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Metabolism of an Antarctic solitary coral, *Flabellum impensum*

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ABSTRACT

Few physiological or behavioral studies have been undertaken on the genus *Flabellum*, particularly on Antarctic species. The present study characterizes the metabolism of the endemic Antarctic coral *F. impensum*, one of the world's largest solitary corals, with measurements of oxygen consumption rate and metabolic enzyme activity. *F. impensum* had a low rate of oxygen consumption at 0 °C, ranging from 0.06 to 0.64 μmol O_2 g^{-1} h^{-1} and averaging 0.31 μmol O_2 g^{-1} h^{-1}, calculated using tissue wet mass. Ammonium excretion averaged 4.21 nmol NH_4^+ g_{wm}^{-1} h^{-1} (range: 0.54–13.99 nmol NH_4^+ g_{wm}^{-1} h^{-1}). The activity values of the metabolic enzymes citrate synthase (CS), malate dehydrogenase (MDH), and lactate dehydrogenase (LDH) fell within the normal range expected for a cnidarian, averaging 0.13 (range: 0.04–0.32), 1.01(range: 0–3.51), and 0.42 (range: 0.18–0.99) activity units (U) g_{wm}^{-1}, respectively. Skeletal density averaged 22% more than the density of pure aragonite and a count of the growth bands on the calyx suggests that this species has a linear extension rate of approximately 1 mm per year. *F. impensum* is a long-lived, slow-growing coral, with a low metabolic rate.

1. Introduction

Seventeen species of scleractinian corals occur in Antarctic waters. As is true of most high-latitude corals, all Antarctic species are azooxanthellate due to the low temperatures and seasonal swings in irradiance typical of the Antarctic system (Cairns, 1990). The genus *Flabellum* is one of two flabellid genera known to occur in the Antarctic region (Cairns, 1990). Corals within the family Flabellidae are exclusively solitary and the family exhibits a cosmopolitan distribution (Cairns, 1990).

Flabellum impensum is endemic to Antarctica and has a circumpolar distribution at depths of 46–2200 m. It is most commonly found from 100 to 1000 m (Cairns, 1982, 1990). *F. impensum* is one of the largest flabellate corals and also one of the largest solitary Scleractinia, achieving a height of up to 8 cm. It exhibits quite a variable range of morphologies (Cairns, 1990), causing smaller specimens to be mistaken for other species of *Flabellum*. Habitat information for Antarctic species of *Flabellum* is sparse, however, in the North Atlantic, corals belonging to the genus are abundant on the soft bottom of the continental slope, in abyssal areas, and on the mid-ocean ridge (Buhl-Mortensen et al., 2007; Hamel et al., 2010; Mercier et al., 2011).

Waller et al. (2008) found that *F. impensum* is gonochoric and females brood several stages of planulae year-round. Studies exist for just a handful of other species of *Flabellum* from various sites around the world. Reproductive strategies have been described for *F. curvatum* (Squires, 1962; Waller et al., 2008), *F. thouarsii* (Waller et al., 2008), *F. alabastrum* (Waller and Tyler, 2011), and *F. angulare* (Mercier et al., 2011; Waller and Tyler, 2011). Those studies revealed that Southern Ocean species of *Flabellum* (*F. curvatum* and *F. thouarsii*) are gonochoric brooders, while North Atlantic species (*F. alabastrum* and *F. angulare*) are gonochoric spawners, producing lecithotrophic larvae. Buhl-Mortensen et al. (2007) studied field/laboratory behavior and respiration in *F. alabastrum* and found that the species is slightly mobile and has a low metabolic rate. Seasonal growth rates described by Hamel et al. (2010) indicated that *F. alabastrum* is also long-lived and slow-growing. Other than what has been ascertained by those few studies, little else is known about the basic biology of corals in the genus *Flabellum*, or that of cold-water corals in general.

Many polar marine species are stenothermal and, with some exceptions, adaptation to their environment includes lower rates of growth and metabolism (Peck, 2002), compared to their non-polar relatives. The present study analyzed the rates of oxygen consumption, nitrogen excretion, and metabolic enzyme activity in order to characterize the metabolism of *F. impensum*.

2. Materials and methods

2.1. Collection

Corals were collected with a small (10 m) otter trawl by the RVIB *Nathaniel B. Palmer*. Trawls were conducted on the western Antarctic Peninsula during March of 2010 off Anvers and Charcot Islands at 600 m and 200 m depth, respectively. Corals were carefully examined after collection for signs of trauma. Individuals that showed no signs of damage were allowed to recover in pre-chilled seawater in a 0 °C incubator from 12 to 22 h before being used in any experiments. After

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the recovery period, only those that were fully extended and that reacted quickly to tactile stimulation were selected for the experiment.

2.2. Oxygen consumption experiments

The apparatus for measuring oxygen consumption consisted of an array of water-jacketed lucite chambers as described in Torres et al. (1994). The chambers' construction allowed for water (temperature-controlled by a circulating refrigerated water bath) to continuously flow between their double-layered walls, keeping the seawater and experimental animals in the inner chamber at a constant temperature (0 °C). Once sealed, no air can enter or leave the inner chamber. Oxygen microelectrodes (Clark, 1956; Mickel et al., 1983) fabricated in-house were inserted into each chamber to measure oxygen levels of the water inside every 30 s, while a magnetic stir bar under a perforated lucite false bottom kept the water well-mixed.

Individual *F. impensum* were placed into chambers appropriate for their size with 0.45 μm Millipore-filtered seawater. To determine the volume of seawater in the chamber, accounting for the animal, the volume of each coral was calculated as an elliptical cone and subtracted from the previously measured water capacity of each chamber (25 replicates). The water was treated with 25 mg L^{-1} each of Streptomycin and Neomycin to minimize bacterial growth and a control chamber was run for each experiment to ensure that any microbial consumption had a negligible effect on respiration measurements. Once the chambers were sealed, the PO_2 of the water was measured continuously for 24 h. To minimize the effects of animal transfer, no data were used until 100 min had elapsed. This was the point by which each coral's respiration rate had stabilized. Measurements were taken on a total of 9 specimens; the small sample size was due to the difficulty of obtaining intact individuals. At the end of the experimental runs, all corals appeared healthy, had their tentacles extended, and reacted to tactile stimulation. They were promptly placed into a −80 °C freezer for later analysis of metabolic enzymes.

Before and after each run, a 20 ml sample of water was taken from each chamber for analysis of ammonium excretion via an auto-analyzer.

2.3. Enzyme analyses

The frozen samples from the respiration experiments were stabilized at 4 °C (the lower limit of the cold room) and weighed using an adaptation of the buoyant weight technique described by Davies (1989). After obtaining the buoyant weight of each sample, the coral tissue was removed from the skeleton using a Waterpik® filled with artificial seawater at 4 °C. Pieces of tissue were separated from the mucus and excess water, weighed, and homogenized in a glass grinder with an imidazole buffer solution that diluted the samples 1:8. The homogenate was spun down in a centrifuge for 10 min at 4500 rpm and the supernatant was used in spectrophotometric analysis of lactate dehydrogenase (LDH), malate dehydrogenase (MDH), and citrate synthase (CS) activity levels at 0 °C using the techniques of Torres and Somero (1988).

2.4. Skeletal observations

After all the tissue had been cleaned off each calyx, they were soaked in a 10% solution of commercial bleach in seawater for 24 h to remove any remaining bits of tissue, rinsed three times in artificial seawater, and buoyantly weighed again (all at 4 °C) to obtain a value for the percentage buoyant weight of tissue versus skeleton. The skeletons were then rinsed three times with milli-Q water and allowed to soak for another 24 h to remove the salt before being put into a 60 °C drying oven until they reached a constant weight (approximately 3 weeks). The dry weight of each calyx was then measured in order to calculate skeletal density. The growth bands were also counted for each specimen. The bands in this species are obvious enough to count under a dissecting microscope with a light illuminating the calyx, without the aid of stains (Fig. 1) that are necessary for smaller, thicker-walled species (e.g. Goffredo et al., 2004; Hamel et al., 2010).

3. Results

The corals exhibited a low rate of oxygen consumption, ranging from 0.06 to 0.64 μmol O_2 g^{-1} h^{-1} and averaging 0.31 ± 0.07 μmol O_2 g^{-1} h^{-1} (±S.E.), using tissue wet mass. Total oxygen consumption increased with increasing wet mass (ANOVA $F = 6.23$ $df = 1$ $p = 0.02$). However, as is typical of most animal groups (Hemmingsen, 1960), the respiration rate per gram of tissue was lower in the larger corals (Fig. 2).

Ammonium excretion fell between 0.54 and 13.99 nmol NH_4^+ g^{-1} h^{-1} and averaged 4.21 ± 1.48 nmol NH_4^+ g^{-1} h^{-1} (±S.E.), resulting in an O:N atomic ratio (oxygen respiration to ammonium excretion) that ranged from 11 to 91 and averaged 39. This indicates that individual corals had different prey spectra, although most were catabolizing lipids to some degree (Ikeda, 1974; Mayzaud and Conover, 1988; Szmant et al., 1990). Nitrogen excretion per gram of tissue was lower than expected for the larger specimens, however, excretion did show a general trend of slowly increasing with wet mass (ANOVA $F = 5.64$ $df = 1$ $p = 0.03$) (Fig. 2).

Activity of CS and MDH fell within the range previously reported for cnidarians, averaging 0.13 ± 0.03 (range: 0.04–0.32) and 1.01 ± 0.34 (range: 0–3.51) activity units (U) g_{wm}^{-1} (±S.E.), respectively, where activity units are micromoles of substrate converted to product per minute. LDH activity was on the higher end of the range for a cnidarian, averaging 0.42 ± 0.08 U g_{wm}^{-1} (range: 0.18–0.99). Mass-specific enzyme activities did not change with increasing mass (all p-values were greater than 0.3).

Tissue weight averaged 20% of total buoyant weight and skeletal density averaged 3.58 g cc^{-1}, which is above the density of pure aragonite (2.94 g cc^{-1}), a value that is sometimes assumed in studies where the density of the coral skeleton is used in a calculation. The difference indicates that other substances are being incorporated into the skeletal matrix. Smaller corals (<5 g tissue wet mass) had skeletons whose densities averaged 3.13 g cc^{-1}, which is fairly close to the density of aragonite, while the larger corals (>25 g tissue wet mass) averaged 4.02 g cc^{-1}. Analysis of two “clean” pieces of two different skeletons with a scanning electron microscope showed that the only element heavier than calcium that was detected at a notable concentration was, as expected, strontium, which averaged about 2% by weight. The high density of the whole skeletons is likely due to the visible boring organisms and sediment incorporated into the skeleton on the “dirty” side of the calyx (Fig. 3), rather than the skeletal matrix taking up heavier elements as it grows.

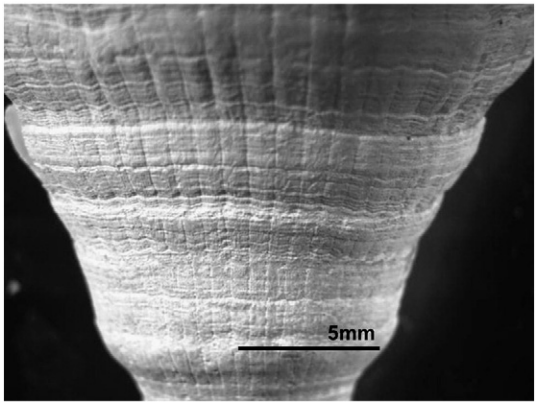

Fig. 1. A close-up of a specimen of *F. impensum*. Growth bands are clearly visible on the calyx surface.

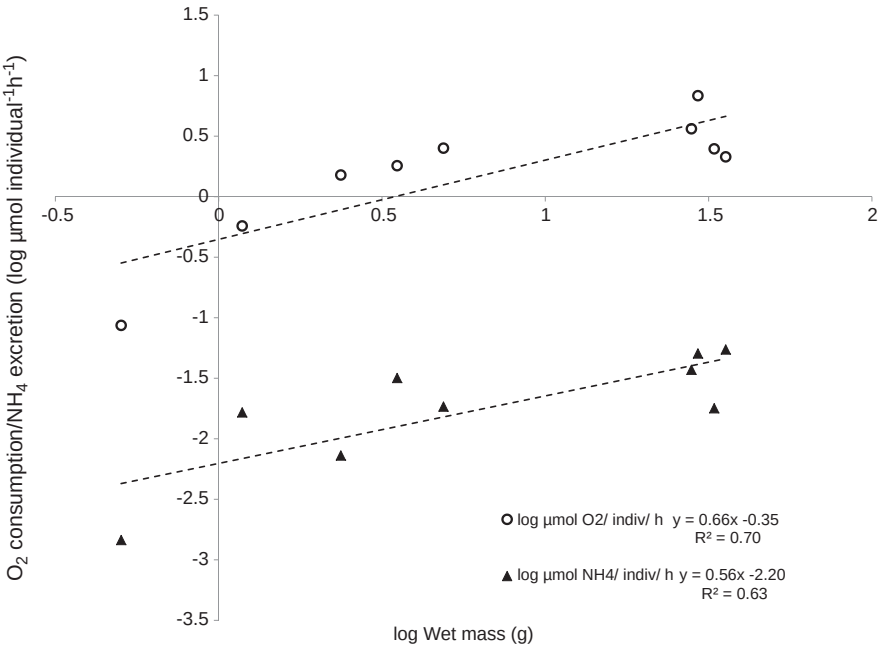

Fig. 2. *F. impensum* respiration and nitrogen excretion rates in relation to wet mass. Increasing body size results in an increased respiratory rate ($p = 0.005$), but as the corals near their maximum size, this increase slows. Nitrogen excretion is variable, but does show some increase with mass in smaller specimens ($p = 0.01$).

The growth bands nearest the bottom of the calyx were the thickest (~3–4 mm) and progressively decrease in thickness from the bottom to the top. If these bands are laid down annually, as in other solitary corals (e.g. Goffredo et al., 2004; Hamel et al., 2010), comparing the number of bands to the height of the calyx yields an average linear extension rate of 1.11 mm per year for these specimens.

4. Discussion

A fairly low rate of oxygen uptake was measured for *F. impensum* (an average of 0.31 ± 0.07 µmol O_2 g^{-1} h^{-1} tissue wet mass), placing it in the lower half of the metabolic spectrum when compared to other scleractinians for which there are such data, even with a Q_{10} correction for temperature (assuming $Q_{10} = 2$) (Table 1).

As sessile species, most corals have low activity costs and are therefore likely to have a low metabolism, particularly in polar or other cold-water environments. Most species of *Flabellum*, however, are more active than other corals; they are free-living individuals as adults and are capable of movement. Captive individuals of *F. alabastrum* have been observed leaving tracks in the sediment at a rate of 3.2 cm mo^{-1}. Moreover, the polyp can inflate to more than 10× its normal, relaxed (not retracted) size, which would give it the ability to use currents as a means of transportation (Buhl-Mortensen et al., 2007). At the end of some experimental runs, the larger coral polyps had expanded within the respiration chamber. Presumably, as the oxygen concentration in the chamber decreased, the polyps expanded in order to facilitate oxygen uptake over a greater surface area. Alternately, it may have been an attempt to "escape" the declining oxygen in the chamber. Despite the behavioral response, the PO_2 within the chambers never dipped below 35 mm Hg and respiratory rate remained constant over the course of the experiment, suggesting that the corals remained well above their P_c.

Buhl-Mortensen et al. (2007) found that *F. alabastrum* had a respiratory rate (2.2 µl O_2 g^{-1} h^{-1} tissue wet mass = 0.10 µmol O_2 g^{-1} h^{-1}) lower than that of *F. impensum*. Further, Hamel et al. (2010) reported that *F. alabastrum* was a slow growing coral, reaching its maximum height of about 43 mm at about 45 years of age. Goffredo et al. (2004)

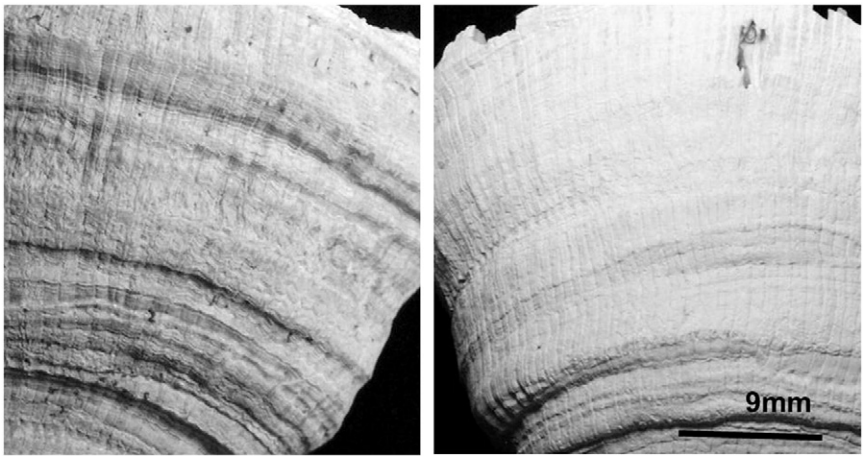

Fig. 3. The "dirty" versus "clean" side of the calyx of an *F. impensum* specimen.

Table 1
Flabellum impensum exhibited an oxygen consumption rate that was fairly low on the metabolic spectrum, as compared to several other corals (Davies, 1980; Hargrave et al., 2004; Shick, 1990), but had a rate 3 times greater than that of *F. alabastrum* (Buhl-Mortensen et al., 2007). This species does, however, have similar respiratory rates to that of other corals, medusae, and ctenophores (Ikeda and Bruce, 1986; Scolardi et al., 2006; Shick, 1990; Thuesen and Childress, 1994). Davies (1980), Shick (1990), and Scolardi et al. (2006) expressed respiration rates in relation to animal dry weight. A 95% water content was assumed in order to convert these values to μmol O_2 g_{ww}^{-1} h^{-1}. Activities of the enzymes citrate synthase (CS), lactate dehydrogenase (LDH), and malate dehydrogenase (MDH) fell within range of other cnidarians. The abbreviation "na" denotes that these parameters were not measured in the cited study and "nd" denotes that the enzyme was not detected.

Animal	Species	O_2 consumption (mean ± S.E.) (μmol O_2 g_{ww}^{-1} h^{-1})	T_{resp} (°C)	CS activity (units g^{-1} ± S.E.)	LDH activity (units g^{-1} ± S.E.)	MDH activity (units g^{-1} ± S.E.)	$T_{enzymes}$ (°C)	Source
Scleractinian	*Flabellum impensum*	0.313 ± 0.074	0	0.126 ± 0.029	0.423 ± 0.083	1.008 ± 0.344	0	This study
Scleractinian	*Flabellum alabastrum*	0.10	7.7	na	na	na	na	Buhl-Mortensen et al. (2007)
Scleractinian	*Montastrea annularis*	3.33	28	na	na	na	na	Davies (1980)
Scleractinian	*Acropora palmata*	7.41	28	na	na	na	na	Davies (1980)
Scleractinian	*Acropora cervicornis*	8.84	28	na	na	na	na	Davies (1980)
Scleractinian	*Montastrea cavernosa*	1.53	28	na	na	na	na	Davies (1980)
Scleractinian	*Agaricia lamarcki*	19.98	28	na	na	na	na	Davies (1980)
Scleractinian	*Agaricia undata*	12.34	28	na	na	na	na	Davies (1980)
Scleractinian	*Agaricia grahamae*	7.14	28	na	na	na	na	Davies (1980)
Alcyonacean	*Gersemia rubiformis*	1.0	3–5	na	na	na	na	Hargrave et al. (2004)
Alcyonacean	*Acanella arbuscula*	1.4	3–5	na	na	na	na	Hargrave et al. (2004)
Zoanthid	*Palythoa tuberculosa*	0.33	30	na	na	na	na	Shick (1990)
Zoanthid	*Protopalythoa* sp.	9.7	30	na	na	na	na	Shick (1990)
Zoanthid	*Zoanthus sociatus*	0.38	25	na	na	na	na	Shick (1990)
Anemone	*Phyllodiscus semoni*	1.9	30	na	na	na	na	Shick (1990)
Anemone	*Heteractis crispa*	0.91	30	na	na	na	na	Shick (1990)
Medusa	*Polyorchis penicillatus*	na	na	0.238 ± 0.029	0.172 ± 0.016	0.939 ± 0.019	20	Thuesen and Childress (1994)
Medusa	*Haliscera bigelowi*	0.128 ± 0.030	5	nd	0.028 ± 0.009	na	20	Thuesen and Childress (1994)
Medusa	*Halitrephes maasi*	0.046 ± 0.006	5	0.004 ± 0.001	0.017 ± 0.005	na	20	Thuesen and Childress (1994)
Medusa	*Crossota rufobrunnea*	0.154 ± 0.024	5	0.147 ± 0.013	0.011 ± 0.007	0.578 ± 0.432	20	Thuesen and Childress (1994)
Medusa	*Vallentinia adherens*	1.932 ± 0.478	15	3.563 ± 0.860	0.057 ± 0.008	na	20	Thuesen and Childress (1994)
Medusa	*Pantachogon* sp.	0.259 ± 0.017	5	0.108 ± 0.012	0.022 ± 0.004	0.915 ± 0.131	20	Thuesen and Childress (1994)
Medusa	*Aegina citrea*	0.185 ± 0.037	5	0.043 ± 0.007	0.085 ± 0.015	0.624 ± 0.084	20	Thuesen and Childress (1994)
Medusa	*Atolla wyvillei*	0.134 ± 0.044	5	nd	0.243 ± 0.055	0.768 ± 0.208	20	Thuesen and Childress (1994)
Medusa	*Paraphyllina ransoni*	0.333 ± 0.104	5	0.124 ± 0.044	0.195 ± 0.088	na	20	Thuesen and Childress (1994)
Medusa	*Periphylla periphylla*	0.094 ± 0.017	5	0.017 ± 0.003	1.711 ± 0.552	0.669 ± 0.144	20	Thuesen and Childress (1994)
Ctenophore	*Callianira antarctica*	0.35 ± 0.18	0.5	na	na	na	na	Scolardi et al. (2006)
Ctenophore	*Beroe* sp.	0.044	−1.5	na	na	na	na	Ikeda and Bruce (1986)
Ctenophore	*Mertensiidae* sp.	0.237	−1.6	na	na	na	na	Ikeda and Bruce (1986)

studied a Mediterranean solitary coral, *Balanophyllia europaea*, and determined its maximum size to be about 20 mm after as many years. The maximum size of specimens used in the present study was 62 mm, and with a metabolic rate in the same range as that of *F. alabastrum*, it is likely that it has a similar growth rate. Cairns (1990) noted a maximum size of 80 mm for *F. impensum*, meaning that the species may live to be around 80 years of age. The specimens examined in the present study appeared to have annual growth bands similar to those described by Goffredo et al. (2004) and Hamel et al. (2010), with the thickest bands occurring before the age of 5 years and gradually thinning as the coral aged, indicating greater linear extension in earlier years. This result correlates well with the oxygen consumption data, as more energy is needed for growth in the early years, accounting for the large differences in metabolic rate among the smaller samples. As the corals age, the metabolic rate still increases, as the calyx is becoming wider and the coral has a larger body to support. However, less linear extension is occurring in the calyx, so the rise in metabolic rate decreases. This may also explain why the smaller corals had skeletal densities closer to that of pure aragonite as compared to their larger counterparts.

Young corals, which grow quickly and live upright, attached to a substrate, may be exposed to fewer particles that could become incorporated into their skeletal matrix than that of older, slower-growing and mobile individuals that are in constant contact with the sediment. Buhl-Mortensen et al. (2007) noted that in addition to lateral movement across the sediment, *F. alabastrum* was also capable of rotating and righting itself if placed upside-down. Cairns (1990) postulated that *F. impensum*, after reaching a size at which it becomes dislodged from the substrate on which it settled as a planula, remains in an upright position, possibly by partially burying itself in the sediment. This was based on his observation of the placement of epibionts on the skeleton. All specimens collected for this study had a worn pedicel, which indicates that they had long been detached from their substrate. The larger *F. impensum* appeared to have been lying in a prone position, as one side of the skeleton appeared "dirtier" than the other, with more bits of debris embedded in the skeleton. This also suggests a "preferred" side upon which to rest, which would be possible if they have the same ability as *F. alabastrum* to rotate. This was less apparent in the smaller specimens, which had no noticeable epibionts or skeletal inclusions.

Oxygen consumption is not the only variable that can differ between a polar coral and its temperate and tropical relatives. The enzyme-mediated metabolic reactions of a polar marine invertebrate can be 10–30 times slower than that of its tropical counterpart (Clarke, 1998). Decreases in environmental temperature reduce the number of enzyme molecules available with enough energy to catalyze their respective reactions. Animals that compensate for such environmental differences exhibit 1) an increase in the number of enzyme molecules present 2) a different type of enzyme used to catalyze a specific reaction, or 3) a modified activity rate of the enzymes (Hochachka and Somero, 1973). With no observable compensation in oxygen uptake, it is unlikely that *F. impensum* has evolved any change in the activity of its metabolic enzymes, as metabolic enzyme activity tends to correlate with respiration.

Lactate dehydrogenase (LDH) is the terminal enzyme in anaerobic glycolysis and its activity in an organism is an indicator of the individual's anaerobic capacity. Citrate synthase (CS) regulates the first step in the Krebs cycle, and malate dehydrogenase (MDH) also plays a role in this cycle, although it has several other functions related to metabolism. The activities of the two Krebs cycle enzymes are indicators of aerobic function. Activities of CS and MDH (0.13 ± 0.03 and 1.01 ±0.34 U g^{-1}, respectively) extracted from *F. impensum* fell within

the ranges measured for medusae (Table 1), indicating that it is similarly aerobically poised. The LDH activity (0.42 ± 0.08 U g^{-1}), however, was on the higher end of the range reported for other cnidarians, indicating a moderate anaerobic potential as well.

F. impensum excreted 4.21 ± 1.48 nmol NH_4^+ g^{-1} h^{-1}. The O:N atomic ratio ranged from 11 to 91 and averaged 39, indicating that lipids are an important component in this coral's diet (Ikeda, 1974; Youngbluth et al., 1988). Many planktonic Antarctic organisms experience a drop in their metabolism during the winter and go into a state of reduced activity. In order to prepare for this, they have a means to store lipids. The lipid-rich animals form part of the coral's diet and contribute to its lipid stores. Lipids then become a significant metabolite when the corals are not feeding.

In summary, the endemic Antarctic coral, *F. impensum*, like other related solitary corals, is slow-growing and has a low metabolic rate. It is one of the largest solitary corals, displays reasonable aerobic and anaerobic capacity, has a lipid-rich diet, and is quite long-lived, possibly capable of reaching 80 years in age. Polar corals are not a well-studied group; this study adds much needed information to the body of knowledge concerning them, as well as contributing new physiological insights pertaining to the genus, *Flabellum*.

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References

Buhl-Mortensen, L., Mortensen, P.B., Armsworthy, S., Jackson, D., 2007. Field observations of *Flabellum* spp. and laboratory study of the behavior and respiration of *Flabellum alabastrum*. Bull. Mar. Sci. 81 (3), 543–552.

Cairns, S.D., 1982. Antarctic and subantarctic Scleractinia. Biol. Antarct. Seas XI Antarct. Res. Ser. 34, 1–74.

Cairns, S.D., 1990. Antarctic Scleractinia. In: Wagele, J.W., Sieg, J. (Eds.), Synopses of the Antarctic Benthos. Koeltz Scientific Books, Koenigstein, pp. 1–78.

Clark, L.C., 1956. Monitor and control of blood and tissue oxygen tensions. Trans. Am. Soc. Artif. Intern. Organs 2, 41–48.

Clarke, A., 1998. Temperature and energetic: an introduction to cold ocean physiology. In: Pörtner, H.O., Playle, R.C. (Eds.), Cold Ocean Physiology. Society for Experimental Biology Seminar Series, 66. Cambridge University Press, Cambridge, pp. 3–30.

Davies, P.S., 1980. Respiration in some Atlantic reef corals in relation to vertical distribution and growth form. Biol. Bull. 158, 187–194.

Davies, P.S., 1989. Short-term growth measurements of corals using an accurate buoyant weighing technique. Mar. Biol. 101, 389–395.

Goffredo, S., Mattioli, G., Zaccanti, F., 2004. Growth and population dynamics model of the Mediterranean solitary coral *Balanophyllia europaea* (Scleractinia, Dendrophylliidae). Coral Reefs 23 (3), 433–443.

Hamel, J.F., Sun, Z., Mercier, A., 2010. Influence of size and seasonal factors in the growth of the deep-sea coral *Flabellum alabastrum* in mesocosm. Coral Reefs 29, 521–525.

Hargrave, B.T., Kostylev, V.E., Hawkins, C.M., 2004. Benthic epifauna assemblages, biomass, and respiration in The Gully region on the Scotian Shelf, NW Atlantic Ocean. Mar. Ecol. Prog. Ser. 270, 55–70.

Hemmingsen, A.M., 1960. Energy metabolism as related to body size and respiratory surfaces, and its evolution. Rep. Steno Meml. Hosp. Nord. Insulin Lab. 9, 6–110.

Hochachka, P.W., Somero, G.N., 1973. Strategies of biochemical adaptation. W.B. Saunders, Philadelphia.

Ikeda, T., 1974. Nutritional ecology of marine zooplankton. Mem. Fac. Fish Hokkaido Univ. 22 (1), 1–97.

Ikeda, T., Bruce, B., 1986. Metabolic activity and elemental composition of krill and other zooplankton from Prydz Bay, Antarctica, during early summer (November–December). Mar. Biol. 92, 545–555.

Mayzaud, P., Conover, R.J., 1988. O:N atomic ratio as a tool to describe zooplankton metabolism. Mar. Ecol. Prog. Ser. 45, 289–302.

Mercier, A., Sun, Z., Hamel, J.-F., 2011. Reproductive periodicity, spawning, and development of the deep-sea scleractinian coral *Flabellum angulare*. Mar. Biol. 158, 371–380.

Mickel, T.J., Quentin, L.B., Childress, J.J., 1983. Construction of a polarographic oxygen sensor in the laboratory. In: Gnaiger, E., Forstner, H. (Eds.), Polarographic Oxygen Sensors. Springer-Verlag, Berlin, pp. 81–89.

Peck, L.S., 2002. Ecophysiology of Antarctic marine ectotherms: limits to life. Polar Biol. 25, 31–40.

Scolardi, K.M., Daly, K.L., Pakhomov, E.A., Torres, J.J., 2006. Feeding ecology and metabolism of the Antarctic cydippid ctenophore *Callianira antarctica*. Mar. Ecol. Prog. Ser. 317, 111–126.

Shick, J.M., 1990. Diffusion limitation and hyperoxic enhancement of oxygen consumption in zooxanthellate sea anemones, zoanthids, and corals. Biol. Bull. 179, 148–158.

Squires, D.F., 1962. Deep sea corals collected by the Lamont Geological Observatory. 3 Larvae of the Argentine coral *Flabellum curvatum* Moseley. Am. Mus. Novit. 2078, 1–11.

Szmant, A.M., Ferrer, L.M., FitzGerald, L.M., 1990. Nitrogen excretion and O:N ratios in reef corals: evidence for conservation of nitrogen. Mar. Biol. 104, 119–127.

Thuesen, E.V., Childress, J.J., 1994. Oxygen consumption rates and metabolic enzyme activities of oceanic California medusae in relation to body size and habitat depth. Biol. Bull. 187, 84–98.

Torres, J.J., Somero, G.N., 1988. Metabolism, enzyme activities and cold adaptation in Antarctic mesopelagic fishes. Mar. Biol. 98, 169–180.

Torres, J.J., Aarset, A.V., Donnelly, J., Hopkins, T.L., Lancraft, T.M., Ainley, D.G., 1994. Metabolism of Antarctic micronektonic Crustacea as a function of depth of occurrence and season. Mar. Ecol. Prog. Ser. 113, 207–219.

Waller, R.G., Tyler, P.A., 2011. Reproductive patterns in two deep-water solitary corals from the north-east Atlantic — *Flabellum alabastrum* and *F. angulare* (Cnidaria: Anthozoa: Scleractinia). J. Mar. Biol. Assoc. U. K. 91 (3), 669–675.

Waller, R.G., Tyler, P.A., Smith, C.R., 2008. Fecundity and embryo development of three Antarctic deep-water scleractinians: *Flabellum thouarsii*, *F. curvatum*, and *F. impensum*. Deep-Sea Res. II 55, 2527–2534.

Youngbluth, M.J., Kremer, P., Bailey, T.G., Jacoby, C.A., 1988. Chemical composition, metabolic rates and feeding behavior of the midwater ctenophore *Bathocyroe fosteri*. Mar. Biol. 98, 87–94.