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 ($Q_{10} \sim 7$ 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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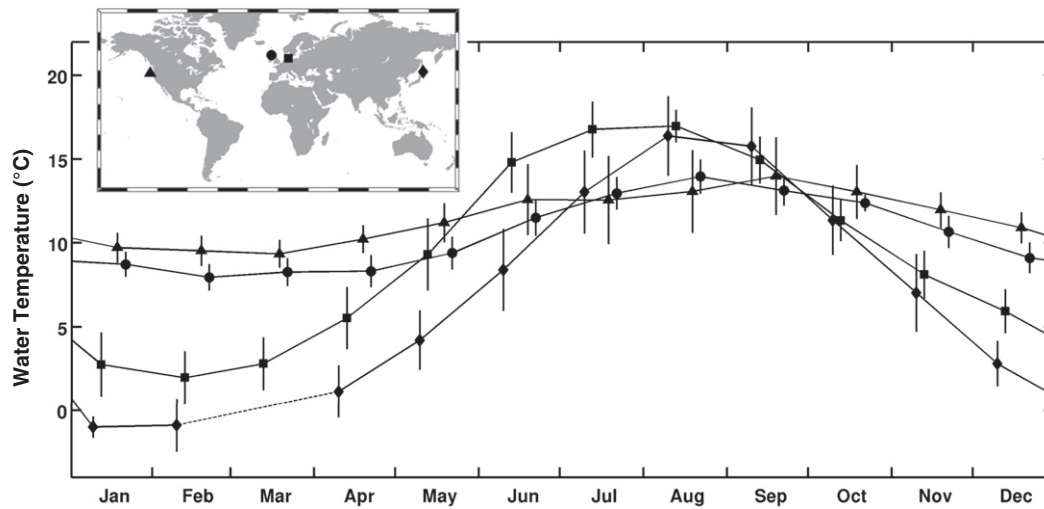 *E-mail address:* myron.peck@uni-hamburg.de (M.A. Peck).

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

LCG) for >16 h, and dry weight (*DW*) was measured (Sartorius, 4503 MP6 microbalance, ± 0.1 μg).

In a second series of trials, the R_R of polyps of *A. aurita* collected from the southern North Sea (Helgoland, 54.18°N, 7.88°E) was measured at acclimation temperatures of 8.0 (n = 2 polyps), 15.5 (n = 4) and 19.0 °C (n = 4). During these trials, polyps were allowed to consume all of the oxygen within the chambers. These runs provided estimates of the point at which R_R was no longer independent of O_2 saturation (the P_c, where oxygen regulators become oxygen conformers). The same technique was used by Rutherford and Thuesen (2005) to examine the P_c in 12 jellyfish (scyphozoan and hydrozoan) species.

2.3. Calculations and statistics

The rate of oxygen consumption was calculated from the slope of the linear decrease in O_2 concentration versus time (predictive regressions). Within each trial, the mean slope of the two control chambers was subtracted from that of each polyp chamber to obtain estimates of R_R (ng O_2 polyp^{-1} h^{-1}). Significant differences in polyp *DW* and R_R within groups among temperatures were tested using ANOVAs followed by a Tukey-HSD post-hoc test. Data were log-transformed to meet assumptions of normality and homogeneity of variances. In the trials examining O_2 saturation, slopes of linear regressions between adjacent measurements of O_2 concentration were calculated (yielding estimates of R_R) and a two-segment (broken stick) regression was fit to R_R vs % O_2 saturation. All statistical tests were conducted using R software (R Core Team, 2012).

3. Results

Significant differences existed in the *DW* of polyps among the different test temperatures in the four groups: (ANOVAs: *A. aurita* Baltic Sea (df = 5, 18) (F = 6.3) (p < 0.01), *A. aurita* northeast Atlantic (df = 5,

17) (F = 5.8) (p < 0.01), *A. labiata* (df = 4, 14) (F = 16.3) (p < 0.001), *C. capillata* (df = 5, 18) (F = 4.5) (p < 0.01)). Therefore, R_R was standardized to a common *DW* within each group using the equation:

$$log(R_{Rcorr}) = log\left(R_{Rp}\right) - \left(log\left(DW_p\right) - log(DW_i)\right) * 0.75 \qquad (1)$$

where DW_p and R_{Rp} are the dry weight (μg) and observed R_R (ng O_2 h^{-1}) of a polyp in group i, and DW_i is the mean dry weight of all polyps within group i. The value 0.75 was the mean slope (b = 0.754) of significant (p < 0.05), inter-specific regressions of polyp R_R versus *DW* ($R_R = aDW^b$) at five temperatures (7 °C, b = 0.676, R^2 = 0.77; 10 °C, b = 0.574, R^2 = 0.75; 12 °C, b = 0.808, R^2 = 0.77; 18 °C, b = 0.829, R^2 = 0.70; 20 °C, b = 0.759 R^2 = 0.74). Using Eq. (1), the R_R of polyps of *A. aurita* Baltic, *A. aurita* NE Atl, *C. capillata*, *A. labiata*, and *A. limbata* was standardized to a DW_i of 300, 525, 400, 150, and 150 μg, respectively.

3.1. Polyp respiration versus temperature

At the six temperatures, R_R was between 150 and 450 ng O_2 polyp^{-1} h^{-1} in *A. aurita* collected from the Baltic Sea (300-μg *DW*) and the northeast Atlantic (525 μg *DW*) as well as *C. capillata* (400 μg *DW*) (Fig. 2A–C). In the somewhat smaller (150 μg-*DW*) polyps of *A. labiata* and *A. limbata*, R_R was generally <200 ng O_2 polyp^{-1} h^{-1}, (Fig. 2D–E). In general, R_R was lower at colder temperatures and increased at warmer temperatures but an exponential increase with increasing temperature was not observed. Moreover, each group displayed relatively large changes in R_R across relatively small changes in temperature as described below.

Between 12 and 15 °C, polyps of *A. aurita* and *C. capillata* collected from the Baltic Sea displayed significant increases in R_R represented by Q_{10} values of ~13 and 7.5, respectively (Fig. 2A and C). Polyps of
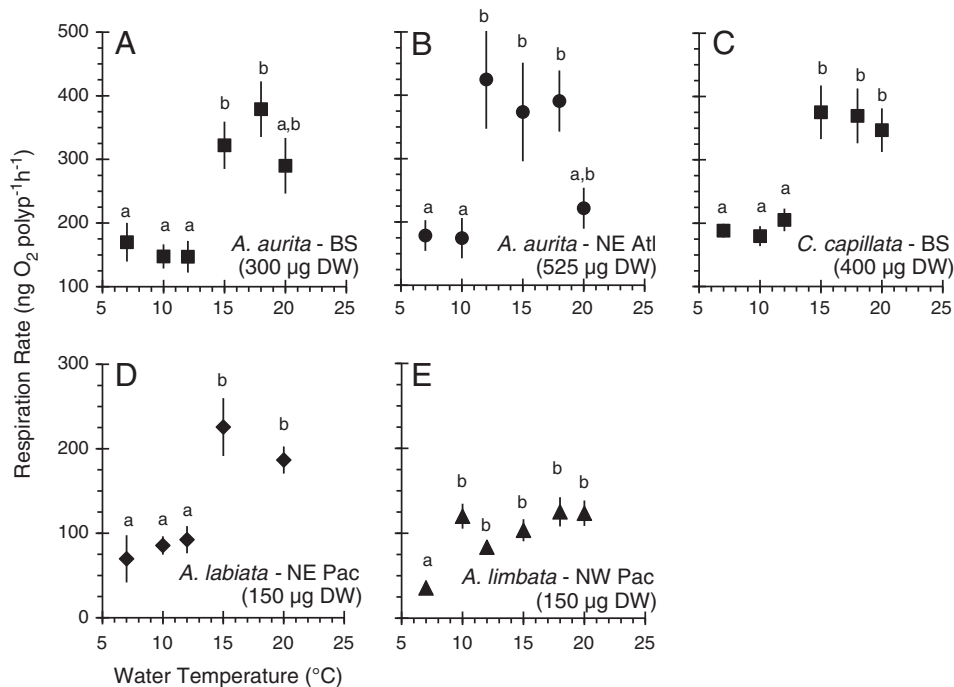
Fig. 2. Mean (±SE) respiration rate (ng O_2 h^{-1}) of individual polyps (n = 3 to 4) acclimated to different water temperatures. Five groups were tested (Panels A–E, symbols refer to collection locations in Fig. 1). For each group, respiration rates were standardized to a common polyp dry weight (*DW*). Within each panel, rates not sharing a common letter were significantly different at the p > 0.05 level. (ANOVA and Tukey HSD), Panel A: F(5, 18) = 9.793, p < 0.001; Panel B: F(5, 17) = 6.248, p < 0.01; Panel C: F(5, 18) = 12.61, p < 0.0001; Panel D: F(4, 14) = 18.27, p < 0.0001; Panel E: F(5, 16) = 10.49, p < 0.001.

A. aurita collected from the northeast Atlantic displayed a significant increase in R_R between 10 and 12 °C, and a significant reduction in R_R at 20 °C (Fig. 2B). In *A. labiata,* a greater than two-fold (significant) increase in R_R also occurred between 12 and 15 °C (Fig. 2D). Finally, mean R_R of *A. limbata* polyps was significantly lower at 7 °C but similar at all warmer temperatures.

3.2. Polyp respiration versus oxygen saturation

The R_R of *A. aurita* polyps remained fairly constant until certain, critical O_2 saturations were reached and then R_R decreased monotonically with decreasing oxygen concentration. Based upon breakpoints in two-segment regressions, the mean ($\pm$SE) P_c at 8.0, 15.5 and 19.0 °C was equal to 10.7 ($\pm$1.7), 24.3 ($\pm$1.3) and 22.1 ($\pm$5.7) % O_2 saturation, respectively. All segmented regressions were significant ($p < 0.001$) and described between 77 and 98% of the variability in polyp respiration rates (2, 4 and 4 polyps at 8.0, 15.5 and 19.0 °C, mean ($\pm$SE) *DW* of 1108.5 ($\pm$155.2), 928.7 ($\pm$119.3), and 948.2 ($\pm$187.1) μg, respectively).

4. Discussion

Optimal and sub-optimal ranges in temperature and critical thermal limits exist in all poikilotherms (Pörtner and Farrell, 2008) and a lack of research on thermal windows in jellyfish limits our ability to project how warming might affect (or potentially limit) life cycle and bloom dynamics. Previous work on benthic polyps of scyphozoans indicates that temperature not only influences respiration rates (Mangum et al., 1972; this study) but also other aspects of growth physiology including the induction and rate of strobilation, the quantity of ephyrae produced (e.g. Di Camillo et al., 2010; Fuchs et al., 2014; Holst, 2012; Liu et al., 2009; Lucas et al., 2012; Purcell, 2007) as well as the rate of asexual reproduction (budding) and growth rate of polyp populations (Di Camillo et al., 2010; Ishii and Katsukoshi, 2010; Lucas et al., 2012; Purcell, 2007).

Polyp budding and strobilation occur at different times of the life cycle (Di Camillo et al., 2010) and these processes appear to be linked to different temperatures (Han and Uye, 2010; Liu et al., 2009). For example, Han and Uye (2010) reported prey level-dependent induction of strobilation (at a specific, cold temperature) and budding (at warm temperatures). Furthermore, the strobilation process is known to be controlled by both retinoic acid signaling and up-regulation of specific proteins in response to a "temperature sensitive timer" (Fuchs et al., 2014). The work of Han and Uye (2010) suggests the presence of "summer" and "winter" metabolic strategies, a distinction that could explain the changes in R_R observed with increasing temperature in the present study. The distinct increase in R_R between 12 and 15 °C in *A. aurelia*, *A. labiata* and *C. capillata* could be due to shifts in metabolic/growth strategy. In ephyrae, a similar threshold-like effect of temperature is evident in respiration rates measured by Møller and Riisgård (2007). In that study, respiration rates from 7 to 11.5 °C were essentially unchanged but strongly, exponentially increased (Q_{10} ~ 4.0) from 11.5 to 22 °C. It is important to note that, although we are confident in the measurements made here, only 3 or 4 polyps were measured at each temperature.

Thermal limits to growth and survival arise from oxygen- and capacity-limited thermal tolerance (Pörtner and Farrell, 2008). Critical thermal limits are normally associated with decreases in aerobic and increases in anaerobic metabolism. Although, the present study did not measure anaerobic metabolism, polyps of *A. aurita* collected from the northeast Atlantic had much lower R_R at 20 °C compared to 15 and 18 °C, and polyps of other groups/species displayed modest declines in R_R at temperatures ≥18 °C. These temperatures are warmer than any monthly mean temperature reported for the sites of collection (44 to 58°N) of these groups of polyps (Fig. 1). Besides the present study, to the best of our knowledge only one previous study (Mangum et al.,

1972) has reported respiration rates of scyphozoan polyps. In that study, *A. aurita* polyps from Chesapeake Bay (37°N) acclimated to 12 and 20 °C exhibited an exponential increase in respiration rates with warming to 32 °C (Fig. 3, inset). After converting to common units, the rates measured here and those reported by Mangum et al. (1972) agree well from 12 to 18 °C but rates at 20 °C were much lower in higher latitude conspecifics measured here (Baltic Sea and NE Atlantic, 54 to 58°N). Furthermore, lower latitude conspecifics died at <12 °C whereas higher latitudes polyps could be acclimated to (and grown at) 7 °C. Common garden experiments with polyps from different latitudes are needed to test for potential adaptation to local thermal conditions.

A. aurita is a particularly well-studied scyphozoan and respiration rates at 15 °C have been measured in medusae (Frandsen and Riisgård, 1997; Ishii and Tanaka, 2006; Kinoshita et al., 1997; Larson, 1987; Uye and Shimauchi, 2005), ephyrae (Frandsen and Riisgård, 1997; Kinoshita et al., 1997; Møller and Riisgård, 2007) and polyps (Mangum et al., 1972; this study). Respiration rates of *A. aurita* polyps, ephyrae and medusae at 15 °C appear to agree well after taking into account differences in body size (Fig. 3). Interestingly, respiration rates of ephyrae (Møller and Riisgård, 2007) appear to be similar to polyps (this study) at similar body masses (and temperatures) despite obvious differences in morphology and activity between these two life stages. Although our study was not designed to test for the effects of *DW* on respiration rate within each species/group, the slopes of inter-specific regressions of R_R versus *DW* (values of b in $R_R = a * DW^b$) were always <1.0 (mean 0.75). Arguments have been made that, with increasing body size, the metabolic rates of pelagic (active) and benthic (inactive) life stages of jellyfish should scale isometrically (b = 1) and allometrically (b ≠ 1), respectively. Intra-specific (*A. aurita*) regressions describing the pooled data collected at 15 °C in 3 studies on ephyrae (<10 mg *DW*) and 5 studies on medusae (>10 mg *DW*) had mean ($\pm$SE) slopes of 0.646 ($\pm$0.039) and 0.904($\pm$0.023), respectively (Fig. 3). Although one should be cautious of pooling data collected in different studies (due to potential differences in methods), our findings support the idea that the slope is closer to isometric in medusae as suggested by Glazier (2006). Ideally, such an intra-specific (inter-stage) comparison would be made on the same population using similar methods.

Various metagenic life stages of jellyfish (medusae, planula larvae, polyps) appear particularly tolerant to low concentrations of dissolved oxygen (Miller and Graham, 2012; Rutherford and Thuesen, 2005; Shoji et al., 2005) likely due to their high body water content and ability to store oxygen within the intragel layer (Theusen et al., 2005). The settlement of planula larvae appeared to be enhanced (more rapid) under hypoxic conditions (Ishii et al., 2008; Miller and Graham, 2012). Polyps of *A. aurita* maintained at 22 °C died within 7 days at 0.2 ml O_2 l^{-1} but grew well at 2.0 ml O_2 l^{-1} (Ishii et al., 2008) which are ~10% and ~40% oxygen saturation, respectively. These results are not unexpected given the marked reduction in R_R at <20% O_2 saturation observed at both 15.5 and 20 °C in the present study. Lower oxygen thresholds (between 10 and 25% saturation = 0.5 and 1.6 mg O_2 l^{-1} at 22 to 24 °C) were found for the survival and growth of polyps of another scyphozoan (*Chrysaora quinquecirrha* (DeSor)) collected from Chesapeake Bay, where seasonal hypoxia is a common feature (Condon et al., 2001).

In conclusion, we observed non-exponential increases in the respiration rates of polyps with increasing temperature which may be related to temperature-dependent changes in life history/growth strategies and warm thermal limits of high-temperate populations. At the same temperature, respiration rates of pelagic ephyrae and medusae appear similar to those of benthic polyps in *A. aurita* after taking into account differences in body size. Polyps originating from lower and higher latitudes appear to have different thermal windows for growth and survival. Common garden experiments are needed to test for potential physiological adaptations of polyps to local temperature regimes and severity of hypoxia. A better understanding of the environmental triggers and physiological constraints of field populations of polyps is
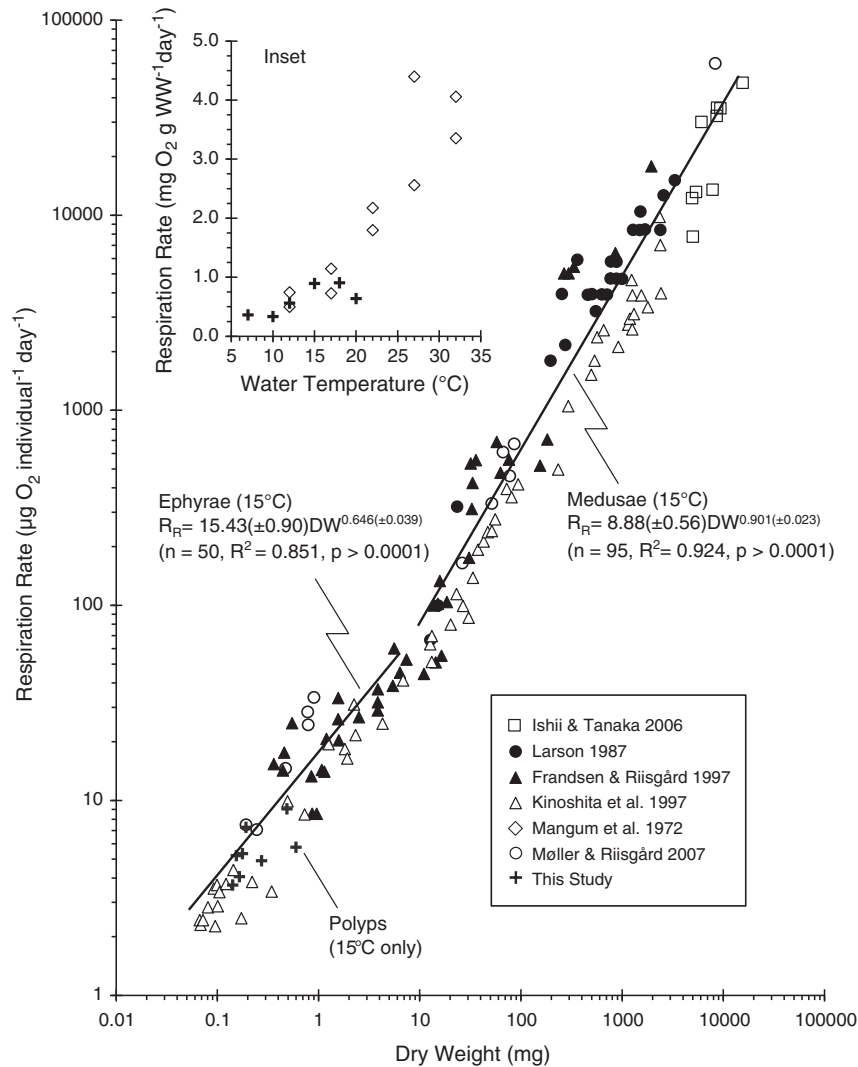
Fig. 3. Respiration rate (μg O₂ individual^{-1} day^{-1}) versus dry weight (mg) of *Aurelia aurita* polyps, ephyrae and medusae at 15 °C. A dry weight (*DW*) of 10 mg separates ephyrae from medusa. The two regression lines (mean ± SE parameter estimates provided) were fit to the pooled data of 3 and 5 studies on ephyrae and medusae, respectively. Inset: effect of water temperature on respiration rate (displayed in units of mg O₂ g wet weight (WW)$^{-1}$ day^{-1}) of polyps of *A. aurita* collected from the Chesapeake Bay (Mangum et al., 1972) and from the Baltic Sea and northeast Atlantic shelf (this study). Note, unlike Fig. 2, *DW* and R_R were measured values (not standardized) and (data for both Baltic and NE Atl groups are shown). For conversion to units of WW, *DW* was assumed to be 5% WW (Uye and Shimauchi, 2005).

needed to advance our predictive capacity of jellyfish blooms using ecosystem models and other tools (Gibbons and Richardson, 2013).

Acknowledgments

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