



Respiration of the sea urchin *Mesocentrotus nudus* in response to large temperature fluctuations



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ABSTRACT

Some subtidal habitats may experience extremely large diel temperature fluctuations. To explore the potential of subtidal animals to regulate their metabolic processes, we investigated how the oxygen consumption rate (MO_2) of the sea urchin *Mesocentrotus nudus* changes in response to extreme temperature fluctuations by mimicking temperature variations recorded at Dokdo Island, Republic of Korea. We compared the MO_2 of urchins before and after a temperature fluctuation. MO_2 was positively correlated with temperature. There was no change in the mean MO_2 values even after exposure to fluctuating temperature. There was no significant difference in mean MO_2 between large and small temperature fluctuations. These results indicate that the metabolic activity of *M. nudus* might be well-adapted to extreme temperature fluctuations. However, given that the temperature coefficient (Q_{10}) values decreased with increasing temperature and Q_{10} values during the temperature decrease was higher than those during temperature increase, temperature rise may still act as a stressor for these animals.

1. Introduction

Water temperature is one of the most influential determinants of metabolism in marine ectotherms. A number of studies have been conducted on the metabolic and physiological responses of ectothermic animals to specific water temperatures (Greenwood, 1980; Oh et al., 2006; Lee et al., 2014). Metabolic activity in ectotherms also depends on the extent, rate, and frequency of temperature changes (Eldridge et al., 2015). Generally, metabolic rate increases with temperature because the rates of biochemical reactions and biological activity increase with temperature.

Because intertidal environments experience large diel temperature variations due to periodic exposures to air at low tides, animals that live in these areas should regulate their metabolic rates as an adaptive response to the frequently changing temperature of their environment (Helmuth and Hofmann, 2001; Denny et al., 2011). Temperatures in subtidal zones are less variable than those in intertidal areas; however, under certain circumstances, subtidal areas can also experience large diel temperature variations (Schoepf et al., 2015; Wall et al., 2015). In the coastal environment at Dokdo Island, located in the East Sea of the Republic of Korea, the water temperature changes rapidly and drastically. The temperature variation is especially dramatic during the

summer months (from July to September), when the water temperature at a depth of 23 m can fluctuate widely twice within a single day; according to a long-term dataset acquired from the Dokdo Oceanographic Observatory, the diel variation in water temperature in the summer ranges from $\Delta 0.6$ to $\Delta 12.4$ °C (Fig. 1). Given that internal waves drive temperature fluctuations at shallow depths near the shore (Farrar et al., 2007; Nakaza et al., 2006; Schmidt et al., 2016; Wall et al., 2015), the diel temperature fluctuations at this site would be also caused by internal waves associated with the tidal cycle. Because the site is located at depths where the thermocline exists (Baek et al., 2018), internal waves might cause extraordinary temperature changes in this region. However, the exact physical mechanism driving the large diel fluctuations in this region is still not fully understood. As this diel variation in water temperature is extraordinarily high compared to that in similar marine subtidal habitats elsewhere in the world (e.g., Diederich and Pechenik, 2013; Putnam and Edmunds, 2011; Schoepf et al., 2015), it is of interest to investigate how the animals living in this area respond or acclimate to these conditions.

The sea urchin *Mesocentrotus nudus* inhabits subtidal rocky areas throughout East Asia, including Dalian in China, the Maritime Territory of Russia, and the East Sea of Korea and Japan (Agatsuma, 2007). *M. nudus* is a highly desirable fisheries resource, which is harvested for its

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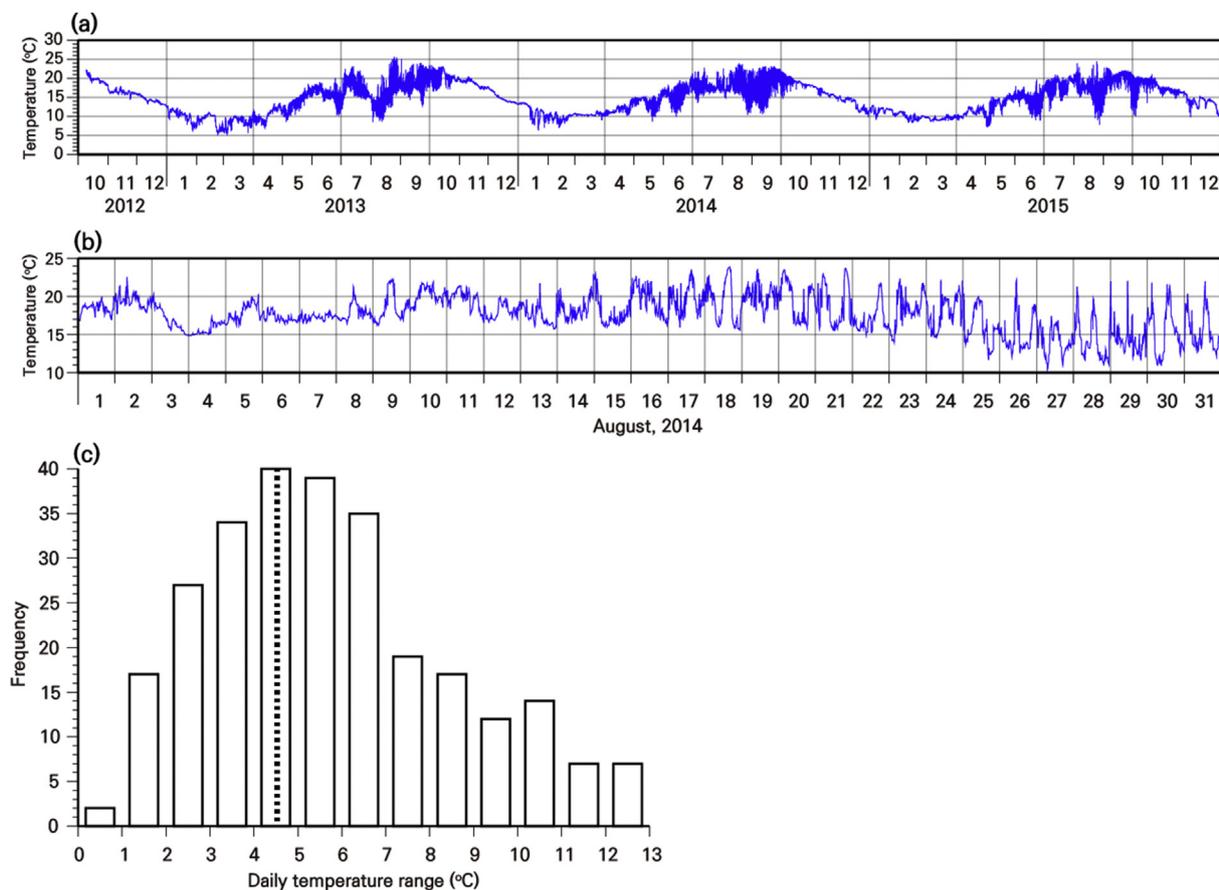


Fig. 1. Water temperature data at Dokdo Island. (a) Water temperature variations from 2012 to 2015. Note that temperature varied widely, especially during the summer from July to September. (b) Temperature variations during August 2014. (c) Frequency distribution of the daily temperature range from July to September 2013, 2014, and 2015, at a depth of 23 m near Dokdo Island. The dotted line represents the mean value of the diel temperature range.

gonads, known as ‘uni’. A number of studies have been conducted on *M. nudus* gonadal development, fertilization, and food selectivity (Kim et al. 2007, 2010; Sung et al., 2014; Unuma et al., 2015). Their spawning season is from September to October, when the water temperature begins to decrease (Agatsuma, 2007). *M. nudus* is a macro-grazer that consumes various seaweeds, and is also one of the major causes of urchin barrens in the East Sea of Korea, including at Dokdo Island (Choi et al., 2006). *M. nudus* is subjected to extreme temperature fluctuations in its natural habitat around Dokdo Island. In contrast to nektonic species, these benthic animals have a limited ability to escape thermal stress by migrating to a less harsh habitat. Therefore, it is important for these animals to acclimate to the temperature variation in their environment, as well as undergo physiological adaptations to these conditions.

In the present study, we hypothesized that even though *M. nudus* can acclimate to fluctuating temperatures in their habitat, they may have trouble maintaining their metabolism under widely fluctuating temperature conditions. Accordingly, we mimicked the fluctuations in water temperature that occur in the habitat of *M. nudus* in the coastal environment near Dokdo Island in the form of two treatments (large and small temperature fluctuations), and compared the oxygen consumption rate (MO_2) values between them. We predicted that under conditions with large temperature fluctuations, the overall MO_2 would be higher than under those with small temperature fluctuations because the animals may need more energy to acclimate to larger temperature variations (Beauregard et al., 2013; Lyytikäinen and Jobling, 1998; Ulbricht and Pritchard, 1972). Furthermore, we predicted that the temperature coefficient (Q_{10}) value would decrease as temperature increases because the high temperature would act as a stressor and affect

the maintenance of physiological functions.

2. Materials and methods

2.1. Measuring temperature at the collection site

A water level recorder (Aanderaa WLR-7; Xylem Incorporated, USA) with a temperature sensor was moored at a depth of 23 m near Dokdo Island (37° 14.267' N, 131° 51.986' E). Water temperature data were then recorded at 20-min intervals from October 2012 to December 2015.

2.2. Experimental animals

Adult *M. nudus* specimens were collected by scuba divers at depths of 20–30 m in the sea around Dokdo Island on May 31, June 23, and September 28, 2016, kept in an ice box, and transported to the Korea Institute of Ocean Science & Technology (KIOST). Urchins were then placed in a closed 500-L water tank (150 × 70 × 80 cm, W × L × H) connected to a well-aerated, recirculating seawater system for more than 2 weeks prior to the experiment to allow acclimation to laboratory conditions. The water temperature was maintained at 18.5 °C (close to the mean ± SD water temperature at Dokdo Island from July to September 2015, which was 18.40 ± 2.28 °C), and the salinity was 33 psu, which was close to the environmental conditions where the sea urchins were captured. The temperature and salinity were measured daily with a YSI 30 water quality analyzer (YSI Incorporated, USA), and every minute with an Aanderaa 3919 conductivity sensor (Xylem Incorporated, USA), respectively. The sea urchins were fed the brown

kelp *Saccharina japonica* three times per week. The photoperiod followed the natural light:dark cycle of the area where the laboratory was located, and the sea urchins were exposed to the light only during the acclimation period. To avoid differences in metabolic activity due to food intake, we stopped feeding the urchins 2 days before measuring respiration (Brockington and Clarke, 2001).

2.3. Experimental setup

To regulate the water temperatures for the two treatments, we used two incubators (VS-1203P5-0; Vision Scientific Co., Korea). Two randomly selected sea urchins were allotted to each incubator, and thus each experimental trial was performed for four individuals (two urchins for each treatment) at the same time. The experiments were conducted five times, and a total of 20 sea urchins were used (10 sea urchins per treatment).

Two water baths (575 × 415 × 255 mm, W × L × H) were placed in each incubator. Seawater (40.6 L), after being filtered twice through two sterilized filters (input, 0.2 μm; output, 0.07 μm; Sartorius, Germany), was poured into each water bath. An air pump was then inserted and turned on to maintain normoxia in the baths. The temperature of both incubators was set at 18.5 °C (Fig. 2a).

An MO₂ measuring chamber (animal chamber: 500 mL; tubing: 54.2 mL) was installed in each water bath. The temperature of both incubators was maintained at 18.5 °C for 24 h. The two incubators were then set at different temperatures to produce the following two experimental water temperature conditions: (i) the water temperature fluctuated between 13.5 °C and 23.5 °C every 6 h (Group L, large temperature fluctuation over a 10 °C range close to the maximum diel temperature range at Dokdo Island); and (ii) the water temperature fluctuated between 16 °C and 21 °C every 6 h (Group S, small temperature fluctuation over a 5 °C range close to the mean diel temperature range at Dokdo from July to September, 2013–2015) (Fig. 3). The water temperature was directly measured by placing a temperature sensor in the water bath. These treatments were replicated within the same incubator each time. In addition, all MO₂ measurements were taken in the dark, because photoperiod can impose a temporal cycle upon the respiration (Lee et al., 2014; Newell, 1973).

2.4. Respirometry

The experiments were conducted five times from June 23 to October 21, 2016. Intermittent measurements of MO₂ that combined closed and flow-through respirometry were taken.

The wet weight (WW) of each sea urchin was measured to the nearest 0.0001 g with an OHAUS-ARG224 precision scale (OHAUS[®], USA), and the test (round shaped skeleton of sea urchin) diameter (TD) was measured to the nearest 0.01 mm with a CD-15PSX digimatic caliper (Mitutoyo Co., Japan). Each urchin was then placed in a respiration chamber, which was sealed to prevent seawater leakage. Each respiration chamber was connected to two pumps (circulation and flush pumps, operating at 5 L/min; Eheim, Germany) and an optode. The flow velocity inside the chamber was 1.3 cm/s, which is less than the velocity (20 cm/s) that affects sea urchin behavior (Agatsuma, 2007). The circulation pump was continuously on throughout the experiment. For the first 30 s, the flush pump was run to provide aerated ambient seawater. After this, there were 30 s intervals when the flush pump did not run and only the circulation pump ran, and thus the water circulated within the loop. The MO₂ was then measured with a dissolved oxygen (DO) sensor for 360 s (Fig. 2b). The DO remained at more than 80% for 360 s in this closed state. This protocol was set up as a cycle (30 + 30 + 360 s) that was repeated for 4 days (24 h at a constant temperature + 72 h with fluctuating temperatures). The pump was controlled using AutoResp respirometry software (Loligo[®] Systems, Denmark).

Values of MO₂ are usually expressed as milligrams of oxygen

consumed per WW per hour (mgO₂/kg/h) (Kim et al., 2016; Lee et al., 2003; Magozzi and Calosi, 2015). Herein, however, MO₂ values are expressed with reference to dry weight (DW) instead of WW because only the soft tissues of the animal, not the calcite skeleton, are involved in respiration (Lee and Kim, 2017; Kim et al., 2018).

2.5. Measuring dry weight

To determine the MO₂ of only metabolically active tissues, we measured the tissue DW of urchins. After the experiment, the soft tissue was scraped out from the test and dried at 80 °C for 24 h using a VS-4172D drying oven (Vision Scientific Co., Korea). In addition, to evaluate the relationship between WW and DW, we measured the DWs of not only the experimental sea urchins, but also those of other sea urchins. The DW of 38 sea urchins was measured in total. For four sea urchins (two from each treatment) whose DW could not be directly measured, we used an equation derived from the results of the 38 measured sea urchins to estimate their DW. Because WW and DW have a very high correlation ratio and the DWs of only a small number of individuals were not measured directly, there is a very low possibility that differences in DW measurements could influence the results.

2.6. Q₁₀ calculations

To determine whether the metabolic activity changed proportionately with changes in the water temperature, we calculated the Q₁₀ values from the MO₂ values. The Q₁₀ values were calculated as follows:

$$Q_{10} = \left[\frac{MO_2'_{DW2}}{MO_2'_{DW1}} \right]^{\frac{10}{T_2 - T_1}}, \quad (1)$$

where T is water temperature (in °C) and MO₂'_{DW} is the MO₂ that was derived from the regression equation of the relationship between the MO_{2,DW} and temperature.

The Q₁₀ was separately calculated for the increasing and decreasing temperature phases. The overall temperature range considered in these calculations of Q₁₀ was 14.5–22.5 °C, with values estimated at 4 °C intervals, i.e., 14.5–18.5 °C, 16.5–20.5 °C, and 18.5–22.5 °C. Calculations were made in both the increasing and decreasing temperature phases.

2.7. Statistical analyses

The total number of experimental sea urchins examined was 20 (10 per treatment); however, we only used data from 19 sea urchins (9 and 10 in groups L and S, respectively) for analyses because one individual died during the experiment from a technical problem (pump failure). When the residuals of the data satisfied the assumption of normality (Kolmogorov–Smirnov or Shapiro–Wilk tests, $P > 0.05$), we used a parametric test to analyze them. If not, we used a non-parametric test. To determine whether there was a difference between the metabolic activity associated with the mean MO_{2,DW} when the temperature was constant (CMO₂) and that associated with the mean MO_{2,DW} when the temperature fluctuated (FMO₂) for each individual in each treatment, a Wilcoxon signed-rank test was used. The MO_{2,DW} data used to calculate the CMO₂ were collected during the first 24 h of each experiment, when the temperature was constant. For the FMO₂, the data were collected during the middle 48 h of the temperature fluctuation phase, because full-day datasets symmetrically aligned with both the temperature increasing and decreasing phases were necessary (Fig. 3). Because the sea urchin size, DW, CMO₂, and FMO₂ data violated the assumption of normality (i.e., $P < 0.05$ for all of these data according to both the Kolmogorov–Smirnov and Shapiro–Wilk tests), the Mann–Whitney U test was used to determine whether the size, DW, CMO₂, and FMO₂ of sea urchins differed significantly between treatment groups. Since there was no significant difference in MO₂ between the sea urchins collected in summer (~ Aug.) and those collected in fall (Sep. ~) (Mann–Whitney

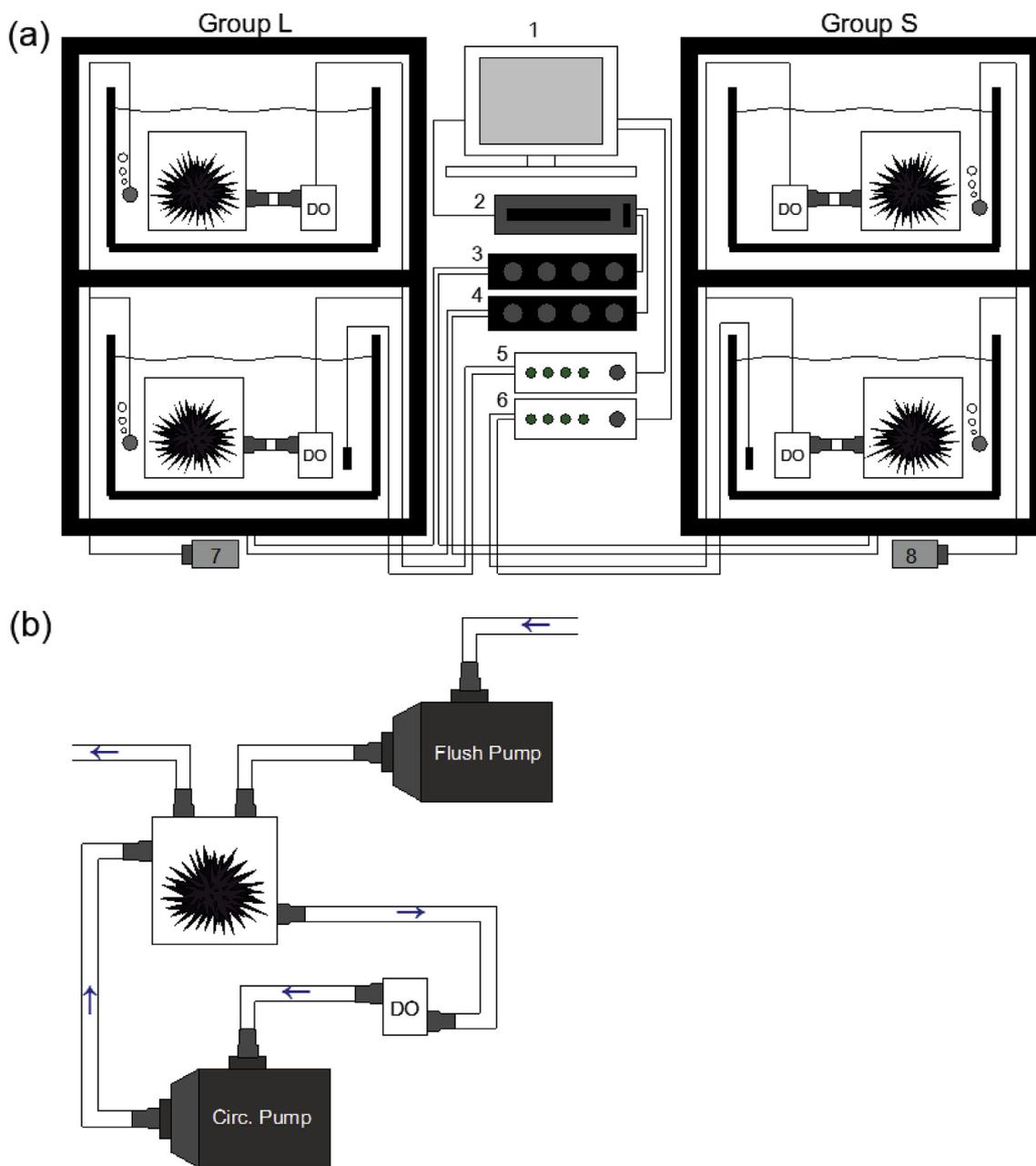


Fig. 2. Diagram of experimental setup. (a) Experimental system: two incubators were used for two treatments at the same time and two sea urchins were located in each incubator per trial. 1: Computer with respirometry software; 2: pump regulator; 3: flush pump power supply; 4: circulation pump power supply; 5: dissolved oxygen and temperature sensor for Group L; 6: dissolved oxygen and water temperature sensor for Group S; 7 & 8: air pump. (b) Respirometry system. Two pumps (flush and circulation), the animal chamber, and a dissolved oxygen (DO) sensor were connected with a water hose. The circulation pump was always on and the flush pump provided normoxic ambient water to the animal chamber in only the flush phase. In the interval between flushes, only the circulation pump ran and MO_2 was not measured.

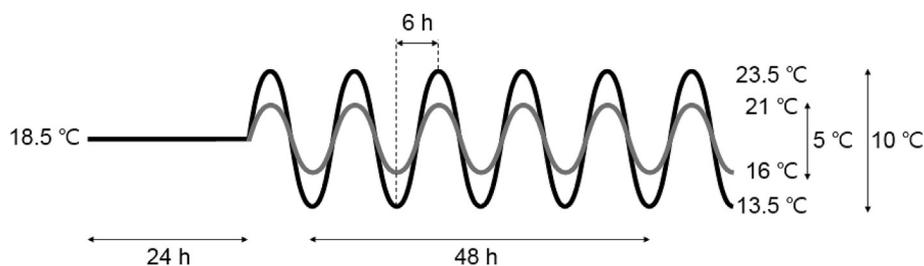


Fig. 3. Experimental water temperatures. The black line represents the temperature change applied to the group exposed to large temperature fluctuations (Group L) and the gray line represents the same applied to the group exposed to small temperature fluctuations (Group S). The bottom arrow shows the periods from which data were selected for the calculation of the constant and fluctuating oxygen consumption rates.

U test, all $P > 0.1$), sea urchin data in each treatment group were pooled. Spearman's rank correlation coefficients were also calculated between the temperature and MO_{2DW} . A Holm–Bonferroni correction was applied to adjust the significance thresholds of P -values to account for the number of tests performed. To remove the outlier of Q_{10} values, the method of Tukey was used (Tukey 1977). To determine if the Q_{10} values were different between groups and between the temperature increase and decrease periods within each group, the unpaired *t*-test was used. Additionally, the difference in Q_{10} values between each temperature interval of group L was determined with the one-way ANOVA. All analyses were carried out using PASW Statistics 18 (SPSS Inc., USA).

3. Results

3.1. Temperature variation at the collection site

Seawater temperature at 23 m depth near Dokdo Island showed intra-annual variation in a seasonal manner. The diel variation in water temperature was especially high during the summer (July–September) of each year compared to that during other seasons. The mean diel temperature range was 4.5 °C, and the maximum diel temperature range was 12.4 °C. When the temperature range was over 12 °C, the maximum temperature was between 19.9 and 25.0 °C and the minimum temperature was between 8.7 and 12.6 °C (Supplemental Table 1). The mean \pm SD temperature from July to September was 17.0 \pm 3.0 °C in 2013, 17.8 \pm 2.4 °C in 2014, and 18.4 \pm 2.3 °C in 2015.

3.2. Experimental treatments

A strong, positive linear relationship was found between the WW, which includes the test and spines, and the DW of the tissue only (Pearson correlation test, $P = 0.001$, $\rho = 0.836$). The equation expressing this relationship is as follows:

$$DW (g) = 0.0373 \times WW (g) + 0.1533. \quad (2)$$

There was no significant difference in the test diameters (Mann–Whitney *U* test: $U = 37$, $N_1 = 9$, $N_2 = 10$, $Z = -0.653$, $P = 0.549$) and DWs (Mann–Whitney *U* test: $U = 44$, $N_1 = 9$, $N_2 = 10$, $Z = -0.082$, $P = 0.968$) between treatment groups L and S.

The mean water temperature was not significantly different between groups L and S, both when the temperature was constant (Group L: 18.29 \pm 0.22 °C; Group S: 18.27 \pm 0.22 °C; Mann–Whitney *U* test: $U = 38$, $N_1 = 9$, $N_2 = 10$, $Z = -0.574$, $P = 0.604$), and when it was fluctuating (Group L: 18.21 \pm 0.12 °C; Group S: 18.14 \pm 0.17 °C, Mann–Whitney *U* test: $U = 36$, $N_1 = 9$, $N_2 = 10$, $Z = -0.737$, $P = 0.497$).

In both groups L and S, the mean water temperature was not significantly different between when the temperature was constant and when the temperature was fluctuating (Wilcoxon signed-rank test – Group L: $Z = -0.059$, $N = 9$, $P = 0.953$; Group S: $Z = -1.687$, $N = 10$, $P = 0.092$).

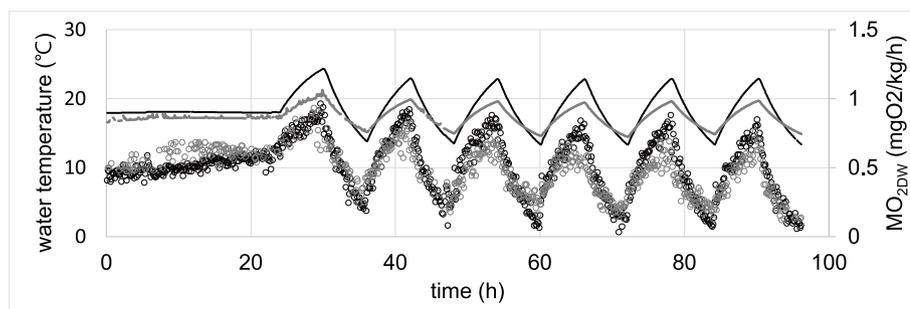


Fig. 4. Example plot showing the response of MO_{2DW} to temperature fluctuation and water temperature. The MO_2 values of sea urchins exposed to large (Group L) and small (Group S) temperature fluctuations are labeled with black and gray dots, and the large and small water temperature fluctuations are shown with black and gray lines, respectively. This figure shows one individual per group. MO_{2DW} is the oxygen consumption rate that was calculated per kg of dry weight.

Table 1

Experimental animal size, dry weight, MO_2 data, and water temperature of different treatments (mean \pm SE).

	Group L (N = 9)	Group S (N = 10)
Test diameter (mm)	51.76 \pm 1.81	53.13 \pm 2.19
Dry weight (g)	2.16 \pm 0.48	2.15 \pm 0.16
Min water temp (°C)	13.29 \pm 0.13	15.55 \pm 0.19
Max water temp (°C)	23.12 \pm 0.12	20.77 \pm 0.17
CMO_2 (mgO ₂ /kg/h)	0.61 \pm 0.10	0.80 \pm 0.10
FMO_2 (mgO ₂ /kg/h)	0.65 \pm 0.11	0.82 \pm 0.09

CMO_2 was the mean oxygen consumption rate when the temperature was constant and FMO_2 was the mean oxygen consumption rate when the temperature was fluctuating. N is the number of individuals. Groups L and S represent the groups exposed to large and small temperature fluctuations, respectively. There was no significant difference in the test diameter, dry weight, CMO_2 , or FMO_2 between groups (Mann–Whitney *U* test, all $P > 0.05$) and no difference between CMO_2 and FMO_2 within each group (Wilcoxon signed-rank test, all $P > 0.05$).

3.3. Oxygen consumption rate

The MO_2 of urchins increased with increasing water temperature, as determined by a positive Spearman's Rank correlation coefficient ($P < 0.01$, Supplemental Table 2, Fig. 4). Within each group, there was no significant difference between the CMO_2 and FMO_2 (Wilcoxon signed-rank test – Group L: $Z = -0.415$, $N = 9$, $P = 0.678$, Group S: $Z = -0.153$, $N = 10$, $P = 0.878$; Table 1). Although both the CMO_2 and FMO_2 values of urchins in Group S were higher than those of urchins in Group L, there was no significant difference between them (Mann–Whitney *U* test; CMO_2 : $U = 27$, $N_1 = 9$, $N_2 = 10$, $Z = -1.470$, $P = 0.156$; FMO_2 : $U = 27$, $N_1 = 9$, $N_2 = 10$, $Z = -1.470$, $P = 0.156$; Table 1).

3.4. Q_{10} values

The Q_{10} value decreased with increasing water temperature for the L group both during the increasing (one-way ANOVA; $F = 25.421$, $df = 2, 24$, $P < 0.001$; Fig. 5) and decreasing temperature phases ($F = 8.649$, $df = 2, 21$, $P < 0.01$; Table 2). Additionally, the Q_{10} values during the decreasing temperature phase were higher than those during the increasing temperature phase in Group L (unpaired *t*-test; all $P < 0.05$; Table 2) but there was no significant difference in these variables in Group S (unpaired *t*-test $t = -1.395$, $df = 16$, $P = 0.182$; Table 2). The Q_{10} values calculated over the range of 16.5–20.5 °C were not significantly different during the increasing temperature phase between the L and S groups (unpaired *t*-test $t = -0.109$, $df = 16$, $P = 0.914$); however, the Q_{10} values of Group L were higher than those of Group S during the decreasing temperature phase (unpaired *t*-test; $t = 2.458$, $df = 14.812$, $P = 0.027$).

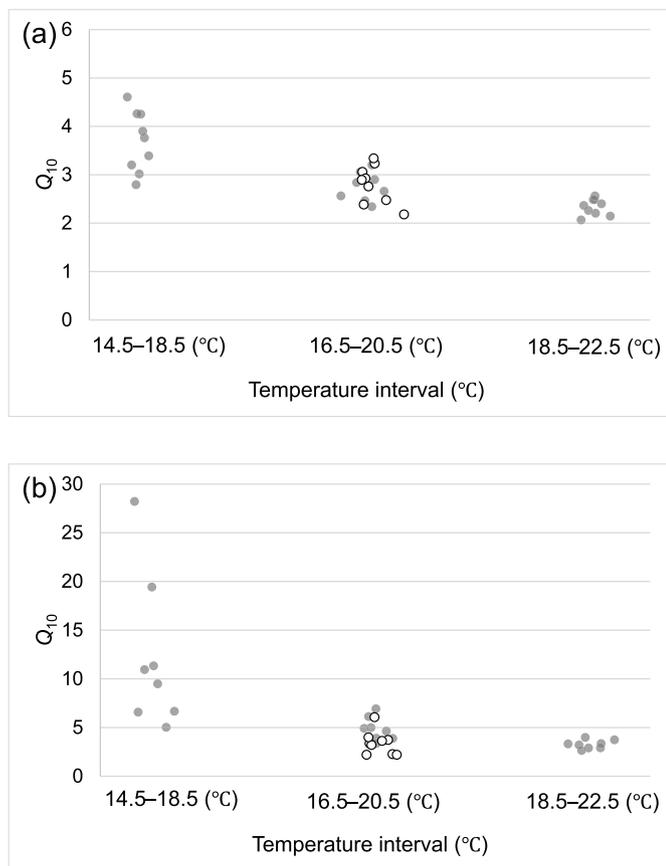


Fig. 5. Jitter plot of Q_{10} values. (a) Q_{10} value during temperature increase. (b) Q_{10} value during temperature decrease. The groups subjected to large (Group L) and small (Group S) temperature fluctuations are represented by gray and white dots, respectively. There was no significant difference in the Q_{10} of the temperature range 16.5–20.5 °C between groups during temperature increase (unpaired t -test; $t = -0.109$, $df = 16$, $P = 0.914$), but there was significant difference during temperature decrease ($t = 2.458$, $df = 14.812$, $P = 0.027$). The Q_{10} value of Group L during the temperature increase was significantly lower than that during the temperature decrease (unpaired t -test; all $P < 0.05$).

4. Discussion

The sea urchin *M. nudus* experiences large temperature fluctuations ranging from $\Delta 0.6$ to $\Delta 12.4$ °C in the coastal areas around Dokdo Island. Therefore, we hypothesized that *M. nudus* may have trouble adjusting their metabolism to widely fluctuating temperatures. When we compared the overall MO_2 of urchins held at a constant water temperature

for 1 day, and then during 3 days of temperature fluctuations, we found that there was no change in the mean MO_2 . Furthermore, the mean MO_2 was not significantly different between high and low fluctuation levels. The MO_2 was positively correlated with temperature within our experimental temperature ranges, with a Spearman's correlation coefficient of 0.386–0.887. These results support the conclusion that *M. nudus* is well adapted to the large temperature fluctuations that occur in its habitat.

Several studies have been conducted on the metabolic responses of other animals to temperature fluctuations. In Arctic char, *Salvelinus alpinus* (Lyytikäinen and Jobling, 1998), and Atlantic salmon, *Salmo salar* (Beauregard et al., 2013), the FMO_2 was found to be higher than the CMO_2 . The sea scallop *Placopecten magellanicus* and the sea cucumber *Apostichopus japonicus*, which are both passively exposed to varying thermal conditions in nature, showed different responses to thermal fluctuations in previous studies. The FMO_2 of *P. magellanicus* was lower than the CMO_2 (Pilditch and Grant, 1999), but the FMO_2 of *A. japonicus* was not significantly different from the CMO_2 (Dong et al., 2006). Similar to *A. japonicus*, in our study, the FMO_2 and CMO_2 values of *M. nudus* were not significantly different. This may suggest that animals that are regularly and passively exposed to environmental changes due to migration limitations might have been forced to adapt to their environmental conditions. Moreover, this adaptation may induce the animal to respond less strongly to temperature variations and prevent their mean MO_2 from increasing, even when the environmental temperature changes (Seebacher et al., 2015).

The rate of temperature change also could affect the metabolic activity (Eldridge et al., 2015). However, even though the rates of temperature change in this study (Group L = 1.67 °C/h; Group S = 0.83 °C/h) were much higher than those in previous studies (0.07–0.25 °C/h) (Lyytikäinen and Jobling, 1998; Pilditch and Grant, 1999; Dong et al., 2006; Beauregard et al., 2013), the FMO_2 of *M. nudus* was not different from that of CMO_2 . This suggests that the *M. nudus* individuals that inhabit areas where rapid temperature fluctuations occur could well adapt to rapid temperature changes.

Although there was no significant difference in the Q_{10} values over the range of 16.5–20.5 °C between groups L and S in this study, the Q_{10} values did decrease as the temperature increased in Group L. In addition, only the Q_{10} value calculated between 18.5 °C and 22.5 °C during the temperature increase was close to exceeding the normal biological range, even though the temperature variation observed in this study appeared normal at the collection site (Bennett, 1980). High Q_{10} values (6.93–12.84) were also exhibited in overwintering turtles due to the change in metabolic rate as a direct effect of temperature on food intake (Hochscheid et al., 2004). The MO_2 of this study was measured 2 days after the last feeding, so that there was no effect of food intake in this study. However, the high Q_{10} value could indicate that some unknown factor, other than the direct thermodynamic factor, is important (Peck

Table 2
 Q_{10} values (mean \pm SE) calculated over each temperature interval.

Temperature interval (°C)	Group L		Unpaired t -test	Group S		Unpaired t -test
	Q_{10} during temperature increase	Q_{10} during temperature decrease		Q_{10} during temperature increase	Q_{10} during temperature decrease	
14.5–18.5	3.69 \pm 0.21	12.20 \pm 2.78	$t = -3.058$ $df = 7.078$ $P = 0.018$			
16.5–20.5	2.79 \pm 0.10	4.84 \pm 0.42	$t = -4.715$ $df = 7.762$ $P = 0.002$	2.81 \pm 0.13	3.40 \pm 0.40	$t = -1.395$ $df = 16$ $P = 0.182$
18.5–22.5	2.33 \pm 0.06	3.25 \pm 0.16	$t = -5.483$ $df = 8.802$ $P < 0.001$			

Groups L and S represent the groups exposed to large and small temperature fluctuations, respectively. In Group L, the Q_{10} values decreased with higher temperature ranges, and Q_{10} values during the temperature decrease were higher than those during the temperature increase (unpaired t -test).

et al., 2006). The Q_{10} value calculated for the lower temperature range of 14.5–18.5 °C was much higher than those for other ranges. Additionally, the Q_{10} values measured during the decreasing temperature phase were higher than those during the increasing temperature phase. This indicates that the metabolism of *M. nudus* is more sensitive to low temperatures, especially during the decreasing temperature phase. *M. nudus* spawn when the water temperature begins to decrease, and the reproductive process is one of the most important things for the survival of the species (Agatsuma, 2007; Unuma et al., 2015). Therefore, they might have adapted to be more sensitive to the temperature decrease than to the temperature increase. The observed reduction in the Q_{10} value of this species' MO_2 with increasing temperature also suggests that *M. nudus* may also experience difficulty in maintaining its metabolic performance under high temperatures, and this may buffer the effects of thermal stress (Kern et al., 2015).

In the purple sea urchin, *Strongylocentrotus purpuratus*, whose distribution is similar to that of *M. nudus*, the MO_2 Q_{10} values over temperature ranges of 12–15 °C, 15–18 °C, and 18–21 °C were 1.16, 1.74, and 0.88, respectively (Ulbricht and Pritchard, 1972). Therefore, a similar tendency of Q_{10} values to decrease with increasing temperature was observed in both this species and *M. nudus*. However, the Q_{10} values and the degree of decreases in Q_{10} with increasing temperature in *M. nudus* were much higher than those in *S. purpuratus* (Ulbricht and Pritchard, 1972). Furthermore, in the green sea urchin, *Strongylocentrotus droebachiensis*, which is distributed throughout circumpolar regions in the northern hemisphere, the MO_2 Q_{10} value over 4–14 °C was 1.46, which is much lower than that of *M. nudus* even at low temperatures (Siikavuopio et al., 2008). This indicates that sea urchins that live in colder regions have reduced their metabolic rate as an adaptation to low water temperatures, and are thus less sensitive to changes in temperature over low temperature ranges. The extraordinarily high Q_{10} values we observed in *M. nudus* may be an adaptation to the widely fluctuating temperatures in its native habitat. The ability to easily acclimatize in response to temperature fluctuations may be essential to its biological functions, and this requires high sensitivity to temperature changes.

Even though sea urchin populations have been threatened by overfishing, urchin grazing may be one of the main ecological reasons for the occurrence of urchin barrens (Glynn, 1993; Hagen, 1983; Kwon et al., 2007; Yoo et al., 2004). However, in most of the cases studied, the critical factor responsible for the formation of urchin barrens has actually been found to be a change in an abiotic environmental factor, such as water temperature (Kwon et al., 2007). In this study, we determined how sea urchins respond to an abiotic factor, i.e., fluctuating water temperature, by investigating their physiological changes. Based on this, *M. nudus* appears to be well adapted to large local temperature fluctuations.

In this study, the sea urchin *M. nudus*, which passively experiences large temperature fluctuations, may possess the ability to address potential thermal stress by adapting its physiology based on its thermal history. However, given that the Q_{10} values increase with temperature increase, local warming may act as a stressor to the population. Further studies on the genetic and phenotypic responses of this species to temperature fluctuation may elucidate the hidden physiological adaptation to changing environments. This may also explain why this species is abundant even in areas with dramatic temperature fluctuations.

Conflicts of interest

All authors declare that they have no conflict of interest.

Ethical approval

All applicable international, national, and/or institutional guidelines for the care and use of animals were followed.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2019.01.003>.

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