Uncoupling temperature-dependent mortality from lipid depletion for scleractinian coral larvae

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Abstract

Predicted increases in sea-surface temperatures due to climate change are likely to alter the physiology of marine organisms and ultimately influence the distribution and abundance of their populations. The consequences of increased temperatures for marine species, including decreased survival and altered rates of development, growth and settlement, are well-known, and often attributed to imbalances between energy supply and demand. To test this hypothesis, we calibrated the effect of temperature on rates of survival and lipid depletion for larvae of the common stony coral *Acropora tenuis* over a seven-degree temperature range. Temperature had a pronounced, linearly increasing effect on larval mortality, with a 6-fold decrease in median survival time. Contrary to expectation, however, temperature had a quasi-parabolic effect on lipid use; rates declined as temperatures either increased above or decreased below the ambient temperature at the time of spawning. This contrasts with previous work suggesting that increased energy depletion is the cause of larval mortality at higher temperatures. Our results highlight the sensitivity of coral larvae to temperature and have implications for dispersal potential because fewer larvae will survive to disperse. Such projected declines in connectivity among coral populations are likely to undermine reef resilience.

Introduction

Temperature has a major effect on the physiology of organisms, most notably by affecting the rates of biochemical reactions that collectively govern organism functions. Typically, biochemical reactions catalysed by enzymes have a unimodal response to temperature, such that reaction rates increase with temperature until an upper tolerance threshold is reached, after which rates rapidly decline (Sibly et al. 2012). Many biological processes, including rates of development, growth, and movement, have a similar trajectory, and the precise shape of this curve demarcates the range of temperatures beyond which performance declines, with the maximum rates achieved at some optimal temperature (Kingsolver 2009). Because ectothermic organisms cannot regulate their internal body temperature to maintain optimum performance, they are particularly dependent on their environment to maintain rates of physiological processes within their range of thermal tolerance. Given increases in global temperatures over the last century and predicted increases in the near future (Kirtman et al. 2013), the ability of ectotherms to cope with increasing temperature, either through migration, acclimation, or adaptation, will play a major role in the changing ecology of ectotherm populations.

In the marine environment, most organisms, including most benthic invertebrate species, are ectothermic, and many have a complex life-cycle consisting of a benthic, mostly sessile, adult stage and a dispersive larval stage. The potential effects of increasing temperature on marine organisms such as these are likely to vary throughout their life stages (Portner 2002; Byrne 2011; Diederich and Pechenik 2013). Reef-building scleractinian corals are key ecosystem engineers of coral reefs, thus their responses to increasing sea temperatures are particularly important determinants of how reefs are likely to change as the climate warms. Although it has long been known that many coral species live close to their upper limit of temperature tolerance

and that temperature anomalies cause bleaching and disease for adult corals (e.g. (Jokiel and Coles 1990; Glynn 1993; Berkelmans and Willis 1999; Bruno et al. 2007), the effects of temperature on coral larvae are less well understood, but likely to be of critical importance for understanding coral reef resilience to climate change.

Most corals are broadcast spawners, releasing their gametes into the water column where fertilization and embryogenesis occurs externally (Baird et al. 2009). The majority of broadcast spawning corals release eggs without symbionts, and although there is some evidence for larval uptake of dissolved organic material in soft corals (Ben-David-Zaslow and Benayahu 2000), it has not been documented in scleractinian corals. Thus most scleractinian coral larvae are dependent upon maternal reserves for energy during the pelagic period. After 1-3 days, depending on the species, larvae are capable of metamorphosing into juvenile corals (Connolly and Baird 2010). During the larval stage, temperature increases of 3-4°C can cause rates of development to increase by 10-25%, the number of larvae developing abnormally to increase by 20-40% (Bassim et al. 2002; Negri et al. 2007; Woolsey et al. 2013), and mortality to increase by 30-80% (Edmunds et al. 2001; Bassim and Sammarco 2003; Brooke and Young 2005; Chua et al. 2013). Although it is generally assumed that increased metabolic rates are the cause of such deleterious effects on larval development (Edmunds et al. 2001; Kipson et al. 2012; Ross et al. 2013), very few researchers have measured the respiration rates of coral larvae at different temperatures (but see (Edmunds et al. 2001; Ross et al. 2013; Rodriguez-Lanetty et al. 2009; Edmunds et al. 2011; Cumbo et al. 2013; Putnam et al. 2013), only one looked at larvae without algal symbionts (Rodriguez-Lanetty et al. 2009), and no studies to date have quantified the effect of temperature on the energy content of larvae. Thus, further studies on aposymbiotic larvae that rely only on endogenous reserves are needed. Without this knowledge, it is difficult to estimate

79 the effect of temperature increases on the energy budgets of coral larvae and consequently the
80 underlying mechanisms of corals' response to warming oceans (Portner 2012).

81 Here, we test the tacit assumption that increasing depletion of stored energy is the cause of
82 larval mortality as temperatures rise, by quantifying the effects of temperature on the survival
83 and energy expenditure of scleractinian coral larvae over the entire period of larval duration. If
84 metabolic rates increase at higher temperatures, then the rate of lipid depletion, the putative
85 energy source for coral larval metabolism (Arai et al. 1993), should also increase at higher
86 temperatures. Higher rates of energy use should then lead to higher mortality rates as larvae
87 deplete their endogenous stores. We test these hypotheses for the common broadcast spawning
88 coral *Acropora tenuis* for all developmental stages, from newly fertilized gametes, through larval
89 development, and for up to two months post fertilization.

90

91 ## Materials and methods

92 ### Study site and sampling procedure

93 Experimental temperature treatments were established at Orpheus Island Research Station
94 (OIRS), part of the Palm Island Group in the Central Section of the Great Barrier Reef (18.61 S,
95 146.48 E), during the austral summer of 2009-2010. The common coral *Acropora tenuis* was
96 selected as the target species because it broadcast spawns gametes at predictable times (Babcock
97 et al. 1986) and its eggs lack symbionts at release. Three days prior to the full moon on 2
98 November, six adult colonies of *A. tenuis*, separated by at least 50m to minimize the chances of
99 their being the same genet, were collected from inshore shallow (<3m) reef flats, three each from
100 Orpheus and Pelorus Islands, and brought to OIRS where they were maintained in flow-through
101 aquaria at ambient temperature at the time of spawning (~27°C). Since 2002, the mean sea

102 temperature for November is 27.0 ± 0.4°C for Orpheus. On November 7, spawned gametes from
103 all colonies were collected, combined into a single culture to maximize fertilization rates (ref)
104 and larval viability (ref), and left to fertilize at ambient temperature. Once cleavage had started in
105 the majority of *A. tenuis* eggs, ~50,000 developing embryos were equally and randomly
106 distributed into five 10 L aquaria containing an air stone to increase oxygenation and 0.2 µm
107 filtered seawater (FSW) and placed in separate water baths maintained at five target
108 temperatures: 25.0°C, 27.0°C (ambient), 28.5°C, 30.0°C, and 31.5°C. A range of temperatures
109 were chosen in order to analyse the data using a regression-based approach, explained below.
110 These temperatures are within the range (22.5°C to 34.8°C) that larvae typically experience
111 around Orpheus Island in austral summer (November through March) months (AIMS 2015).
112 Although the developing embroys were not gradually acclimated to the treatment temperatures,
113 because coral larvae typically lyse within 24 hours of death, we do not believe this affected the
114 results. The aquaria were maintained in a temperature controlled room with a 12:12 h light:dark
115 cycle. Temperature was controlled to within 0.2°C using submerged thermoregulators (TH1,
116 Ratek) and recirculating pumps, and checked several times daily. Water quality was regularly
117 monitored and aquaria were completely refreshed with heated FSW as required. Although
118 scleractinian coral larvae generally do not settle without the proper cue, any spontaneously
119 metamorphosing larvae were promptly removed.
120 Sampling commenced immediately after transfer of larvae into the treatment tanks and
121 was then repeated: 1) every 12 h until time to motility (i.e. all larvae were actively swimming; up
122 to 36 h); 2) daily until larvae in all treatments were competent to settle (5 days after spawning
123 [DAS]); 3) every 3 d in the remainder of the first month (29 DAS); and 4) every 7 d in the
124 second month (up to 63 DAS in treatments with larvae remaining). At each sampling time, five

125 replicate samples of 50 randomly selected larvae from each treatment were immediately frozen
126 in liquid nitrogen for subsequent lipid analysis. Lipids were extracted using a modified Bligh-
127 Dyer chloroform:methanol procedure, adding ketone as a standard for lipid recovery (Sewell
128 2005). A thin layer chromatography-flame ionization device (Iatroscan, Iatron Corporation,
129 Japan) was used to measure lipids, which enabled the individual lipid classes to be quantified
130 separately from the total amount of lipid. The wax esters (WE) and triacylglycerols (TAG) lipid
131 classes were combined for analyses, as these have been identified as the primary energy storage
132 lipids in many marine invertebrates (Villinski et al. 2002, Kattner et al. 2007). The total amount
133 of WE and TAG in each replicate was divided by the number of larvae to obtain the amount of
134 energetic lipid per larva.
135 To measure larval survival at 4 DAS, when larvae in all treatments were swimming, a
136 single set of 500 randomly selected larvae were permanently removed from each temperature
137 treatment, evenly distributed into five replicate 70 ml specimen jars filled with heated FSW (100
138 larvae each), and placed into water baths maintained at the same temperatures, in the same
139 manner, as the treatment aquaria. At each sampling time, the number of larvae surviving from
140 the initial 100 larvae in each jar was recorded and the remaining larvae transferred into a clean
141 specimen jar with fresh, heated FSW. Sampling continued for up to 63 DAS in treatments with
142 larvae remaining.
143
144 **Modelling approach**
145 A regression-based approach was used to determine how temperature affects rates of mortality
146 and lipid depletion of *A. tenuis* larvae. In our approach, temperature is treated as a continuous
147 variable, in contrast to the standard approach typically used to analyse temperature effects on

148 marine invertebrate larvae, which treats temperature as a categorical variable and uses analysis of
149 variance (ANOVA). While ANOVA can determine if temperature effects differ among
150 treatments, it cannot calibrate how effect size varies as a continuous function of temperature.
151 Temperature effects were predicted to have one of two response types, linear or quasi-parabolic.
152 For the linear response, response rates (mortality and lipid depletion) were modelled as changing
153 linearly with temperature. Alternatively, if the response to temperature is quasi-parabolic,
154 response rates should increase (or decrease) to a maximum (or minimum) value, before
155 decreasing (or increasing). As experimental temperatures move away from this value, effects on
156 response rates should become increasingly large. Thus, the squared deviation of absolute
157 temperature from ambient was used instead of absolute temperature as the predictor variable to
158 test for a quasi-parabolic response in lipid depletion rates. Both types of response were tested for
159 in analyses of the larval survival and lipid data. All analyses were done using R (R Development
160 Core Team 2008).
161 Multiple linear regression implemented by the "lm" function in the "stats" R package was
162 used to model the energetic lipid data as a continuous function of temperature, with time and
163 temperature as the explanatory variables. A log-log transformation of the data was used because
164 an approximately power-law relationship between days after spawning and lipid content was
165 observed after the initial pre-swimming period had ended (Fig. S1). Prior to this point, in each
166 treatment, energetic lipids were approximately constant (Fig. S2). The time to motility
167 corresponded to 36 h for the lowest three temperatures and 24 h for the highest two temperatures.
168 We tested for differences in lipid content after development and rates of lipid depletion as a
169 function of temperature. Akaike's Information Criterion (AIC) was then used to select the model
170 that provided the best fit to the data. In each case, the relevant parameter (slope and/or intercept

171 of lipid levels as a function of time) was modelled as a linear function of either temperature, or
172 the squared deviation of temperature from ambient, as described above.
173 To directly compare larval survival between treatments and obtain a quantitative estimate
174 of survival as a function of temperature, a parametric regression was used to fit a Weibull
175 distribution to the survival times using the function "survreg" in the "survival" package in R. The
176 Weibull distribution is one of the most commonly used distributions for survival analysis
177 (Mudholkar et al. 1996). It is a two-parameter model with the initial parameter (λ) denoting the
178 overall level of hazard, or instantaneous risk of death, and the shape parameter (γ) allowing
179 mortality rates to increase ($\gamma > 1$) or decrease ($0 < \gamma < 1$) monotonically, or to remain constant (γ
180 $=1$), over time (t). The survival function for the Weibull distribution is:
181 $$S(t) = e^{-\lambda t^{\gamma}};$$
182 Incorporating temperature dependence into the hazard function for the Weibull distribution when
183 testing for a monotonic response (linear model) means:
184 $$\lambda = a + b * T_{\circ\mathrm{C}};$$
185 where *a* and *b* are the coefficients of the linear predictors produced by the model fit and T°C is
186 the actual temperature in °C. When modelled for a parabolic response the survival function
187 becomes:
188 $$\lambda = a + b * (T_{\circ\mathrm{C}} - T_A)^2;$$
189 where *T*°A is ambient temperature. Random effects of replicates were included in the model
190 using the "frailty" function (Therneau et al. 2003). Analyzing the time-specific survival of *A.*
191 *tenuis* larvae in this manner allows us to incorporate the non-independent carry-over effects of
192 time on the population and provides for more robust estimates of survival compared to analyses
193 which ignore the longitudinal nature of our data. Median survival times were estimated for each

194 replicate with the “rms” package in R (Harrell 2012) and used to calculate the average median
195 survival time for each temperature treatment. Finally, independent two-sample t-tests were
196 performed between each ordered pair of temperatures to identify significant differences in
197 median lifetimes.
198
199 # Results
200 ## Survival
201 Temperature had a substantial effect on the survival of *Acropora tenuis* larvae. Mortality rates
202 increased linearly with increasing temperature, even though there was variation among replicates
203 (Fig. 1; Table S1). Estimated median survival times for each temperature indicated a 6-fold
204 decrease in median lifetime between the lowest (54 d) and highest temperatures (9 d) (Fig. 2).
205 The difference in median lifetimes between each ordered temperature pair was significant
206 ($p<0.5$).
207
208 ## Lipid
209 The best model for the change in energetic lipids through time assumed that larvae in all
210 treatments had the same amount of lipid when they started swimming (i.e. same intercept) and
211 that rates of lipid depletion varied among treatments (i.e. different slopes). (Fig. 3; Table S2).
212 There was a quasi-parabolic response of lipid depletion rate to temperature; maximum depletion
213 rates of energy lipids occurred at ambient temperatures, with larvae in the low and the higher
214 temperature treatments consuming fewer lipids (Fig. 4).
215

Discussion

Temperature has a strong effect on larval survival of the broadcast spawning coral *Acropora tenuis*; however, temperature-dependent mortality is not the result of increased lipid depletion. Rising temperatures have the greatest impact on larval survival, with a 6-fold decrease in median survival times occurring between the lowest and highest temperature treatments. In contrast to the linearly decreasing survival, we identify a quasi-parabolic response for lipid depletion, with the greatest rates occurring at ambient temperature and declining on either side, reflecting the characteristic thermal sensitivity of biochemical reaction rates (Kingsolver 2009), and suggesting an optimum temperature for coral larvae in terms of physiological rates is at or near ambient temperature at the time of spawning.

Increased larval mortality due to increasing sea temperatures is likely to play an important role in the regulation of coral populations in a warming world. Significantly, the highest temperature treatment in this study, 31.7°C, is within the present-day summer temperature range (22.5°C to 34.8°C) recorded for inshore shallow reef flats at Orpheus Island (AIMS 2015). Temperatures greater than or equal to 31.7°C have occurred on 20 days between 2002 and 2013, for as long as 12 hours (AIMS 2015). Although the duration of exposure to the higher temperatures used here is longer than has been experienced on the reef in the recent past, even conservative predictions suggest that sea temperatures will rise above the highest temperatures tested here by 2100 (Collins et al. 2013). The likelihood that larvae will be exposed to these and higher temperatures in the near future, together with evidence indicating that, under current conditions, adult corals of many species are already close to the upper range of their tolerances (e.g. Berkelmans and Willis 1999; Rodolfo-Metalpa et al. 2014), highlights the vulnerability of coral reefs in a warming ocean.

Our finding that larval lipid stores are not depleted at greater rates as temperatures increase, but in fact, the opposite occurs (Fig. 3), provides important insights into the potential cause of temperature-dependent mortality of coral larvae. The fact that energy reserves were depleted more slowly at all temperatures higher than ambient indicates that energy depletion is not the cause of higher mortality at higher temperatures, as typically assumed in most studies of marine invertebrate larvae, the idea being that higher metabolic rates will deplete limited energy reserves more rapidly (e.g. Edmunds et al. 2001; Pechenik 1987). These results, together with previous work demonstrating a similar parabolic response between respiration rates and temperature (Edmunds et al. 2011), indicate metabolic suppression may be occurring at even small temperature deviations from ambient.

Physiological performance generally increases over most of a species' temperature range, with a peak and rapid decline as an upper temperature threshold is reached (Sibly et al. 2012). This threshold temperature might be expected to be at or near ambient temperature, since over time, temperature tolerances of ectotherms become closely associated with local environmental conditions (Portner 2002; Angilletta 2009). Moving outside this optimum can lead to impaired function, such as decreasing calcification rates of the adult coral *Siderastrea siderea* (Castillo et al. 2014) and potentially terminal effects (Willmer et al. 2002). The fact that lipid depletion is lower on either side of optimum in this study is also likely due to the inefficiency of enzymes at lower temperatures and enzyme inactivation at higher temperatures. It might also suggest that *A. tenuis* larvae around Orpheus Island may have adapted to their present conditions.

Since depletion of energy reserves cannot account for the linear increase in mortality with temperature, it is important to consider other potential causes. Although lipids make up a substantial proportion of coral eggs (Arai et al. 1993; Figueiredo et al. 2012) and appear to be the

primary energy source for coral larvae (Harii et al. 2007), it is possible that depletion of another energy source (i.e. protein or carbohydrate) may contribute to larval mortality at high temperatures although these macronutrients have not been measured in non-feeding coral larvae before. Other potential causes of mortality include carry-over effects from developmental abnormalities (Negri et al. 2007), disruption of the normal balance of metabolic reactions (Pechenik 1987), problems with membrane structures so that transport systems into and between cells become unbalanced or inoperative (Hofmann and Todgham 2010), a molecular response, such as downregulation of metabolism, (Rodriguez-Lanetty et al. 2009), or increased mitochondrial reactive oxygen species (ROS) formation (Keller et al. 2004). Determining which of these mechanisms cause larval mortality at high temperatures will require further research.

Regardless of the mechanism, our results and other work documenting the adverse effect of temperature on fertilization (Negri et al. 2007; Krupp et al. 2006), development (Bassim et al. 2002; Woolsey et al. 2013), and settlement (Edmunds et al. 2001; Bassim and Sammarco 2003) strongly suggest that the dispersal potential of corals is likely to change fundamentally in the near future, particularly given the expected increases in temperature due to anthropogenic climate change. While the total number of larvae surviving to settlement is likely to decrease, localized recruitment may increase due to shorter development times (Figueiredo et al. 2014). Moreover, long distance dispersal is likely to decrease as a result of warming oceans. For sessile marine organisms, such as reef building corals, the dispersing larval stage is vital for population connectivity and reef resilience.

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288

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459 Figure Legends

460 **Fig. 1** (a-e) Estimated parametric survival function for larvae of *Acropora tenuis* fitted to the
461 empirical survival data with the Weibull distribution (heavy line). Each light line represents a
462 replicate vial containing 50 initial larvae (these vials were the random effects in the analysis). (f)
463 Survival function (± 1 SE) at each temperature for comparison. Ambient temperature at the time
464 of spawning ~27°C. Note the y-axis is on a square root scale

465

466 **Fig. 2** Estimated median survival times for larvae of *Acropora tenuis* for each temperature
467 treatment. Error bars represent one standard error. Ambient temperature at the time of spawning
468 ~27°C

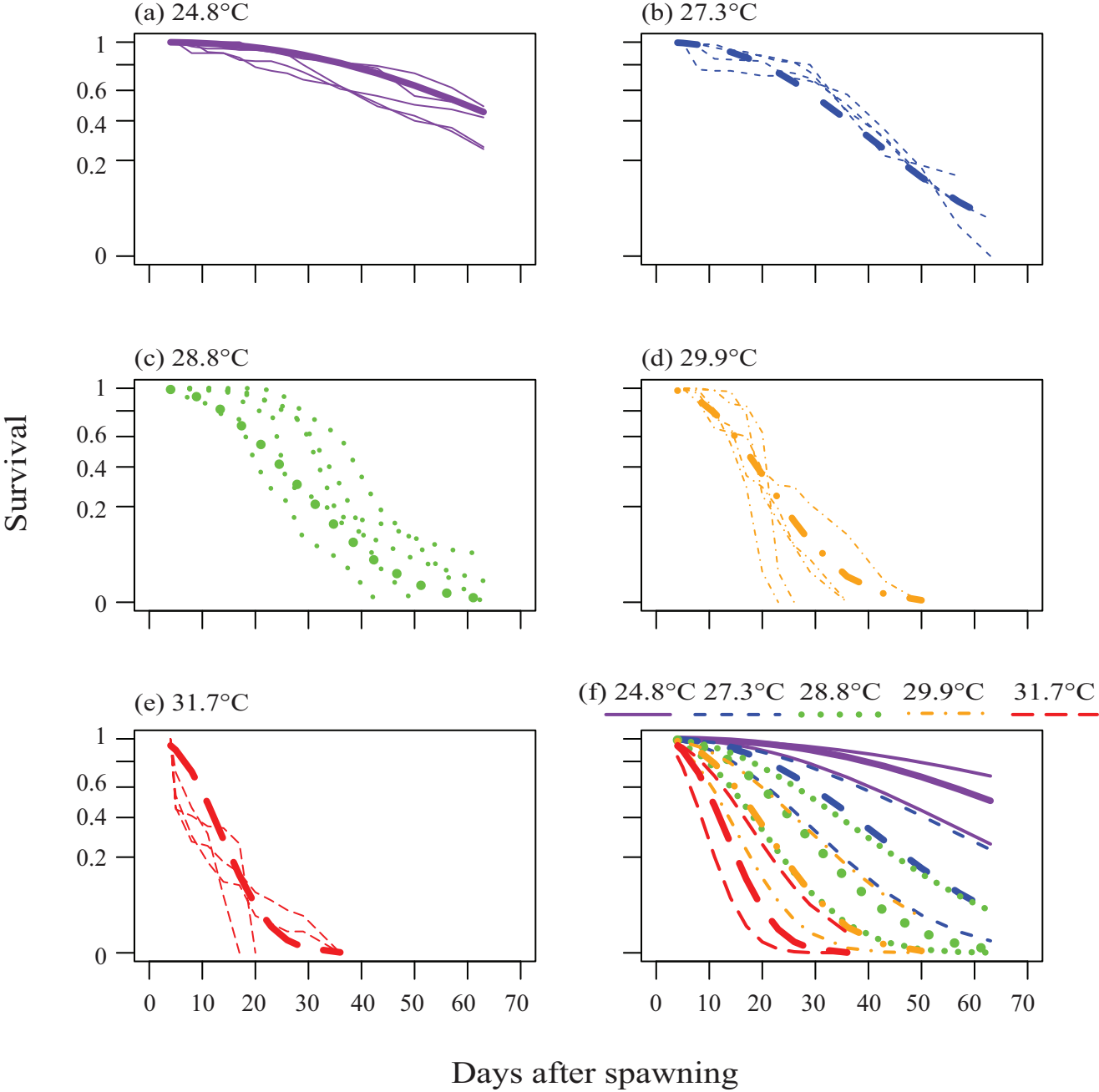
469

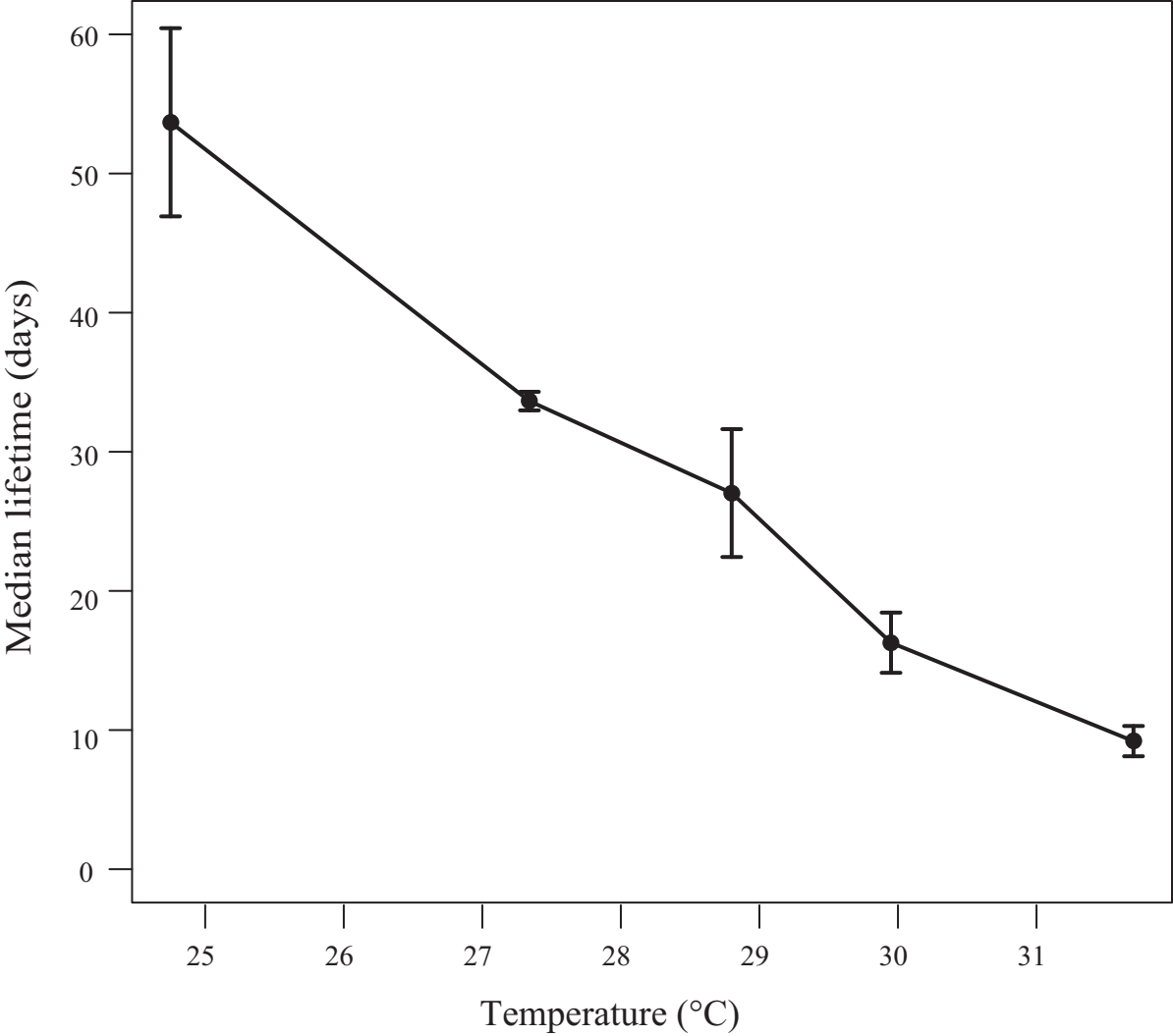
470 **Fig. 3** (a-e) Best-model fits for the depletion of energetic lipids through time by *Acropora tenuis*
471 larvae maintained at five different temperatures. Each circle represents a replicate measurement,
472 with lines for each fit. Time series starts at larval motility (see *Methods*). The model with the
473 best-fit to the data was the model with the same amount of lipid remaining after development to
474 a swimming larvae and a parabolic function of temperature for rates of lipid depletion (Table
475 S2). (f) Lipid depletion (± 1 SE) at each temperature for comparison. Note 29.9°C (dot-dash line)
476 lies on top of 24.8°C (solid line) and may be indistinguishable. Ambient temperature at the time
477 of spawning ~27°C. Note both axes are on a natural log scale (see *Methods*)

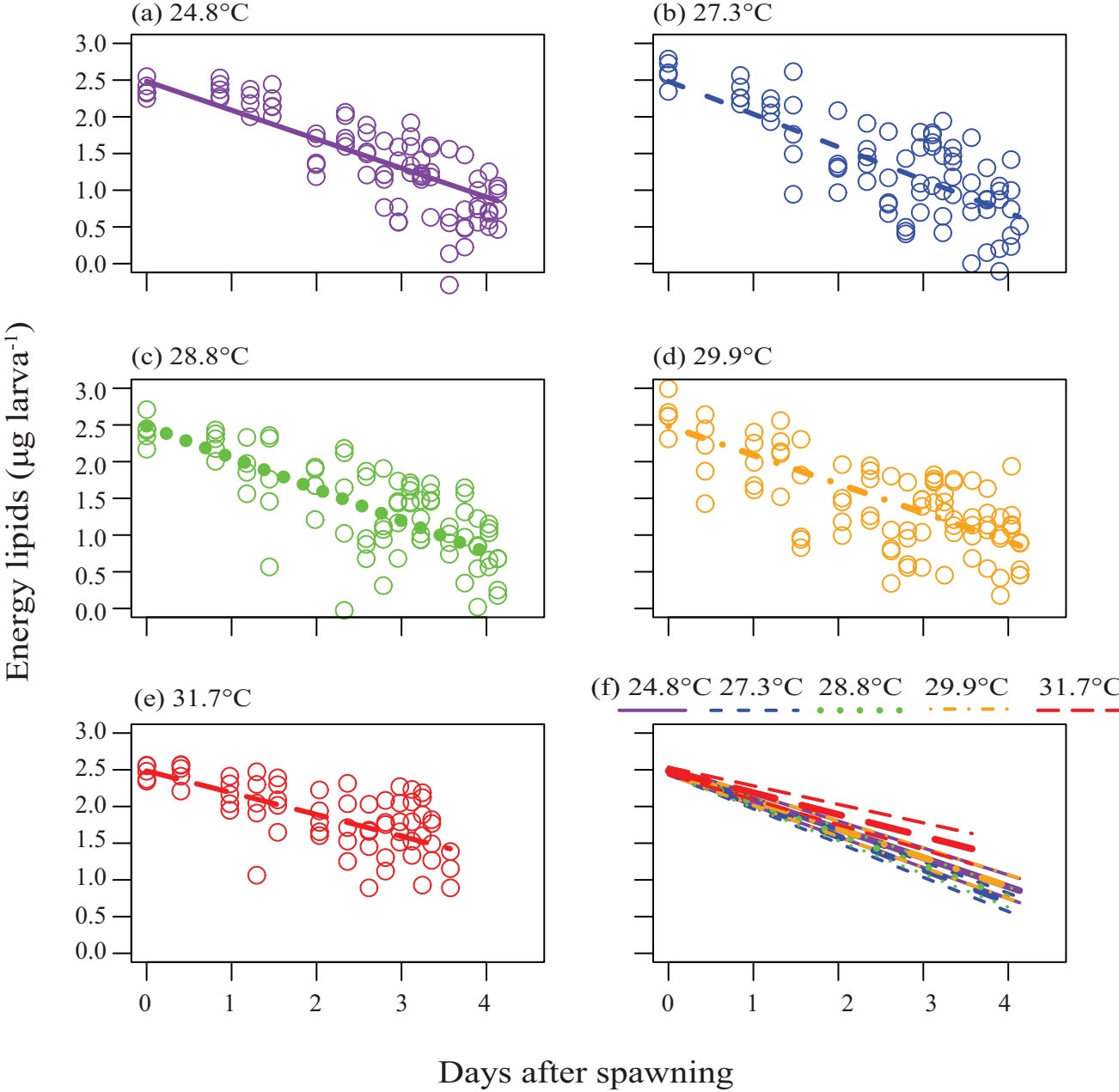
478

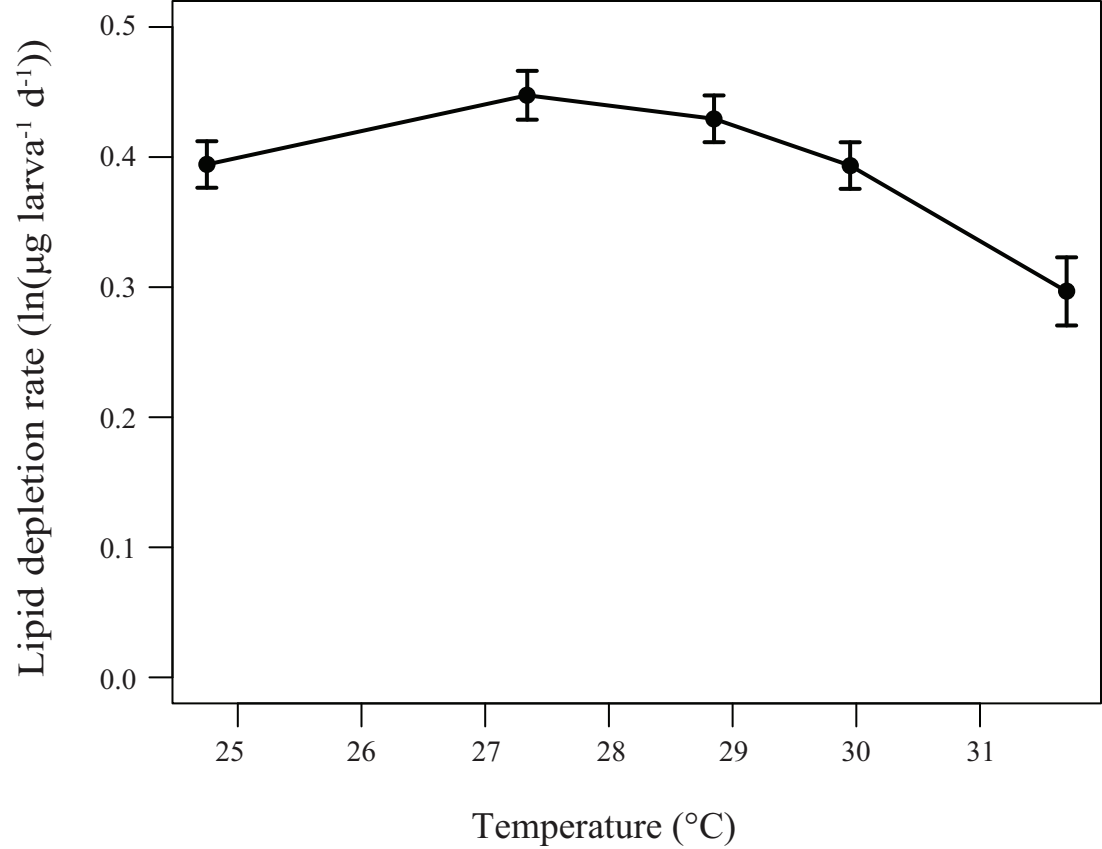
479 **Fig. 4** Estimated lipid depletion rates for *Acropora tenuis* larvae maintained at different
480 temperatures (i.e. estimated slopes from the best-fit lipid depletion model shown in Fig. 3 and
481 Table S2). Error bars are standard errors produced by the regression analysis. Ambient

482 temperature at the time of spawning ~27°C


(a) 24.8°C
(b) 27.3°C
(c) 28.8°C
(d) 29.9°C
(e) 31.7°C
(f) 24.8°C 27.3°C 28.8°C 29.9°C 31.7°C
Survival
Days after spawning
0
0.2
0.4
0.6
1
0
10
20
30
40
50
60
70


Median lifetime (days)
60
50
40
30
20
10
0
25
26
27
28
29
30
31
Temperature (°C)


(a) 24.8°C
(b) 27.3°C
(c) 28.8°C
(d) 29.9°C
(e) 31.7°C
(f) 24.8°C 27.3°C 28.8°C 29.9°C 31.7°C
Energy lipids (µg larva-1)
Days after spawning
0.0
0.5
1.0
1.5
2.0
2.5
3.0
0
1
2
3
4


Lipid depletion rate (ln(μg larva-1 d-1))
0.5
0.4
0.3
0.2
0.1
0.0
25
26
27
28
29
30
31
Temperature (°C)