Distinct realized physiologies in green sea urchin (*Strongylocentrotus droebachiensis*) populations from barren and kelp habitats

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Abstract

Overgrazing of habitat-forming kelps by sea urchins is reshaping reef seascapes in many temperate regions. Loss of kelp, in particular as a food source, may alter individual consumer physiology, which in turn may impair ability to respond to climate warming. Here, we measured the temperature dependence of absolute and mass-independent oxygen consumption ($\dot{M}O_2$) using two different exposure protocols (acute exposure and temperature 'ramping'), as proxies of realized physiology, between green sea urchin (*Strongylocentrotus droebachiensis)* populations from neighbouring barren and kelp habitats. Sea urchins from kelp habitats consumed 8-78% more oxygen than sea urchins from barrens, (across a range of temperatures tested [4-32 ºC]), and had higher maximum $\dot{M}O_2$ values (by 26%). This was in part because kelp urchins typically had greater body masses. However, higher mass-independent $\dot{M}O_2$ values of kelp urchins suggest metabolic plasticity in response to habitat per se. In addition, the $\dot{M}O_2$ of sea urchins from kelp habitats was less sensitive to increases in temperature. We conclude that sea urchins from barren and kelp habitats of comparable body mass represent different energetic units. This highlights that habitat type can drive population-level variation which may shape urchins' activities and environmental impact. Such variation should be integrated into energy-based models.

Keywords: sea urchin barrens, oxygen consumption, habitat loss, thermal response curves, energetics

Introduction

Sea urchin populations are rapidly expanding across shallow rocky reef habitats in many temperate regions (Filbee-Dexter & Scheibling 2014). Urchins can reach high densities and form feeding (grazing) fronts that rapidly overgraze macroalgae, including bioengineering kelps (Filbee-Dexter

& Scheibling 2014; Frey & Gagnon 2015; Ling *et al.* 2015). The proliferation of sea urchins, and the associated expansion of barrens, have been primarily linked to the over-exploitation of natural predators such as large groundfish and sea otters (Jessup *et al.* 2004; Pederson & Johnson 2006; Bonaviri *et al.* 2009; Sangil *et al.* 2012), but also to climate perturbations (e.g., heat waves) and disease-driven food web changes (McPherson *et al.* 2021; Smith *et al.* 2021). As kelp beds transition to barrens, habitat complexity, sediment accumulation and the availability of 3D-structures and shade decrease markedly, whereas wave exposure increases (Reed & Foster 1984; Rosman *et al.* 2007; Watanabe *et al.* 2016; Layton *et al.* 2019; Morris *et al.* 2020), and this limits both food sources and refugia. This shift to a more simplified ecosystem can impose strong 'environmental filters', defined as a set of environmental conditions that select a subset of species from a regional species' pool (Lebrija-Trejos *et al.* 2010). Thus, the presence and absence of kelp may differentially select for subsets of traits or phenotypes (Kraft *et al.* 2015), and hence lead to shifts in assemblage structure, as well as the functional and genetic structure of populations.

The paucity of food (including kelp) in sea urchin barrens suggests that there is a fundamental difference in the selection pressures on sea urchin phenotypes as compared to those in kelp habitats (Benjamin *et al.* 2010; Hollins *et al.* 2018; Duncan *et al.* 2019). Multiple species of macroalgae are commonly present in kelp habitats, and support preferential and selective feeding by grazers, whilst grazers in barrens often experience prolonged starvation, and rely on drift kelp, filamentous algae and biofilms for their nutrition (Vanderklift & Wernberg 2008; Filbee-Dexter & Scheibling 2014; Renaud *et al.* 2015). The quantity and quality of food influences metabolic rate, which ultimately controls the pace of life and underpins an organism's physiology and functioning (Brown *et al.* 2004; Huey & Kingsolver 2019; Norin & Metcalfe 2019). Metabolic rate is the sum of all life-sustaining chemical reactions that create and use energy, and is typically estimated by measuring oxygen consumption ($\dot{M}O_2$). Metabolic plasticity is often observed under different environmental conditions and in relation to food (Norin & Metcalfe 2019). Therefore, metabolic rates may differ between sea urchins living in kelp and barren habitats because of contrasting food availabilities and quality.

Understanding how metabolic rates are shaped by a species' habitat also has implications in the context of climate change and population-level resilience. Organisms that cannot meet their basic energetic needs because of resource limitations may not be able to regulate and optimize their metabolic response to environmental stress. Metabolic rate can be used as a proxy to estimate an organism's overall physiological state and to characterize its sensitivity to environmental change (Silbiger *et al.* 2019), since metabolic rate fuels all organism functioning and is strongly temperature-dependent (Boltzmann 1872; Gillooly *et al.* 2001; Dell *et al.* 2011). Populations with different physiological trait distributions can respond differently when exposed to challenging thermal conditions, such as heat waves (Padfield *et al.* 2016; Silbiger *et al.* 2019). For example, two populations with different thermal tolerance ranges, temperature optima (where performance is maximal) and thermal safety margins (i.e., the difference between a species' optimal temperature and its critical upper thermal limit) may respond differently to the same heat wave event, with only one population experiencing adverse effects. Yet, there has been limited research into how habitat shifts may shape physiological trait distribution within coastal populations (but see: Bernhardt & Leslie 2013; Miller & Dowd 2019; Spindel *et al.* 2021), and what the implications are for climate resilience.

The northwest Atlantic represents a model system where green sea urchin (S*trongylocentrotus droebachiensis* [O.F. Müller, 1776]) populations typically reach high densities, and can transform kelp habitats into extensive barrens (Scheibling & Hatcher 2001). Green sea urchins in this region play a key ecological role as consumers, and exert strong top-down control on marine communities by removing foundational kelps (Scheibling *et al.* 1999; Gagnon *et al.* 2004; Scheibling & Lauzon-Guay 2007; Frey & Gagnon 2015). Even so, kelp beds and kelp patches of mainly *Alaria esculenta* and *Laminaria* spp. are present in the northwest Atlantic, in areas where sea urchin populations die-off cyclically because of disease outbreaks or where high currents limit sea urchin grazing (Keats *et al.* 1990; Feehan & Scheibling 2014; Frey & Gagnon 2016). This system provides an opportunity to directly compare sea urchin populations in terms of their physiology from these adjacent, yet contrasting, habitats.

In the present study, we use a standardized experimental approach to, first, determine whether green sea urchins from barren and kelp habitats differ in their realized physiological state (metabolic rate and thermal sensitivity) by measuring their absolute, mass-independent and mass-specific $\dot{M}O_2$ over a range of temperatures. Absolute $\dot{M}O_2$ estimates the energy required per unit time to maintain biological functions, whilst mass-specific $\dot{M}O_2$ gives metabolic rate scaled to the organisms' mass (Peters 1983; Brown *et al.* 2004). Because absolute $\dot{M}O_2$ and body mass are typically correlated (Brown *et al.* 2004), and because sea urchin mass itself may vary across barrens and kelp habitats, we also calculate mass-independent $\dot{M}O_2$ to compare populations without the confounding effect of body mass. Second, we test whether the thermal sensitivity of metabolism differs between sea urchins from barren and kelp habitats. Third, we compare two experimental approaches to investigate the effects of short-term increases in sea water temperature on urchin metabolism: (Method 1) an 'acute' temperature exposure protocol, where sea urchins are transferred to a novel (stable) temperature, and oxygen consumption is measured at that temperature; and (Method 2) a temperature 'ramping' (dynamic) exposure protocol, in which the same set of individuals are exposed to stepwise increases in temperature (Terblanche *et al.* 2007).

The latter experiment allowed us to construct thermal response curves (TRCs) for each individual (Huey & Stevenson 1979), and enabled us to evaluate an individual's response to a temperature gradient. We used these two approaches to test if the different methods result in similar, or different, temperature-dependent changes in $\dot{M}O_2$, and to examine whether 'heat-hardening' [i.e., an increase in heat tolerance following a sub-lethal exposure to elevated temperatures (Maness & Hutchison 1980)] occurs during temperature ramping.

Methods

Sea urchin collections

Green sea urchins (N=225) were collected by snorkelers from three sites along the northeastern arm of the Avalon Peninsula: Biscayan Cove, Tors Cove, and Bauline (ordered by collection date; see Fig. 1 and Table 1 for details on the collection sites). Sites were chosen as comparable replicates of barren and kelp habitats with similar depth profiles, extent and exposure to waves, as well as shore access and distance from the laboratory. Sea urchins with test diameters of ~7-8 cm were haphazardly hand collected from habitats within the same depth range (see Table 1, Fig. S1) that resembled kelp or barrens habitats (i.e., with or without kelp) as assessed visually. Kelp areas were sections of rocky reef, at least 10 x 5 m in size, with dense, continuous kelp cover, whilst barren areas (also at least 10 x 5 m) were rocky reefs devoid of fleshy seaweeds, with bare rock substrate covered in encrusting coralline algae. Prior to collection, sea urchin densities were quantified in kelp and barren areas by counting the number of individuals in a 0.5 x 0.5 m quadrat. Seven quadrats were haphazardly placed in each kelp and barren area of the three sites (N=42 quadrats). Sea urchins collected in each habitat were kept separate at all times and placed into individual seawater-filled coolers for immediate transport to the Ocean Science Centre (OSC) in Logy Bay, Newfoundland, within 2 hours of collection. At the OSC, the sea urchins were placed into holding tanks with seawater at 14ºC (the average ambient summer temperature) and a 12-hour light: 12-hour dark photoperiod, and left to recover from transport and handling stress for 24 hours. To measure the routine $\dot{M}O_2$ of the urchin populations in a 'field-fresh' physiological state, $\dot{M}O_2$ measurements were started after the initial 24-hour recovery period, and completed within seven days of collection. Sea urchins were not fed at any point to avoid post-feeding increases in metabolic rate (i.e., specific dynamic action).

Experimental system for measuring oxygen consumption

We used a custom-built experimental system to measure the $\dot{M}O_2$ of individual sea urchins (see Fig. S2). The system built by the Technical Services Department at Memorial University of Newfoundland and Labrador, consists of a table with 10 removable acrylic chambers (each 650 mL in volume and 9 cm in diameter) with magnetic stir plates, located inside an insulated seawater tank (YETI Tundra cooler, 125 L; Austin, Texas, USA). A heater (submersible aquarium heater, 300 Watts; Aqueon, Franklin, Wisconsin, USA) and chiller (Isotemp Model 3016S; Fisher Scientific, Waltham, Massachusetts, USA) controlled by a thermostat (Inkbird ITC-308 Temperature Controller; Inkbird Tech, London, UK) were used to adjust seawater temperatures in the insulated cooler. A water pump connected to the chiller circulated the seawater from one end of the cooler to the other, ensuring consistent temperatures across the 10 chambers. Seawater within the cooler was continuously aerated with an air pump (Top Fin Aquarium, Air-200; PetSmart LLC, Phoenix, Arizona, USA) attached to an air stone. Each chamber was fitted with a temperature (PreSens dipping probe, Pt1000) and a fiber-optic oxygen probe (PreSens dipping probe, DP-PSt7-10-L2.5-ST10-YOP), and measurements of temperature and water oxygen level (in % saturation) were made every second via a computer running PreSens software (PreSens Measurement Studio 2, Version 3.0.3; Precision Sensing GmbH, Regensburg, Germany). Water oxygen level (in mL O_2 / L) was automatically calculated by the PreSens software. Oxygen probes were calibrated prior to each experimental set (sampling site) with air saturated, room temperature, seawater and sodium sulfite (no O_2; 1 g Na_2SO_3 dissolved in 100 mL of distilled water at room temperature).

Oxygen consumption measurements

Pre-measurement procedures and containment of sea urchins

We used a standardized experimental approach to test for differences in the response of metabolism to temperature between sea urchin populations from barren and kelp habitats. To estimate routine metabolic rate at the eight seawater temperatures (4, 6, 10, 14, 18, 22, 26 or 30°C), the $\dot{M}O_2$ of sea urchins was measured using closed respirometry with the system described above. We chose these temperatures to capture the entire response range (increase, peak and decrease in oxygen consumption) of sea urchins, to allow us to compare the response shape and limits across populations. The coldest and warmest temperatures were experimentally constrained by the heater and cooler capacities, and the intervals were chosen based on logistics and feasibility. Twelve (12) hours before the start of each run, nine urchins were selected for measurement (4 barren urchins and 5 kelp urchins, or vice versa). These nine sea urchins were weighed (to the nearest 0.1 g), and had their individual volumetric displacement measured [volumetric displacement = volume of seawater with urchin - volume without urchin]. One individual was placed into each of the nine chambers, with no urchin in the 10^{th} chamber so that background oxygen consumption (i.e., due to microbial respiration) could be measured in a blank control chamber that contained only seawater. The chambers were then covered with fine-mesh netting to prevent the urchins from crawling out of the chamber, and returned to the holding tank overnight to allow the urchins to adjust to confinement in the chambers and to recover from handling.

‘Acute’ temperature exposure protocol (Assay Method 1)

To examine the temperature-dependent $\dot{M}O_2$ response of sea urchins from all three sites to acute temperature changes, the YETI cooler was filled with fresh, filtered (10 μm), seawater and set to one of eight target temperatures: 4, 6, 10, 14, 18, 22, 26 or 30°C. Each independent assay was conducted on a different day, and target temperatures were randomized for each day so that warmer temperatures did not relate to longer timespans during which the urchins were held in aquaria. For each assay, all 10 chambers (9 urchins, one blank) with mesh tops were moved from the holding tank to the insulated cooler (pre-set to the target temperature for the day) and the urchins were given 1 hour at their new temperature (standardized to 1 hour because this was the maximum time to equilibrium across all temperatures). Then $\dot{M}O_2$ measurements were made by closing the lids on each chamber and allowing oxygen levels in the chambers to fall by 5-10%. This decrease in oxygen concentration allowed reliable estimates of $\dot{M}O_2$ to be obtained. The total measurement time varied from 15 min to ~ 1.5 h, with shorter measurement times at higher temperatures because $\dot{M}O_2$ increases with temperature (Gillooly *et al.* 2001). Once the measurements were completed for each of the 10 chambers, all sea urchins included in the assay were removed from their chambers and immediately frozen prior to ash-free dry mass determination (see below). The cooler and chambers were then emptied, cleaned with warm freshwater, and refilled with seawater for the next assay. The above procedures were repeated with new urchins until measurements were made at all target temperatures (N=9 sea urchins per measurement; N=72 sea urchins per collection site; N=216 sea urchins in total across all sites and replicates).

Temperature ‘ramping’ exposure protocol (Assay Method 2)

To examine the metabolic response of sea urchins to a temperature ‘ramping’ protocol, and to assess how comparable values are between this method and the previous protocol (i.e., acute transfer to a new temperature), we constructed thermal response curves (TRC) for individuals from Biscayan Cove (only one site was included due to logistical constraints). Nine sea urchins from a fresh collection were weighed and prepared as detailed in the 'pre-measurement procedures' section. After overnight recovery period, nine urchin-containing chambers and a blank chamber were placed into the cooler with temperature pre-set to 4°C, and 1 hour was allowed before testing began. Oxygen consumption measurements were then made at each of nine temperature steps: 4, 6, 10, 14, 18, 22, 26, 30 and 32°C with a 30-minute period between each temperature during which the next target temperature was reached and maintained (see Fig. S3). The final temperature step (32°C) was added to ensure we accurately defined the sea urchins' TRC as completely as possible. The first experiment ('acute' protocol) showed that $\dot{M}O_2$ peaked at around 26°C. The same nine sea urchins had their $\dot{M}O_2$ measured at all temperatures, and the chamber lids were removed and replaced with the mesh lids between measurements to allow for the replacement of seawater from the cooler in which the chambers were held. After the final measurement was taken, the sea urchins were immediately frozen.

Ash-free dry mass

We determined ash-free dry mass to quantify the amount of organic tissue per sea urchin, which corresponds to the amount of metabolically active tissue. To measure ash-free dry mass, empty aluminum weigh boats were first placed in a muffle furnace (500°C) for 12 h to remove any trace of organic matter, and thereafter, stored in a sealed container until use. Sea urchins frozen at the end of both temperature challenges were thawed prior to weighing. The urchins were then placed on pre-weighed (to 0.001 g accuracy) weigh boats, and dried in a combustion oven (at 60°C) for 12 to 24 h until their dry mass stabilized. The sea urchins were then ashed in a muffle furnace at 500°C for 12 h. Ash-free dry mass (i.e., metabolically active tissue) was calculated as dry mass (with boat) minus ashed mass (with boat). Individual dry mass was calculated as dry mass minus the empty weigh boat weight, where dry mass was the total mass of an individual (organic and inorganic) after drying. Finally, an individual's inorganic mass was calculated as ashed mass minus the empty boat weight. This inorganic mass primarily represents an individual's calcified endoskeleton (test), although small traces of sediment or inorganic gut content may also be present in the ashed sample.

Data Processing and Analyses

Values of $\dot{M}O_2$ were calculated for each individual using the respR package in R (Harianto *et al.* 2019). $\dot{M}O_2$ values were adjusted for salinity and water volume in the chamber (i.e., after correction for an individual's volumetric displacement). Mass-independent $\dot{M}O_2$ was calculated by regressing absolute $\dot{M}O_2$ on individual wet body mass (non-linear regression) and extracting the residuals. Mass-specific values were adjusted for wet-mass or ash-free dry mass (i.e., absolute $\dot{M}O_2$ divided by mass), with the latter accounting for the mass of metabolically active tissue only. All $\dot{M}O_2$ measurements were also corrected for background respiration using the $\dot{M}O_2$ values for the blank chamber of each run. Background respiration values were typically < 0.1 mL / O_2 / h. The $\dot{M}O_2$ data were visually inspected to confirm that a linear decrease in water % air saturation of 5-10% occurred. We set a minimum r^2 of 0.98 (Chabot *et al.* 2021) to identify non-linear measurements and discarded eight measurements (all from Assay Method 1; Fig. S6) with an r^2 value below this threshold.

To compare the temperature sensitivity of barren and kelp sea urchins, we calculated temperature coefficients (Q_{10} values) from the 'acute' protocol assays, based on the mean absolute $\dot{M}O_2$ for each site and habitat group, and for the temperature 'ramping' (TRC) protocol, using absolute values of $\dot{M}O_2$ for each individual sea urchin. Q_{10} values were calculated for each group or individual urchin based on the equation:

$$Q_{10} = \frac{R_2}{R_1}^{\left(\frac{10}{T_2 - T_1}\right)}, \qquad \text{(Eqn. 1)}$$

where R_1 = $\dot{M}O_2$ at temperature T_1, R_2 = $\dot{M}O_2$ at temperature T_2. Separate Q_{10} values were calculated for the lower temperature range (cold-range Q_{10}; T_1 = 4ºC and T_2 = 14ºC) and the warm-range (i.e., temperatures above the average summer /holding temperature (warm-range Q_{10}; T_1 = 14ºC and T_2 = 26ºC)). We calculated these Q_{10} values separately because temperature sensitivity may change at more stressful temperatures that lie outside the sea urchins' realized range. Additionally, we determined the maximum metabolic rate and estimated the T_{max} (temperature at which $\dot{M}O_2$ peaked) from each thermal response curve, by identifying the maximum $\dot{M}O_2$ achieved by each individual across temperatures, and the temperature that corresponded with this maximum value. Finally, temperature-induced metabolic scope (AS_T) was calculated as the difference between the maximum recorded metabolic rate (MMR_T; $\dot{M}O_2$ at 26ºC) and the lowest metabolic rate measured (LMR_T; the $\dot{M}O_2$ at 4ºC).

To test for differences in the urchins' $\dot{M}O_2$ between barren and kelp sites using Assay Method 1, we used generalized additive mixed models within the package 'mgcv' in R (R Core Team 2014) using the 'gamm' function (Wood 2011; Pinheiro *et al.* 2015). The random effect of site was included to account for variation in the response variables due to site. A random effect of 'individual' was also used in models resulting from Assay Method 2 (the 'ramping' protocol), since temperature ramping led to repeated measurements on the same individuals. Habitat (barrens vs. kelp) was included as a fixed effect in all models to test for habitat-dependent variation in the

$\dot{M}O_2$ responses of the sea urchins, with temperature included as a covariate. For models with absolute $\dot{M}O_2$ as the response variable, we also included body mass as a covariate, to account for the potentially confounding effect of individual mass.

We visually inspected Gaussian model fits to ensure test assumptions were met (normality of residuals and homogenous error structure), and compared model results across different distribution families (Poisson and quasi-Poisson, both with a log-link function) to ensure the results were consistent. Additionally, we compared gamm results with results from linear mixed-model fits with a polynomial term (function 'lme' in R package 'nlme'), again ensuring reported model results were robust (Zuur *et al.* 2009).

To compare sea urchin mass (wet mass, ash-free dry mass, inorganic mass and AFDM to wet mass ratio), metabolic parameters (MMR_T and AS_T), and the thermal sensitivity of $\dot{M}O_2$ (i.e., Q_{10} values), we fit one-way or two-way ANOVAs using the function 'aov' in the R 'stats' package (R Core Team 2014) with habitat, or habitat and site as main effects, and with an interaction term, as appropriate. We visually checked that test assumptions were met, and ran a Shapiro-Wilk normality test using the function 'shapiro.test' in the R 'stats' package (Team 2014). We performed Tukey's HSD post-hoc tests to compare data between the three sites using the function 'tukeyHSD' in the R 'stats' package.

Results

Sea urchin density averaged 25 ± 9 individuals per 0.25 m^2 in barrens, and 7 ± 5 individuals per 0.25 m^2 in areas with kelp across the three sites (26 ± 7 vs. 6 ± 7 at Biscayan Cove, 22 ± 13 vs. 8 ± 4 at Tors Cove and 26 ± 9 vs. 7 ± 5 at Bauline, in kelp vs. barrens, respectively). Across the three sites, green sea urchins from kelp habitats had a greater overall mass (by 8 %; two-way ANOVA, $F(1,2) = 17.80$, $p < 0.01$), more metabolically active tissue [i.e., higher AFDM values by 48 %

(two-way ANOVA, $F(1,2) = 138.24$, $p < 0.01$)] and more inorganic mass (by 16 %; two-way ANOVA, $F(1,2) = 23.66$, $p < 0.01$) than sea urchins from barrens (Fig. S4, Tables S5-S6). Green sea urchin masses ranged across the sites from 23.3-113.4 g (wet mass) and 0.9-8.5 g (AFDM) in kelp and 15.2-99.0 g (wet mass and) and 0.8-5.3 g (AFDM) in barrens. Sea urchins from kelp habitats also had significantly higher AFDM to wet mass ratios (two-way ANOVA, $F(1,2) = 47.15$, $p < 0.01$, Table S5, Fig. 2, Fig. S5) than individuals from barrens.

Green sea urchin populations from barren and kelp habitats differed in their oxygen consumption (Figs. 3-4). Overall, sea urchins from kelp habitats had significantly higher absolute $\dot{M}O_2$ values (by 8-78 %) than sea urchins from adjacent barrens (Figs. 3-4; Table S1; Fig. S7) across the three study sites (Fig. 1), and this pattern was generally consistent across temperatures (Figs. 3-4). This was in part due to body mass (Table S1), as urchins from kelp habitats having a higher wet mass and a greater AFDM: wet mass ratio (Fig. 2; Figs. S4-5), as their $\dot{M}O_2$ per g of AFDM was, in fact, lower as compared to sea urchins from barren habitats (Figs. S9-10). However, after accounting for body mass, the mass-independent $\dot{M}O_2$ of sea urchins from kelp habitats was still significantly higher than that of sea urchins from barrens (Fig. 3 C-D; Table S1; Fig. S7 C-D).

The temperature sensitivity (i.e., Q_{10} value) of sea urchin $\dot{M}O_2$ was significantly higher in animals from barrens than those from kelp habitats over the cold temperature range (Q_{10} 4-14°C; one-way ANOVA; $F(1,6) = 27.47$, $p = 0.002$, Table S3), but only when assessed using the temperature 'ramping' protocol (Table 2, Fig. 5A, C). Similarly, the temperature sensitivity of $\dot{M}O_2$ in sea urchins from barrens was significantly higher in the warm temperature range (Q_{10} 14-26°C) when measured using the 'acute' protocol (one-way ANOVA; $F(1,4) = 11.35$, $p = 0.028$, Table S3). Mean Q_{10} values ranged from 1.50 to 3.14, and from 1.31 to 1.84 across the two temperature ranges (4-14°C and 14-26°C, respectively) when sea urchins were exposed to the 'acute' protocol. These values were similar to those measured using the 'ramping' protocol, where Q_{10} values ranged from 1.72 to 2.69 and from 1.46 to 1.93, respectively.

$\dot{M}O_2$ generally peaked between 26-30ºC when considering all site by habitat combinations (Table 2), with urchins inhabiting areas with kelp having significantly (by 26 %) higher maximum $\dot{M}O_2$ values (one-way ANOVA; $F(1,7) = 8.008$, $p = 0.025$; Fig. 5E; Table S3) than sea urchins from barrens. Despite the finding that sea urchins from kelp habitats had higher values for MMR_T, there was no significant difference in the temperature-induced metabolic scope (AS_T; $p = 0.254$; Table S3; Fig. 5F; Table 2). There were also no significant differences in values of MMR_T or AS_T when standardized for wet mass (MMR_T; $p = 0.946$; AS_T; $p = 0.397$) or ash-free dry mass (MMR_T; $p = 0.090$; AS_T; $p = 0.123$), although sea urchins from kelp habitats had lower MMR_T and AS_T values than sea urchins from barren habitats when standardized for ash-free dry mass (Fig. S11). Overall, the $\dot{M}O_2$ of Biscayan Cove urchins did not differ significantly when measured using the two methods ('acute' temperature protocol vs. the 'ramping' protocol: Fig. 6, Table S2, Fig. S8).

Discussion

We showed that green sea urchins from barren and kelp habitats in Newfoundland differ in their realized physiological states, with those from kelp habitats having higher metabolic rates, but reduced temperature sensitivity, compared to urchins from barren areas. The average urchin from areas with kelp consumed 8-78% more oxygen than urchins from areas without kelp (i.e., barrens), across the range of typical ocean temperatures. The higher overall energetic requirements of sea urchins in kelp habitats was in part due to their greater mass. Yet, significant differences remained between sea urchins from areas with and without kelp when their mass-independent oxygen consumption rates were compared, which indicates that metabolic plasticity exists between habitat types regardless of mass-effects. In contrast, when considering metabolism standardized per gram of animal, sea urchins from kelp habitats consumed less oxygen than barren urchins, which suggests a larger investment in energy-storing tissues with low oxygen demand in populations from areas with kelp. We conclude that sea urchin populations from kelp and barren habitats have fundamentally different mass-specific and mass-independent energy requirements, and hence, represent ecologically distinctive "units". Such distinct populations may respond to, and interact with, their environment in unique but predictable ways.

Variation in individual energy requirements is ecologically important because biomass-energy relationships and the energetic status of a population form the basis of an organisms' ability to respond to environmental variability. Energetic models, such as the metabolic theory of ecology (Brown *et al.* 2004) or dynamic energy budget models (Kooijman 1986), are built upon mass-energy scaling laws and are commonly used to predict organismal responses to environmental variability. Yet, most energetic models are average-based, and predict a species' mean response (rather than population specific responses) with unexplained, but often substantial, variation around the mean (Saito *et al.* 2021). This can lead to inaccurate predictions. Integrating habitat-based energy relationships into energetic models could explain some of this variation, and improve the forecasting of a species' vulnerability to environmental change.

The differences we detected in the metabolic performance of green sea urchins from barrens and kelp habitats presumably relate to habitat characteristics, and the physical challenges and environmental filters that each habitat presents (as summarized in the introduction). Yet, differences in food availability/quality emerges amongst a number of abiotic and biotic differences as the most likely driver of differences in the energetic demand and physiology of sea urchins (Mueller & Diamond 2001; Huey & Kingsolver 2019). This is because populations in kelp habitats have access to nutritious and rich food sources, whilst high density urchin barren populations experience prolonged periods of starvation, and compete for scarce food sources such as drift kelp, encrusting algae, and biofilms (Norderhaug *et al.* 2003; Vanderklift & Wernberg 2008; Filbee-Dexter & Scheibling 2014; Renaud *et al.* 2015; Wells *et al.* 2017). Increased competition for scarce food resources in barrens intensifies food shortages, and this also appeared to be the case in the present study. Sea urchin densities were over three-fold higher in barren areas than in kelp areas across all sites.

Organisms that cannot meet their basic energetic demands because of reduced food availability or quality, or starvation, have limited capacity to regulate and optimize their metabolic response to environmental change (Boersma *et al.* 2008; O'Connor *et al.* 2009). Compared to sea urchins from kelp habitats, urchins from barrens in our experiments had lower absolute MMR_T values (by 26 %), and their $\dot{M}O_2$ was also more sensitive to increasing temperature (i.e., they had higher Q_{10} values). Perhaps green sea urchins from barrens are more sensitive to temperature change because prolonged starvation reduces their ability to maintain homeostasis as a lower underlying plasticity of cellular traits cannot buffer for environmental change, and this leads to stronger temperature-induced metabolic responses (Brett *et al.* 1969; Huey & Kingsolver 2019). Although data on the longevity of the barrens-state at these specific sites is not available, personal observations indicate that these barrens have existed at least since 2019, and urchin barrens are a persistent community state across the majority of the northwest North Atlantic (Adey & Hayek 2011; Frey & Gagnon 2015), suggesting extended starvation is likely. Additional studies on differences in protein expression in response to heat stress (e.g., heat shock proteins) between barren and kelp populations could prove insightful. It has been previously reported that various ectotherms lower their preferred body temperatures (reviewed in Angilletta 2009) and metabolic rates (Schuster *et al.* 2019) under starvation or reduced food regimes.

Green sea urchins in kelp habitats had larger body masses, more metabolically active tissue, and more inorganic (ashed) mass in comparison to urchins of the same test size from barrens (which contain relatively more water for a given body mass) across our study sites. Limited food availability in sea urchin barrens may limit urchins from shunting energy into tissue growth and storage. Sea urchins in areas with kelp, by contrast, may invest more energy into the growth of metabolically active tissues, but also the development of robust and larger body structures (e.g. ossicles or jaw length) and gonad growth (Meidel & Scheibling 1998; DeVries *et al.* 2019). This hypothesis is supported by our findings of relatively lower $\dot{M}O_2$, MMR_T and AS_T values in urchins from kelp compared to barren urchins when standardized to the mass of metabolically active tissue (i.e., AFDM). Greater investment in energy stores (e.g., lipids and glycogen) that consume little oxygen would explain why urchins from kelp habitats consume less oxygen per unit mass. Evidently, the internal structures of sea urchins from barren and kelp habitats are different, even though the populations appear visually similar (at a macroscopic level).

Variation in the body structure of green sea urchins from barrens and kelp may also emerge because of differing abiotic conditions across the two habitats. For example, kelp forests can alter local pH and dissolved oxygen (Cornwall *et al.* 2013; Krause-Jensen *et al.* 2016), and influence hydrodynamics which in turn changes the residence time of chemically altered seawater (Gaylord *et al.* 2012; Hirsh *et al.* 2020). Thus, kelp forests present unique biochemical habitats compared to areas where kelp are absent. As such, areas with productive kelp have been suggested to act as deoxygenation and acidification refugia relative to surrounding waters (Frieder *et al.* 2012). Thus, our finding that barren urchins have lower inorganic masses than kelp urchins suggests that a compelling direction for future investigations is whether differences in seawater biochemistry between barrens and kelp beds affect calcification processes in sea urchins (e.g., Hoshijima & Hofmann 2019).

We also report that the temperature at which oxygen consumption ($\dot{M}O_2$) of green sea urchins peaks (T_{max}; 26 - 30ºC) exceeds summer maximal coastal temperatures in Newfoundland, where sea temperatures typically reach 14ºC, and rarely exceed 20ºC (Frey & Gagnon 2015; Bélanger & Gagnon 2020). Thus, it is unlikely that ≥26ºC represents the realized maximum performance for this species, as longer-term experiments with green sea urchins show signs of deterioration at temperatures greater than 15ºC, and grazing rates rapidly decline above 12ºC (Frey & Gagnon 2015). Instead, the temperatures where aerobic scope is highest would give a better indication of the optimum for sea urchin physiological performance, and would likely lie well below the temperature where $\dot{M}O_2$ peaks. In addition, the impact of disease dynamics on sea urchin performance under warming scenarios needs to be evaluated to predict how populations will fare in the future (but see: Scheibling *et al.* 1999; Lafferty *et al.* 2004; Lester *et al.* 2007). Disease dynamics in high density urchin barrens may interact with the heightened temperature sensitivity of barren urchins (i.e., impaired physiological states due to disease may further modify the shape of thermal response curves, or increased temperature sensitivity may increase disease vulnerability), leading to reduced population performance. Collectively, these data show that TRCs alone (and the T_{max} value) have limited capacity to predict population performance in the wild, or at what temperatures urchins begin to be impacted under slower rates of warming then our experimental protocols. We advise caution with regards to applying temperature tolerance data from rapid, short-term exposures to species' population models that predict species' success in future climates and inform conservation decisions.

In this study, we also found that exposure to an ‘acute’ temperature protocol versus a ‘ramping’ temperature protocol yielded similar $\dot{M}O_2$ values (for this urchin species and ecological context). This was unexpected as there is much debate about which physiological assay designs are most suited to particular lines of investigation, and different assay protocols can lead to different physiological responses (Terblanche *et al.* 2007; Bates & Morley 2020). In the ‘acute’ protocol, individuals were moved from the ambient holding temperature to a target temperature, and, each individual was used for one independent measurement. Consequently, there was a greater temperature “shock” at increasingly warmer temperatures. Acute approaches are also both time and replication intensive, as each individual organism is only exposed to a single temperature challenge. By contrast, ‘ramping’ approaches repeatedly measure the same individuals across multiple temperature steps. In such approaches, cumulative temperature effects as organisms are exposed to longer durations of heat stress can limit the inferences from the results of ramping approaches (Overgaard *et al.* 2012).

Accumulated temperature effects may also lead to ‘heat-hardening’, where thermal tolerance is impacted by previous sub-lethal heat exposures during ramping, which can impact rate measurements (Dahlgaard *et al.* 1998; Kelty & Lee 2001). However, many researchers now recognize that ‘ramping’ protocols that use ‘ecologically-relevant’ rates of heating (e.g., that reflect acute temperature changes in smaller water bodies or tide pools, or seasonal changes in coastal water temperatures) are the most appropriate method when the question relates to species in their natural environment, and the goal of the study is not specifically to study the maximum or minimum temperature at which a particular physiological mechanism fails (e.g. Leeuwis *et al.* 2019; Zanuzzo *et al.* 2019; Gamperl *et al.* 2020). Further, in this study there was no evidence of ‘heat-hardening’ (when urchins were exposed to increasing temperature steps), or a time/cumulative heat load effect on $\dot{M}O_2$. The slightly higher $\dot{M}O_2$ values with the 'ramping' protocol may have been related to differences in ambient seawater temperature at the time of sea urchin collection (urchins collected for the 'acute' protocol in mid-August [~13ºC ambient seawater] versus collection for the 'ramping' protocol during early November [~7ºC ambient seawater]). This interpretation is supported by rate differences at the first temperature step (4ºC), where stress resulting from incremental temperature ramping had not accumulated yet (i.e., the first temperature step of a 'ramping' protocol is equivalent to that of an 'acute' protocol). Impacts of 'heat-hardening', would manifest in diverging $\dot{M}O_2$ values at higher temperatures during the 'ramping' protocol, relative to $\dot{M}O_2$ values recorded during the 'acute' protocol, but we found no evidence of this in the present study.

Our results suggest that, at least for green sea urchins, the 'acute' and 'ramping' protocols provide comparable data, and do not lead to different oxygen consumption values when the same equipment is used. Even so, researchers should match their experimental design to their research question, in particular when laboratory assays are used to infer or predict climate vulnerability, and when 'heat-hardening', acclimation and adaptation are fundamentally important and ecologically-relevant (Bates & Morley 2020). Therefore, in some cases faster 'ramping' approaches, which require less time and fewer replicates, may be a practical choice for comparison when the goal is to compare amongst many individuals and species. Developing realistic temperature 'ramping' protocols that reflect current rates of change experienced by wild populations, or those predicted in the future (e.g. Zanuzzo *et al.* 2019; Gamperl *et al.* 2020) are crucial to produce accurate bounds on which to base predictions.

Overall, habitat type emerged as a driver of population-level variations in realized physiology. Green sea urchins (and likely other sea urchin species) from barrens are ecologically different ‘units’ than those from kelp habitats in terms of their metabolic responses to temperature change. Our findings have important implications for the application of energy-based models (e.g., metabolic theory of ecology or dynamic energy budget models) that aim to understand and predict a species’ vulnerability under climate change. We show that habitat may play a fundamental role when considering organisms as energetic units, and in explaining differences between individuals. Testing our observations in different species that occupy several distinct habitats (including species occurring in both forests and deforested areas on land) could reveal whether habitat complexity produces consistent energetic sub-units within species that can be integrated into forecasting approaches.

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Figure captions:

Figure 1. Green sea urchin collection sites along the easternmost side of the Avalon Peninsula, Newfoundland, Canada (plot inset shows the province of Newfoundland, with the red box outlining the Avalon Peninsula). Urchins were hand collected from Biscayan Cove (A), Tors Cove (B) and Bauline (C) (see Table 1 for further details). Panels on the right (A-D) show kelp beds (A, B) and sea urchin barrens (C, D) on the Avalon Peninsula. Pictures were taken by snorkelers at ~4m depth in August 2020. B and C show count quadrats with a size of 0.5 x 0.5 m, placed in a kelp bed and barren, respectively.

Figure 2. Ash-free dry mass (AFDM) to wet mass ratios for green sea urchins collected from barren and kelp habitats in Newfoundland. The temperatures on the x-axis indicate the temperature steps each set of urchins was exposed to during oxygen consumption measurements. Data for each habitat and temperature combination represent 27 urchins, N=216 in total. Boxplots show maximum, minimum and median values, as well as 25^{th} and 75^{th} percentile values.

Figure 3. Absolute (A) oxygen consumption ($\dot{M}O_2$) and mass-independent (B) oxygen consumption of green sea urchins collected from barren and kelp habitats as a function of experimental seawater temperature, and measured using the 'acute' protocol. Individuals were collected from three sites in Newfoundland and for each site, nine fresh urchins were acutely exposed to each temperature (N=27 urchins per temperature). Boxplots show maximum, minimum and median values, as well as 25^{th} and 75^{th} percentile values. N=216 urchins across all sites. Note: sea urchins from Bauline (N=9 urchins) were mistakenly measured at 8ºC instead of 6ºC, thus boxplots at 6ºC represent sea urchins from Biscayan Cove and Tors Cove only (N=18 urchins).

Figure 4. Absolute oxygen consumption ($\dot{M}O_2$) of green sea urchins from barren and kelp habitats in Biscayan Cove when exposed to the 'ramping' protocol. Boxplots (A) show maximum, minimum and median absolute $\dot{M}O_2$ values, as well as 25^{th} and 75^{th} percentile values. (B) Shows thermal response curves for each urchin (N=9 urchins), with dashed lines and triangles denoting urchins from kelp habitats, and solid lines and circles indicating those from urchin barrens.

Figure 5. Temperature sensitivity (Q_{10}) of absolute oxygen consumption ($\dot{M}O_2$) in green sea urchins collected from barren and kelp habitats (A-D). Q_{10} values were calculated from 4 – 14 ºC and 14 – 26 ºC based on mean $\dot{M}O_2$ values for each site and habitat measured during the 'acute' protocol (A-B, N=3), and for each individual urchin using the 'ramping' protocol (C-D, Biscayan Cove, see data in Fig. 4: N=9). Note: mean summer water temperature was ~14ºC. (E) Shows the difference in maximum oxygen consumption (MMR_T) between sea urchins from barren and kelp habitats, and (F) shows the difference in temperature-induced metabolic scope (AS_T). Both of these parameters were calculated using data from the 'ramping' protocol. N=9 urchins per habitat type. Boxplots show maximum, minimum and median values, as well as 25^{th} and 75^{th} percentile values for each habitat type. Asterisks indicate a significant difference (* = $p < 0.05$, ** = $p < 0.01$, *** $p < 0.001$) between values for sea urchins collected from barren and kelp habitats.

Figure 6. Comparison of temperature-dependent changes in $\dot{M}O_2$ when measured using the 'acute' (red) vs. the temperature 'ramping' protocol (blue). (A) Absolute $\dot{M}O_2$ and (B) mass-

independent $\dot{M}O_2$. Boxplots show maximum, minimum and median values, as well as 25th and 75th percentile values, for each temperature exposure protocol ('acute' and 'ramping'). N=72 urchins across both protocols.

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Figures & Tables:

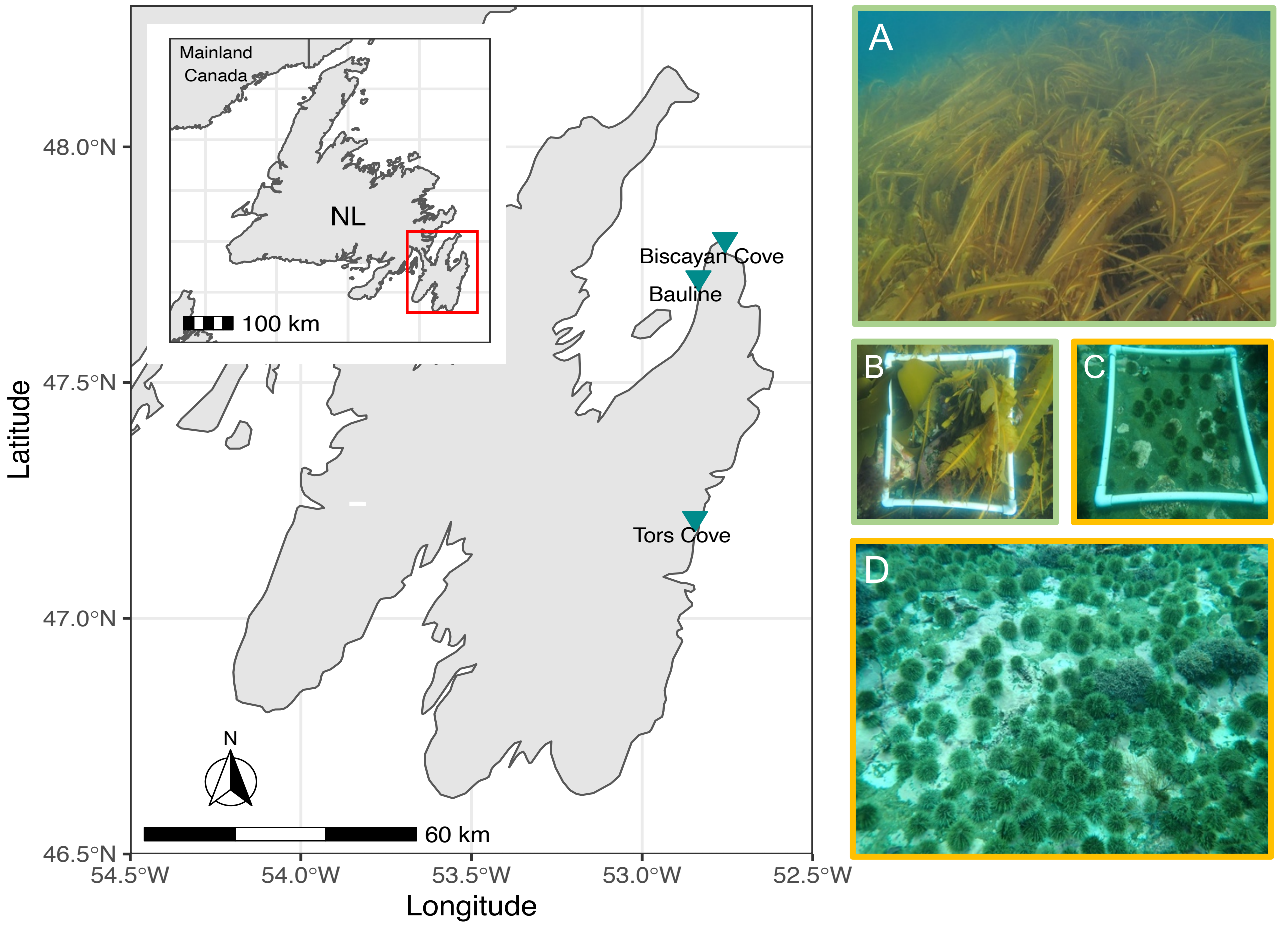
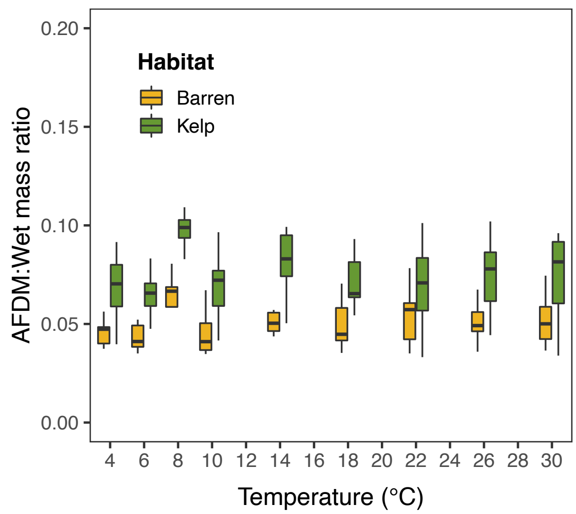


Figure 1. The map shows green sea urchin collection sites along the easternmost side of the Avalon Peninsula, Newfoundland, Canada (plot inset shows the province of Newfoundland (NL), with the red box outlining the Avalon Peninsula). Urchins were hand collected from Biscayan Cove, Tors Cove and Bauline (see Table 1 for further details). Panels on the right (A-D) show kelp beds (A, B) and sea urchin barrens (C, D) on the Avalon Peninsula. Pictures were taken by snorkelers at ~4m depth in August 2020. B and C show count quadrats with a size of 0.5 x 0.5 m, placed in a kelp bed and barren, respectively.



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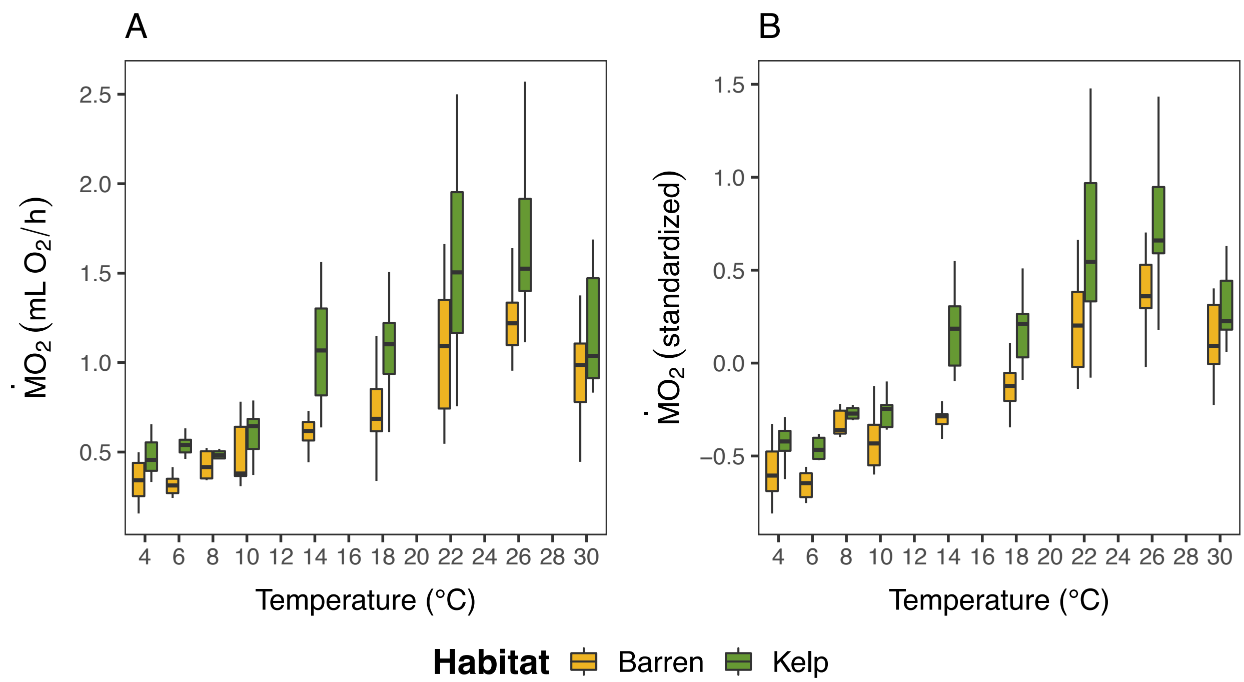

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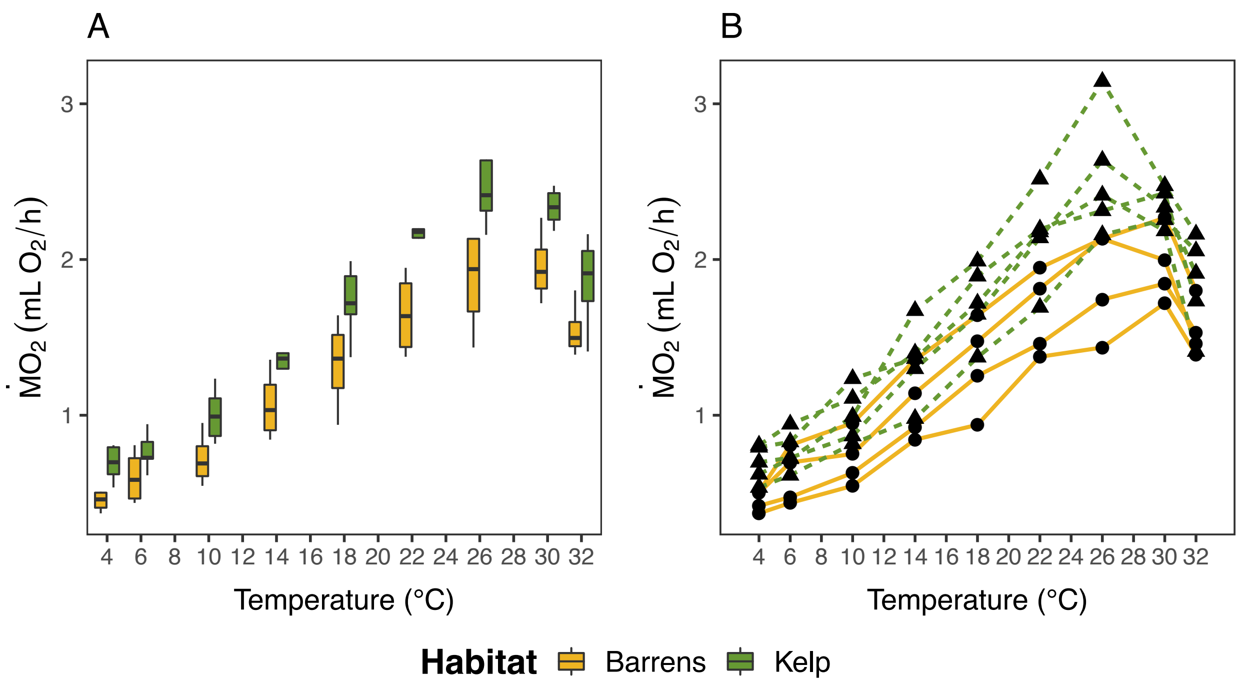

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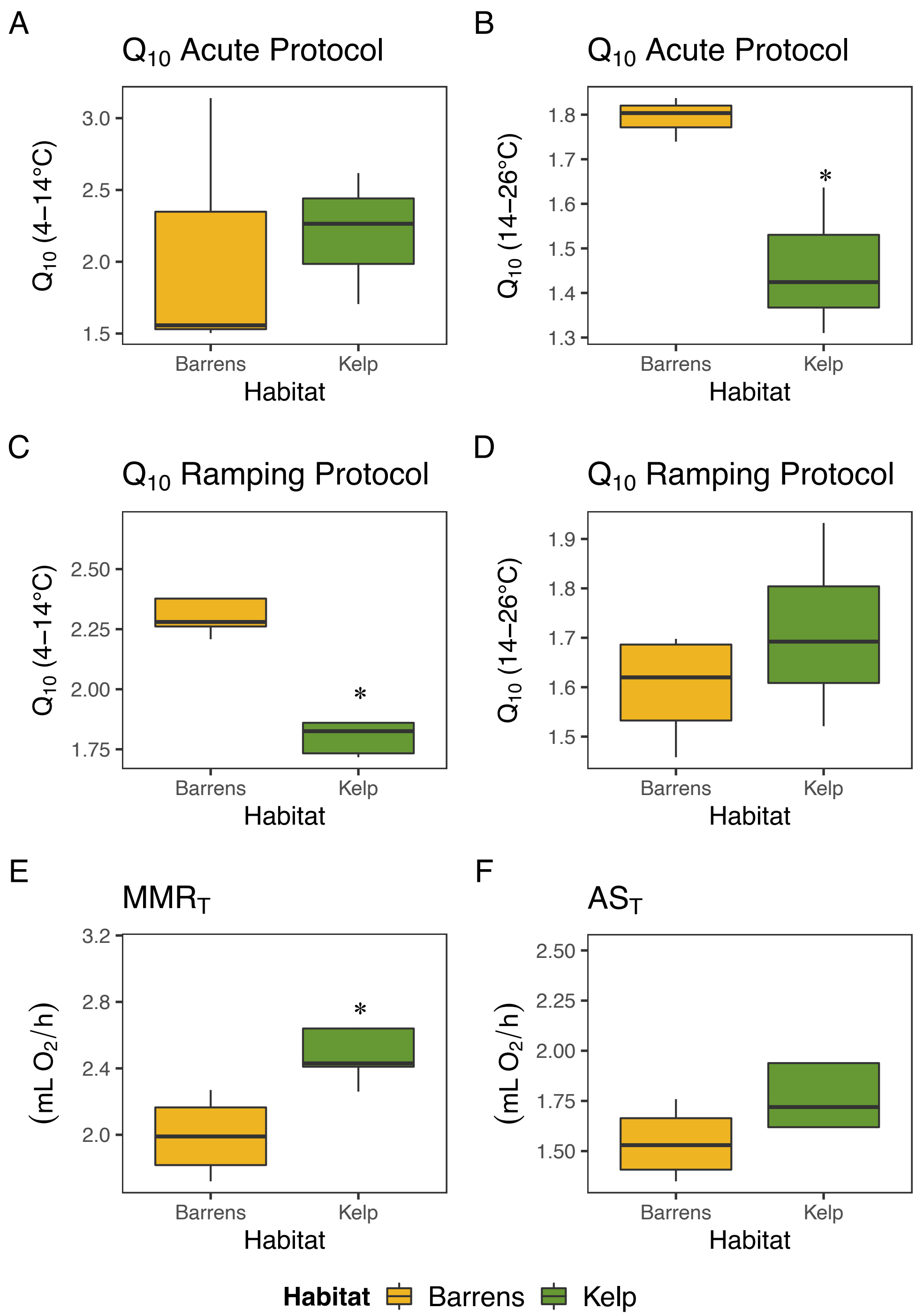

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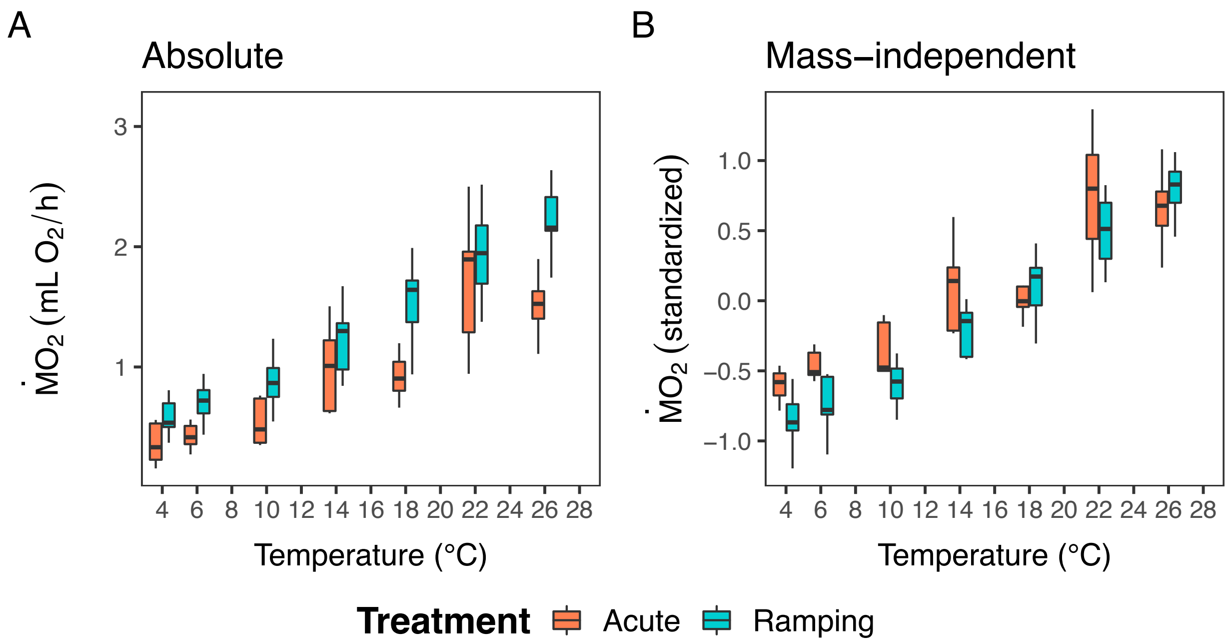

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Table 1. Details on the green sea urchin collection sites used in these experiments. The 'Protocol' column indicates in which experiment a given group of urchins was used. Two experimental protocols were used; an 'acute' temperature protocol and a 'ramping' protocol (see methods). The latter was used for the construction of individual thermal response curves (TRCs). 'SW Temp.' indicates ambient seawater temperature (ºC) at the time of collection.

Collection Site	º Latitude	º Longitude	Collection depth (m)	Date (DD-MM-YY)	SW Temp.	Protocol	# of sea urchins collected
Biscayan Cove	47.803947	52.787087	1.4-5.6	12-08-20	14ºC	'Acute'	72
Tors Cove	47.212302	52.844915	2.5-4.5	06-09-20	11ºC	'Acute'	72
Bauline	47.722456	52.835011	0.7-3.0	21-09-20	11ºC	'Acute'	72
Biscayan Cove	47.803947	52.787087	2.0-3.0	06-11-20	7ºC	'Ramping'	9

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Experiment	Population or Replicate	Q_{10} (4-14 ºC)	Q_{10} (14-26 ºC)	MMR_T (mL O_2 / h)	T_{max} (ºC)	AS_T (mL O_2 / h)
'Acute'	Barrens Bauline	1.56	1.80	1.31	26	NA
'Acute'	Kelp Bauline	1.81	1.64	1.42	26	NA
'Acute'	Barrens Biscayan Cove	3.14	1.84	1.63	26	NA
'Acute'	Kelp Biscayan Cove	2.62	1.31	2.50	22	NA
'Acute'	Barrens Tors Cove	1.50	1.74	1.80	22	NA
'Acute'	Kelp Tors Cove	2.26	1.42	2.57	26	NA
'Ramping'	Barrens #1	2.28	1.68	2.13	26	1.63
'Ramping'	Barrens #2	2.67	1.45	2.27	30	1.76
'Ramping'	Barrens #3	2.28	1.56	1.72	30	1.35
'Ramping'	Barrens #4	2.21	1.70	1.85	30	1.43
'Ramping'	Kelp #1	1.86	1.80	2.64	26	1.94
'Ramping'	Kelp #2	1.83	1.93	2.26	30	1.72
'Ramping'	Kelp #3	1.73	1.52	2.43	30	1.62

‘Ramping’	Kelp #4	1.72	1.61	2.41	26	1.62
‘Ramping’	Kelp #5	2.69*	1.69	3.14	26	2.52