina) and held in aquaria.

### Holding and acclimation conditions

Animals were maintained for 2 weeks in aquaria at simulated summer conditions (similar to natural conditions at the moment of the capture) of temperature and daylight hours (10 °C; photoperiod 17:7 h light:darkness, respectively) and fed twice a week with chopped hake filet meat until satiation. Salinity of the water was maintained at 30 psu from capture to the beginning of the experiment. For acclimation, fish were divided into three groups of ten animals and accommodated in 15 l aquaria (five fish per aquarium). Then, animals were acclimated gradually for 10 days to experimental salinities (1, 12 and 30 psu). For this acclimation, the same quantity of water (marine or a mix of fresh-marine water) was changed in each aquarium and salinity was diminished progressively. In order to maintain the rate of change, the quantity of changed water was progressively greater, from 1.5 to 10 l. In aquaria destined for acclimation to 30 psu, water was replaced by

marine water. For groups of 12 and 1 psu, the rate of change was 1.8 and 3 psu per day, respectively.

Experimental salinities were chosen because the extremes (30 and 1 psu) are the upper and lower limits respectively where *E. maclovinus* could be found in Fuegian estuaries, and the intermediate (12 psu) was frequently observed by the current authors in the mixing zone as described by Isla et al. (1999) in the Lapataia estuarine complex. This intermediate salinity (12 psu; 349.46 mOsm/kg) is also near the mean plasma/serum osmotic concentration as described in Nordlie (2009) for isosmotic estuarine and near-shore marine teleosts (345.1 mOsm/kg). Temperature, feeding and photoperiod were maintained constant from holding conditions. After reaching the desired salinities, these conditions were maintained throughout a period of 3 days until the respirometric experiment start and feeding was suspended. This period of time was considered enough to reach a chronic regulatory period of plasma osmolality (Sangiao-Alvarellos et al. 2005). Then, the animals were transferred to the respirometric system which was filled with water of the same salinity.

### Respirometry

The experiments were carried out under simulated summer conditions of temperature and daylight (10 °C; 17:7 h light:darkness, respectively). Stop-flow respirometry chambers were made of translucent plastic material to prevent visual stimulation from external sources. The volume of the chambers (490 ml) was found large enough to allow spontaneous fish movements (Vanella, pers. obs.). In order to measure oxygen consumption, chambers were closed and water flow stopped for 1–3 h to make sure O<sub>2</sub> saturation was never lower than 80 %. The oxygen consumption values suspected to be influenced by the photoperiod (starting of dark period) were removed.

Oxygen concentration was measured using a 928 6-Channel Oxygen Strathkelvin System, equipped with 1302 Microcathode Oxygen Electrodes, which were inserted into the respirometric chambers. For this kind of electrode, medium homogenization under actual conditions is not required. After 3 days inside the chambers, animals were fed with chopped hake filet in order to study Specific Dynamic Action (SDA).

### Measured variables

The following variables were measured during respirometry experiments. Definitions were taken principally from Secor (2009):

**Baseline:** Metabolic rate of postabsorptive individuals, quantified as routine oxygen consumption (mg O<sub>2</sub>/g/h),

calculated by the mean of data from the last day after feeding.

**Peak:** Post-prandial peak in metabolism, quantified as oxygen consumption (mg O<sub>2</sub>/g/h).

**Scope:** Post-prandial peak divided by Baseline.

**Duration:** Time from feeding when metabolic rate is no longer greater than baseline values (h).

**Meal size:** Dry mass of ingested food as percentage of body mass.

**Meal energy:** Meal energy determined by bomb calorimetry (kJ).

**SDA:** Accumulated energy expended above baseline for duration of SDA response. It was calculated as caloric equivalent (1 mg O<sub>2</sub>: 14.6 J; Johnston and Battram 1993) of additional oxygen consumed after a single feeding, relativized by body mass (kJ/g).

**SDA coeff:** SDA coefficient, calculated as the percentage of ingested energy used over routine values during the SDA process.

### Statistics

A one-way analysis of variance (ANOVA) was carried out in order to test differences between treatments on the proposed respirometric variables measured. The assumptions required by the parametric test (normality and/or homogeneity of variances) were reached by all variables studied. Multiple Tukey–Kramer post hoc comparisons were made when the ANOVA was significant. In all cases,  $\alpha = 0.05$ .

## Results

### Physicochemical analysis of the estuarine zone and distribution of *E. maclovinus* juveniles

A clear predominance of marine conditions was observed in sites 8 and 9, located in Lapataia Bay (Salinity overall average: 26.2 and 27.4 psu, respectively; Table 1; Fig. 1). The more external site, number 9, presented the upper mean value of salinity even at high and low tide.

The mixing zone extends to sites 2 and 3 in Lapataia River, and to site 4 in Ovando River, respectively (salinity overall average: 3.9, 15.0 and 0.5 psu, respectively; Table 1; Fig. 1). Upstream of these sites, the influence of seawater measured by salinity is zero (site 1; Lapataia River) or very low and unusual (fall, site 5; Ovando River). This area shows the greatest temperatures in summer (12.30 °C, site 3; 12.50 °C, site 7; low tide).

Analyzing historical sampling in rivers and streams of the National Park, it was observed that the distribution

**Table 1** Physicochemical variables measured in Lapataia estuary

Site	Variables	Summer		Fall		Winter		Spring		Mean $\pm$ SD	
		23 Feb 09		29 May 09		23 Jul 09		02 Oct 09		LT	HT
		LT	HT	LT	HT	LT	HT	LT	HT		
1	pH	7.97	7.93	8.95	8.52	7.95	8.59	8.02	7.82	8.22 $\pm$ 0.49	8.22 $\pm$ 0.40
	Cond. (mS/cm)	0.069	0.069	0.105	0.071	0.073	0.78	0.073	0.072	0.08 $\pm$ 0.02	0.25 $\pm$ 0.35
	Temp. ( $^{\circ}$ C)	11.3	11.8	6.30	5.30	3.80	4.40	4.70	5.50	6.53 $\pm$ 3.35	6.75 $\pm$ 3.40
	Salinity (psu)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0 $\pm$ 0.0	0.0 $\pm$ 0.0
2	pH	7.90	8.03	8.32	8.42	7.60	8.19	8.08	7.93	7.98 $\pm$ 0.30	8.14 $\pm$ 0.21
	Cond. (mS/cm)	0.076	8.49	7.25	14.10	0.52	22.20	0.081	3.88	1.98 $\pm$ 3.52	12.17 $\pm$ 7.89
	Temp. ( $^{\circ}$ C)	11.00	11.20	6.10	5.50	3.80	5.30	4.60	5.50	6.38 $\pm$ 3.23	6.88 $\pm$ 2.88
	Salinity (psu)	0.0	4.7	3.7	7.2	0.1	13.5	0.0	1.9	1.0 $\pm$ 1.8	6.8 $\pm$ 4.9
3	pH	8.29	8.07	8.04	8.29	7.55	8.20	8.64	7.90	8.13 $\pm$ 0.46	8.12 $\pm$ 0.17
	Cond. (mS/cm)	27.2	44.80	22.20	24.70	30.60	23.90	8.39	19.10	22.10 $\pm$ 9.77	28.13 $\pm$ 11.39
	Temp. ( $^{\circ}$ C)	12.30	10.20	5.40	4.00	4.30	4.08	5.70	6.60	6.93 $\pm$ 3.63	6.22 $\pm$ 2.92
	Salinity (psu)	16.4	28.4	12.9	14.7	17.9	13.9	4.4	11.0	12.9 $\pm$ 6.0	17.0 $\pm$ 07.8
4	pH	8.00	7.89	8.34	8.70	8.20	8.22	8.12	7.71	8.17 $\pm$ 0.14	8.13 $\pm$ 0.43
	Cond. (mS/cm)	0.081	0.072	2.39	1.01	1.37	5.62	0.90	0.091	1.19 $\pm$ 0.96	1.70 $\pm$ 2.65
	Temp. ( $^{\circ}$ C)	10.8	11.90	4.90	3.40	2.50	3.30	4.50	5.40	5.68 $\pm$ 3.57	6.00 $\pm$ 4.05
	Salinity (psu)	0.0	0.0	1.1	0.1	0.5	2.1	0.0	0.0	0.4 $\pm$ 0.5	0.6 $\pm$ 1.0
5	pH	7.95	8.25	8.36	8.71	8.30	8.42	8.05	7.94	8.17 $\pm$ 0.20	8.33 $\pm$ 0.32
	Cond. (mS/cm)	0.081	0.082	2.10	0.86	0.25	0.092	0.15	0.22	0.65 $\pm$ 0.97	0.31 $\pm$ 0.37
	Temp. ( $^{\circ}$ C)	11.50	13.2	4.20	4.30	2.70	3.30	5.20	7.10	5.90 $\pm$ 3.87	6.98 $\pm$ 4.45
	Salinity (psu)	0.0	0.0	0.9	0.0	0.0	0.0	0.0	0.0	0.2 $\pm$ 0.5	0.0 $\pm$ 0.0
6	pH	8.28	8.34	8.11	8.28	7.88	8.13	8.50	8.15	8.19 $\pm$ 0.26	8.23 $\pm$ 0.10
	Cond. (mS/cm)	7.78	18.30	18.00	16.50	9.60	7.63	1.51	12.00	9.22 $\pm$ 6.80	13.61 $\pm$ 4.79
	Temp. ( $^{\circ}$ C)	11.30	11.30	5.50	4.60	3.80	3.00	4.90	6.10	6.38 $\pm$ 3.36	6.25 $\pm$ 3.60
	Salinity (psu)	4.2	11.0	10.0	8.3	5.0	3.8	0.4	6.6	4.9 $\pm$ 3.9	7.4 $\pm$ 3.0
7	pH	7.99	7.86	8.32	8.92	8.29	8.36	7.92	8.01	8.13 $\pm$ 0.20	8.29 $\pm$ 0.47
	Cond. (mS/cm)	0.71	1.38	1.09	7.32	0.26	0.57	1.14	0.45	0.80 $\pm$ 0.41	2.43 $\pm$ 3.29
	Temp. ( $^{\circ}$ C)	12.50	12.80	3.10	1.30	2.70	1.80	6.20	8.20	6.13 $\pm$ 4.53	6.03 $\pm$ 5.50
	Salinity (psu)	0.3	0.6	0.4	0.2	0.0	0.2	0.0	0.1	0.2 $\pm$ 0.2	0.3 $\pm$ 0.2
8	pH	8.13	7.93	8.24	8.39	7.81	8.10	8.42	8.32	8.15 $\pm$ 0.26	8.19 $\pm$ 0.21
	Cond. (mS/cm)	44.60	43.30	47.10	42.40	46.50	21.20	47.00	45.80	46.30 $\pm$ 1.16	38.18 $\pm$ 11.41
	Temp. ( $^{\circ}$ C)	9.30	9.60	6.60	2.20	6.00	3.40	6.30	7.60	7.05 $\pm$ 1.52	5.70 $\pm$ 3.48
	Salinity (psu)	27.5	27.5	29.4	25.6	29.2	12.1	29.4	28.8	28.9 $\pm$ 0.9	23.5 $\pm$ 7.7
9	pH	8.10	8.09	8.38	8.52	7.96	8.15	8.77	8.44	8.30 $\pm$ 0.36	8.30 $\pm$ 0.21
	Cond. (mS/cm)	45.20	42.20	47.00	45.00	46.50	33.70	46.70	44.50	46.35 $\pm$ 0.79	41.35 $\pm$ 5.24
	Temp. ( $^{\circ}$ C)	9.50	9.70	6.60	3.30	5.80	4.00	6.20	7.40	7.03 $\pm$ 1.68	6.10 $\pm$ 2.99
	Salinity (psu)	28.5	26.8	29.5	27.9	28.9	20.6	29.3	27.9	29.1 $\pm$ 0.4	25.8 $\pm$ 3.5

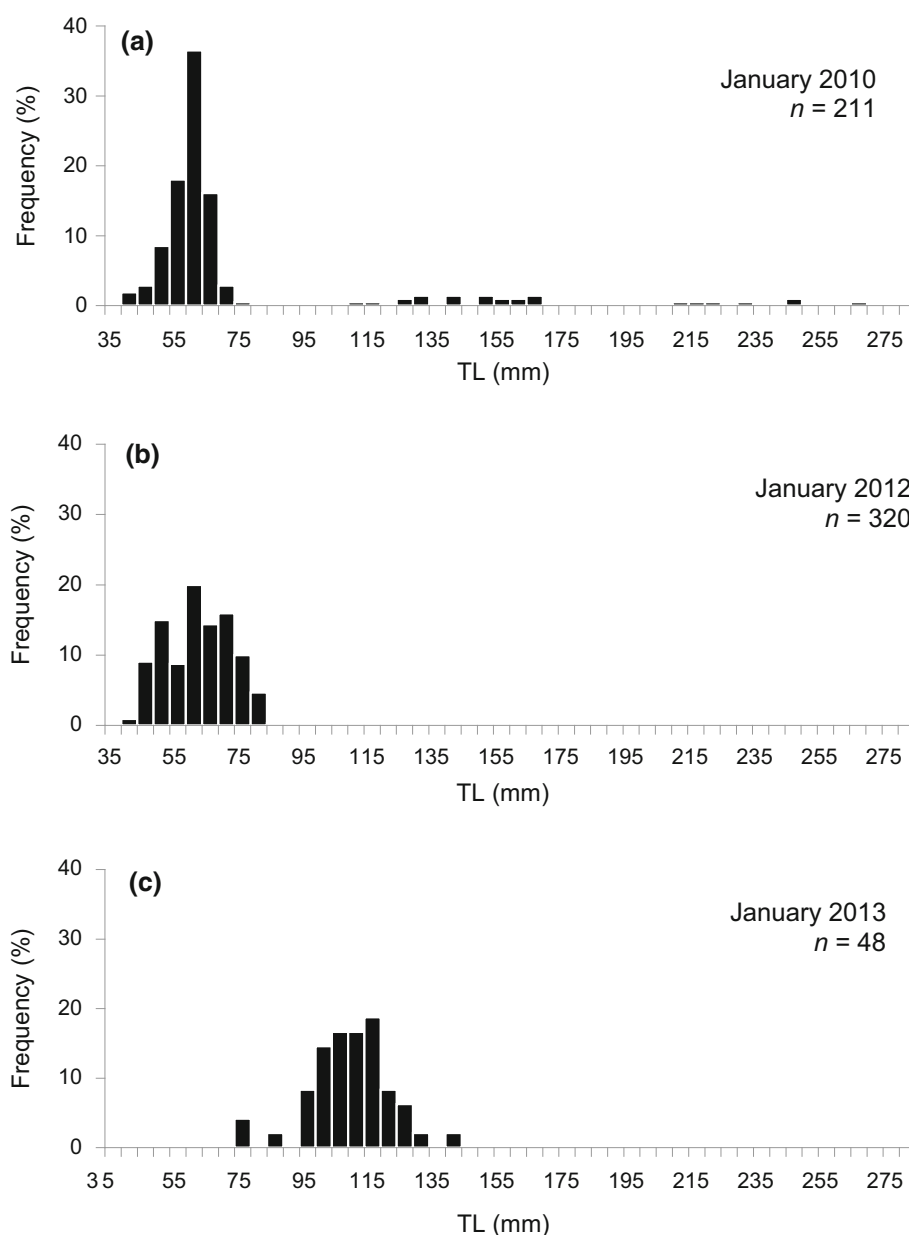
LT low tide, HT high tide. Measured variables: pH; Conductivity (Cond); Temperature (Temp); Salinity

range of juvenile *E. maclovinus* is restricted to the mixing zone of marine and fresh water (see Fig. 1).

A few individuals of *E. maclovinus* were captured at each sampling site (Fig. 1), except at site 3 (Cormoranes Bay), where captures were highest. Figure 2 shows size-frequency distributions at Cormoranes Bay in January 2010 and 2012, which were the most abundant captures. In 2010, the distribution

shows a mode at about 60 mm TL and with a few individuals of greater sizes; whereas in 2012 a bimodal distribution is observed, with one peak similar to 2010 and the other one smaller (about 50 mm TL). In January 2011 no individuals were captured, whereas in January 2013 and 2014 a few individuals were captured (3 and 22, respectively), which were larger than 130 mm TL, except one of them of 55 mm TL.

**Fig. 2** Size-frequency distributions of *Eleginops maclovinus* in Tierra del Fuego National Park: **a**, **b** Cormoranes Bay; **c** Negro Stream. Only years with  $n > 45$  individuals are shown (see “Results” section). TL total length



At site 7, 6 individuals were captured measuring between 40 and 55 mm TL (January 2013); and 48 between 70 and 145 mm TL (January 2014; Fig. 2). The individuals captured at site 8 ( $n = 3$ ) were larger than 115 mm TL (January 2011). Finally, at site 9 only one individual of 85–90 mm TL (January 2013) and another one individual of 105–110 mm TL (January 2014) were captured.

### Respirometry

Measured variables of respirometric experiment are synthesized in Table 2.

The baseline was not affected by salinity, showing an average value of  $0.080 \pm 0.015$  mg/h/g. Nevertheless, differences in metabolic response were observed after a punctual meal, during the SDA process.

At a salinity of 12 psu, the SDA process was significantly longer (duration:  $\sim 69$  h), and peak and scope were higher. The peak showed a value that was 1.2 and 1.5 times greater, compared with the one measured at a salinity of 1 and 30 psu, respectively, whereas scope was 1.24 and 1.59 times greater in animals acclimated to 12 rather than to 1 and 30 psu, respectively.

Salinity also affected food ingestion by *E. maclovinus*. Meal size and meal energy showed significant differences



**Table 2** Variables measured during respirometric experiment at diverse salinities

	Salinity (psu)			Test
	30	12	1	
Body mass (g)	4.65 ± 0.97	4.72 ± 0.81	5.86 ± 1.53	ANOVA <i>p</i> = 0.1237
Baseline (mg O <sub>2</sub> /h/g)	0.081 ± 0.01	0.078 ± 0.01	0.077 ± 0.02	ANOVA <i>p</i> = 0.7102
Peak (mg O <sub>2</sub> /h/g)	0.19 ± 0.04 <sup>a</sup>	0.29 ± 0.06 <sup>b</sup>	0.23 ± 0.05 <sup>a</sup>	ANOVA <i>p</i> = 0.0006
Scope	2.40 ± 0.57 <sup>a</sup>	3.81 ± 0.88 <sup>b</sup>	3.07 ± 0.75 <sup>a</sup>	ANOVA <i>p</i> = 0.0012
Baseline/peak				
Duration (h)	66.67 ± 20.86 <sup>a</sup>	69.27 ± 4.44 <sup>b</sup>	47.02 ± 3.13 <sup>a</sup>	ANOVA <i>p</i> < 0.0003
Meal size	1.72 ± 0.61 <sup>a</sup>	2.43 ± 0.39 <sup>b</sup>	1.03 ± 0.43 <sup>c</sup>	ANOVA <i>p</i> < 0.0001
Meal energy (kJ)	1.73 ± 0.47 <sup>a</sup>	2.53 ± 0.36 <sup>b</sup>	1.34 ± 0.83 <sup>a</sup>	ANOVA <i>p</i> < 0.0004
SDA (kJ/g)	0.05 ± 0.02 <sup>a</sup>	0.11 ± 0.06 <sup>b</sup>	0.04 ± 0.01 <sup>a</sup>	ANOVA <i>p</i> < 0.0055
SDA coeff	14.12 ± 8.54	21.76 ± 13.37	17.59 ± 8.97	ANOVA <i>p</i> = 0.2922

Different superscript letters indicate significant differences between treatments

between groups. The greatest meal size was reached by fish maintained at 12 psu, exhibiting a value of 2.36 and 1.36 times that of the one obtained at 1 and 30 psu, respectively. In consequence, meal energy was affected similarly, being higher at 12 psu, in 1.46 and 1.89 times that at 30 and 1 psu, respectively.

Regarding the energy allocated to digestion and absorption, SDA was significantly greater in animals maintained at a salinity of 12 rather than at 30 and 1 psu, being the approximate two-fold value. SDA coeff showed a similar tendency, but without significant differences.

## Discussion

No effect of salinity was observed in the baseline of *E. maclovinus*. This result is not in agreement with the general idea of the “isosmotic hypothesis” (Jobling 1994) that when euryhaline species are held in media that are isosmotic with their body fluids, their metabolic rates are lower than those individuals held in either fresh water or seawater. Our oxygen consumption results did not show energetic evidence of the Vargas-Chacoff et al. (2014) findings, although these authors calculated an isosmotic salinity (11 psu) very near to the one used by us (12 psu). They described, with decreasing salinities under chronic conditions, an increased concentration of cortisol, lactate and protein, and an elevated Na<sup>+</sup>K<sup>+</sup>-ATPase activity in

posterior intestine. However, Vargas-Chacoff et al. (2015) have described no differences in plasma cortisol level in individuals exposed to 5, 15 and 31 psu, and they interpreted this in the same way as for *E. maclovinus* which do not appear to exhibit chronic stress. Those authors hypothesize that there could be a discrepancy which can be explained by different times of acclimation. It is remarkable that the rate of exchange of salinity used in this work was designed to reach chronic acclimation. The baseline of ~0.08 mg O<sub>2</sub>/h/g calculated for *E. maclovinus* in the current work agrees with the values predicted by the mass equation described in Vanella and Calvo (2005) for animals of this size. Nevertheless, the well-known euryhaline condition of *E. maclovinus* could keep this species in the “Type I” response group described by Morgan and Iwama (1991). According to these authors, euryhaline fishes which move freely through waters generally demonstrate that metabolic rate does not change over a wide range of salinities. A possible explanation for this lack of effect in baseline could be a compensation between the enhancement of some metabolic pathways at extreme salinities and a downregulation of others, resulting in a similar net balance. However, this tendency was not observed in almost all other respirometric variables, measured after a punctual meal.

Peak, Scope and Duration clearly demonstrate an influence of salinity which is not apparently related to a drop in routine metabolic rate, since those variables

showed the greatest values at intermediate salinity. The explanation could be in the quantity of food ingested by *E. maclovinus*. Meal size at 12 psu was 41.2 and 135.9 % greater than the meal sizes observed at 30 and 1 psu, respectively. This is in accordance with the findings of Vargas-Chacoff et al. (2015) that acclimation of *E. maclovinus* to near-isosmotic conditions enhanced growth and confirms partially the low ingestion rate proposed by those authors, related with a lower acid digestive proteolytic activity at low salinity. This feeding behavior was observed previously for other fishes. Boeuf and Payan (2001) conclude that there are many indications suggesting that better growth in brackish water would depend on controlled food intake, because many species adapt their food ingestion to the external water salinity. A possible advantage of an increased ingestion could be hypothesized. Brodeur et al. (2003) have described for *Harpagifer bispinis* (Forster, 1801), another sub-Antarctic notothenioid, a direct stimulation of myogenic cell proliferation by feeding and a close relationship between time-courses of the SDA and the activation and proliferation of the myogenic progenitor cells. Given that the axial muscle represents approximately 65 % of the total muscle mass (Weatherley et al. 1979), increased proliferation of myogenic progenitor cells would influence on somatic growth of individuals. According to Brodeur et al. (2003), this cell proliferation may contribute to increasing the energetic expenditures that constitute the SDA. The greatest aerobic scope found here at intermediate salinity indicates an increased capacity to support an elevated metabolic rate by juvenile *E. maclovinus* within this condition.

Lapataia Bay showed a clear prevalence of marine characteristics, with a pattern of temperature and salinity similar to the one observed at the open Beagle Channel (Vanella et al. 2007). Data from captures in rivers and streams of the Tierra del Fuego National Park show that the distribution range of juvenile *E. maclovinus* is restricted to the mixing zone of marine and fresh water. Following Isla et al. (1999), the complex conformed from Lapataia Bay to Acigami Lake could be understood as an estuary. This coastal water system has a fluent but limited connection with the Beagle Channel. In the midsection of the estuary, in the vicinity of Cormoranes Bay, water has an intermediate salinity (site 3, Table 1; Isla et al. 1999). In this site the smallest and most abundant captures of *E. maclovinus* were found and their sizes, mostly about 60 mm TL, correspond to 1-year old individuals as described by Huergo et al. (1996). Many fish species select intermediate water salinities of estuaries as nurseries, where they find advantageous conditions for their development (Beck et al. 2001; da Silva Rocha et al. 2005). These conditions could be altered by environmental events that modify physical characteristics, such as

droughts (Dolbeth et al. 2008) or fresh water inputs in coastal zones (Quiñones and Montes 2001). However, an environment that stimulates food acquisition and offers enough resources could constitute a considerable advantage for a species with the metabolic capacity to allocate energy in the rise of metabolic rate caused for SDA. Further, this environment would be particularly advantageous for species which show a considerable rise in their growth rate at high temperatures (Vanella et al. 2012). These two conditions (allocation of energy by raising the metabolic rate, and increasing growth with increasing temperatures) are satisfied by *E. maclovinus*, which shows the greatest metabolic scope at intermediate salinity. Of the three sectors of an estuary defined by Fairbridge (1980), marine or lower estuary, middle estuary and upper or fluvial estuary, juveniles of *E. maclovinus* clearly select the intermediate salinity zone of Lapataia estuarine complex, characterized by a high mixture of fresh water and seawater. This idea is clearly supported by the findings of Vargas-Chacoff et al. (2014) about the time-course changes of plasma osmolality after osmotic challenge, that indicate a better capacity of *E. maclovinus* to acclimatize to lower rather than to higher environmental salinities.

## Conclusions

The strong association found between the distribution of juvenile *E. maclovinus* and the mixing zone of the studied estuary might be related to the higher energetic scope at intermediate salinities. Present work shows that this increased scope is reached by increasing the energy intake and not through a decrease in the standard metabolic rate, which seems to be an extended mechanism across fish species.

**Acknowledgments** This research was supported by PICT 0580, PIP 0321 and Administración de Parques Nacionales (Projects 957, 1038, 032 CPA). We are very grateful to the laboratory technicians Daniel Aureliano, Sonia Rimbau, and Marcelo Gutiérrez for their help and to Isabel Ledesma for assistance with the English language.

## References

- Beck MW, Heck KL Jr, Able KW, Childers DL, Eggleston DB, Gillanders BM, Halpern B, Hays CG, Hoshino K, Minello TJ (2001) The identification, conservation, and management of estuarine and marine nurseries for fish and invertebrates: a better understanding of the habitats that serve as nurseries for marine species and the factors that create site-specific variability in nursery quality will improve conservation and management of these areas. *Bioscience* 51:633–641
- Boeuf G, Payan P (2001) How should salinity influence fish growth? *Comp Biochem Physiol C* 130:411–423

- Boy CC, Morriconi E, Calvo J (2007) Reproduction in puyen, *Galaxias maculatus* (Pisces: Galaxiidae), in the southernmost extreme of distribution. *J Appl Ichthyol* 23:547–554
- Brodeur JC, Calvo J, Johnston IA (2003) Proliferation of myogenic progenitor cells following feeding in the sub-antarctic notothenioid fish *Harpagifer bispinis*. *J Exp Biol* 206:163–169
- 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* 40:157–164
- Cardona L (2000) Effects of salinity on the habitat selection and growth performance of mediterranean flathead grey mullet *Mugil cephalus* (Osteichthyes, mugilidae). *Estuar Coast Shelf Sci* 50:727–737
- Cardona L (2006) Habitat selection by grey mullets (Osteichthyes: Mugilidae) in Mediterranean estuaries: the role of salinity. *Sci Mar* 70:443–455
- Ceballos SG, Lessa EP, Victorio MF, Fernández DA (2012) Phylogeography of the sub-Antarctic notothenioid fish *Eleginops maclovinus*: evidence of population expansion. *Mar Biol* 159:499–505
- Ceballos SG, Lessa EP, Licandeo R, Fernández DA (2015) Genetic relationships between Atlantic and Pacific populations of the notothenioid fish *Eleginops maclovinus*: the footprints of Quaternary glaciations in Patagonia. *Heredity*. doi:10.1038/hdy.2015.106
- Cousseau MB, Perrota RG (2000) Peces Marinos de Argentina. Instituto Nacional de Investigación y Desarrollo Pesquero, Mar del Plata
- da Silva Rocha AJ, Gomes V, Van Ngan P, de Arruda Campos Rocha Passos MJ, Rios Furia R (2005) Metabolic demand and growth of juveniles of *Centropomus parallelus* as function of salinity. *J Exp Mar Biol Ecol* 316:157–165
- Dolbeth M, Martinho F, Viegas I, Cabral H, Pardal MA (2008) Estuarine production of resident and nursery fish species: conditioning by drought events? *Estuar Coast Shelf Sci* 78:51–60
- Fairbridge RW (1980) The estuary: its definition and geochemical role. In: Olausson E, Cato I (eds) *Chemistry and geochemistry of estuaries*. Wiley, New York, pp 1–35
- Fernández DA, Ciancio J, Ceballos SG, Riva-Rossi C, Pascual MA (2010) Chinook salmon (*Oncorhynchus tshawytscha*, Walbaum 1792) in the Beagle Channel, Tierra del Fuego: the onset of an invasion. *Biol Invasions* 12:2991–2997
- Herrera M, Araújo C, Hachero I, Ruiz-Jarabo I, Vargas-Chacoff L, Mancera JM, Conceição LEC (2012) Physiological short-term response to sudden salinity change in the Senegalese sole (*Solea senegalensis*). *Fish Physiol Biochem* 38:1741–1751
- 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 Atlántico Sur. Antártida e Islas del Atlántico Sur Government, Tierra del Fuego, Ushuaia
- Isla F, Bujalesky G, Coronato A (1999) Procesos estuarinos en el canal Beagle, Tierra del Fuego. *Rev Asoc Geol Argent* 54:307–318
- Jobling M (1994) *Fish bioenergetics*. 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
- Morgan JD, Iwama GK (1991) Effects of salinity on growth, metabolism, and ion regulation in juvenile rainbow and steelhead trout (*Oncorhynchus mykiss*) and fall chinook salmon (*Oncorhynchus tshawytscha*). *Can J Fish Aquat Sci* 48:2083–2094
- Nordlie FG (2009) Environmental influences on regulation of blood plasma/serum components in teleost fish: a review. *Rev Fish Biol Fish* 19:481–564
- 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* 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. In: Falabella V, Campagna C, Croxall J (eds) *Atlas del mar patagónico. Especies y espacios*. Wildlife Conservation Society and Birdlife International, Buenos Aires, pp 56–75
- Pritchard DW (1967) What is an estuary: physical viewpoint. *Estuaries* 83:3–5
- Quiñones RA, Montes RM (2001) Relationship between fresh water input to the coastal zone and the historical landings of the benthic/demersal fish *Eleginops maclovinus* in central-south Chile. *Fish Oceanogr* 10:311–328
- Riva Rossi CM, Pascual MA, Aedo Marchant E, Basso N, Ciancio JE, Mezga B, Fernández DA, Ernst-Elizalde B (2012) The invasion of Patagonia by Chinook salmon (*Oncorhynchus tshawytscha*): inferences from mitochondrial DNA patterns. *Genetica* 140:439–453
- Sangiao-Alvarellos S, Laiz-Carrión R, Guzmán JM, Martín del Río MP, Míguez JM, Mancera JM, Soengas JL (2003) Acclimation of *S. aurata* to various salinities alters energy metabolism of osmoregulatory and nonosmoregulatory organs. *Am J Physiol-Regul Integr Comp Physiol* 285:897–907
- Sangiao-Alvarellos S, Arjona FJ, Martín del Río MP, Míguez JM, Mancera JM, Soengas JL (2005) Time course of osmoregulatory and metabolic changes during osmotic acclimation in *Sparus auratus*. *J Exp Biol* 208:4291–4304
- Secor SM (2009) Specific dynamic action: a review of the postprandial metabolic response. *J Comp Physiol B* 179:1–56
- Vanella FA, Calvo J (2005) Influence of temperature, habitat and body mass on routine rates of Subantarctic teleosts. *Sci Mar* 69:317–323
- 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. *Polar Biol* 30:449–457
- Vanella FA, Boy CC, Fernández DA (2012) Temperature effects on growing, feeding, and swimming energetics in the Patagonian blennie *Eleginops maclovinus* (Pisces: Perciformes). *Polar Biol* 35:1861–1868
- Vargas-Chacoff L, Moneva F, Oyarzún R, Martínez D, Muñoz JLP, Bertrán C, Mancera JM (2014) Environmental salinity-modified osmoregulatory response in the sub-Antarctic notothenioid fish *Eleginops maclovinus*. *Polar Biol* 37:1235–1245
- Vargas-Chacoff L, Saavedra E, Oyarzún R, Martínez-Montaña E, Pontigo JP, Yáñez A, Ruiz-Jarabo I, Mancera JM, Ortiz E, Bertrán C (2015) Effects on the metabolism, growth, digestive capacity and osmoregulation of juvenile of Sub-Antarctic notothenioid fish *Eleginops maclovinus* acclimated at different salinities. *Fish Physiol Biochem* 41:1369–1381
- Weatherley AH, Gill HS, Rogers SC (1979) Growth dynamics of muscle fibers, dry weight, and condition in relation to somatic growth rate in yearling rainbow trout (*Salmo gairdneri*). *Can J Zool* 57:2385–2392