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Respiration rates of the polyps of four jellyfish species: Potential thermal triggers and limits

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ABSTRACT

The bloom dynamics of metagenic jellyfish are regulated, to a large degree, by the asexual reproduction of benthic polyps. The ecophysiology of polyps is poorly studied compared to pelagic (ephyrae and medusae) life stages. We measured unfed (routine) respiration rates (R_R) of the polyps of four scyphozoan species (*Cyanea capillata*, *Aurelia aurita*, *Aurelia labiata* and *Aurelia limbata*) acclimated to six temperatures between 7 and 20 °C and one species (*A. aurita*) under hypoxic conditions. Strong increases (Q_{10} ~ 7 to 13) in R_R occurred after subtle warming across specific test temperatures (e.g., 12 to 15 °C for *C. capillata*, *A. labiata*, and *A. aurita*). In some species, R_R at 20 °C was lower than at 15 or 18 °C suggesting that sub-optimally warm temperatures were approached. Polyps of *A. aurita* were unable to maintain R_R below 11, 22 and 24% O_2 saturation at 8.0, 15.5 and 19.0 °C, respectively. Despite obvious differences in activity and habitat, rates of respiration in polyps, ephyrae and medusae of *A. aurita* at 15 °C appear similar after taking into account differences in body size. A literature comparison of polyp respiration rates suggests a narrowing of thermal windows in individuals collected from higher latitudes. Common garden experiments are needed to thoroughly examine potential local adaptation.

1. Introduction

Global water temperatures are expected to rise during the next decades which, along with increases in other anthropogenic pressures, are expected to increase blooms of pelagic scyphozoans in marine systems (e.g. Duarte et al., 2012; Purcell et al., 2007). Regardless of whether recent increases in the frequency of jellyfish blooms are due to climate change or natural oscillations in populations (Condon et al., 2013), warming waters have been correlated with increased abundance of scyphozoan jellyfish in some marine systems (Han and Uye, 2010; Holst, 2012; Lynam et al., 2004). Gaining a mechanistic (cause-and-effect) understanding of the factors that control bloom dynamics is important to project the ecological impacts such as altered food web dynamics as well as the consequences to various economic sectors such as fisheries and aquaculture (reviewed in Purcell et al., 2007).

In the metagenetic life cycle of scyphozoans, benthic polyps play a critical role in population persistence. Polyps strobilate to produce ephyrae which mature into adult medusae which sexually reproduce to form planula larvae which settle and metamorphose into polyps thus closing the life cycle. Polyps are most often found in shallow (0 to 15 m) coastal areas but can occur to depths of 120 m (Hernroth and Gröhndahl, 1983; Miyake et al., 2002; Toyokawa, 2011). Polyps of some species display high tolerance to hypoxia which increases their likelihood of persisting in benthic habitats and successfully outcompeting other fouling organisms such as mussels or barnacles (Condon et al., 2001; Ishii and Katsukoshi, 2010; Ishii et al., 2008; Miller and Graham, 2012). Temperature and prey availability interact to affect the reproduction and growth of polyps (Di Camillo et al., 2010; Lucas et al., 2012) with the former acting as a trigger for asexual reproduction such as budding and/or strobilation (Holst, 2012; Liu et al., 2009) and the en/excystment of polyps (Brewer and Feingold, 1991). Surprisingly, to the best of our knowledge only one previous study (Mangum et al., 1972) has examined the effect of temperature on respiration rates of scyphozoan polyps.

The present study measured the unfed (routine) respiration rate (R_R) of polyps of four scyphozoan species (*Cyanea capillata, Aurelia aurita, Aurelia limbata and Aurelia labiata*) acclimated to six temperatures between 7 and 20 °C. Polyps of the five groups (two populations of *A. aurita*) originated from either oceanic or coastal waters displaying different annual ranges in water temperature (Fig. 1) which could provide interesting contrasts in thermal windows of R_R. The effect of oxygen concentration on R_R of *A. aurita* polyps was also examined. Since changes in R_R have important consequences for the energy available for growth and reproduction, these measurements could shed light on how thermal windows (and oxygen concentrations) constrain the distribution and productivity of polyp populations in nature.

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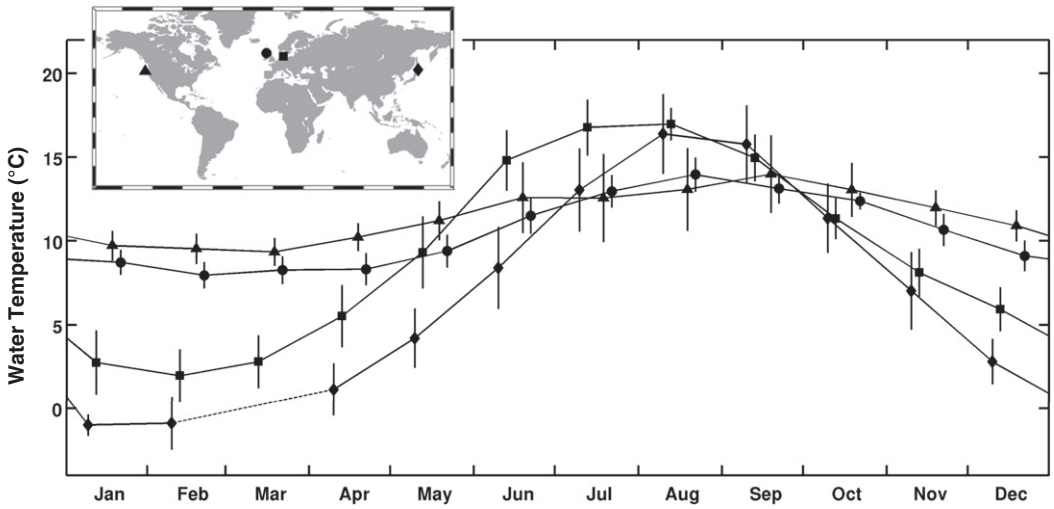

Fig. 1. Mean (±SD) monthly water temperatures at each of the four areas where scyphozoan polyps were collected for this study. The region of field collection is shown on the inset map. Temperatures were compiled from the World Ocean Atlas (WOA) database. The points were slightly shifted along the x-axis for visual clarity.

2. Material and method

2.1. Origin and maintenance of the polyps

Polyps of *A. aurita* and *C. capillata* were collected from Kiel Bight (southwest Baltic Sea, 54.4°N, 10.2°E) and polyps of *A. aurita* were also obtained from the Hebrides, west coast of Scotland (North Atlantic, 57.6°N, 7.0°W). Two other *Aurelia* species originated from Pacific waters: polyps of *A. labiata* were from Coos Bay, Oregon (northeast Pacific 43.4°N, 142.2°W) and *A. limbata* was collected from northern Japan (Sea of Okhotsk, 44.2°N, 144.3°E) (Fig. 1). Polyps were maintained in laboratory cultures for >5 years at 15 °C using 0.7 μm filtered seawater at a salinity of 32. Polyps were maintained without aeration in darkness (except a brief period each week when polyps were fed and the water changed). For several months prior to testing, polyps were fed late-stage copepodites (C5–C6) of a calanoid copepod (*Acartia tonsa*). Prior to the experiment, polyps were slowly acclimated (2.5 °C week^{-1}) to one of six test temperatures and maintained at that temperature for at least 2 weeks prior to measurements. Polyps had not received food for 2 or 3 days prior to respiration measurements.

2.2. Respiration measurements

The R_R of individual polyps was measured at six temperatures: 7, 10, 12, 15, 18 and 20 °C (except *A. labiata* not measured at 18 °C) using a Unisense A/S Micro-respiration System (Århus, DK, OX-10 sensor) equipped with 750-μl chambers submerged within a temperature-controlled (±0.2 °C) water bath. Oxygen diffusion between the chambers and the water bath, tested prior to the start of each experiment, was negligible. The water within each chamber was well mixed by a small stir magnet (120 rpm) separated from the polyp by a mesh screen. The chambers were large enough to easily accommodate the largest polyps (diameter and height of the chamber were roughly twice the width and height of those polyps) but small enough to ensure that the respiration of polyps was easily registered. Seawater was filtered (0.7 μm) and autoclaved to avoid bacterial contamination. All components of the system were cleaned with ethanol prior to each trial. A total of 24 trials was conducted (Table 1) with, most often, six chambers with one polyp and two control (blank) chambers with only seawater and a small volume of transfer water from polyp cultures. Trials were conducted over a 3-month period during which two or three scyphozoan groups/species were run in the same trial (except *A. limbata*) and test temperatures were always run in a random order.

During each trial, each polyp had a short (7-min) acclimation period to the chamber prior to the first measurement period. Over the course of several hours, the oxygen concentration in each chamber was repeatedly measured four to seven times (a measurement lasted 7 to 10 min with only the middle 3 min used for analyses to avoid noise). In each temperature trial, oxygen within the chambers was never <55% saturation (pilot tests suggested that R_R was constant until O_2 was <30% saturation — see below). Differences between the two blank chambers were always <10% and the mean rate of oxygen consumption in these two chambers was always <50% of that of chambers with polyps and was often much less (<30% in the majority of trials). Directly after each trial, polyps were dipped into distilled water to wash away salt and frozen at −80 °C. Samples were subsequently freeze-dried (Christ

Table 1
Summary information for trials measuring the respiration rate (R_R) of the polyps of five groups of scyphozoans: *Aurelia aurita* collected in the Baltic Sea (Aa1) and northeast Atlantic (Aa2), *Aurelia labiata* (Ala), *Aurelia limbata* (Ali) and *Cyanea capillata* (Cc).

Trial	T	Species	Polyps	Polyp dry weight (μg)	
ID	(°C)	(ID)	(n)	Minimum	Maximum
1	15	Aa1, Cc, Ala	2, 2, 2	117	263
2	15	Aa1, Cc, Ala	2, 2, 2	190	303
3	18	Aa1, Cc	2, 2	219	464
4	18	Aa1, Cc	2, 2	263	397
5	20	Aa1, Cc, Ala	2, 2, 2	186	413
6	20	Aa1, Cc, Ala	2, 2, 2	119	366
7	12	Aa1, Cc, Ala	2, 2, 2	132	346
8	12	Aa1, Cc, Ala	2, 2, 2	123	257
9	10	Aa1, Cc, Ala	2, 2, 2	78	240
10	10	Aa1, Cc, Ala	2, 2, 2	55	176
11	10	Aa2	4	177	370
12	12	Aa2	4	279	490
13	15	Aa2	4	204	377
14	18	Aa2	4	249	405
15	20	Aa2	4	137	172
16	7	Aa1, Cc, Ala	2, 2, 2	66	260
17	7	Aa1, Cc, Ala	2, 2 ,1	56	276
18	7	Aa2	4	217	346
19	10	Ali	4	83	212
20	7	Ali	4	21	59
21	15	Ali	4	81	140
22	12	Ali	4	83	95
23	18	Ali	4	82	119
24	20	Ali	4	82	156