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Temperature influence on post-prandial metabolic rate of sub-Antarctic teleost fish

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ABSTRACT

The influence of temperature on the aerobic metabolism and the energetic cost of food intake (Specific Dynamic Action; SDA) have been investigated in four species of Sub-Antarctic teleosts. The species were the notothenioids *Paranotothenia magellanica*, *Patagonotothen sima* and *Harpagifer bispinis* and the zoarcid *Austrolycus depressiceps*. Individuals were captured in the vicinity of Ushuaia Bay. Experimental temperatures were 10, 4 and 2 °C, which correspond to summer, winter and extreme winter respectively. Individual respirometry chambers and calorimetric techniques were used. Different food items were provided: crustaceans (isopods and amphipods) and Argentinean hake muscle. Interspecific analysis was done on species fed with isopods. A rapid increase in oxygen consumption was registered after meals, indicating a typical SDA response. The Duration of the SDA was longer at low temperatures. The extra energy spent during the process itself, and when expressed as a percentage of consumed food energy, decreased with decreasing temperature. The SDA Coefficient was higher for *H. bispinis* that were fed with isopods. We suggest that decreases in temperature diminish the metabolic cost and extend SDA. Energy-saving mechanisms could be an evolutionary advantage to minimize the energetic cost of living at low sub-Antarctic temperatures. A general model of exponential decay is suggested for the duration of SDA and Temperature, based on the present study and compiled from literature data.

1. Introduction

Notothenioids evolved from a stock of Perciformes, mostly in coastal waters of the Antarctic continent during the cooling process of the Southern Ocean that started about 125 mya (Near, 2004). The colonization of sub-Antarctic waters exposed the notothenioids that evolved in cool waters to a wider range of temperatures, probably developing increased thermal tolerance (Eastman, 1993). At present, the suborder notothenioidei is the best represented group of teleosts in the Beagle Channel (Fig. 1), with about 33–34% species of Fuegian fish fauna belonging to this group (Lloris and Rucabado, 1991; López et al., 1996).

The family Zoarcidae (Order Perciformes) is another group with several species present in Beagle Channel (Moreno and Jara, 1984; Lloris and Rucabado, 1991; López et al., 1996), but there is scarce information about its biology in this region. Two species of the group inhabit the holdfast of *Macrocystis pyrifera* (L.) (Vanella et al., 2007), sharing their habitat with benthic notothenioid species. During low tide, small size zoarcidae can be found in wet refuges under flat rocks in the intertidal zone (Lloris and Rucabado, 1991). These fish are regularly exposed to a wide temperature range in winter and summer (Vanella, personal observations).

After the ingestion of food, animals of different taxonomic groups exhibit an increase in their metabolic rates. This reaction to feeding is known as Specific Dynamic Action (SDA), and is usually studied in fish using respirometric techniques (Jobling, 1993). Several metabolic processes such as digestion, absorption and storage of nutrients, synthesis of excretory products and the increased synthesis of proteins and other molecules are associated with the rise in metabolism during the SDA (Willmer et al., 2000). SDA could be affected by different conditions, such as diet composition. The source of nutrients and protein content in food can change the magnitude of SDA in fish *Etroplus suratensis* (Bloch, 1790) (Somanath et al., 2000). Particularly for ectotherms, another important variable is Temperature. It appears to be a general condition that SDA is prolonged by low temperatures (see review of McCue, 2006). The aerobic scope between standard metabolic rate and peak produced after ingestion appears to be stable, at least along the normal thermal range of a given species (Secor, 2009). Nevertheless, it is not clear if the proportion of ingested energy inverted in SDA, normally called SDA Coefficient, and the quantity of consumed energy itself are affected by temperature (Secor, 2009). The subtropical freshwater fish *Sparus aurata* (Guinea and Fernandez, 1997) and *Silurus meridionalis* (Luo and Xie, 2008) showed an SDA Coefficient directly related to temperature but Johnston and Battram (1993) did not find a significant difference in SDA Coefficient of the Antarctic *Notothenia neglecta* (Nybelin, 1951), the temperate *Myoxocephalus scorpius* (Linnaeus, 1758) and the tropical *Cirrhitichys bleekeri* (Day, 1874, under winter and summer conditions.

The comparative study of physiological responses of species that live in different environments is conditioned by their specific capability to survive in a thermal range and the phylogeny. This last point

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has been verified in the relationship between Temperature and resting oxygen consumption in teleost at order level (Clarke and Johnston, 1999). Marine fish bioenergetics has been extensively studied in species that live in tropical (temperature ≥25 °C), subtropical (temperature ≥15 °C) or polar waters (temperature ≤5 °C). Clarke and Johnston (1999) summarized 59 points for perciform fish, in a general approach to the relationship of Temperature and resting oxygen consumption. No points were located between 16 and 4 °C. In another extensive review about SDA, Secor (2009) reported that for a total of 86 works about *actinopterigii*, none was in the range between 8 and near 0 °C. Sub-Antarctic thermal range has been scarcely investigated, although most of the fish fauna that lives in those seawaters belongs to groups that are present in an extended latitudinal gradient. This offers an opportunity for comparative studies related to physiological responses in intermediate temperatures, filling the gap between both extremes of thermal and latitudinal range.

The main objective of this research was to study the influence of Temperature on the energetic cost of food assimilation of four species of sub-Antarctic teleost: *Paranotothenia magellanica, Patagonotothen sima, Harpagifer bispinis* and *Austrolycus depressiceps*. A comparative context with teleost species from different environments was also discussed.

2. Materials and methods

2.1. General techniques

Fish were captured by hand, trammel nets or traps near Ushuaia Bay, Tierra del Fuego, Argentina (54°48′S, 68°18′W) and Ensenada Bay (54°50′S; 68°28′W) (Fig. 1) and transported to the laboratory (CADIC – Centro Austral de Investigaciones Científicas) in well-aerated seawater tanks during the summer months between 1999 and 2003. In the sampling zone, water temperature ranged from 4 to 9.5 °C in winter and summer, respectively (Vanella et al., 2007).

The studied species were the Nototheniidae *P. magellanica* (Hutton, 1875) and *P. sima* (Richardson, 1845); the Harpagiferidae *H. bispinis* (Schneider, 1801) and the zoarcid *A. depressiceps* (Regan, 1913). Habitat and body sizes of the studied species, as well as the food provided in the experiments, are displayed in Table 2.

The arrangement of experiments was described previously in Vanella and Calvo (2005). Experiments were carried out with a photoperiod of 12 h dark/12 h light and a salinity of 30‰. Stop flow respirometric chambers were made of translucent plastic material to prevent visual stimulation from external sources. Two types of respirometric chambers were used, in agreement with fish size (3.17 L, ~12 times the volume of biggest *P. magellanica,* and 316 mL,

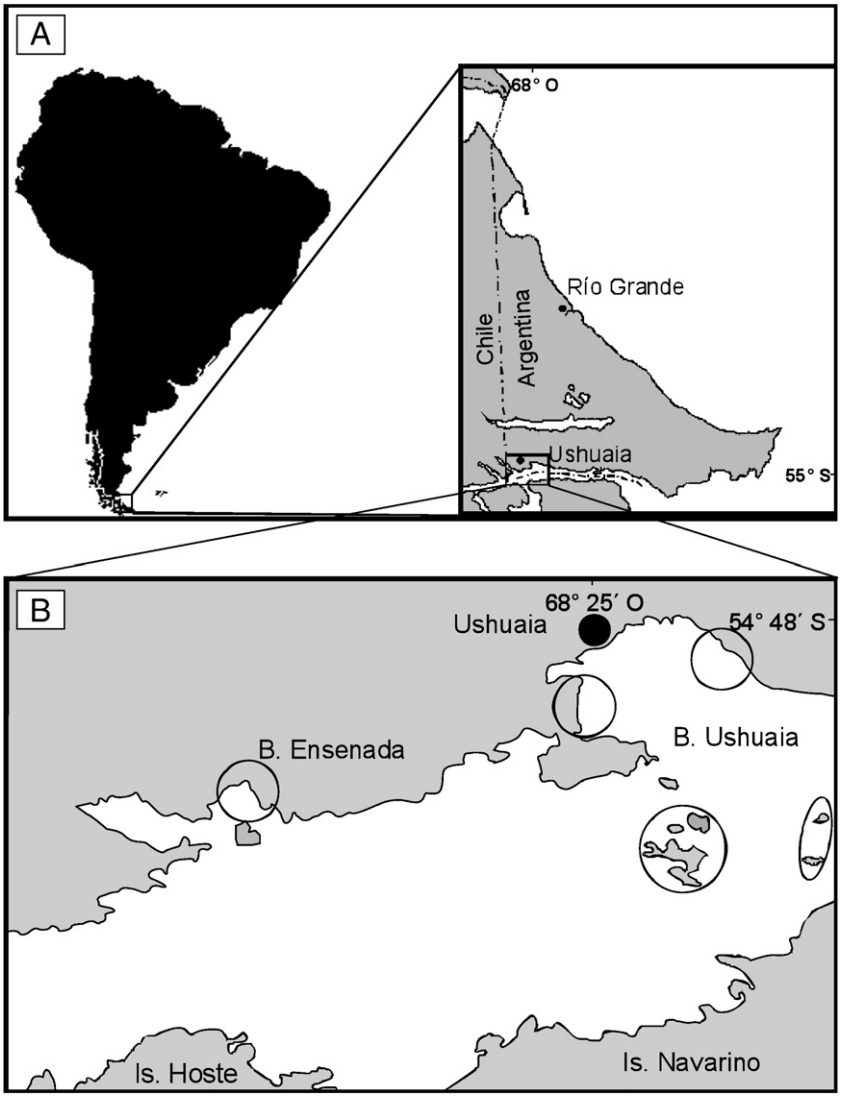

Fig. 1. Geographical reference of the sampling area: A General position of Beagle Channel in Tierra del Fuego and South America. B Sampling areas near Ushuaia City (enclosed in circles).

~30 times the volume of the biggest *A. depressiceps*). In all cases, the volume of the chambers was found large enough to allow spontaneous fish movements.

Fish were fasted for 15 days in order to obtain stable oxygen consumption values and acclimatized to 10 °C (±1) inside individual respirometric chambers, immersed in a tank of air-saturated seawater (acclimatization time following Shrode et al., 1982). In order to measure oxygen consumption, chambers were closed for 1–6 h to make sure that O_2 saturation never descended from 80% at any given temperature and fish size. Samples of 10 mL of water were taken through a rubber cup with a syringe. Oxygen concentration was measured using a Rank Brothers (model U 10) Clark-type polarographic electrode (resolution: 0.1% saturation). Oxygen consumption data were taken 1–2 times a day. Last 5 days of routine O_2 consumption were used to calculate Baseline (see "Measured variables") by mean.

After Baseline was measured at 10 °C, fish were fed to satiation inside the respirometric chambers. Frozen isopods (*Exosphaeroma* spp.) were fed to *P. sima, A. depressiceps* and *H. bispinis* (*H. bispinis* (I)). A second group of *H. bispinis* (*H. bispinis* (A)) were fed with amphipods (*Paramoera* spp.), following the same procedure. *P. magellanica* did not accept crustaceans as food and therefore they were fed on Argentinean hake muscle (*Merluccius hubbsi*; Marini, 1933). The food was weighed before its introduction into the respirometric chamber. After 12 h, remaining food was removed from the chambers and weighed again in order to quantify the ingested food (see "Experimental food items"). Oxygen consumption rate was measured until its value returned to Baseline level. After that, the temperature was lowered 1 °C per day until a temperature of 4 °C was reached. Fish were maintained fasting in this temperature for 10 days in order to determine Baseline and oxygen consumption after meals. The same procedure was followed at 2 °C. No negative effects were verified visually after experiment.

2.2. Measured variables

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

Baseline Metabolic rate of postabsorptive individuals, quantified as routine oxygen consumption (mg O_2/kg/h).
Peak Post-prandial peak in metabolism, quantified as oxygen consumption (mg O_2/kg/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 Wet 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_2: 14.06 J; Johnston and Battram, 1993) of additional oxygen consumed after a single feeding (kJ).
Meal Energy/g and SDA/g In order to compare assimilation cost in different species, Meal Energy and SDA were standardized according to Body Mass.
SDA Coeff SDA Coefficient, calculated as the percentage of ingested energy used over routine values during the SDA process.

To avoid possible differences originated by the type of food, *P. magellanica*, fed with hake, and the group of *H. bispinis* fed with amphipods were not included in the interspecific analysis of sub-Antarctic. Q_{10} was obtained for this variable using the formula $Q_{10} = (\text{SDA Coeff.}_2/\text{SDA Coeff.}_1)^{10/(t2-t1)}$ (Jobling, 1994), between 10 and 2 °C.

2.3. Experimental food items

The selection of the crustaceans as a food item was based on their presence in the intertidal and sub-tidal zone of Beagle Channel. In the case of *H. bispinis*, crustaceans have been observed in their stomach contents (Vanella, personal observations).

Measurement of offered and uneaten crustaceans weight was made in fresh, after its drain on a tissue paper. Measurement of *M. hubbsi* meal was made in fresh. The remainder was calculated after being dried at 60 °C and compared with a curve fresh–dry weight.

The biochemical proximal composition of isopods, amphipods and hake meal was determined by using standard techniques: percentage of water (by drying in an oven at 60 °C until constant weight), ash (by burning at 450 °C), protein (Lowry et al., 1951), glycogen (by anthrone method; Seifter et al., 1949) and lipids (by subtraction of the other components). The energy density was obtained by burning dry pellets in a Parr 1425 micro-calorimeter bomb. The values were corrected for ash and acid contents and were expressed as kJ/g ash-free, dry weight (AFDW) (Beukema and De Bruin, 1979). However, the values without ash correction were also obtained to know the quantity of energy ingested by fish. Hake fillet contains a higher percentage of water, proteins and energy but lower ash than both of the crustacean species. Isopods and amphipods contain a similar proportion of lipids and glycogen, but isopods contain the double proportion of ash and 10% less proteins than amphipods (Table 1).

2.4. Statistics

A repeated measures design was applied (Friedman test and Dunn's multiple comparisons) at each experimental temperature and species in order to test differences between Baseline and Peak and Temperature effect. Interspecific comparisons at equal experimental temperatures were analyzed using a Kruskal–Wallis test and Dunn's multiple comparisons. A Mann–Whitney test was used to compare groups of *H. bispinis* fed with different items, and to compare the biochemical composition of isopods and amphipods.

A bibliographic search of fish feeding bioenergetics data was carried out, focusing on the variables Scope, Duration and SDA Coeff. From the relatively large number of scientific work available, only the ones made with marine teleost and using crustaceans or fish meat as alimentary items were considered. A regression analysis was performed using the variables previously mentioned and Temperature. In order to diminish possible influence of phylogeny, a general model was performed using the complete data collection (Marine

Table 1

Alimentary items	% Water	% Ash	% Proteins	% Glycogen	% Lipids	Energy (kJ)	Energy (ash-free; kJ)
Hake	82.28 ± 1.48	5.5 ± 1.08	78.24 ± 6.16	–	9.07 ± 5.15	22.44 ± 4.89	25.11 ± 5.31
Amphipods	71.62 ± 4.54	25.07 ± 3.53	51.79 ± 5.31	0.19 ± 0.032	10.74 ± 2.66	16.96 ± 2.25	20.79 ± 3.45
Isopods	67.42 ± 1.31	54.45 ± 11.36	41.84 ± 4.57	0.18 ± 0.081	6.62 ± 3.81	10.31 ± 1.23	17.62 ± 2.85
Significance (amphipods vs. isopods)		**	*			**	

Proximal composition of alimentary items on a dry matter basis. % Water; % Ash, % Protein, % Glycogen, % Lipid and Energy. ± = standard deviation. Differences tested with Mann–Whitney test between crustaceans; significant differences ($p<0.05$) indicated by asterisk: * = significant (<0.05) and ** highly significant (<0.01).

teleost) but also another one with only notothenioids and zoarcids. In order to study possible correlations between Body Mass and Duration, Scope or SDA Coeff, a Spearman Rank analysis was made. Zar (1984) was the main statistics reference.

3. Results

3.1. Oxygen consumption

Post-prandial increase in oxygen consumption rate rapidly reached values significantly higher than those of the routine oxygen consumption (Friedman test, $P<0.05$) at all temperatures and for all species assayed, except for *A. depressiceps* fed at 2 °C. The Scope in different sub-Antarctic species varied from 1.35 to 4.22 (Table 2).

3.2. Intraspecific temperature effects

In general, the Meal Size, Meal Energy and Scope were not affected by Temperature in the studied species (Table 2). The only exception was *H. bispinis* (I). In this specie, Scope resulted significantly higher at 10 °C than at 4 °C. On the contrary, in *H. bispinis* (A), Scope was higher at 4 °C (Table 2). Duration was longer at low temperatures for *P. magellanica*, *P. sima* and *H. bispinis* (I). Although SDA was higher at higher temperatures (10 °C) than at lower temperatures (2 and 4 °C) in all species studied, significant differences were observed only in *P. sima* and *H. bispinis*.

SDA Coeff. diminishes at lower experimental temperatures. *P. magellanica* and *H. bispinis* (A) showed a reduction from 10 to 2 °C, while *A. depressiceps* showed a significant difference between 10 and 4 °C, being higher at 10 °C. However, *A. depressiceps* exhibited a very

Table 2

Species, total weight habitat and food	Te °C	*n*	Baseline mg O_2/kg/h	Peak mg O_2/kg/h	Meal Size	Scope	Duration (h)
P. magellanica	10	6	38.57 ± 8.60^{a}	73.76 ± 20.97^{ab}	6.3 ± 1.91	1.84 ± 0.33	99 ± 14^{a}
120.17 ± 39.39	4	6	12.78 ± 4.95	29.40 ± 10.47^{a}	5.69 ± 2.41	2.36 ± 0.48	148 ± 57
Habitat: pelagic	2	6	9.89 ± 2.46^{a}	26.38 ± 6.87^{b}	5.97 ± 1.45	2.86 ± 1.21	168 ± 37^{a}
Food: hake			**	**			*
P. sima	10	5	16.95 ± 2.36^{a}	41.70 ± 4.39^{a}	2.67 ± 0.61	2.48 ± 0.23	123 ± 37
31.55 ± 7.99	4	5	10.44 ± 1.46	18.79 ± 3.28	2.61 ± 0.68	1.82 ± 0.36	$48 \pm 0{,}19^{a}$
Habitat: benthopelagic	2	5	6.12 ± 0.9^{a}	14.63 ± 3.55^{a}	2.32 ± 0.58	2.37 ± 0.30	134 ± 29^{a}
Food: isopods			***	***			*
H. bispinis (I)	10	4	28.33 ± 5.13^{a}	77.02 ± 11.58^{a}	3.80 ± 0.85	2.74 ± 0.31^{a}	81 ± 3^{a}
6.32 ± 0.55	4	4	12.40 ± 2.29	35.26 ± 5.62	4.00 ± 1.08	2.01 ± 0.05^{a}	110 ± 16
Habitat: benthic	2	4	10.74 ± 2.44^{a}	24.72 ± 6.80^{a}	5.51 ± 1.26	2.28 ± 0.24	178 ± 54^{a}
Food: isopods			**	**		**	**
H. bispinis (A)	10	4	47.21 ± 4.57^{a}	83.05 ± 6.05^{a}	4.44 ± 1.95	1.77 ± 0.12^{a}	57 ± 20
5.68 ± 1.55	4	4	15.89 ± 1.22	38.10 ± 5.65	6.79 ± 1.79	2.40 ± 0.37^{a}	56 ± 40
Habitat: benthic	2	4	6.35 ± 1.08^{a}	13.83 ± 3.52^{a}	4.14 ± 1.02	1.72 ± 0.20	59 ± 13
Food: amphipods			**	**		*	
A. depressiceps	10	7	36.62 ± 19.46^{a}	60.61 ± 27.97^{a}	1.24 ± 1.15	1.71 ± 0.28	67 ± 18
4.43 ± 1.78	4	7	16.06 ± 16.20	22.80 ± 17.34	1.93 ± 0.89	2.42 ± 1.20	55 ± 31
Habitat: benthic	2	7	4.56 ± 4.30^{a}	9.89 ± 5.65^{a}	1.64 ± 0.89	3.31 ± 2.20	80 ± 45
Food: isopods			*	*			

Species	Meal energy (kJ)	Meal energy/g	SDA (kJ)	SDA/g	SDA Coeff	Q_{10} 2–10 °C SDA Coeff
P. magellanica	33.58 ± 14.77	0.283 ± 0.090	6.01 ± 2.43	0.052 ± 0.020	19.97 ± 12.09^{a}	1.97
	28.47 ± 13.41	0.268 ± 0.120	3.51 ± 1.45	0.032 ± 0.012	13.00 ± 2.18	
	33.16 ± 11.88	0.292 ± 0.123	3.65 ± 0.73	0.032 ± 0.009	11.63 ± 2.31^{a}	
					***	
P. sima	2.30 ± 1.02	0.072 ± 0.016	0.41 ± 0.20^{a}	0.014 ± 0.007^{a}	21.23 ± 12.76	2.14
	2.21 ± 0.80	0.070 ± 0.018	0.08 ± 0.04^{a}	0.002 ± 0.001^{a}	3.60 ± 1.86	
	1.86 ± 0.12	0.062 ± 0.015	0.22 ± 0.11	0.007 ± 0.003	11.57 ± 5.71	
			*	*		
H. bispinis (I)	0.64 ± 0.20	0.100 ± 0.023	0.28 ± 0.06^{a}	0.044 ± 0.005^{a}	44.70 ± 5.32	2.43
	0.67 ± 0.20	0.106 ± 0.029	0.12 ± 0.02	0.019 ± 0.004^{a}	18.95 ± 5.65	
	0.93 ± 0.27	0.147 ± 0.034	0.19 ± 0.07^{a}	0.030 ± 0.010	21.97 ± 10.53	
			**	**		
H. bispinis (A)	1.22 ± 0.54	0.284 ± 0.109	0.18 ± 0.06^{a}	0.034 ± 0.034	16.09 ± 5.23^{a}	8.78
	1.95 ± 0.93	0.338 ± 0.090	0.09 ± 0.07	0.014 ± 0.007	4.13 ± 1.41	
	1.17 ± 0.34	0.208 ± 0.052	0.03 ± 0.02^{a}	0.006 ± 0.001	2.83 ± 0.99^{a}	
			*	*	*	
A. depressiceps	0.11 ± 0.09	0.030 ± 0.030	0.04 ± 0.04	0.009 ± 0.006	64.24 ± 63.94^{a}	13.62
	0.14 ± 0.13	0.031 ± 0.025	0.01 ± 0.01	0.002 ± 0.002	6.12 ± 6.80^{a}	
	0.18 ± 0.10	0.050 ± 0.034	0.01 ± 0.01	0.002 ± 0.001	7.95 ± 8.24	
					*	

Feeding metabolism of sub-Antarctic teleosts. Species name, habitat and provided food. Te: experimental temperature. *n*: number of specimen used. Meal Size, Scope, Duration, Meal Energy, Meal Energy/g, SDA, SDA/g, SDA Coeff. and Q_{10} SDA Coeff. 2–10 °C: variables defined as in Materials and methods. Data provided with ± standard deviation. Habitat definition taken from Froese and Pauly (2009).

Statistical results of Friedman test for each variable at different temperatures. Significant differences ($p<0.05$) indicated by asterisk: * = significant (<0.05), ** highly significant (<0.01); and *** very highly significant (<0.001). Equal letters indicate significant differences between temperatures of Dunn's multiple comparisons.

dispersive response. In *P. sima* and in *H. bispinis* (I), there is a similar trend, but differences were not significant (Table 2). The Q_{10} (2–10 °C) obtained for this variable showed a wide range of values, from 1.97 (*P. magellanica*) to 13.62 (*A. depressiceps*).

3.3. Interspecific comparison in species fed with isopods (Tables 2, 3)

Meal Size of *H. bispinis* (I) was higher than in the other experimental species at all temperatures, but significantly greater only for *A. depressiceps* (the mean in the former was two-fold higher).

The Scope at 4 and 2 °C did not show differences between species. At 10 °C, *P. sima* and *H. bispinis* showed a higher Scope than *A. depressiceps*.

Duration was longer for *P. sima* than for *A. depressiceps* at 10 °C, but *H. bispinis* (I) did not show significant differences with neither of them. At 4 °C, the highest mean was exhibited by *H. bispinis* (I), differences being significant with the other species. At 2 °C the value of *H. bispinis* (I) was almost twice the value of *A. depressiceps*.

For SDA Coeff, at 10 °C no significant differences between species were observed. At 4 °C *H. bispinis* (I) showed a greater SDA Coeff. than *P. sima* but there were no significant differences with *A. depressiceps*. At 2 °C, the SDA Coeff. for *H. bispinis* (I) was significantly greater than for *A. depressiceps*, but not for *P. sima*.

For Meal Energy/g and SDA/g at all temperatures, although *H. bispinis* (I) and *P. sima* did not differ significantly, the values of the former species were higher. Compared with *A. depressiceps*, *H. bispinis* (I) displayed the greatest value in all cases.

3.4. Effect of different food items consumed by H. bispinis (Table 2)

The SDA Coeff. in *H. bispinis* (I) was three to four times significantly higher than for the same species fed with amphipods.

Meal Size at all temperatures for both food items reached similar values.

Scope resulted greater for *H. bispinis* (I) at 10 °C, but no significant differences were found at lower temperatures.

At 2 °C, *H. bispinis* (A) had a shorter Duration, but no differences were found at 10 or 4 °C.

Meal Energy became lower in specimens fed with isopods at 4 °C. However, at 10 and 2 °C a considerable difference was observed, but it was not statistically significant.

SDA of *H. bispinis* (I) at 2 °C was greater than that of *H. bispinis* (A), but at 10 and 4 °C SDA did not differ between fish fed with both food items.

Table 3

Te °C	Meal Size	Scope	Duration (h)	Meal energy/g	SDA/g	SDA Coeff
10	*	**	*	**	**	$p>0.05$
	1–2 ns	1–2 ns	1–2 ns	1–2 ns	1–2 ns	
	1–3 ns	1–3*	1–3*	1–3 ns	1–3 ns	
	2–3*	2–3*	2–3 ns	2–3*	2–3*	
4	***	$p>0.05$	*	***	**	*
	1–2 ns		1–2*	1–2 ns	1–2 ns	1–2*
	1–3 ns		1–3 ns	1–3 ns	1–3 ns	1–3 ns
	2–3*		2–3*	2–3*	2–3*	2–3 ns
2	*	$p>0.05$	*	*	***	**
	1–2 ns		1–2 ns	1–2 ns	1–2 ns	1–2 ns
	1–3 ns		1–3 ns	1–3 ns	1–3 ns	1–3 ns
	2–3*		2–3*	2–3*	2–3*	2–3*

Interspecific comparison of the feeding metabolism of three sub-Antarctic teleosts fed with isopods. References: *P. sima* = 1; *H. bispinis* (I) = 2; *A. depressiceps* = 3. Differences were tested with Kruskal–Wallis test and Dunn's multiple comparisons test; * = significant (<0.05), ** highly significant (<0.01); and *** very highly significant (<0.001).

3.5. Comparative context

The linear regression analysis performed with Scope and SDA Coeff. vs. Temperature of data summarized in Table 2, 4 showed no relationship. For Duration, the best fit was performed for an exponential decay regression model (Fig 2).

The Spearman analysis performed between Body Mass and Scope, Duration and SDA Coeff. did not show a significantly correlation, even using the total data collection or only notothenioid and zoarcid data.

4. Discussion

4.1. Temperature and SDA process. Present work and comparative context

Meal Size, and consequently also Meal Energy, was not influenced by Temperature (Table 2). A possible explanation of the similar quantity of food ingested across the temperature range could be related to the experimental feeding protocol, given that individuals were fed punctually after a prolonged starvation period in order to obtain the Baseline. A similar lack of difference in Meal Size after a punctual feeding under winter and summer conditions in both Antarctic and North Sea species (*N. neglecta* and *M. scorpius*) was observed by Johnston and Battram (1993). However, a direct relationship between temperature and feeding rate has been reported in several studies (Jobling, 1994). In other experimental study, *Eleginops maclovinus* (Cuvier, 1830; Eleginopsidae) ingested more food at summer than at winter temperatures when fed periodically (Vanella, personal observation). The particular response to punctual and continuous feeding should be considered in future experimental design.

The usual rise in the oxygen consumption rate after meals generally reaches between 2 or 3 times, independent of the Baseline (Jobling, 1993). Scope was independent of the Temperature in almost all species tested. However, *H. bispinis* displayed significant differences between 10 and 4 °C (I and A), but the pattern was not clear. *H. bispinis* (I) showed a bigger Scope at 10 °C, while *H. bispinis* (A) showed the counter reaction (see "*H. bispinis* fed with two different items"). Johnston and Battram (1993) concluded that the metabolic rates in fish fed to satiation are ~2 to ~3 times higher than the fasting rate in sedentary species, independent of environmental temperature. In coincidence, Willmer et al. (2000) assert that the rise in the oxygen consumption caused by ingestion is independent of the body temperature of fish. A general analysis of the aerobic scope of feeding from previous and present papers in a range from polar to tropical temperatures (Fig. 2A) shows an extremely conservative response. From the analysis of general data, no variations across a Body Mass gradient were observed.

In some species (Table 2), Duration was shorter at higher temperatures. The scope between Duration at 2 °C and at 10° was 1.7 for *P. magellanica* and 2.20 for *H. bispinis* (I). For *P. sima*, significant difference was found between 4 and 2 °C. No significant differences were found in *A. depressiceps* and *H. bispinis* (A). The analysis of published literature shows a negative correlation between Temperature and the length of SDA in species living in different kinds of environments (Fig. 2B). The best fit was obtained with an exponential decay model. A similar effect of temperature was found in gut evacuation time (Vanella, unpublished data) of sub-Antarctic teleost species. Again, the analysis of general data showed no direct relationship between Body Mass and Duration.

SDA Coeff. decreased at lower temperatures. Only in the case of *P. sima* and *H. bispinis* (I) the difference was not significant, but the tendency was observed. This drop in the relationship of Meal Energy and SDA could be associated with a reduction of metabolism at the lower experimental temperatures registered for sub-Antarctic fish (Vanella and Calvo, 2005). Although *S. aurata* (Linnaeus, 1758) is a

Table 4

Species (alphabetical order)	Body mass (g)	Temperature (°C)	Meal type	Meal Size %	Scope	Duration h	SDA Coeff. (%)	References
Cirrhitichthys bleekeri	21.1	25	Shrimp	5.3	1.97	39	14.9	Johnston and Battram (1993)
Gadus morhua	147	10	Fish	5.0	2.25	95	9.7	Jordan and Steffensen (2007)
Harpagifer antarcticus•	1.43	0.25	Krill	2.44	2.53	243	56.4	Boice and Clarke (1997)
Harpagifer antarcticus•	3.48	0.25	Krill	3.04	2.48	324	56.2	Boice and Clarke (1997)
Harpagifer antarcticus•	1.91	0.25	Krill	12.62	2.11	264	8.9	Boice and Clarke (1997)
Harpagifer antarcticus•	4.33	0.25	Krill	14.61	2.38	390	10.1	Boice and Clarke (1997)
Harpagifer bispinis•	3.0	10	Amphipod	15.0	3.6	118		Brodeur *et al* (2003)
Myoxocephalus scorpius	95.4	5	Shrimp	12.9	3.48	190	17	Johnston and Battram (1993)
Myoxocephalus scorpius	44.2	15	Shrimp	15.5	2.6	152	17	Johnston and Battram (1993)
Myoxocephalus scorpius	74.5	15	Shrimp	12.7	2.86	162	16	Johnston and Battram (1993)
Notothenia neglecta•	34.3	−1	Shrimp	6.8	2.03	168	17	Johnston and Battram (1993)
Notothenia neglecta•	39.1	0	Shrimp	8.4	2.08	199	23.3	Johnston and Battram (1993)
Notothenia neglecta•	62.4	−1	Shrimp	7.6	2.12	191	17.2	Johnston and Battram (1993)
Notothenia neglecta•	95.3	0	Shrimp	8.7	2.34	211	20	Johnston and Battram (1993)
Thunnus maccoyii	10000	19.3	Fish	5.5	2.2	31	35	Fitzgibbon *et al* (2007)

SDA information from published literature. Body Mass (g) and Temperature (°C). Meal Type, Meal Size, Scope, Duration (h) and SDA Coeff. as defined in Materials and methods section. •Notothenioid.

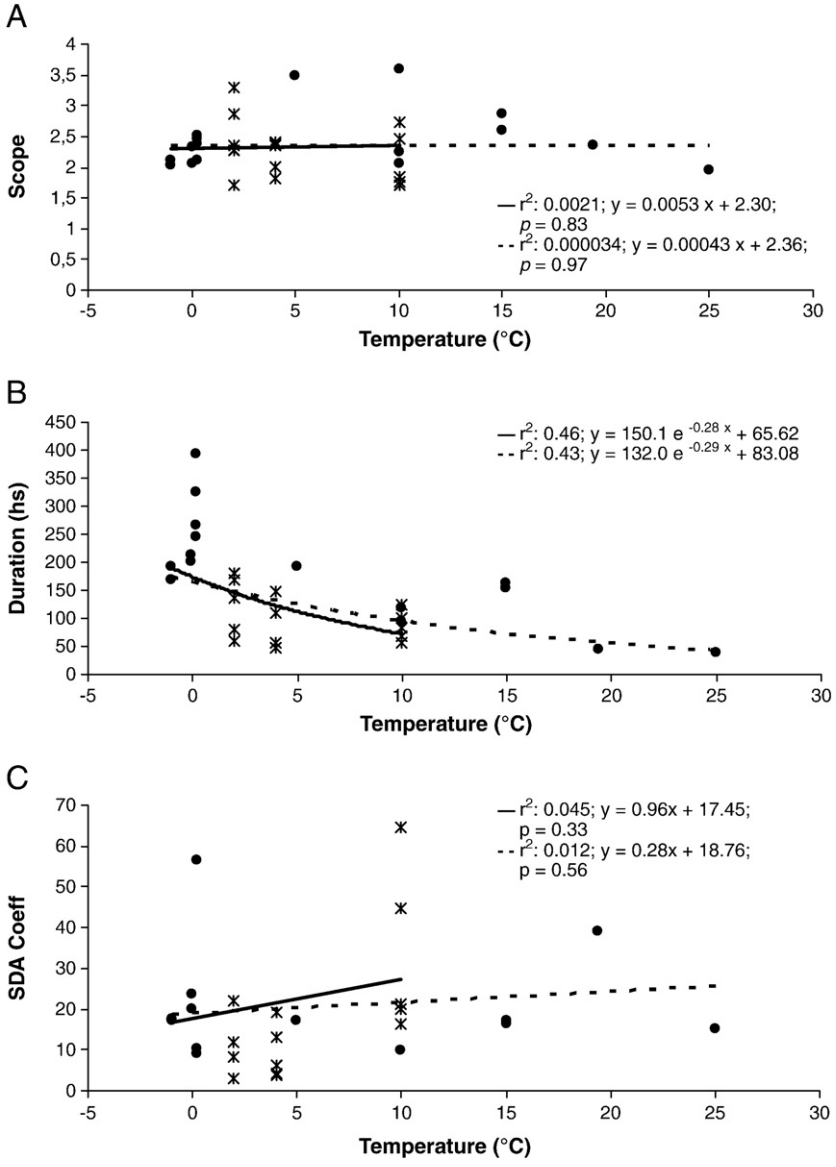

Fig. 2. Curves fitted from data of Tables 1 and 4. — All selected teleost species; — only notothenioid and zoarcid species. A Scope vs. Te. B Duration vs. Te. C SDA Coeff. vs. Te.

freshwater fish, thus not included in Table 4 and Fig. 2, a similar drop in SDA Coeff. was observed by Guinea and Fernandez (1997). The SDA Coeff. decrease could be a way to improve the efficiency of transforming ingested energy into live tissue at low temperatures when the food acquisition capacity is limited. However, a plot of SDA Coeff. for present and previous research shows little variation in the allocation of energy in digestion and absorption among temperatures (Fig. 2C). A similar lack of response to temperature was observed by Johnston and Battram (1993) for demersal sedentary species from Antarctic, North Sea and Indian Ocean. Likewise, no dependency on Body Mass was observed. Nevertheless, general comparisons of SDA Coeff. between different species are limited in their applicability, as stressed for McCue (2006), and more intraspecific research should be conducted.

As regards sub-Antarctic species, a relationship could be established between several variables: Baseline and Q_{10} at 10 and 2 °C (Vanella and Calvo, 2005), habitat (Moreno and Jara, 1984; Vanella et al., 2007) and the buoyancy of these species (Fernández, pers. com.). *P. magellanica*, the most mobile species, exhibits a high Baseline and buoyancy, but a low Q_{10} for routine metabolism and for SDA Coeff. On the contrary, the benthic *H. bispinis* and *A. depressiceps* show a low Baseline, but a high Q_{10} for the Baseline and SDA Coeff. Apparently, species with a more sedentary lifestyle present a higher intraspecific temperature effect on both routine and post feeding metabolism. Johnston et al. (1998) found a highly inverse correlation between mitochondrial volume density in red pectoral fin adductor muscle and the habitat temperature in demersal and moderately active fish, but not in active pelagic or semi-pelagic species. It is possible that less mobile species require more compensation than active ones on their aerobic process at low temperature in order to maintain an adequate performance.

4.2. Analysis between species (fed with isopods)

Interspecific differences were evident among the three species and may indicate variations in energetic strategy. *H. bispinis* (I) consumes more food and energy than *A. depressiceps* at all temperatures, and the notothenioid expended more energy during the SDA. The SDA Coeff. was higher for *H. bispinis* at 4 °C and 2 °C in comparison with *P. sima* and *A. depressiceps* respectively. The Scope for *H. bispinis* was greater at 10 °C than in the other species. As regards this matter, a high SDA Coeff. was noted for *Harpagifer antarcticus* (Nybelin, 1947) fed with small rations. This can be explained by a high start-up cost of digestion in this specie (Boice and Clarke, 1997). This explanation could be applied to the Harpagiferidae from Beagle Channel.

Fu et al. (2009) describes a correlation between the foraging and metabolic characteristics of four species distributed along the Yangtze River. According to these authors, the effect of feeding in metabolism and swimming capacity is greater in less mobile than in more active species. These differential effects were not found in the present study. However, the SDA Coeff of *A. depressiceps*, the more sluggish species studied, shows a greater Q_{10}.

4.3. H. bispinis fed with two different items

The Meal Size of *H. bispinis* that were fed different alimentary items (isopods or amphipods) at all temperatures did not differ significantly. This indicates no preference for one type of crustacean food item. Whereas Scope was higher for *H. bispinis* (I) at 10 °C, there were no differences at 4 °C and 2 °C. (Table 2).

SDA Coeff. was higher for *H. bispinis* (I) at all temperatures. The higher metabolic cost of isopod assimilation could be a consequence of the differences in the energy density of these crustaceans (10.31 kJ/g) in relation to amphipods (16.96 kJ/g), in the ash proportion (almost double in isopods), and in protein content (~20% greater in amphipods). Meal Size was very similar at all temperatures, but Meal Energy/g was higher for *H. bispinis* (A) at 10 and 4 °C. At these temperatures, the same energy was expended for SDA. A different SDA Coeff. could be explained if the same energy was expended in digestion and absorption for both food items. This explanation is supported by Boice and Clarke's (1997) findings in *H. antarcticus*. These authors found that when the species had eaten a small ration (2.44–3.04% body mass) they showed a greater SDA Coeff. than animals that had eaten a large ration (12.62–14.61% body mass), since the absolute energy cost of assimilation was the same. For Boyce and Clarke, an important proportion of SDA is determined by fixed metabolic cost. However, other authors (Fu et al., 2005) found that SDA Coefficient did not vary with Meal Size. At very low temperatures, the Meal Energy was not significantly different between alimentary items, but the energy used in SDA was higher for the *H. bispinis* (I) group. In this case, the Duration was perhaps responsible for the elevated energy used in this process.

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