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Metabolism of gymnosomatous pteropods in waters of the western Antarctic Peninsula shelf during austral fall

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ABSTRACT: Two species of Southern Ocean gymnosomatous pteropods with dissimilar distributional ranges were collected from western Antarctic Peninsula (WAP) shelf waters in the vicinity of Anvers, Lavoisier, Adelaide and Charcot Islands from March to April 2010 and between 0 and 500 m. The sub-Antarctic gymnosome species, *Spongiobranchaea australis*, typically occupies regions north of the Polar Front, whereas the true Antarctic gymnosome species, *Clione antarctica*, inhabits colder waters and higher latitudes. Oxygen consumption rates, ammonia excretion rates, proximate body compositions and the activities of 3 metabolic enzymes — lactate dehydrogenase, malate dehydrogenase, and citrate synthase (CS) — were determined in both gymnosome species. Oxygen consumption rates of *S. australis* and *C. antarctica* were found to be similar; however, the mean ratio of oxygen consumed to ammonia excreted (O:N, 61.26 ± 18.68:1) indicated that *S. australis* was oxidizing primarily lipids while *C. antarctica* was oxidizing a mixture of proteins and lipids (26.41 ± 14.82:1). Proximate body compositions based on percent protein, percent lipid, and carbon to nitrogen ratios, suggested larger lipid storage in *C. antarctica* (~5%) than in *S. australis* (~3%). CS activities among gymnosomes were dissimilar, and comparisons of enzyme activities were made to other Antarctic organisms. Observed differences in *S. australis*' physiological indicators may be related to prolonged starvation, whereas *C. antarctica* appears ready to survive overwintering in Antarctica. Water mass advection from the Antarctic Circumpolar Current is thought to be transporting *S. australis* onto the WAP shelf, and away from its typical sub-Antarctic habitat.

KEY WORDS: Pteropod · Zooplankton · Western Antarctic Peninsula · Oxygen consumption rate · Starvation

INTRODUCTION

Pteropods are holoplanktonic gastropod molluscs divided into 2 orders, Thecosomata (shelled pteropods) and Gymnosomata (naked pteropods), which collectively are food for zooplankton (e.g. chaetognaths and heteropods), fish, whales, seals, and birds (Lebour 1932, Dunbar 1942, LeBrasseur 1966, Lalli & Gilmer 1989, Hunt et al. 2008, Karnovsky et al. 2008). In the Southern Ocean surrounding Antarctica there are only 2 gymnosome species, *Spongiobranchaea australis* (d'Orbigny 1836), common north of the Polar Front (PF), and *Clione antarctica* (Smith 1902), considered to be an exclusively Antarctic species (Hunt et al. 2008). Southern Ocean gymnosomes have therefore likely adapted physiologically to live within narrow thermal ranges called 'climate envelopes' as dictated by their habitat (Pearson & Dawson 2003, Seibel et al. 2007).

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Antarctic gymnosomes are physiologically specialized predators that have coevolved with their thecosome prey (Lalli & Gilmer 1989). For instance, *C. antarctica* exhibits a suite of cold-adapted characteristics including a single locomotory gait (Rosenthal et al. 2009) and elevated oxygen consumption rates (Seibel et al. 2007). Gymnosomes have greater abundances in colder, temperate, and polar waters (Lalli & Gilmer 1989, van der Spoel et al. 1999, Hunt et al. 2008), which are geographic regions currently experiencing rapid climate change (e.g. Meredith & King 2005). Describing the physiology of Antarctic gymnosomes is an important first step for understanding their responses to a changing polar climate (e.g. Pörtner et al. 2007, Pörtner & Farrell 2008), and currently no studies have reported the physiological characteristics of any gymnosome pteropods along the western Antarctic Peninsula (WAP), where they may experience higher seasonal temperatures than the previously studied Ross Sea populations.

The polar marine ecosystem is usually characterized by permanently low, stable temperatures (Clarke & Peck 1991), and a tradeoff for life adapted to permanently low temperatures is a decreased tolerance of changing temperatures (Clarke 1988, Peck et al. 2004, Somero 2004, 2010, Cheng & Detrich 2007, Pörtner et al. 2007). For the Antarctic gymnosome *C. antarctica*, which lives permanently at temperatures near −1.89°C over much of its range (Seibel et al. 2007), or the sub-Antarctic *S. australis* that experiences an annual water temperature range of 0 to 4°C from sea surface to depth within the Antarctic Circumpolar Current (ACC) and near the WAP (Gordon et al. 1986), temperature has a considerable potential for influencing both their physiological conditions and therefore their distributional ranges (e.g. Roy et al. 1998, Astorga et al. 2003, Pörtner et al. 2005).

The purpose of the present study was to assess the physiological characteristics of Southern Ocean gymnosomes along the WAP. Specifically, we measured the oxygen consumption rates, ammonia excretion rates, atomic ratios of oxygen consumed to nitrogen excreted, proximate body compositions, carbon: hydrogen:nitrogen ratios, and enzymatic activities of polar gymnosomes captured from a latitudinal gradient along the WAP. Oxygen consumption rates are strongly influenced by growth, reproduction, activity level, feeding rates, and resource utilization (Pörtner et al. 2007, Seibel & Drazen 2007). Most gymnosomes swim continuously (Lalli & Gilmer 1989, Seibel et al. 2007), and, while *C. antarctica* has only one swimming gait (Rosenthal et al. 2009), visual observations during the present study suggested that *S. australis* may have two. Direct measurements of oxygen consumption rates have been made on a few species of gymnosomes (Conover & Lalli 1974, Ikeda 1985, Seibel & Dierssen 2003, Seibel et al. 2007, Maas et al. 2011a), but no physiological study, other than details of lipid composition (e.g. Phleger et al. 1999), currently exists in the literature for *S. australis* from anywhere around Antarctica.

Measurements of the activities of key enzymes in the intermediary metabolism are useful as proxies for the whole animal metabolic rate and as indicators of anaerobic and aerobic potential. Lactate dehydrogenase (LDH), malate dehydrogenase (MDH), and citrate synthase (CS), because of their essential roles in producing ATP (Childress & Somero 1979, Seibel & Drazen 2007), are especially useful indicators. Maximal activities of the key enzymes LDH, MDH, and CS have traditionally been used as proxies for metabolic rate (Shapiro & Bobkova 1975, Torres & Somero 1988, Seibel et al. 2000, González et al. 2008), but until now have only been measured in wing muscle of *C. antarctica* (Dymowska et al. 2012).

As *S. australis* and *C. antarctica* are reported to have dissimilar distributional ranges around Antarctica (Hunt et al. 2008), and because of the seasonal transition occurring during the time of the present study, we also explored the physiological characteristics of both gymnosomes in relation to the latitudinal gradient of this study's sampling sites along the WAP. In this exploration we postulated that there would be significant differences in gymnosome physiology given their dissimilar distributional ranges around Antarctica.

MATERIALS AND METHODS

Gymnosome and hydrographic data collection

Gymnosomes were collected in MOCNESS (multiple opening and closing nets and environmental sampling system) trawls from March to May 2010 along a latitudinal gradient in WAP shelf waters from the research vessel ice breaker (R.V.I.B.) 'Nathaniel B. Palmer'. The cruise track ranged from Charcot Island in the south to Anvers Island in the north (Fig. 1, Sites 1 to 4). A 10 m^2 MOCNESS fitted with 3 mm mesh nets and capable of collecting vertically stratified samples was used for sample collection (MOC-10; Wiebe et al. 1976, 1985, Donnelly & Torres 2008, Parker et al. 2011). Vertically stratified sampling was performed within 5 discrete depth layers between 0 and 500 m. The initial, or drogue net,

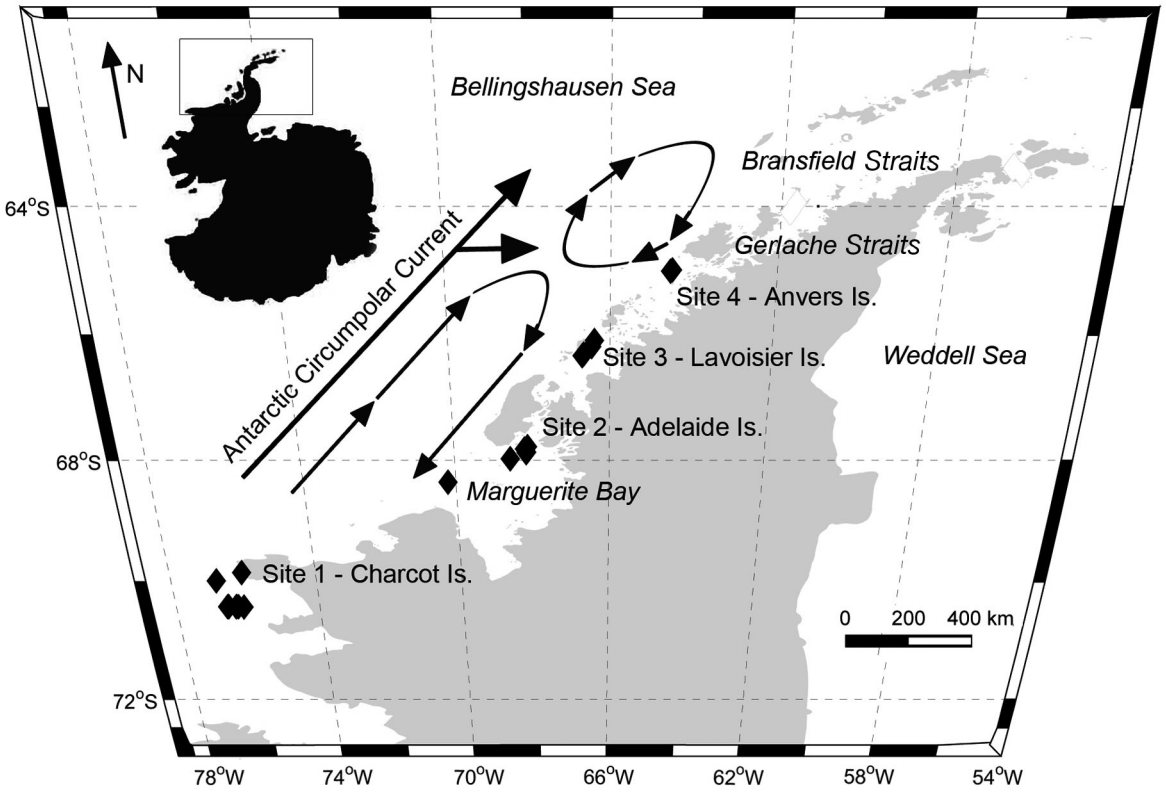

Fig. 1. Western Antarctic Peninsula (WAP) with inset map denoting sampling area from which gymnosomes were sampled for physiological determinations. Black diamonds at Sites 1 to 4 represent locations of the 10 m^2 multiple opening and closing net and environmental sampling system (MOC-10) trawls. Circulation of the Antarctic Circumpolar Current and sub-gyres in the Bellingshausen Sea at 400 to 200 m along the WAP are adapted from Smith et al. (1999) and denoted by arrows

trawled obliquely to 500 m, with subsequent nets sampling 500–300, 300–200, 200–100, 100–50, and 50–0 m (Nets 1–5, respectively). Towing speeds ranged from 1.5 to 2.5 knots. Upon retrieval, contents of each MOC-10 net were emptied into 19 l buckets, and the gymnosomes present in each bucket were removed, enumerated, and identified to species level. Thirty-six trawls were made: Site 1 (11), Site 2 (11), Site 3 (6), and Site 4 (8). Captured gymnosomes observed to be in good condition were pooled from all depths and placed in jars containing filtered seawater (0.45 µm), then acclimated to 0.5°C. Details of the WAP water column among sites are detailed in Suprenand et al. (2013).

The main goals of the field work required nearly exclusive use of the MOC-10 at each site. However, at each of the 4 sites at least one 1 m^2 MOCNESS (MOC-1) trawl was taken using nine 333 µm mesh nets, primarily for archival purposes. MOC-1 trawls confirmed that adult gymnosomes were present only at Sites 1 to 4, and the gymnosomes collected for physiological tests were a composite from discrete depth layers. Additionally, no thecosome species were captured along the WAP during this study's sampling period by either MOC-10 or MOC-1 trawls.

Respirometry (oxygen consumption rates) and ammonia excretion measurements

Each gymnosome specimen was placed in an individual 5 ml styrene syringe containing filtered (0.45 µm pore size) seawater treated with streptomycin and neomycin (each 25 mg l^{-1}). Clark polarographic oxygen electrodes (Clark 1956) formed an airtight seal at the end of the syringes, opposite the plunger, and care was taken to ensure no air bubbles were in the syringe (Ikeda et al. 2000, Kawall et al. 2001). Each electrode was calibrated using air- and nitrogen-saturated seawater at experimental temperature (Childress 1971). The syringe and electrode were kept submerged in a circulating water bath to maintain a temperature of 0.5°C, and kept in the dark. Respirometry runs were conducted continuously, through the day and night. To control for possible consumption by microorganisms, a syringe con-

taining only filtered seawater treated with antibiotics was measured for oxygen consumption. Microbial oxygen consumption was negligible.

Oxygen partial pressures (PO_2) were continuously recorded using a computer-controlled digital data-logging system (Donnelly et al. 2004). Each oxygen probe was scanned once per minute, its signal was averaged over a period of 1 s and then recorded. Data were reduced by first averaging the 30 recorded values in each 30 min increment of an entire 12 h run, producing twenty-four 30 min points per run. Data obtained during the first hour were discarded due to the activity of experimental gymnosomes immediately after being introduced into the syringe. All 30 min points were averaged to produce a mean rate for each gymnosome. Respirometry runs were concluded when oxygen had been approximately 80% depleted.

After each run water samples were taken from each syringe for ammonium concentration analyses (ultimately yielding ammonia excretion rates), and gymnosomes were frozen at −80°C for enzyme assays to be conducted at the University of South Florida (USF), College of Marine Science — Physiology Laboratory. Samples for ammonium concentration were analyzed by the USF-College of Marine Science nutrient chemistry laboratory using a Technicon autoanalyzer following the methods of Gordon et al. (2000), with minor modifications to extend the dynamic range to 30 µM for anoxic and other high ammonium waters by decreasing the flow rates for the nitroprusside, hypochlorite, phenolate, citrate, sample, air bubble, and waste draw to 50, 50, 50, 320, 600, 160, and 1200 µl min^{-1}, respectively. The ammonia concentration in each aliquot was used to calculate an ammonia excretion rate that was used along with the respiration data to calculate O:N molar ratios. Mass-specific oxygen consumption rate (µmol O_2 g^{-1} wet mass h^{-1}) and mean mass-specific ammonia excretion rate (MNH_4, NH_4 g^{-1} wet mass h^{-1}) were used to calculate the atomic ratio of oxygen consumed to nitrogen excreted (O:N) for each species.

Wet, dry, and ash-free dry mass measurements

Wet mass was initially obtained for each whole gymnosome. After a gymnosome was homogenized in deionized water with a glass tissue grinder, a 50 µl aliquot of homogenate was dispensed into pre-combusted, pre-weighed crucibles and dried to a constant mass in a 60°C oven. Water level (% wet mass) per gymnosome was calculated from the homogenate dry mass (DM) allowing for the volume added during homogenization (Donnelly et al. 1990). Ash content (% DM) per gymnosome was calculated following combustion of the dry mass in crucibles at 500°C for 3 to 4 h.

Protein analyses

Protein concentration per gymnosome was determined from a 50 µl aliquot of the homogenate. If not analyzed immediately, then each homogenate sample was air-evacuated using nitrogen, and placed in a −40°C freezer until protein analyses were conducted. Protein composition was measured per homogenate (gymnosome) using a bicinchoninic acid (BCA) kit made by Thermo Scientific and adding the hydrolysis of proteins with NaOH from the method established in Lowry et al. (1951). Absorbance was measured at 750 nm using a CARY 1E UV/Visible spectrophotometer with data analysis software. Values were then compared to a standard curve created from BCA standards also subjected to acid hydrolysis with NaOH to obtain protein concentrations within homogenates.

Lipid analyses

Lipid concentration was determined from a 200 µl aliquot from the homogenate using the methods of Torres et al. (1994). Briefly, lipids were extracted using a methanol:chloroform:water extraction (2:1:0.8 by volume), and filtered to remove particulates. Samples were extracted overnight, and the phases were separated the following day by the addition of chloroform and water to reach the final solvent ratio (1:1:0.9 by volume). Concentrations were determined using the charring method of Marsh & Weinstein (1966) with stearic acid as a standard (Bligh & Dyer 1959, Marsh & Weinstein 1966, Reisenbichler & Bailey 1991). Sample absorbance was measured at 375 nm using a CARY 1E UV/Visible spectrophotometer with data analysis software. Values were then compared to a standard curve created from stearic acid standards to obtain values for lipid concentrations within homogenates.

CHN analyses

Carbon:hydrogen:nitrogen (CHN) analyses for percent mass were done by the Marine Science Institute at the University of California at Santa Barbara.

Dried gymnosomes were analyzed individually using an Automated Organic Elemental Analyzer (Dumas combustion method) to yield simultaneous determinations of carbon, hydrogen, and nitrogen.

Enzyme analyses

Gymnosomes were thawed and homogenized individually by hand in 50 mM imadazole/HCl buffer (pH 7.2 at 20°C) using a ground-glass homogenizer. Homogenates were centrifuged at 4500 rpm (2500 × *g*) for 10 min at 10°C. Samples were then placed on ice, and the supernatant was used within 3 h to measure enzyme activities. Supernatant solution was drawn from beneath the lipid layers present on top of the samples. Substrate and cofactor concentrations yielding maximum reaction velocities were used in all assays. Activities were measured at 10 ± 0.2°C using a thermostatted CARY 1E UV/Visible spectrophotometer with data analysis software. The temperature, 10°C, has been used successfully to determine enzymatic activities in Antarctic organisms (e.g. Torres & Somero 1988, Fields & Somero 1998). The structural stability of enzymes allows them to remain effective at the physiological concentrations of substrates, even at temperatures exceeding those normally encountered by whole organisms (Hochachka & Somero 2002). Enzyme activity was expressed in units (µmol substrate converted to product min^{-1}) per gram wet tissue. All enzyme assays were done with replicates and followed the procedure of Torres & Somero (1988), with slight modifications. The modifications were as follows: The activity of LDH was measured by adding 20 µl of the supernatant to 1.0 ml of assay mixture consisting of 80 mM imadazole buffer, 5.0 mM sodium pyruvate, and 0.15 mM of NADH. The reaction was followed by recording the decrease in absorbance at 340 nm resulting from oxidation of NADH. The slope of the initial portion of the tracing was used as the reaction rate.

The activity of MDH was measured by adding 20 µl of the supernatant to 1.0 ml of assay mixture containing 40 mM Lesley's special buffer (0.2 M imadazole, 0.2 M $MgCl_2$), 0.4 mM oxaloacetate, and 0.15 mM NADH. The reaction was followed by recording the decrease in absorbance at 340 nm resulting from oxidation of NADH. The slope of the initial portion of the tracing was used as the reaction rate.

The activity of CS was measured in an assay mixture containing 30 µl of the supernatant, 50 mM imadazole, 0.4 mM 5,5-dithio-bis(2-nitrobezoic acid) (DTNB), and 0.1 mM acetyl-coenzyme-A. The reaction was followed by recording the increase in absorbance at 412 nm due to the reaction of the reduced coenzyme-A liberated from the enzymatic reaction with DTNB. The rate of absorbance increase was first recorded in the absence of oxaloacetate and then after addition of oxaloacetate to compute the true CS activity. The blank (no oxaloacetate) was subtracted from the total activity to compute true CS activity.

Statistical analyses

Statistical analyses were performed using the FATHOM toolbox (Jones 2012) in MATLAB (MathWorks Inc. 2010). Analysis of covariance (ANCOVA) was used to test for relationships between biological data such as oxygen consumption, proximate composition, and enzyme activities with regards to wet mass. A distribution-free, permutation-based variant of MANOVA (NP-MANOVA; Anderson 2001) was also used to test for significant relationships between the explanatory variables such as site, temperature, salinity, and species with the physiological indicators oxygen consumption rate, MNH_4, protein content, lipid content, water content, wet mass, dry mass, ash-free dry mass, and enzyme activity. NP-MANOVA was utilized because it removes the reliance on the assumptions of any single distributional model (Anderson 2001, McArdle & Anderson 2001). To select for the most significantly relevant predictor or independent variable(s) explaining the variability in the physiological indicator(s) as indicated by NP-MP-MANOVA, hypothesis testing was done with stepwise forward selection of the explanatory variables in redundancy analysis (RDA) based on Akaike's information criterion (AIC). In RDA physiological indicators were transformed in some cases using square-root or fourth-root transformations to find the most parsimonious subset of explanatory variable(s) to explain physiological indicators. For assessing whether the means of the physiological indicators between species were significant from one another, a Student's *t*-test was used. Statistical significance for each method was set at $p < 0.05$ and evaluated with distribution-free randomization tests (n = 1000 iterations).

RESULTS

Gymnosomes and hydrographic data

As discussed in Suprenand et al. (2013), gymnosome distributions along the WAP during the present

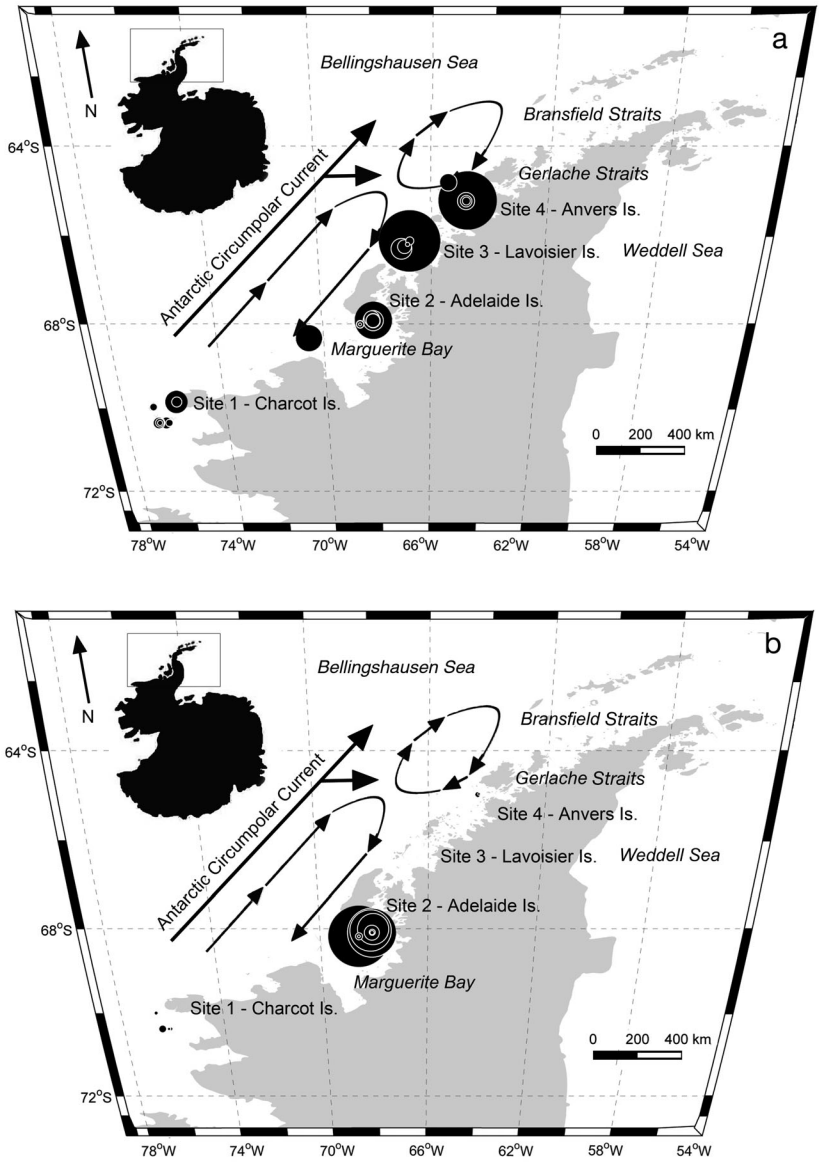

Fig. 2. Distribution bubble plots of (a) *Spongiobranchaea australis* and (b) *Clione antarctica* across study sampling area, including western Antarctic Peninsula water mass circulation. Bubbles were produced using numbers of gymnosomes captured (10^4 m^3) per volume of seawater filtered (m^3; see Suprenand et al. 2013) in 10 m^2 multiple opening and closing net and environmental sampling system (MOC-10) trawling events (n = 44) with respect to latitude and longitude. Bubbles are proportional to the range of densities of gymnosomes captured along the western Antarctic Peninsula; larger bubbles indicate greater densities. *S. australis* was captured more frequently per trawl at sites closer to the Antarctic Circumpolar Current (Sites 3 and 4), whereas *C. antarctica* was primarily caught in Marguerite Bay (Site 2)

study were influenced primarily by Southern Ocean water masses (e.g. Upper Circumpolar Deep Water [UCDW]), seawater temperatures, sampling sites, trawl net depths, and trawling latitudes. The highest densities of *Spongiobranchaea australis* were associated with lower latitudes nearest the ACC and warmer water temperatures influenced by advection of UCDW from the ACC, whereas the highest vertical densities of *Clione antarctica* were associated with less saline, colder waters at Site 2 and further from the ACC (Fig. 2a,b). It is evident that gymnosome distributions are influenced by environmental conditions (e.g. Loeb & Santora 2013).

Physiological indicators in gymnosomes

According to the power equation, $Y = aM^b$, where Y is the oxygen consumption rate, a is a normalization constant independent of mass, b is a scaling coefficient that describes the slope of the relationship, and M is wet mass (Table 1), oxygen consumption rates varied from 3.95 ± 1.89 µmol O_2 g^{-1} wet mass h^{-1} in *S. australis* ($Y = 2.30M^{-0.20}$) and 2.86 ± 1.29 µmol O_2 g^{-1} wet mass h^{-1} in *C. antarctica* ($Y = 1.86M^{-0.17}$). The mean oxygen consumption rate (MO_2) for *C. antarctica* was within the range reported in Seibel et al. (2007), and was significantly lower than that of *S. australis* (NP-MANOVA: $F = 6.09$, $p = 0.029$, N = 55 observations). However, the main difference between the gymnosomes' oxygen consumption rates was likely due to a dissimilar range of wet masses between the species. To determine if this were true, we used the scaling coefficient −0.25 (Seibel et al. 2007), as well as individually observed oxygen consumption rates and corresponding wet masses to calculate a new normalization constant for each respirometry run. With the new normalization constant we then normalized the oxygen consumption rate to a common wet mass (0.1 g) and ran a t-test. Results revealed no significant differences between the oxygen consumption rates of *S. australis* and *C. antarctica* ($t = 1.87$, $p = 0.068$).

The mean oxygen consumption rate found for *S. australis* is higher than many other gelatinous zooplankton of equivalent size (e.g. polychaetes and

Table 1. Metabolism, enzyme activities, and composition of Southern Ocean gymnosomes. Data are mean ± SD. LDH: lactate dehydrogenase; MDH: malate dehydrogenase; CS: citrate synthase; n: number of samples

	n	*Spongiobranchea australis*	n	*Clione antarctica*
Oxygen consumption rate (µmol O_2 g^{-1} wet mass h^{-1})	25	3.95 ± 1.89	27	2.86 ± 1.29
Oxygen to nitrogen ratio	11	61.26 ± 18.68	10	26.41 ± 14.82
Ammonia excretion rate (µmol NH_4 g^{-1} wet mass h^{-1})	11	0.10 ± 0.10	10	0.21 ± 0.09
LDH activity (µmol substrate converted to product min^{-1} g^{-1} wet mass)	17	1.03 ± 0.78	11	0.94 ± 0.50
MDH activity (µmol substrate converted to product min^{-1} g^{-1} wet mass)	17	9.48 ± 5.61	11	5.06 ± 1.74
CS activity (µmol substrate converted to product min^{-1} g^{-1} wet mass)	17	0.29 ± 0.13	11	0.56 ± 0.23
% Water	9	96.45 ± 0.02	8	92.07 ± 0.07
% Protein	9	2.13 ± 0.81	8	1.82 ± 0.46
% Lipid	9	3.04 ± 1.72	8	5.15 ± 2.42
Wet mass (g)	33	0.13 ± 0.09	32	0.20 ± 0.09
Dry mass (mg)	33	0.66 ± 0.34	32	0.73 ± 0.30
Ash-free dry mass (mg)	10	0.17 ± 0.08	10	0.21 ± 0.03
% Carbon	6	45.68 ± 1.84	6	54.34 ± 4.94
% Hydrogen	6	6.49 ± 0.27	6	8.00 ± 0.79
% Nitrogen	6	8.28 ± 0.72	6	6.51 ± 0.41
Carbon to nitrogen ratio	6	5.5:1	6	8.4:1

chaetognaths ranging from 0.01 to 1.0 g as reviewed in Seibel & Drazen 2007). A comparison of pteropod oxygen consumption rates from the Southern Ocean to the eastern tropical Pacific to the Atlantic Ocean revealed that *S. australis*' oxygen consumption rate is most similar to that of *C. antarctica* (Table 2). *C. antarctica*'s mean oxygen consumption rate in the present study was slightly higher than that reported in *C. antarctica* from other Antarctic regions at experimental temperatures ranging from approximately –2 to 2°C (Table 2, Fig. 3). Fig. 3 and Table 2 show oxygen consumption rate values adjusted with a Q_{10} of 2.5 to account for differences in experimental temperatures between studies and in order to estimate the gymnosome and thecosome mass-specific oxygen consumption rates (Y; µmol O_2 g^{-1} wet mass h^{-1}). *S. australis* is included in Fig. 3 for comparison as well.

Analyses with ANCOVA showed no significant covariability between explanatory variables and response variables (with the exception of MNH_4 and protein content in *S. australis* as discussed below); therefore, reported values for physiological data in Table 1 are reported per unit wet mass. The mean O:N value for *S. australis* was 61.26 ± 18.68, indicating that the primary substrates being oxidized for energy were lipids. *C. antarctica*'s mean O:N value was 26.41 ± 14.82, indicating that the primary substrates being oxidized in this species were a mixture of lipids and proteins. Ammonia excretion rates in *S. australis* decreased as its oxygen consumption rate decreased (r^2 = 0.67), whereas *C. antarctica*'s MNH_4 decreased as its oxygen consumption rate increased (r^2 = 0.51). *S. australis* demonstrated a significant covariate relationship between protein content (mg g^{-1}) and MNH_4 (ANCOVA: F = 5.31, p = 0.027, N = 9 observations).

Mean wet mass and dry masses in both species were similar. *S. australis* had a mean protein composition similar to *C. antarctica*, roughly 2% of wet mass; however, the mean lipid composition of *C. antarctica* was significantly higher than that in *S. australis* at approximately 5% of its wet mass (NP-MANOVA: F = 9.68, p = 0.003, N = 65 observations). Lipid and protein compositions in the 2 gymnosome species were consistent with the CHN results reported in Table 1; percent water was very similar in both gymnosome species, between 93 and 95% wet mass.

The mean LDH activity in *S. australis* was 1.03 ± 0.78 units g^{-1} wet mass, and 0.94 ± 0.50 units g^{-1} wet mass in *C. antarctica* (Table 1). Similar results were observed in MDH activities with values varying from a high of 9.48 ± 5.61 units g^{-1} wet mass in *S. australis*, to a low of 5.06 ± 1.74 units g^{-1} wet mass in *C. antarctica* (Table 1). However, CS activities varied from a high of 0.56 ± 0.23 units g^{-1} wet mass in *C. antarctica* to a low of 0.29 ± 0.13 units g^{-1} wet mass in *S. australis* (Table 1).

Mass relationships

Mass-specific LDH activity (y, units g^{-1} wet mass) decreased with increasing mass in the gymnosome species examined, according to the power equation $y = ax^b$ (Fig. 4a,b). In this case, b values were nega-

Table 2. Comparisons of pteropod oxygen consumption rates. Mass-specific oxygen consumption rate (Y; µmol O^2 g^{-1} wet mass h^{-1}) is calculated at the standard mass of 0.1 g. Temperature coefficient (Q_{10}) represents the factor by which the rate (R) of a reaction increases for every 10°C rise in the temperature (T), according to the equation: $Q_{10} = (R_2/R_1)^{[10/(T_2 - T_1)]}$, where R_1 is the oxygen consumption rate at temperature (°C) or T_1 reported in the studies below, and R_2 is the adjusted oxygen consumption rate at 0.5°C or T_2. This yields each study's mean oxygen consumption rate (MO_2) at T_2 (0.5°C) for comparison to the present study's MO_2. Q_{10} is assumed to be 2.5

	Location	T_1	R_1	R_2	Y	Reference
Gymnosomes						
Spongiobranchaea australis	Western Antarctic Peninsula	0.50	3.95 ± 1.89	3.95	3.65	Present study
Clione antarctica	Western Antarctic Peninsula	0.50	2.86 ± 1.29	2.86	2.75	Present study
	McMurdo Sound	−1.86	1.93 ± 0.21	2.39	0.82	Seibel & Dierssen (2003) (Years: 1998–1999)
	McMurdo Sound	−1.86	2.04 ± 0.12	2.53	0.82	Seibel & Dierssen (2003) (Years: 2000–2001)
	Ross Island, Antarctica	2.00	2.83 ± 0.18	2.47	2.55	Seibel et al. (2007)
	Ross Island, Antarctica	−2.00	1.00 ± 0.28	1.26	1.23	Maas et al. (2011a) (Year: 2002)
	Ross Island, Antarctica	−2.00	1.11 ± 0.23	1.23	No eq. published	Maas et al. (2011a) (Year: 2007)
	Ross Island, Antarctica	−2.00	1.20 ± 0.46	1.51	No eq. published	Maas et al. (2011a) (Year: 2008)
	Ross Island, Antarctica	2.00	1.62 ± 0.72	1.41	No eq. published	Maas et al. (2011a) (Year: 2008)
Clione limacina	Newfoundland	5.00	1.36 ± 0.16	0.90	1.56	Seibel et al. (2007)
	Newfoundland	10.00	1.95 ± 0.15	0.82	2.25	Seibel et al. (2007)
Thecosomes						
Hyalocylis striata	Eastern tropical Pacific	20.00	7.31 ± 3.64	1.23	1.32	Maas et al. (2011b)
Creseis virgula	Eastern tropical Pacific	20.00	7.75 ± 4.17	1.29	1.42	Maas et al. (2011b)
Clio pyramidata	Eastern tropical Pacific	20.00	9.96 ± 4.80	1.67	1.42	Maas et al. (2011b)
Cavolinia longirostris	Eastern tropical Pacific	20.00	12.29 ± 7.60	2.05	1.29	Maas et al. (2011b)
Diacria quadridentata	Eastern tropical Pacific	20.00	10.62 ± 5.63	1.78	2.28	Maas et al. (2011b)
Cavolinia tridentata	Gulf of California	18.00	10.99 ± 3.23	2.21	No eq. published	Seibel et al. (2007)
Corolla spp.	Monterey, California	5.00	0.23 ± 0.11	0.15	No eq. published	Seibel et al. (2007)
	Gulf of California	18.00	0.58	0.12	No eq. published	Seibel et al. (2007)
Limacina helicina (Antarctic species)	McMurdo Sound	−1.86	5.51 ± 0.4	6.84	No eq. published	Seibel & Dierssen (2003) (Years: 1998–1999)
	McMurdo Sound	−1.86	3.78 ± 0.20	4.69	No eq. published	Seibel & Dierssen (2003) (Years: 2000–2001)
	Ross Island, Antarctica	−2.00	5.51 ± 0.44	6.93	No eq. published	Seibel et al. (2007)
	Ross Island, Antarctica	−2.00	4.00 ± 1.13	5.03	2.41	Maas et al. (2011a) (Year: 2007)
	Ross Island, Antarctica	−2.00	3.37 ± 0.89	4.23	1.49	Maas et al. (2011a) (Year: 2008)
	Ross Island, Antarctica	2.00	4.30 ± 1.11	3.75	1.49	Maas et al. (2011a) (Year: 2008)
Limacina helicina (Arctic species)	Monterey, California	5.00	6.37 ± 0.87	4.22	No eq. published	Seibel et al. (2007)

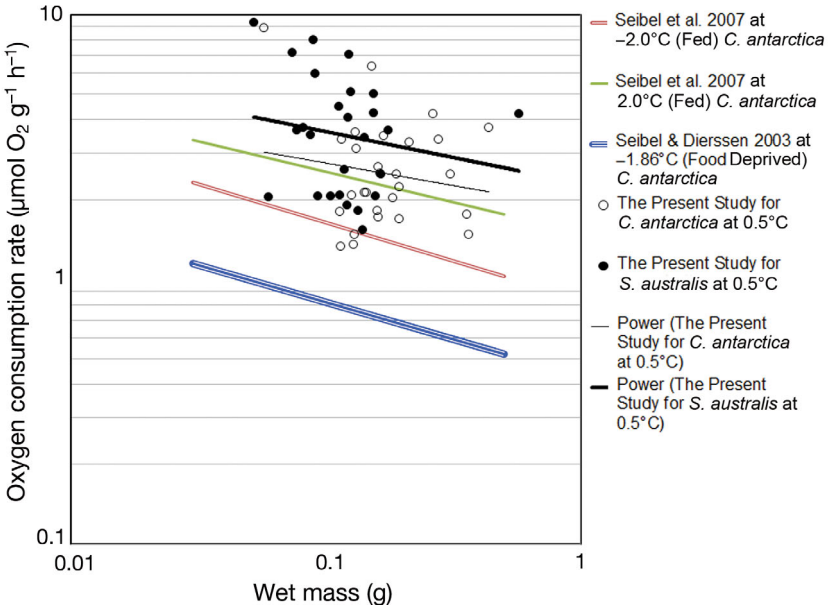

Fig. 3. Comparisons of observed and predicted mean oxygen consumption rate (MO_2) for *Clione antarctica* and *Spongiobranchaea australis*. Using the range of wet mass observed in the austral fall 2010 and the power equations from Seibel et al. (2007) and Seibel & Dierssen (2003) to predict MO_2, the present study's MO_2 values observed for *C. antarctica* indicated normal physiological conditioning. The 'power' equations displayed represent the oxygen consumption equation determined for gymnosomes in the present study. Q_{10} is assumed to be 2.5

tive and varied from −2.1 in *S. australis* to −1.3 in *C. antarctica*. Mass-specific MDH and CS activity (*y*, units g^{-1} wet mass) also decreased with increasing mass in both species. In regards to MDH activity, *b* values were negative and varied from −1.8 in *S. australis* to −1.5 in *C. antarctica*. CS activity *b* values were approximately −1.3 for both species (Fig. 4a,b).

Correlations between physiology and location

Ammonia excretion rates and O:N values observed in *S. australis* showed significant variability between sampling sites. MNH_4 in *S. australis* was found to significantly increase at higher latitudes, with the highest mean value of 0.17 µmol NH_4 g^{-1} wet mass h^{-1} at Site 2, which was significantly different from the mean value of 0.06 NH_4 g^{-1} wet mass h^{-1} at Site 3 (NP-MANOVA: $F = 5.77$, p = 0.004, N = 10 observations). When MNH_4 was expressed on a protein-specific basis (µmol NH_4 mg^{-1} protein h^{-1}), the trend remained significant (NP-MANOVA: $F = 5.31$, p = 0.027, N = 9 observations). An associated significant decrease in O:N was also observed with increasing latitude, explaining approximately 63% of the variability in O:N values in *S. australis* (RDA: $F = 15.25$, p = 0.010), as lipid oxidation was lowest at Site 2, with a mean O:N of 56 compared to a mean O:N of 122 at Site 3. The decrease in lipid oxidation with latitude suggested a small increase in protein oxidation at higher latitudes, as trends with latitude were most evident between Sites 2 and 3.

DISCUSSION

Physiological indicators in gymnosomes

The energetic demands of polar organisms drive selection for high metabolic efficiency (Seibel et al. 2007). *Spongiobranchaea australis* is found most commonly north of the PF (Hunt et al. 2008), and reported distributions around Antarctica indicate it is found axially within the ACC. Within the ACC and near the WAP, *S. australis* experiences an annual water temperature range of 0 to 4°C, from sea surface to depth (Gordon et al. 1986). The sub-Antarctic habitat of *S. australis* is a region of higher and more variable temperature than the Antarctic, causing an increase in its energetic costs (e.g. Pörtner et al. 2005, Pörtner 2008). In keeping with that observation, the mean oxygen consumption rate found for *S. australis* is higher than that for many other gelatinous zooplankton of equivalent size (e.g. polychaetes and chaetognaths), ranging from 0.01 to 1.0 g (Seibel & Drazen 2007), and is most similar to that for krill and salps (Ikeda & Mitchell 1982). Pteropod oxygen consumption rates from the Southern Ocean, the eastern tropical Pacific, and the Atlantic Ocean show that *S. australis*' rates align most closely with those of *Clione antarctica* and other polar gymnosomes and thecosomes (Table 2). Table 2 demonstrates oxygen consumption rates among species once corrected for mass, but only reports those values from published power equations describing oxygen consumption rates. Considering *S. australis*' oxygen consumption and MNH_4, the resulting O:N values are greater than those of many ctenophores, polychaetes, copepods, amphipods, euphausiids, and thaliaceans (Ikeda & Mitchell 1982).

Austral fall mean lipid content of *S. australis* is similar to that reported in the austral summer study of

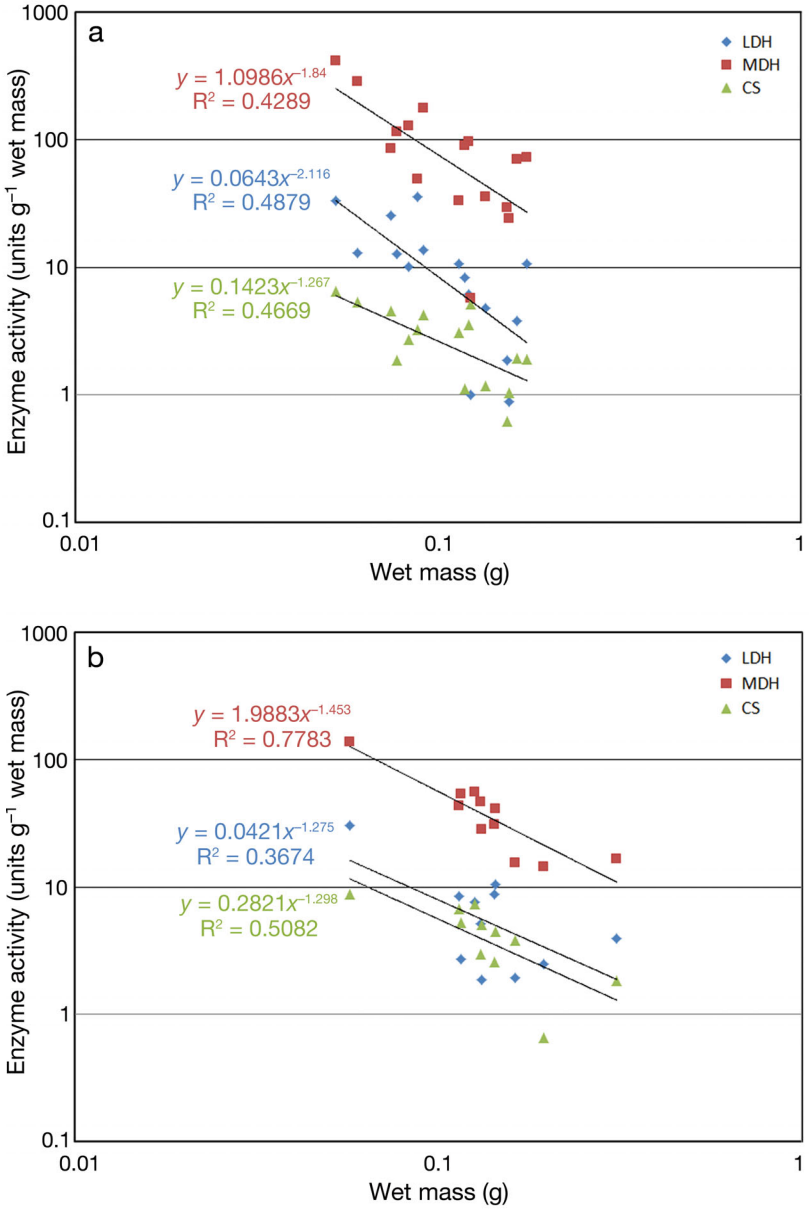

Fig. 4. Lactate dehydrogenase (LDH), malate dehydrogenase (MDH), and citrate synthase (CS) activities in (a) *Spongiobranchaea australis* and (b) *Clione antarctica* as a function of total wet mass. Number of samples per species are reported in Table 1

Phleger et al. (1999), approximately 3% of wet mass, indicating minimal lipid storage in this sub-Antarctic gymnosome, but it is similar to some bathydermersal notothenioid fishes (Friedrich & Hagen 1994). CHN analysis, providing C:N ratios used for estimating proximate body compositions (e.g. Torres et al. 1994), supports O:N ratio results indicating lipid catabolism in *S. australis*. Both gymnosomes' C:N ratios fall in the range of other pteropods' values (Curl 1962, Omori 1969, Ikeda & Mitchell 1982, Ikeda 2014), and, although ratios are higher than those for many Antarctic seals (Burns et al. 1998, Zhao et al. 2004), they generally follow the relationship between habitat and temperature noted in Ikeda (2014). The C:N ratios of *S. australis* are most similar to those of the snail *Neobuccinum eatoni*, the limpet *Nacella concinna*, the bivalve *Laternula elliptica* (Burns et al. 1998, Dunton 2001), some copepods (Ikeda et al. 2007, Ikeda 2013, 2014), and the polar/sub-polar gymnosome *Clione limacina* caught in the Barents Sea during the Arctic summer (Ikeda & Skjoldal 1989).

C. antarctica's mean oxygen consumption rate in the present study was higher than those reported from other Antarctic regions at experimental temperatures ranging from approximately –2 to 2°C (Fig. 3, Table 2). Given the local distribution of *C. antarctica* (Hunt et al. 2008), this gymnosome likely experiences annual water temperatures from sea surface to depth of about –2 to 2°C along the WAP (Gordon et al. 1986), the temperature range utilized in the respirometry studies that are compared in Table 2. *C. antarctica*'s O:N ratios were most similar to the ratios of recently fed gymnosomes from the Ross Sea (Maas et al. 2011b), and higher than those reported for this species near Wilkes Land (Antarctica; Ikeda & Mitchell 1982).

The present study's observed mean lipid content in *C. antarctica* was greater than that found in the austral summer study of Phleger et al. (2001), equal to the 5% of wet mass required for overwintering in Antarctica to survive for the production and release of eggs in the spring (Phleger et al. 1997, Seibel & Dierssen 2003, Böer et al. 2005), and similar to the content of other Southern Ocean species (e.g. Clarke 1980, Friedrich & Hagen 1994, Hagen et al. 1996, Geiger et al. 2001). CHN analysis providing C:N ratios used for estimating proximate body compositions also supported O:N ratios indicating a mixture of protein and lipid catabolism in *C. antarctica* (Table 1). The C:N ratios of *C. antarctica* are more similar to those of the Antarctic

toothfish *Dissostichus mawsoni*, the Antarctic silverfish *Pleuragramma antarcticum*, the euphausiid *Euphausia superba* (Burns et al. 1998, Dunton 2001), and its northern congener *Clione limacina* (Curl 1962).

The present study's observed oxygen consumption rate, MNH_4, CHN, and O:N ratio indicating a mixture of protein and lipid catabolism for *C. antarctica* suggested healthy specimens heading into winter with a well-developed lipid depot and a high oxygen consumption rate. This observation was supported when comparing the present study's mean oxygen consumption to the predicted oxygen consumption rate using this study's wet mass values and the power equation for fed *C. antarctica* at −2.0°C ($Y = 0.84M^{-0.29}$) and 2.0°C ($Y = 1.50M^{-0.25}$) reported in Seibel et al. (2007) and for food-deprived *C. antarctica* at −1.86°C ($Y = 0.43M^{-0.28}$) reported in Seibel & Dierssen (2003; Fig. 3). The oxygen consumption rates in Fig. 4 are based on a Q_{10} of 2.5 per Seibel et al. (2007) and a temperature of 0.5°C to adjust for differences in experimental temperatures, and we find that the range of oxygen consumption rates observed in *C. antarctica* for the present study are most closely associated with fed oxygen consumption rates for *C. antarctica* in the Ross Sea (Seibel & Dierssen 2003, Seibel et al. 2007). *S. australis* is included in Fig. 4 for comparison.

Both Southern Ocean gymnosomes exhibit a decline in mass-specific enzyme activities with increasing mass, mirroring the trends observed in other molluscs (e.g. Seibel et al. 2000, Seibel 2007) and other Southern Ocean species (e.g. Donnelly et al. 2004). Similar mass-specific CS and LDH activities were observed between *S. australis* and the pelagic, oceanic squid *Abraliopsis pacificus*, Tsuchiya & Okutani (1991), and between *C. antarctica* and the pelagic squid *Gonatus pyros*, Young (1972) and Seibel et al. (2000). Although, both are active swimmers (Borrell et al. 2005, Seibel et al. 2007), the present study's observed dissimilarities in gymnosome CS activity and swimming gaits (*C. antarctica* has only 1, whereas *S. australis* was observed to have 2) may be derived from their dissimilar distributional ranges, as demonstrated among polar gymnosomes (e.g. Dymowska et al. 2012).

Correlations between physiology and location

WAP water mass circulation is influenced by a large cyclonic gyre bounded by the ACC and the Antarctic continent (Hofmann et al. 1996, Smith et al. 1999, Vaughan et al. 2003). Within the large cyclonic gyre are 2 cyclonic sub-gyres that circulate most of the UCDW from the ACC onto the WAP shelf at depth and then southward into higher latitudes along the coast (Smith et al. 1999, Shevenell & Kennett 2002, Klinck et al. 2004, Martinson et al. 2008). The ACC water mass circulation has changed significantly over the last 40 yr, increasing warmer UCDW intrusions onto the WAP shelf and predominantly in deep water trenches near Lavoisier and Anvers Islands, Sites 3 and 4, respectively (Martinson et al. 2008, Dinniman et al. 2012, Martinson 2012, Suprenand et al. 2013). This results in a latitudinal temperature gradient with warmer waters at this study's more northern sites which then transition to colder waters at more southern sites.

Since the 1970s UCDW upwelling has increased along the WAP, and is expected to increase over the remainder of this century (Dinniman et al. 2012). Increased UCDW upwelling from the ACC is correlated with a consistent decrease in annual sea ice extent, as well as a southward ecological shift of important marine species along the WAP (Fraser et al. 1992, Trivelpiece & Fraser 1996, Rott et al. 1996, Smith et al. 1998, Moline et al. 2004, Ducklow et al. 2007, Lawson et al. 2008, McClintock et al. 2008, Moline et al. 2008, Turner et al. 2009a, Martinson 2012). The changing WAP circulation is the result of a persistent hole in the ozone layer above Antarctica and concurrent increases in greenhouse gases that have caused a 20% increase in westerly wind strength since the 1970s, thereby increasing the intrusions of UCDW onto the WAP (Shindell & Schmidt 2004, Schiermeier 2009, Turner et al. 2009b, Trathan et al. 2011, Dinniman et al. 2012). At present the WAP marine ecosystem is thought to be changing from that of a colder polar environment to one that is warmer and sub-polar (Ducklow et al. 2007, Martinson 2012).

Spongiobranchaea australis is likely being advected from the ACC with UCDW, entrained in the ACC, and, with mesoscale water mass circulation, passively transported into higher latitudes along the WAP (Figs. 1 & 2a). This passive advection may also be confirmed with *S. australis* densities, which were observed to be highest at sites most influenced by waters advected from the ACC, Sites 3 and 4, and significantly correlated to UCDW and warmer water temperatures (Suprenand et al. 2013; Fig. 2a, this study). Passive advection of *S. australis* would carry it away from food and the temperature range characteristic of its sub-Antarctic habitat. As *S. australis* is carried further from food, the observed latitudinal

increase in MNH_4 and decrease in O:N ratios, as well as summer C:N ratios and lipid compositions, collectively reveal persistent starvation, which becomes more acute at higher latitudes. If this is correct, *S. australis*' oxygen consumption rate will generally be higher than reported in the present study (e.g. Brett & Groves 1979). Using a simple calculation, it would take nearly 2 mo for *S. australis* to passively travel from Site 3 to Site 2 via the Laubouf Fjord (approximately 250 km) at the mean current velocity of the ACC (5 cm s^{-1}; e.g. Fahrbach et al. 1994) and over 5 mo to travel from Site 4 to Site 1 (approximately 700 km). Thus, given the distances from the ACC that *S. australis* was captured along the WAP, it has likely been without food for an extended period and depleted its available lipid reserves. In contrast, *C. antarctica* was mostly captured at Site 2 (Fig. 2b), and indicated little starvation in its typical Antarctic habitat.

During the austral fall, average Antarctic pteropod abundances rapidly decline (Hunt et al. 2008). This is particularly true for *Clio pyramidata* and *Limacina helicina*, the prey items of the monophagous predators *S. australis* and *C. antarctica*, respectively. Given the austral fall to winter transition, and the observed absence of thecosomes in MOC-10 and MOC-1 trawls along the WAP, both Antarctic gymnosomes are expected to be experiencing some level of starvation. However, the present study's observations indicate that *S. australis* is experiencing a greater level of starvation than *C. antarctica*. With its 5% lipid stores *C. antarctica* could survive almost 6 mo of overwintering without food in its Antarctic habitat (Seibel & Dierssen 2003), and during the austral fall may have only recently reduced its food intake, as evidenced by its oxygen consumption rates (Fig. 3) and O:N ratios (Table 1).

A reduction in organismal metabolism is observed during austral winter in many species, and the onset of starvation leads primarily to the catabolism of high-energy lipids (e.g. Brockington & Clarke 2001). In polar gymnosomes, lipid stores are often used for overwintering and/or when food becomes scarce in their natural habitat (Phleger et al. 1997, 1998, 1999, 2001, Kattner et al. 1998, Böer et al. 2005). The metabolic response for some polar gymnosomes to food deprivation or other depressive ecological influences is to reduce the oxygen consumption rate and MNH_4, thereby reducing the energy required for survival (Hand & Hardewig 1996, Maas et al. 2011b). As revealed in other organisms, if starvation continues after available lipid reserves are combusted, the cells in the body begin to break down muscle protein, and MNH_4 increases to keep ammonia concentrations below toxic levels (Castellini & Rea 1992, Caloin 2004, McCue 2010). This occurs when protein is the last remaining fuel source available in the body to combust for the ATP necessary to maintain fundamental physiological functions (McCue 2010 and references therein). According to Mommsen et al. (1980), the sockeye salmon *Oncorhynchns nerka* demonstrates a progressive change in substrate oxidation during prolonged starvation when migrating upriver, first catabolizing primarily lipids and then progressively changing to catabolism of proteins at a critical threshold.

Advection of water masses from the ACC is thought to be transporting *S. australis* onto the WAP shelf and away from its sub-Antarctic habitat. As *S. australis* moves onto the WAP shelf it survives prolonged starvation by first combusting lipids for ATP production, and then, in higher latitudes, it shifts to combustion of muscle proteins to maintain essential physiological functions. As protein is a fuel of last resort for producing ATP after available lipid stores have been necessarily depleted, *S. australis* is thought to be experiencing prolonged starvation as it is carried further from the ACC and into higher latitudes by the ACC.

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