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RESEARCH ARTICLE

Effects of temperature on the respiration of brooded larvae from tropical reef corals

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SUMMARY

This study describes the effects of temperature on the respiration of brooded larvae of scleractinian corals, and evaluates the implications of these effects relative to seawater temperature when peak larval release occurs. Respiration rates of larvae from *Pocillopora damicornis*, *Seriatopora hystrix* and *Stylophora pistillata* were quantified in darkness as oxygen uptake during 1–3 h exposures to five temperatures between 26.4 and 29.6°C. To assess the biological significance of these experiments, the temperature of the seawater into which larvae of *P. damicornis* and *S. hystrix* were released was measured for 32–34 months over 5 years between 2003 and 2008. Mean respiration varied from 0.029 to 0.116 nmol O_2 larva^{-1} min^{-1}, and was related parabolically to temperature with a positive threshold at 28.0°C. The temperature coefficients (Q_{10}) for the ascending portion of these relationships (Q_{10}=15–76) indicate that the temperature dependency is stronger than can be explained by kinetics alone, and probably reflects behavioral and developmental effects. Larval release occurred year-round in synchrony with the lunar periodicity when seawater temperature ranged from 21.8 to 30.7°C, and more than half of the sampled larvae were released at 27.5–28.9°C. The coincidence on the temperature scale of peak larval release with the thermal threshold for respiration suggests that high metabolic rates have selective value for pelagic coral larvae. The large and rapid effects of temperature on larval respiration have implications for studies of the effects of climate change on coral reproduction, particularly when seawater temperature exceeds ~28°C, when our results predict that larval respiration will be greatly reduced.

Key words: temperature, larvae, respiration, Scleractinia.

INTRODUCTION

Biphasic life cycles with pelagic larvae and benthic adults are common in marine invertebrates, and considerable effort has been expended to understand the evolutionary origin and ecological consequence of this arrangement (Raff, 2008). Describing the biology of pelagic larvae has been a centerpiece of this effort, particularly with regard to the factors determining pelagic larval duration (PLD) and the potential for dispersal prior to settlement (Cowan and Sponaugle, 2009). The extent to which larvae are planktotrophic and capable of feeding *versus* lecithotrophic and dependent on energy reserves is a key feature modulating PLD (Strathmann, 1985), but the nutritional strategy is discounted against the metabolic rate, which determines the speed with which food is consumed to meet the energetic costs of development. Accordingly, measurements of respiration have featured prominently in studies of marine pelagic larvae (Crisp, 1976; Hoegh-Guldberg and Manahan, 1995; Marsh and Manahan, 1999).

The respiration of pelagic larvae is strongly affected by biological and physical processes, for example, scaling with larval size (Manahan, 1990), changing with development to reflect the metabolic costs of ontogeny (Hoegh-Guldberg and Manahan, 1995; Marsh and Manahan, 1999) and covarying with temperature (Sprung, 1984). The influence of temperature on respiration is a well-known example of biophysical coupling affecting pelagic larvae (e.g. Lough and Gonor, 1973; Sprung, 1984; Edmunds et al., 2001), and the response is characterized by a parabola whose apogee represents a threshold beyond which the stimulatory effect of temperature is reversed. In the simplest form, this relationship is described by the Q_{10} coefficient – the proportional change in respiration caused by a 10°C increase in temperature (Hochachka and Somero, 2002) – but the magnitude of the coefficient varies with the temperature range over which it is calculated. If the effects of temperature on metabolism are driven solely by enzyme kinetics, respiration can be expected to increase approximately twofold with a 10°C rise in temperature (Hochachka and Somero, 2002), although the accuracy of this prediction is determined by the relationship between the temperature range investigated and the thermal threshold, which is often unknown. The effect of temperature on larval metabolism has intrinsic importance to the ecological objective of elucidating the role of abiotic factors in determining community structure (Agrawal et al., 2007), because temperature can serve as a density-independent factor modulating the contribution of pelagic larvae to adult populations. The effects of temperature have, however, acquired new significance in the context of global climate change because rising temperature increases larval metabolism, which tends to accelerate overall development, shorten PLD, reduce dispersal distances and modify population connectivity (O'Connor et al., 2007).

Tropical scleractinian corals provide an interesting system in which to study the effects of temperature on larval metabolism, because members of this taxon are classically viewed as living close to their upper thermal limit and, therefore, are susceptible to increases in temperature such as those occurring through global climate change (Hoegh-Guldberg et al., 2007). This notion is

supported by the widespread mortality of corals as a result of thermal bleaching (Hoegh-Guldberg et al., 2007). Moreover, strong reproductive synchrony within a coral population (Harrison et al., 1984; Levitan et al., 2004) and in concert with external cues, such as lunar phases (Fan et al., 2002), creates a situation where the success of gametes and larvae is dependent, in part, on their metabolic response to the thermal conditions at the time of spawning. It is reasonable, therefore, to expect that the metabolism of pelagic coral larvae responds to temperature in ways that promote success, specifically to ensure that the energetic costs of development [e.g. fig. 5 in Hoegh-Guldberg and Manahan (Hoegh-Guldberg and Manahan, 1995)] can be matched by the supply of ATP though respiration. This process is fueled by a variety of respiratory substrates, including lipids – which comprise a large fraction of the biomass of coral larvae (Richmond, 1987) – and food resources obtained through heterotrophy and, for larvae containing *Symbiodinium*, autotrophy (Richmond, 1987).

The objectives of this study were to describe the effects of temperature on newly released brooded coral larvae and evaluate whether the responses are ecologically significant relative to the timing of larval release and the contemporaneous seawater temperature. Although only 17% of scleractinians brood their larvae, this amounts to 74 species (Harrison, 2011), many of which are ecologically important; most have been overlooked in favor of spawning corals as model systems for contemporary studies of coral larvae (Harrison, 2011). In the present analysis, three brooding pocilloporid corals from shallow fringing reefs in southern Taiwan were studied, and were selected because their reproductive biology in this location is well known (Fan et al., 2002; Fan et al., 2006). The study consisted of two parts: first, the metabolic response of larvae to temperature was assessed by measuring their oxygen uptake during short periods (<3 h) at one of five temperatures; second, the timing of larval release from two of the species over multiple years was combined with records of seawater temperature to characterize the thermal environment into which the larvae were released. These data were used as a framework to interpret the biological significance of the temperature–metabolism relationships. Finally, a compilation of published values for the respiration of coral larvae was used to contextualize the present results and evaluate the extent to which they are likely to be representative of the Scleractinia.

MATERIALS AND METHODS

Experiments were completed in 2010 at the National Museum of Marine Biology and Aquarium (NMMBA), Taiwan, using corals from the shallow fringing reefs of Nanwan Bay. To obtain larvae, colonies (*ca.* 20 cm diameter) of the brooding corals *Pocillopora damicornis* (Linnaeus 1758), *Seriatopora hystrix* Dana 1846 and *Stylophora pistillata* Esper 1797 were collected from ~6 m depth at Hobihu Reef (21°56.799′N, 120°44.968′E), 1 week before the new moon of 15 March, when the ambient seawater temperature was 25.3°C. Eight colonies of each species were placed into individual aquaria exposed to partially shaded natural sunlight (noon irradiances of ~500 μmol photons m^{-2} s^{-1}); aquaria received sand-filtered seawater (at the ambient temperature of 25.3°C) that spilled into a cup fitted with plankton mesh to retain larvae. The corals were checked daily for larval release (at ~07:00 h), which occurs just before dawn in these species (Fan et al., 2006), and freshly released larvae were harvested and combined among colonies of each species. Although larvae were obtained from all eight colonies, the number released on any one day differed among colonies; therefore, maternal genotypes were represented unequally in the pooled larvae for each species. The pooled larvae were stirred gently to ensure a haphazard sampling from parent colonies, and larvae were allocated to various experiments, one of which is described here. A small number of freshly released larvae were selected haphazardly and measured for length and width using a dissecting microscope and an eyepiece micrometer. Although brooded coral larvae differ among days of release within a single spawning (Putnam et al., 2010), logistical constraints prevented a contrast of temperature effects on respiration among release days. The possible consequences of such variation were minimized by the random application of temperature treatments, with each treatment applied on a separate day using larvae released on that day, and by completing the experiments on lunar days over which the variation in larval phenotype was small (V.C., T.-Y.F. and P.J.E., unpublished data) (Putman et al., 2010).

The aerobic respiration of larvae was measured between 18 and 24 March, using batches of six larvae in a glass vial. Trials in which the oxygen consumption (% O_2 h^{-1}) of *P. damicornis* larvae in darkness was titrated against the number of larvae (two to nine) revealed a significant linear relationship ($F_{1,4}$=89.630, P=0.001) for which the y-intercept did not differ significantly from zero (t=2.068, d.f.=5, P=0.107); respiration rates (nmol O_2 $larva^{-1}$ min^{-1}) stabilized with approximately five larvae in the chamber, and therefore subsequent trials were completed with six larvae. Respiration rates were measured in 2 ml glass Wheaton vials filled with filtered seawater (50 μm) aerated and equilibrated to the treatment temperature. Temperatures were maintained using chillers (Hipoint, Taiwan, models LC-06 and LC-10, stability ±0.1°C), and measured with a certified digital thermometer (Fisher Scientific, Pittsburgh, PA, USA; model 15-077-8, accuracy ±0.05°C). Trials were completed at 26.4°C (18–19 March), 29.6°C (20 March), 28.0°C (22 March), 27.0°C (23 March) and 28.9°C (24 March).

Larval respiration was calculated from the O_2 concentration at the start and end of 1–2 h incubations, as measured using an optrode (FOXY-R, 1.58 mm diameter, Ocean Optics, Dunedin, FL, USA) attached to a spectrophotometer (USB2000, Ocean Optics) and computer running the manufacturer's software (OOISensors, version 1.00.08, Ocean Optics, Dunedin, FL, USA). This technology relies on O_2-dependent quenching of fluorescence from an encapsulated Ruthenium compound, and it is well suited to studies of larval metabolism as the optrode does not consume O_2 and is unaffected by flow speed (Klimant et al., 1995). The optrode was calibrated with a zero solution (sodium sulphite and 0.01 mol l^{-1} sodium tetraborate) and an O_2 maximum created in water-saturated air within a vial held at the measurement temperature. Percentage O_2 saturation was converted to concentration in seawater of a known temperature and salinity (measured with a refractometer) using tabulated constants [N. Ramsing and J. Gundersen at http://www.unisense.com/Default.aspx?ID=1109, based on Garcia and Gordon (Garcia and Gordon, 1992)]. O_2 concentrations were measured with the sample immersed in a water bath held at the same temperature as the incubation conditions.

Wheaton vials were stocked with six larvae from a single species, with four vials per temperature for each of the three species when sufficient larvae were obtained; this target was not always obtained, particularly for *S. pistillata*. One incubation temperature was completed each day, and four control vials without larvae accompanied vials with larvae. The initial O_2 concentration was determined by analyzing the water used to fill the vials, with preliminary analyses demonstrating that this concentration was identical to that of the vial immediately after the larvae were added. Vials were sealed with Parafilm™, immersed in darkness in the water reservoir of the chillers, and left for 1–3 h for respiration to deplete the O_2. This regimen ensured that the mean O_2 saturation

remained ≥87% throughout the incubations, thereby reducing the likelihood that respiration was affected by O_2 saturation (Edmunds and Spencer Davies, 1988; Shick, 1990). As Parafilm^{TM} is slightly permeable to O_2, we measured the O_2 flux into Wheaton vials filled with filtered seawater depleted to 83% O_2 saturation (by bubbling with nitrogen gas) and capped with either Parafilm^{TM} or Parafilm^{TM} plus an impermeable polypropylene cap fitted with a foil insert. The change in O_2 concentration within the vials was unaffected by the type of cap (t=0.067, d.f.=18, P=0.948); therefore, diffusion of O_2 through the Parafilm^{TM} did not appreciably alter the measurement of O_2 uptake by coral larvae.

Periodic inspection of the vials using a weak red light revealed that the larvae of *P. damicornis* and *S. pistillata* swam actively throughout the dark incubations, although *S. hystrix* larvae tended to settle on the glass. At the conclusion of incubations, vials were removed from the water, inverted gently to ensure mixing, and analyzed for O_2 saturation using the optrode described above. The styling of the optrode as a needle allowed it to be inserted into the vial, through the Parafilm^{TM} top, without exposing the seawater in the vial to air. The O_2 saturation in the seawater within the vial was then measured at the incubation temperature and converted to O_2 concentration, with the change in concentration serving as the measure of aerobic dark respiration after adjusting for O_2 fluxes in control vials.

Larval respiration was expressed as nmol O_2 larva^{-1} min^{-1} and analyzed using two approaches. First, respiration was compared among temperatures and species using a fixed effects (model I) two-way ANOVA, with the statistical assumptions of this procedure tested through graphical analyses of the residuals. Where main effects were detected, Tukey's honestly significant difference (HSD) *post hoc* analyses were used to identify the paired contrasts that differed significantly. Second, the non-linear relationships between respiration and temperature were characterized by second-order polynomials fitted to the mean respiration rates by least squares techniques.

To provide a context to interpret the respiration rates of coral larvae, we used (1) an earlier study to quantify the seawater temperature into which coral larvae are released in Nanwan Bay, and (2) a compilation of published results to gain insights into the generality of the present results. In the earlier study (Fan et al., 2006) (T.-Y.F., unpublished data), the number of larvae released daily was recorded for *P. damicornis* and *S. hystrix* retained in aquaria for month-long periods spanning multiple lunar phases in up to 5 years between 2003 and 2008. For each sampling, a mean of six (*P. damicornis*) and four (*S. hystrix*) colonies (range=1–8 colonies) were collected monthly from ~6 m depth in Nanwan Bay and returned to NMMBA where they were placed into the same larval collection apparatus used in the present study. Corals were replaced monthly to ensure that the laboratory measurement of larval release reflected larval release *in situ*, and to avoid acclimatization to laboratory conditions. Larvae were collected daily from each coral, pooled within species, and counted to evaluate larval release by day throughout each lunar month. Seawater temperature on the day of larval release was assessed from records obtained from thermisters (Hobo Aquapro II, Onset Computing, Bourne, MA, USA; resolution ±0.2°C) placed at 5 m depth in Nanwan Bay and programmed to sample every hour; the hourly values were averaged by day to describe the seawater temperature on the day of larval release. This approach assumes that the temperature of seawater over shallow reefs in Nanwan Bay is the same as that flowing through the aquaria at NMMBA and, moreover, that the timing of larval release is determined by a chronology of events beginning before the period of coral retention at NMMBA.

The cumulative number of larvae released daily by *P. damicornis* and *S. hystrix* was expressed as a function of the daily seawater temperature on the day of release. Temperature was partitioned in 0.5°C increments, and bar graphs of the results were juxtaposed with the temperature–respiration relationships to gain insight into the functional consequences of the timing of larval release with regard to the impacts on metabolism.

The compilation of published results describing the respiration rate of planula larvae of tropical reef corals was created through bibliographic search techniques of peer-reviewed literature. When suitable studies were found, rates of aerobic respiration were compiled in units of nmol O_2 larva^{-1} min^{-1}.

Data are presented as means ± s.e.m.

RESULTS

Larvae released from the three species were actively swimming when collected at ~07:00 h, and all contained dense populations of *Symbiodinium*; one or two *S. pistillata* larvae had unusual pale yellow animal tissue (Fig. 1). *Symbiodinium* were distributed throughout the larvae, but tended to be concentrated at the oral pore and along the mesenteries. Larvae of *P. damicornis* and *S. hystrix* were similar in length (938±73 μm and 996±44 μm, respectively; N=10), but not diameter (690±51 *versus* 344±34 μm, respectively; N=10), and larvae of *S. pistillata* were long (1698±97 μm) with an intermediate diameter (536±25 μm; N=10); there were no striking differences in the size of larvae used on each of the six days of the experiment. Assuming larvae were cylindrical, their volumes were 0.39±0.08 mm^3 (*P. damicornis*), 0.10±0.02 mm^3 (*S. hystrix*) and 0.38±0.03 mm^3 (*S. pistillata*) (all N=10). As cnidarian tissue has a density slightly above that of seawater (Spencer Davies, 1989), the density of tropical seawater (~1.023 mg mm^{-3}; P.J.E., unpublished data) can be used to estimate larval biomass; with this approach, the biomass of larvae was approximately 399, 104 and 392 μg larva^{-1} for *P. damicornis*, *S. hystrix* and *S. pistillata*, respectively.

In the respiration trials, mean control O_2 fluxes were small (≤0.063±0.002 nm O_2 chamber^{-1} min^{-1}), and those attributed to the six larvae in each vial were a mean of 5.9±0.4-fold larger (N=50). In replicate trials, aerobic respiration rates ranged from 0.008 nm O_2 larva^{-1} min^{-1} for *S. hystrix* at 26.4°C to 0.128 nm O_2 larva^{-1} min^{-1} for *P. damicornis* at 28.0°C. Mean respiration ranged from 0.073±0.019 (at 26.4°C) to 0.116±0.009 nm O_2 larva^{-1} min^{-1} (at 28.0°C) for *P. damicornis*, and from 0.029±0.011 (at 26.4°C) to 0.058±0.007 nm O_2 larva^{-1} min^{-1} (at 27.0°C) for *S. hystrix* (N=3–4). Larval respiration differed significantly among temperatures ($F_{4,31}$=4.137, P=0.008) and between *P. damicornis* and *S. hystrix* ($F_{1,31}$=48.900, P<0.001), but there was no interaction between the two ($F_{4,31}$=0.479, P=0.751). The respiration rate of *P. damicornis* was 1.5- to 2.6-fold greater than for *S. hystrix*, and for both species, it displayed a non-linear response to temperature, increasing to a threshold value at ~28.0°C and decreasing thereafter. Tukey's HSD *post hoc* analyses demonstrated that respiration differed between 26.4 and 28.0°C (P=0.007) and between 28.0 and 29.6°C (P=0.047); no other contrasts of marginal means were significant (P≥0.150). The respiration–temperature relationships were fitted well by second-order polynomials (r^2≥0.76; Fig. 2).

Larval biomass was not measured, but larval volume and density (described above) allowed biomass-normalized respiration to be estimated. Although the non-linear relationship between respiration and temperature was unaffected by biomass normalization, on a biomass scale, the range of mean respiration rates for *P. damicornis* was 0.183 to 0.291 nm O_2 mg^{-1} min^{-1}, and for *S. hystrix*, 0.275 to

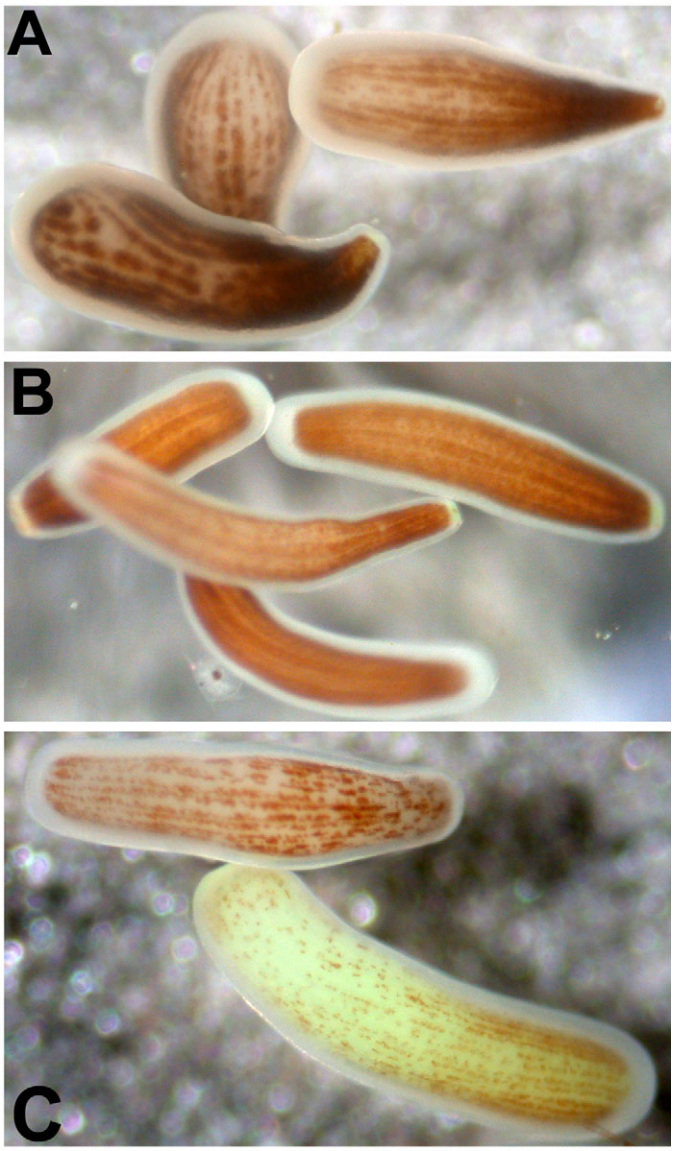

Fig. 1. Planula larvae freshly released from (A) *Pocillopora damicornis*, (B) *Seriatopora hystrix* and (C) *Stylophora pistilla* at the National Museum of Marine Biology and Aquarium, Taiwan. The mean (±s.e.m.) length of planulae from *P. damicornis*, *S. hystrix* and *S. pistillata* was 0.94±0.07, 1.00±0.04 and 1.70±0.10 mm, respectively (all N=10). These larvae were released on 21 and 22 March 2010; similar larvae were used in respiration trials.

0.558 nm O_2 mg^{-1} min^{-1}. The relative difference between these species was, therefore, reversed when standardized to biomass (because the mean volume of *P. damicornis* larvae was 3.9-fold greater than that of *S. hystrix* larvae), with the respiration rate for *S. hystrix* larvae 1.5- to 2.5-fold greater than that of *P. damicornis* larvae. For the larvae of *S. pistillata*, which were less numerous and measured at only three temperatures, mean respiration varied from 0.063 nm O_2 $larva^{-1}$ min^{-1} (at 29.6°C, N=1) to 0.097±0.005 nm O_2 $larva^{-1}$ min^{-1} (at 28.0°C, N=2; Fig. 2); on a biomass scale, these mean rates corresponded to 0.161 and 0.248 nm O_2 mg^{-1} min^{-1}, respectively. The respiration rates for *S. pistillata* were similar in magnitude to those of *P. damicornis*, and appeared to display a similar functional relationship to temperature.

The analysis of larvae released from corals held at NMMBA included data for up to 5 years with 4–12 months sampled annually. For *P. damicornis*, larval release was scored with lunar periodicities for 12 months in 2003, 5 months in 2005 (February, March and May–July), 9 months in 2007 (February–June, August and October–December) and 6 months in 2008 (January–June). For *S. hystrix*, larval release was scored with lunar periodicities for 12 months in 2003, 4 months in 2004 (January–April), 6 months in 2005 (January–March and May–July), 6 months in 2007 (February–May, August and December) and 6 months in 2008 (January–June). As the sampling for both species favored more uniform representation of cooler months (e.g. January–March) than warmer months (e.g. July–September), the analysis is biased towards emphasizing larval release on cooler days.

Based on all the data for larval release, both *P. damicornis* and *S. hystrix* released a large percentage (56%) of their larvae on days defined by a narrow range of warm temperatures (27.5–28.9°C). The largest proportion of larvae released in any 0.5°C temperature bin was coincident with the thermal threshold for respiration for both species (~28.0°C). When the same analysis was repeated for the year in which larval release was documented for all 12 months (2003), the pattern of larval release as a function of temperature was broadly unchanged (data not shown).

DISCUSSION

This study evaluated the metabolic responses of newly released brooded coral larvae to temperature, and used the results to gain insight into the consequences of their synchronous release (Harrison and Wallace, 1990; Fan et al., 2006). The results demonstrate that the respiration of three sympatric pocilloporids, *P. damicornis*, *S. hystrix* and *S. pistillata*, responded in rapid and distinctive ways to temperature with thresholds at ~28°C. Analysis of the seawater temperature into which larvae of *P. damicornis* and *S. hystrix* were released in Nanwan Bay (Fan et al., 2002) revealed modal temperatures that were close to the thermal threshold for larval respiration. Together with the negative skewing and leptokurtosis of these temperatures, we interpret the concordance of this modal temperature with the thermal threshold for respiration as having beneficial consequences for the larvae. Given the selective pressure for rapid growth in small life stages of corals (Jackson, 1977; Vermeij and Sandin, 2008), the enhanced supply of ATP through temperature-stimulated respiration is probably advantageous, whereas the reduction in ATP supply at temperatures above the threshold is probably detrimental.

Measurement of respiration has long been recognized as an important objective for understanding the biology of pelagic larvae (Zeuthen, 1947; Crisp, 1976), but this task has been hindered by the difficulty of accurately recording the slow rate of larval O_2 consumption (Hoegh-Guldberg and Manahan, 1995). In the present study, larval O_2 consumption was measured using optical sensor technology, which avoided the traditional problems of the leading alternative technology, polarographic oxygen sensors. These problems include flow-dependency of the sensor, and O_2 consumption by the sensor itself (Klimant et al., 1995). The efficacy of the optical technology was assessed by titrating O_2 consumption against the number of larvae, and using the results to predict the O_2 consumption in the absence of larvae. The outcome created a linear relationship whose intercept on the ordinate was not statistically discernible from zero, thereby confirming that only larvae were consuming O_2 at a measurable rate (Marsh and Manahan, 1999). This interpretation is consistent with the similarity of the present respiration rates with those previously recorded for coral larvae (Table 1).

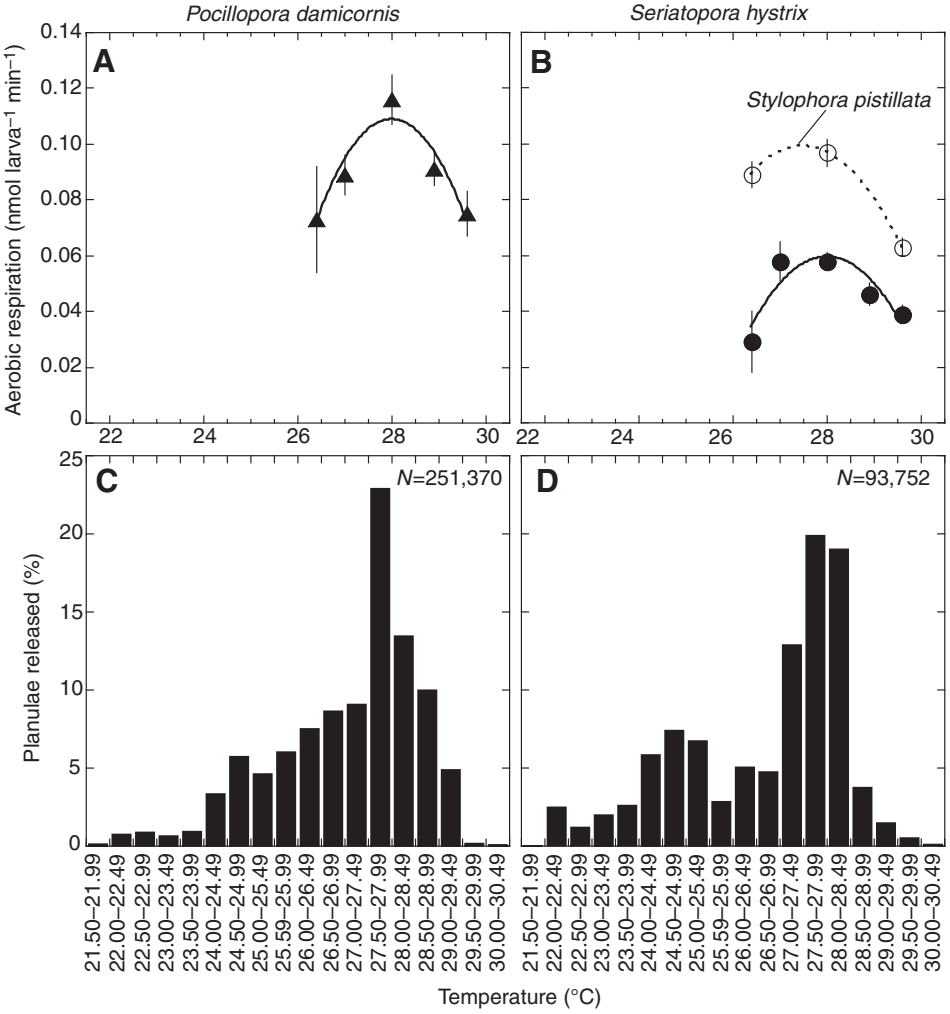

Fig. 2. Aerobic respiration of planulae (mean ± s.e.m.) as a function of temperature (upper panels), and the number of planulae released as a function of mean daily seawater temperature (lower panels). (A) Respiration of *Pocillopora damicornis* planulae (N=5–6 for each temperature), with the line displaying the best-fit second-order polynomial (y=–11.11+0.80x–0.01x^2, r^2=0.89). (B) Respiration of *Seriatopora hystrix* planulae, with the line displaying the best-fit second-order polynomial (y=–7.46+0.54x–0.01x^2, r^2=0.76). Aerobic dark respiration is also displayed for planulae from *Stylophora pistillata*, although these results are not considered in detail because of incomplete sampling across temperatures and small sample sizes (N=1–4). (C) Cumulative release of *P. damicornis* planulae over 2003, 2005, 2007 and 2008 by mean daily seawater temperature (in 0.5°C bins) on the day of release. (D) Cumulative release of *S. hystrix* planulae over 2003, 2004, 2005, 2007 and 2008 by mean daily seawater temperature (in 0.5°C bins) on the day of release. Refer to Results for further details.

Positive temperature dependency of respiration in poikilotherms is a consequence of kinetic principles (Hochachka and Somero, 2002), at least until harmful temperatures are reached, and the consequences reflect a greater availability of ATP. Rates of enzyme-catalyzed reactions typically double for each 10°C increase in temperature (Hochachka and Somero, 2002), with greater increases possible when enzyme kinetics are augmented by changes in the fundamental biochemical systems (Hochachka and Somero, 2002) and behavioral mechanisms. Thermal stimulation of respiration necessitates an immediate response because ATP supply is usually balanced with ATP use (Hochachka and Somero, 2002), and typically the ATP is used to fuel chemical synthesis and mechanical work. However, the production of ATP through respiration consumes food reserves, and thermal stimulation of this process can have deleterious effects when the reserves cannot be replaced. When severely depleted, diminished food reserves are a leading cause of metabolic depression (Hand and Hardewig, 1996). Therefore, the extent to which thermal stimulation of respiration is beneficial depends on the demands for cellular energy and the speed with which reserves can be replaced, but regardless of the benefits, the effects reverse when temperature declines. Beyond the threshold, however, further increases in temperature result in metabolic depression, and these effects are less readily reversed because they reflect the effects of damage (Hochachka and Somero, 2002).

Against this backdrop, the present analysis of larval respiration – with a distinctive threshold at 28°C – represents a predictable example of a general response. Remarkably, there are so few empirical analyses of larval respiration in scleractinians that it has not previously been possible to describe the shape of this relationship, or to pinpoint with accuracy the threshold temperature. This is unfortunate, because the high thermal sensitivity of adult corals (Jokiel and Coles, 1990) provides good reason to study similar effects in the life stage (i.e. larvae) that is critical to reef recovery following damage (Richmond and Hunter, 1990). Further, studies of the effects of temperature on a variety of pelagic larvae underscore the profound impacts of high temperature in shortening PLD and dispersal distances (O'Connor et al., 2007). The proximal cause of the effect of temperature on PLD is the acceleration of metabolism (O'Connor et al., 2007), yet to our knowledge, this critical example of biophysical coupling has been studied in only two species. For *Porites astreoides*, larval respiration increased 1.4-fold between 26 and 28°C (Q_{10}≈6.1), but did not change further between 28 and 33°C (Q_{10}≈1.9 between 26 and 33°C (Edmunds et al., 2001); for *Acropora millepora*, larval respiration increased 1.6-fold between 24 and 31°C (Q_{10}=1.9) (Rodriguez-Lanetty et al., 2009). The results from the small number of other studies of larval respiration in corals are difficult to compare with those of the present study owing to incongruent methodology and the use of a single temperature in virtually all studies. Nevertheless, together they are consistent with the notion of parabolic thermal effects with a threshold at ~27–28°C, although the statistical fit to this functional relationship is weak and more data are required to characterize the general temperature–respiration response (Fig. 3).

Table 1. Respiration rates of larvae from tropical scleractinians

Species	Location	Temperature (°C)	Respiration rate (nmol O_2 larva^{-1} min^{-1})	Reference
Porites astreoides	Conch Reef	26	0.09±0.02 (4)	Edmunds et al., 2001
Porites astreoides	Conch Reef	28	0.13±0.02 (6)	Edmunds et al., 2001
Porites astreoides	Conch Reef	33	0.14±0.02 (4)	Edmunds et al., 2001
Pocillopora damicornis	Heron Island, GBR[a]	26	0.11±0.02 (3)	Harii et al., 2010
Pocillopora damicornis	Heron Island, GBR[b]	26	0.18±0.02 (3)	Harii et al., 2010
Pocillopora damicornis	Heron Island, GBR[c]	26	0.10±0.01 (3)	Harii et al., 2010
Pocillopora damicornis – Type B	Kaneohe Bay	28	0.10±0.01 (4)	Richmond, 1987
Pocillopora damicornis – Type Y	Kaneohe Bay[d]	28	0.18±0.03 (4)	Richmond, 1987
Pocillopora damicornis	Guam[e]	28	0.10±0.01 (7)	Gaither and Rowan, 2010
Pocillopora damicornis	Guam[f]	28	0.08 (8)	Gaither and Rowan, 2010
Montipora digitata	Heron Island, GBR[a]	26	0.02 (3)	Harii et al., 2010
Montipora digitata	Heron Island, GBR[b]	26	0.09±0.01 (3)	Harii et al., 2010
Montipora digitata	Heron Island, GBR[c]	26	0.07±0.03 (3)	Harii et al., 2010
Acropora intermedia	Bise, Okinawa	27	0.05±0.01 (9)	Okubo et al., 2008
Stylophora pistillata	Okinawa	24	0.28±0.04 (3)	Titlyanov et al., 1998
Acropora millepora	Heron Island, GBR[g]	24	0.04±0.01	Rodriguez-Lanetty et al., 2009
Acropora millepora	Heron Island, GBR[g]	28	0.04	Rodriguez-Lanetty et al., 2009
Acropora millepora	Heron Island, GBR[g]	31	0.06	Rodriguez-Lanetty et al., 2009

Location describes the site from which the larvae were obtained, and temperature the conditions under which measurements were made.
Respiration rates are means ± s.e.m., with sample size in parentheses (except for *A. millepora*, for which sample sizes were not provided). Where s.e.m. are not given, values were <0.01.
[a]Larvae were freshly released.
[b]Larvae were retained for 30 d under light (~100 μmol photons m^{-2} s^{-1}) conditions.
[c]Larvae were retained for 30 d under dark conditions.
[d]Calculated only from symbiotic larvae.
[e]Larvae were freshly released under high light (57% of ambient PAR).
[f]Larvae were freshly released under low light (11% of ambient PAR).
[g]Larvae were 10 days old and exposed to each temperature for 10 h.

A rise in temperature from 26.4 to 28.0°C had large effects on larval respiration compared with a kinetic expectation with a Q_{10} of ~2. For *P. damicornis*, larval respiration increased 1.6-fold over this range (Q_{10}=18); for *Seriatopora hystrix*, it increased 2.0-fold (Q_{10}=76); and for *S. pistillata*, it increased 1.1-fold (Q_{10}=1.7). Although these Q_{10} values differ from the kinetic expectation, respiration rates for scleractinians (mostly adult) suggest that they are not exceptional (Coles and Jokiel, 1977; Hoegh-Guldberg and Smith, 1989; Edmunds et al., 2001; Howe and Marshall, 2001; Edmunds, 2005; Edmunds, 2008). For newly settled, juvenile and adult corals, behavior is a leading cause of high Q_{10} values because it can modify metabolic rate through expansion and contraction of tissues (Patterson, 1992; Shick et al., 1979), mechanical work (e.g. tentacle movement and larval swimming) and specific dynamic action following feeding (Edmunds and Spencer Davies, 1988; Secor, 2009). For larvae, however, development is also an important factor that could contribute to the functional relationship between temperature and metabolism, and indeed, coral larvae appear to develop very quickly. For instance, brooded larvae are released after just ~14 d following fertilization [in *P. damicornis* (Stoddart and Black, 1985; Permata et al., 2000)], with pre-release growth rates as fast as 62 μm d^{-1} (Stoddart and Black, 1985), and for broadcast spawning corals, swimming larvae develop from externally fertilized eggs within ~4 days [in *Acropora millepora* (Ball et al., 2002)]. Within the plankton, development to settlement competency usually takes days to weeks (Ball et al., 2002; Graham et al., 2008), and sometimes many months (Vermeij et al., 2009), but among some brooded corals, this period can be as short as a few minutes (Best and Resing, 1987; Carlon and Olson, 1993). We suspect that inherently rapid development in coral larvae plays an important role in translating small increases in temperature into to large responses (Heyward and Negri, 2010), here involving metabolism, and suggest that rapid ontogeny offers a parsimonious explanation of why time (i.e. larval age) can have strong effects in analyses of larval physiology (Putnam et al., 2010).

To gain insights into the ecological significance of the effect of temperature on larval respiration, the temperature of the seawater into which larval *P. damicornis* and *S. hystrix* were released in Nanwan Bay was analyzed for 2529 days between 1 May 2003 and 2 April 2010. Although the sampling effort was uneven over this period, and tended to favor cooler months, nevertheless, these data represent a globally unique record of the release of larvae from corals spanning multiple years. In Nanwan Bay, *P. damicornis* and *S. hystrix* release brooded larvae year-round in synchrony with lunar phases, and typically show peak larval release ~5–15 days following the new moon (Fan et al., 2002). The phase relationship with the new moon varies through the year as the temperature of the seawater changes, with warmer temperature advancing the release date relative to the new moon, and cooler temperatures delaying release (T.-Y.F., unpublished data). The distributions of seawater temperature into which these larvae were released were negatively skewed for both species, with modal temperatures corresponding to the thermal threshold for respiration, with few larvae (<5%) released at higher temperatures. This coincidence of modal release temperature and thermal threshold for respiration supports the hypothesis that brooding corals experience metabolic advantages from the timing of larvae release, with most larvae benefiting from these effects. If this assertion is correct, then high respiration upon release would be correlated inversely with PLD, and directly with survivorship, settlement and metamorphosis.

It is premature, however, to infer that Orton (Orton, 1920) was correct with regard to the timing of invertebrate reproduction, and

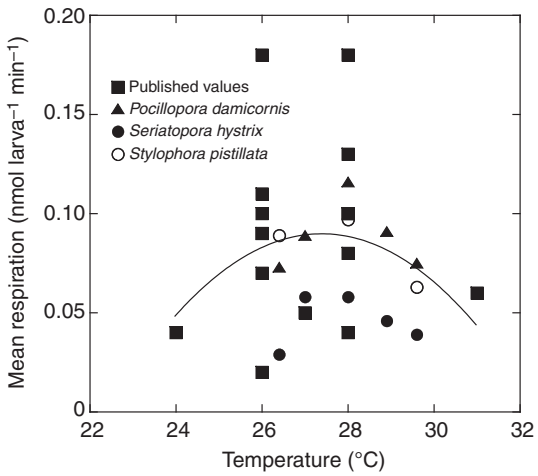

Fig. 3. Mean respiration rates of coral larvae in the present study (see Fig. 2) and from the literature (Table 1), with the line displaying the best-fit second-order polynomial (y=–2.590+0.196x–0.004x^2, r^2=0.288); refer to Table 1 and Fig. 2 for s.e.m. Two extreme values in Table 1 are omitted (respiration for *Stylophora pistillata* at 24°C and *Porites astreoides* at 33°C).

conclude that natural selection has acted on the timing of coral reproduction to maximize the respiration of newly released larvae. The correspondence of peak larval respiration and modal release temperature is likely just one piece in the complex puzzle determining when corals spawn and, indeed, compelling cases have been made that the ultimate causes of reproductive timing in corals are avoidance of hybridization (Levitan et al., 2004), predator satiation (Babcock et al., 1986), enhanced fertilization success and larval retention (Van Woesik, 2009), and evading heavy rainfall (Mendes and Woodley, 2002). The timing of larval release clearly cannot solely be determined by maximizing larval respiration, because 48–54% of the larvae in the present analysis were released at temperatures cooler than the thermal threshold for respiration (i.e. <27.5°C), and in months when the present results suggest that the seawater was too cold to facilitate the highest metabolic rate. This possibility remains to be tested, for the present analysis involved measurements completed in a single month and cannot, therefore, address the possibility that seasonal acclimatization of respiration occurs (Al-Sofyani and Spencer Davies, 1992; Edmunds 2009), thereby altering the shape of the temperature–respiration response. Further, although this study did not address the metabolic rate of the maternal coral, it is likely that their respiration also varied with temperature (Jokiel and Coles, 1990), and probably with a threshold close to that of the larvae. Therefore, we cannot exclude the possibility that the timing of peak larval release is gauged to maximize the respiration of the maternal coral, perhaps to meet the metabolic costs associated with final larval development and spawning.

One interesting possibility that deserves further research attention is that the release of a large number of larvae at sub-optimal temperatures with regard to maximizing respiration could be construed as a bet-hedging strategy (Slatkin, 1974; Kaplan and Cooper, 1984). In this theoretical construct, larvae released into warm seawater would have short PLD because of their enhanced metabolism, and have the potential to settle more locally relative to the parents. In contrast, larvae released into cool water would have longer PLD, because the lower temperature would slow metabolism, and thus would be likely to disperse to more distant locations. Interestingly, our results suggest that an outcome similar to that predicted for low temperature could result from warming of seawater through global climate change, because temperatures >28°C also favor depressed metabolism. Together, these patterns suggest that, for brooding corals that are reproductively active year-round, larvae released in warm months would favor self-seeding, which is a beneficial strategy when local conditions are favorable. In contrast, those released in cooler months would favor distant dispersal, which can be beneficial when local conditions are unfavorable and there is a good chance of finding more suitable conditions elsewhere (Olson, 1985). This prediction is consistent with the settlement of *S. pistillata* in the Red Sea, where early-release larvae (in March) settled less quickly than late-release larvae (June) on the first night following planulation (Amar et al., 2007). If our assertion is correct, then *P. damicornis* and *S. hystrix* may utilize bet-hedging strategies on two temporal scales, both within a brood and among release days (Putnam et al., 2010) and among broods and throughout the year (present study) (Amar et al., 2007).

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