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Effects of elevated temperature on the performance and survival of pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*)

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Abstract

Population irruptions of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) have caused substantial damage to coral reefs, but it is largely unknown how this asteroid will fare in a warmer ocean. We exposed these starfish to one of four thermal treatments, with final temperatures of 26 °C (control, annual average), 28 °C (summer average), 30 °C (summer maximum) and 32 °C (predicted summer maximum by 2100). We measured the righting time, movement rate, standard metabolic rate and probability of survival of the crown-of-thorns starfish at various timepoints over ~ 60 days. We found that while temperature did not affect righting time, it did significantly affect movement rate. The movement rate of starfish increased across the 26 to 30 °C range, with those at 28 °C and 30 °C moving 18 and 27% faster than those at the control temperature. Similarly, the standard metabolic rate of starfish increased from 26 to 30 °C, with metabolism 100% and 260% faster at 28 °C and 30 °C compared to those at the 26 °C control. At 32 °C, individual starfish exhibited a 14% slower movement rate, a 33% slower metabolic rate, and also exhibited a fourfold lower probability of survival than those at 30 °C. These results indicate that 32 °C is above the thermal optimum of crown-of-thorns starfish, suggesting that prolonged exposure to temperatures that are expected to be regularly exceeded under near-future climate change may be detrimental to this species.

Keywords Climate change · Coral reefs · Behaviour · Movement · Metabolic rate · Mortality

Introduction

Population irruptions of the coral-feeding Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*; CoTS) and climate change are considered two of the greatest contributors to coral loss, especially in the western Pacific (De'ath et al. 2012; Baird et al. 2013; van Hooidonk et al. 2016; Mellin et al. 2019; Castro-Sanguino et al. 2021). The tropical and subtropical waters surrounding coral reefs have warmed approximately ~ 1 °C since pre-industrial times (Lough et al. 2018; Negri et al. 2020), and climate change projections

indicate that they will likely heat further over the coming decades (IPCC 2013, 2021). Climate change is already having significant impacts on coral reef ecosystems in the form of a higher incidence and severity of marine heatwaves in recent years (GBRMPA 2019; Bureau of Meteorology 2020; IPCC 2021). These short-term periods of abnormally high ocean temperatures (by definition, when the temperature exceeds the 90th percentile for at least five consecutive days; Hobday et al. 2016), have resulted in mass coral bleaching events (van Hooidonk et al. 2016; Bureau of Meteorology 2020). Extreme temperatures and CoTS predation are considered to have cumulative or synergistic negative effects on corals, reducing the resilience of coral reef ecosystems (Vercelloni et al. 2017; Kamya et al. 2018; Haywood et al. 2019; Keesing et al. 2019; Castro-Sanguino et al. 2021). However, in order to predict the future resilience of the reef, the direct impact of ocean warming on this coral predator must be considered (Lang et al. 2021).

For ectothermic species, such as asteroids, environmental temperature is a strong determinant of the rate of physiological processes, which affects the ability of these individuals

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to move in their natural environment (Kidawa et al. 2010; Nguyen et al. 2011; Brothers and McClintock 2015; Illing et al. 2020). Measuring the time it takes for an individual to return to its natural orientation following inversion (righting time) is a useful measure of neuromuscular coordination (Kleitman 1941; Reese 1966; Binyon 1972) and has been used as a proxy for overall performance in response to temperature in echinoderms (Peck et al. 2008; Kidawa et al. 2010; Wood et al. 2010; Brothers and McClintock 2015). In the starfish *Odontaster validus*, while temperatures of 2 °C above ambient had little effect on righting time, starfish righted more slowly when heated by a further degree (Kidawa et al. 2010). Likewise, the sea urchin *Heliocidaris erythrogramma* righted at similar speeds at ambient temperature and with a 2 °C temperature increase, but a further degree of warming more than doubled the righting time (Minuti et al. 2021). In contrast, several studies have found that the righting time of echinoderms, such as the sea urchin *Strongylocentrotus intermedius* (Zhang et al. 2017) and the brittle star *Ophiura ophiura* (Wood et al. 2010), changed very little with 3 °C and 4.5 °C of warming (above ambient), respectively. Rates of movement along a surface serves as another useful proxy for performance in a warmer environment, but is rarely studied in echinoderms (but see Kidawa et al. 2010). This behaviour may be even more thermosensitive than righting, with the movement rate of *O. validus* increasing only until 1 °C above ambient temperature, but declining with an additional degree of warming (Kidawa et al. 2010). Activity rate declines in marine organisms at high temperatures may diminish the ability to effectively escape predators and seek out suitable prey, lessening the capacity to meet the heightened energetic demands in a warmer ocean (Pörtner and Knust 2007; Peck et al. 2008; Kidawa et al. 2010; Wood et al. 2010; Brothers and McClintock 2015; Sun et al. 2018).

It is a general physiological rule that the standard metabolic rate (SMR) increases with temperature, in an attempt to meet the greater energy requirement for maintenance of homeostasis (Peck and Prothero-Thomas 2002; Clarke and Fraser 2004). However, there are limits to the capacity to supply sufficient oxygen to sustain metabolism, produce enough energy to support normal cellular processes, and maintain organism performance and fitness (Lawrence 1984; Pörtner 2001, 2002; Pörtner et al. 2017). Harianto et al. (2018), for instance, observed significant declines in SMR and survival at 26 °C (~ 4 °C above the average summer temperature, AST) in the temperate sea urchin *H. erythrogramma*. Observed metabolic depression at elevated temperatures is largely a consequence of the increased reliance on anaerobic metabolism, which is much less efficient at producing energy than aerobic metabolism (Pörtner 2001, 2002; Pörtner et al. 2017; Lang et al. 2021). Evidence for this has been observed in CoTS at the biochemical level, with reduced activity of citrate synthase (a proxy for aerobic capacity) and increased activity of lactate dehydrogenase (a proxy for anaerobic capacity) at warmer temperatures (Lang et al. 2021). The consequent hypoxia contributes towards the disruption of cellular oxidative phosphorylation, protein denaturation, mitochondrial failure and ultimately mortality, which often occur after extended exposure to elevated temperatures (Chen and Chen 1993; Pörtner 2001, 2002; Peck et al. 2009; Fang et al. 2015a, b; Christensen et al. 2011, 2017; Pörtner et al. 2017; Harianto et al. 2018).

In many marine ectotherms, including CoTS, thermal sensitivity is not uniform across life stages, and sensitivity to elevated temperature often varies depending on the measures assessed (e.g., Rupp 1973; Kashenko 2006; Rahman et al. 2009; Byrne et al. 2013; Uthicke et al. 2015; Caballes et al. 2017). Laboratory-based investigations have demonstrated that gametogenesis and the early life stages of CoTS are thermosensitive, whereby 2 to 4 °C warming (above AST) results in smaller eggs and a lower gonado-somatic index (Hue et al. 2020), as well as reduced fertilisation success (Caballes et al. 2017; Hue et al. 2020), and proportion of embryos and larvae undergoing normal development (Kamya et al. 2014; Caballes et al. 2017; Sparks et al. 2017). In contrast, the same degree of warming either enhances or does not affect the development rate (Lamare et al. 2014; Uthicke et al. 2015), survival (Lamare et al. 2014; Uthicke et al. 2015) and growth (Lamare et al. 2014) of larvae, as well as the growth of algae-feeding (Kamya et al. 2016) and coral-feeding juveniles (< 1.5 cm; Kamya et al. 2018). Larger coral-feeding CoTS may be more thermally robust, as shown in a recent study where the metabolic rate of sub-adults was found to increase with temperature to at least 36 °C, and metabolic depression was only observed in adult CoTS from 33 °C (> 5 °C above AST; Lang et al. 2021). However, these individuals were exposed to acute ramping trials (rate of increase, 1 °C h^{-1}; Lang et al. 2021) and thus may not experience additional physiological costs that are associated with the longer durations of heat exposure that naturally occur on the reef (Pörtner 2001, 2002; Pörtner et al. 2017). Whether coral-feeding juvenile (> 1.5 cm), sub-adult and adult CoTS experience compromised performance at cooler temperatures with prolonged exposure, remains to be tested.

Understanding how the coral-feeding life stages of CoTS perform in a warmer environment is essential for predicting the future impact of this predator on the reef. Herein, we explored the effect of prolonged (~ 60 days) exposure to various thermal treatments in Pacific CoTS from Australia's Great Barrier Reef (GBR). The size range tested incorporates large coral-feeding (> 5.5 cm) juveniles, as well as sub-adults and adults (Pratchett et al. 2014; 2021; Caballes 2017). The measures used to assess the effect of temperature on this species were: righting

time, average movement rate, SMR (weight-specific) and probability of survival. Because it is considered that species that inhabit coral reefs are living particularly close to their thermal limits (Stuart-Smith et al. 2015; Negri et al. 2020), we hypothesised that temperatures of only a few degrees above the AST will compromise performance during prolonged exposure to elevated temperatures (Lang et al. 2021). Compromised performance and increased mortality of CoTS in a warmer ocean will unequivocally lead to population contractions (Eisenlord et al. 2016), and possibly re-distributions (Ling 2013; Sill and Dawson 2021), with variable impacts on the corals that they interact with.

Materials and methods

Collection and maintenance

We collected Pacific crown-of-thorns starfish ($n = 48$, 10–1556 g, 5.5–38 cm diameter), from mid-shelf reefs in the central GBR between 28 and 30th January 2020, at depths of 2–8 m. These reefs were Big Broadhurst (18°58′S, 147°43′E), Keeper (18°45′S, 147°17′E), Kelso (18°26′S, 146°59′E), Little Broadhurst (18°56′S, 147°41′E), Little Kelso (18°28′S, 146°59′E), Lodestone (18°42′S, 147°06′E), and Rib (18°28′S, 146°53′E). Sea surface temperatures at the collection locations generally range from 24 °C to 29 °C annually (AIMS 2021a), and at the time of collection the temperature of the water was 28–29 °C. These CoTS were transported to the Marine and Aquaculture Research Facilities Unit (MARFU), James Cook University, Townsville, in flow-through aquaria. Upon arrival, we placed the starfish individually in 42 L tanks attached to one of four semi-closed recirculating systems (which would eventually become the four temperature treatments). The water temperature was set to 26 °C, which is the annual average temperature in the collection vicinity (AIMS 2021a). The seawater was naturally at pH 8.24 and had a salinity of 37.5 ppt. The systems were housed within a temperature-controlled room with a 12 h:12 h light:dark cycle. We acclimated the CoTS to laboratory conditions in these tanks for 25 days. We did not feed the CoTS throughout the acclimation period and the duration of experiments, to avoid any potential effect of differential feeding on individual performance (sensu Caballes et al. 2016). This starvation unlikely impacted energy reserves to a significant extent, due to the low levels of activity of CoTS in the laboratory, and the fact that they are known to survive for many months without feeding (Moran 1988).

Experimental design

We commenced the experiments to assess righting time and average movement rate after the acclimation period on 24th February 2020. Starfish were distributed evenly among four treatments (26, 28, 30 and 32 °C, $n = 12$ per treatment). The treatment names represent the final temperatures experienced by the starfish rather than the temperatures at the beginning of the experiments (26 °C in all treatments, Fig. 1). The mean weights of these starfish were 313, 193, 309 and 294 g for the 26, 28, 30 and 32 °C treatment, respectively. The weights of the starfish were not significantly different among treatment groups (LM, $F = 0.30$, $df = 3$, $p = 0.819$). We initially tested the starfish in each of the temperature treatments at the control temperature of 26 °C (day 1), after which we raised the temperatures in the 28, 30 and 32 °C treatments to 28 °C, before repeating the experiments on all 48 starfish (week 2, day 8). Upon completion, we further raised the temperatures of the 30 °C and 32 °C treatment systems to 30 °C, and again repeated the experiments (week 3, day 15). Finally, we raised the temperatures of the 32 °C treatment to 32 °C, and we completed the last round of righting and movement experiments, with all starfish being at their final temperatures (week 4, day 22, Fig. 1). In between each week, we raised the temperatures in the relevant treatments at rates of 0.5 °C day^{-1}, which allowed for a three-day acclimation period at the testing temperature before experiments commenced. The treatments were warmed gradually rather than immediately exposing starfish to their final temperatures, in order for the environmental conditions to be more representative of those that may be experienced by CoTS in nature, during a warming event (AIMS 2021a, b). The temperature of the seawater in the systems was on average ± 0.25 °C around the set-point level throughout the experiments.

We tested the SMR of each starfish twice unless mortality occurred before testing. One run (same week, SW) involved testing the SMR of all surviving starfish between days 32–35 for the 26 ($n = 12$), 28 ($n = 12$), 30 ($n = 11$) and 32 °C ($n = 8$) temperature treatments (Fig. 1). The CoTS were tested over the same four days in order to control for an effect of time in the laboratory. To further control for an effect of time, we tested starfish from all four treatments each day. The other run (consecutive weeks, CW) involved testing the SMR of the same starfish exactly 4 weeks after first exposure to the final temperatures for each treatment (except in the case of the 26 °C control). Specifically, testing occurred on days 29–30 for the 26 °C treatment ($n = 12$), day 36 for the 28 °C treatment ($n = 11$), day 43 for the 30 °C treatment ($n = 11$) and day 50 for the 32 °C treatment ($n = 3$) (Fig. 1). On each of the warmer testing days (days 36, 43 and 50), we re-tested the same six starfish from the 26 °C control treatment in order to control for any effect of time, however there was no
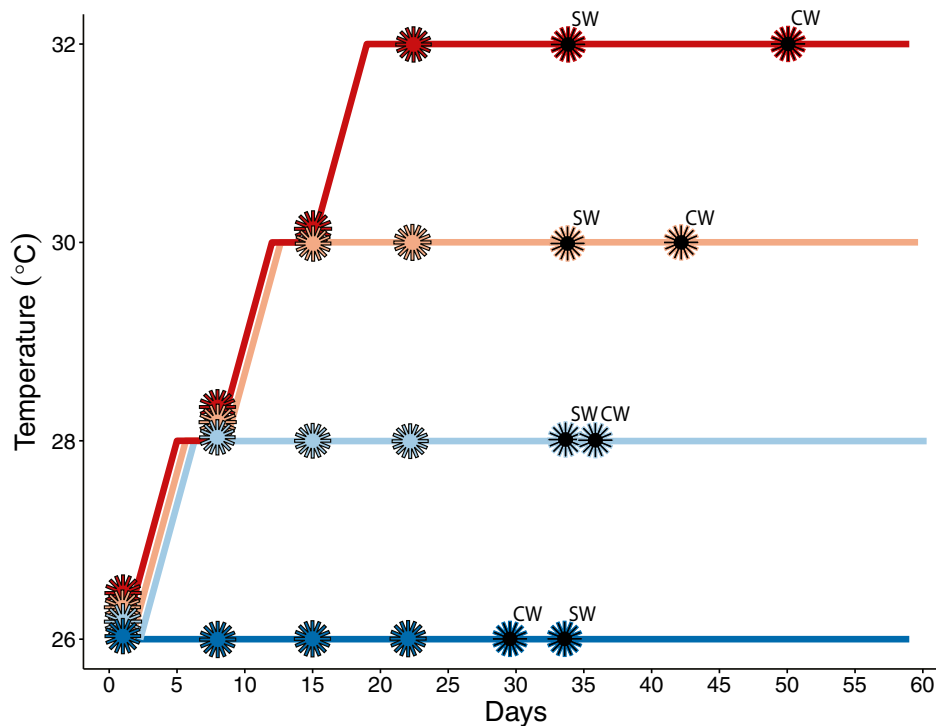
Fig. 1 Experimental design timeline. The figure indicates the temperature profiles for the 26 °C (dark blue), 28 °C (light blue), 30 °C (orange) and 32 °C (red) treatments, from day 1 of the study until day 59. Experiments to assess righting time and average movement rate (symbols with coloured fill) were carried out on days 1, 8, 15 and 22 for all *Acanthaster* cf. *solaris* during the temperature ramping period. Experiments to measure the standard metabolic rate of the starfish (symbols with black fill) took place after endpoint temperatures were reached. The same week 'SW' run was carried on days 32 to 35 on all starfish, while the consecutive weeks 'CW' run was conducted on days 29–30, 36, 43 and 50 for the 26, 28, 30 and 32 °C treatments, respectively. The overlapping lines of the four treatments were offset horizontally, so that their complete temperature profiles could be visualised. The overlapping symbols were offset vertically. Experiments began with $n = 12$ starfish per treatment, and any mortality was recorded over the 59 days

significant effect of this variable ($p = 0.529$). We conducted the CW run in order to account for an effect of differing lengths of time at the final temperatures among temperature treatments, and to allow for better assessment of the exposure-time dependence of thermal effects on physiological performance.

We checked the CoTS once or twice per day for mortality from day 1 until day 59 (Fig. 1). Starfish were considered deceased when they exhibited all or a number of typical indicators of mortality, such as flattened or detached spines, lesion formation, exposure of internal organs and loss of turgor. Upon death, we immediately removed the starfish in order to avoid system contamination, and they were not replaced. We recorded the time of death for later analysis.

Righting time and movement rate

We conducted the experiments to measure the righting time and average movement rate for each CoTS in one of four 1.1 m diameter round aquaria, connected to their respective recirculation systems to ensure consistency of environmental conditions. To measure righting time (s),

we inverted the starfish and placed them in the centre of the aquarium, and permitted them to return to their natural orientation. Once righted, we allowed the starfish to move from the centre to the edge of the aquarium. We video recorded all responses using GoPro Hero 7 cameras (GoPro Inc., California, USA) for later analysis. We determined the righting time and mode of righting (the style of movement used to return to the correct orientation) from the videos. Three modes of righting were utilised by the CoTS. Mode 1 involved the starfish raising all arms upwards so that they were almost touching, causing them to tip to side. The top arms finally moved over the bottom arms until they reached the surface. Starfish utilising mode 2 raised some arms upwards so that they were almost touching, while the other arms bent backwards in order for them to flip themselves over. Mode 3 involved the starfish bending their arms backwards and flipping themselves over without raising their arms up first. We used Adobe After Effects software (Adobe Systems Inc., California, USA) to establish the average rates of movement (cm min^{-1}) over the total distance travelled (the sum of the distance travelled in all directions).

Standard metabolic rate

To assess the SMR of the starfish in the four temperature treatments, we used intermittent-flow respirometry (Clark et al. 2013; Svendsen et al. 2016; Kühnhold et al. 2019; Lang et al. 2021). We placed four acrylic respirometry chambers of various sizes (4.12, 9.99 and 21.77 L) within a 1000 L capacity water bath. Flush pumps (flow rate; 400 to 500 L h^{-1}) delivered oxygenated water from the water bath into the chambers between measurement periods, and snorkels attached to the top of the chambers expelled oxygen depleted water. Recirculatory pumps (flow rate; 400 to 500 L h^{-1}) enabled the water within the chambers to constantly mix. We glued oxygen sensor spots to the recirculatory tubing with silicone gel, and aligned them with Firesting oxygen probes (PyroScience, Aachen, Germany). These probes delivered oxygen depletion data via a Pyro oxygen meter into the PyroScience program installed on a computer via fibre-optic cables. A chiller and two heaters (1 kW) cooled/heated the water to the final temperature for the 26, 28, 30 and 32 °C treatments prior to the introduction of the starfish. We ran four chambers at once (three containing starfish, with one left empty to control for background respiration). We allowed the starfish to settle in the chambers for 45 min with the flush pumps switched on, after which we sealed the chambers, and measured oxygen depletion in each chamber over 30 min. After the measurement period we again switched on the flush pumps, enabling oxygen levels in the chambers to return to ~100%. We tested four to six cohorts of starfish each day between 09:00 and 20:30.

For consistency we removed the first eight minutes from all oxygen depletion slopes, as a consequence of a delay in the water within the sealed chambers becoming completely mixed. We subtracted the slopes for background respiration from each run from the CoTS respiration slopes. We calculated the weight-specific SMR in mg O$_2$ g^{-1} h^{-1} following Svendsen et al. (2016).

Statistical analysis

We carried out all statistical analyses in R Studio (version 1.1.463, RStudioTeam 2016). We analysed the effect of temperature (at the time of testing) on righting time (s) using a linear mixed effects model. We log-transformed the response in order to meet the normality assumption. We also included the experimental week, the log-transformed starfish wet weight (g) and mode of righting as covariates, to control for differences in these variables among temperature treatments. We included Starfish ID as a random effect to account for the repeated measures design. In addition, we conducted a Fisher's exact test in order to establish whether there was an association between temperature and the mode of righting utilised by the starfish.

We used an additional linear mixed effects model to establish the effect of temperature on the average movement rate (cm min^{-1}). Again, we included the experimental week, the log-transformed wet weight (g) and starfish ID in the model, in addition to the log-transformed distance travelled (cm). We excluded observations from the analysis if the starfish did not move within 20 min of righting ($n=3$). As a result of the significance of wet weight in influencing the average movement rate, we explored this relationship further by establishing the scaling exponent (*b*), which is the slope value of this factor and the response. This value was calculated for each temperature using linear ordinary least squares regression analyses. We extracted the estimated marginal means for the righting time (on the response scale) and average movement rate of the starfish for all temperatures. These are the means that have been adjusted for covariates in the model i.e., weight, mode of righting and distance travelled. These estimated marginal means were used for further data investigation including post-hoc comparisons using the Tukey method.

We analysed the SMR (log-transformed, mg O$_2$ g^{-1} h^{-1}) using a further linear mixed effects model. We included temperature treatment and run as interacting fixed effects, and starfish ID as a random effect. We removed observations from the analysis that were so low that they could not be distinguished from background respiration ($n=3$). We used the estimated marginal means (on the response scale) of SMR in the four treatments for post-hoc analysis, including comparisons using the Tukey method. As a result of there being little effect of the run in the model, we only report the compiled estimated marginal means for the four treatments. However, these estimated marginal means adjust for other factors in the model. We calculated the temperature (Q$_{10}$) coefficient between the estimated marginal means of the four treatments in order to establish thermal sensitivity, using the equation by Prosser (1991). For each treatment we also established the scaling exponents (*b*) for the relationship between the natural logarithms of SMR at the organism level (mg O$_2$ h^{-1}) and weight (g). These was calculated using linear ordinary least squares regression analyses.

We explored the survival probability (%) for the starfish in the four temperature treatments using a Kaplan–Meier survival plot and an accompanying log-rank test. Pairwise comparisons were conducted using the Benjamini–Hochberg method. We also conducted a Cox proportional hazards model in order to determine the hazard ratios associated with the three elevated treatments. These models are unable to include groups with no 'events', and therefore we eliminated the 26 °C control treatment (no mortality, see results) from this analysis. We also conducted a Cox proportional hazards model to observe the hazard ratios for the effect of wet weight (g) on the probability of survival.

Results

Righting time and movement rate

We found no significant impact of temperature on righting time (Fig. 2a, Table 1, see S1 in Online Resource), and no significant effect of the experimental week or the wet weight of the starfish (Table 1). Likewise, we did not find that temperature significantly influenced the mode of righting utilised (Fisher's exact test, $p = 0.328$), although we did find that there was a significant effect of mode of righting on righting time (Table 1). Starfish utilising mode 3 righted the fastest, with an average righting time of 158 ± 35 s. This was also the rarest mode of righting ($n = 4$). Mode 1 was the second fastest mode of righting (194 ± 13 s), and was the most commonly used by the CoTS ($n = 161$). Starfish utilising mode 2 of righting were the slowest ($n = 26$, 258 ± 27 s).

We found a significant effect of temperature on the average movement rate of the starfish (Table 1). There was an 18 and 27% faster movement rate of starfish at 28 °C and 30 °C, respectively, compared to those at 26 °C. However, starfish at 32 °C were 14% slower than those at 30 °C (Fig. 2b, see S1 in Online Resource). Rates of movement did not vary significantly among experimental weeks, although we did find a significant effect of distance travelled and wet weight on average movement rate. Starfish that had faster rates of movement travelled further to reach the edge of the aquaria and were heavier (Table 1). The positive relationship between wet weight and movement rate was similar between 26 and 30 °C ($b = 3.58–3.93$), but was lower at 32 °C ($b = 1.80$, see S2 in Online Resource).

Standard metabolic rate

We found that temperature treatment significantly influenced the SMR (Table 2). The SMR was 100% (Q_{10}: 32.0) and 260% (Q_{10}: 24.6) higher in the 28 °C and 30 °C treatments compared to the 26 °C treatment, respectively. However,
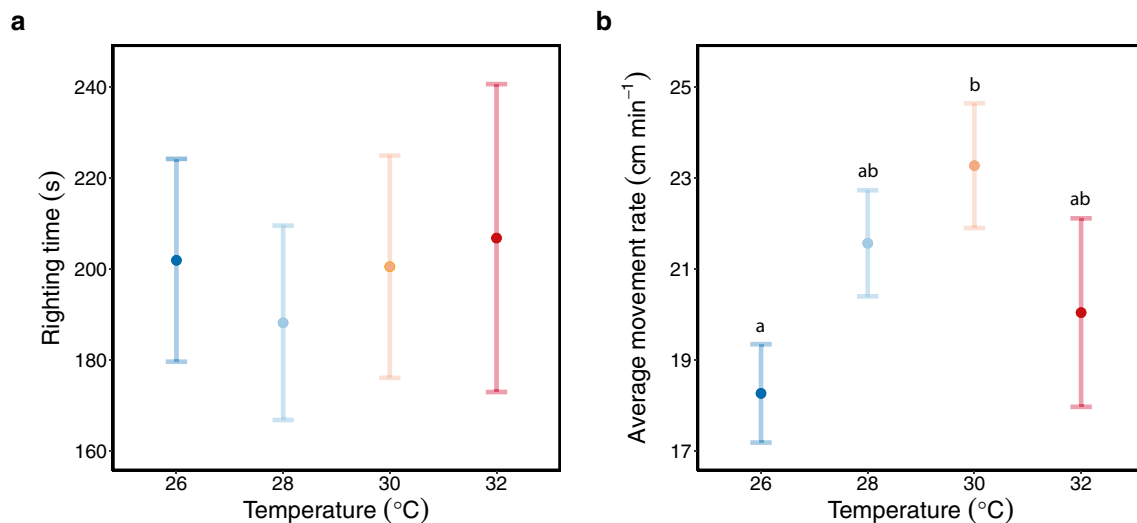
Table 1 Output of the linear mixed effects models on the effect of temperature on righting time (s) and average (Av) movement rate (cm min^{-1}) in *Acanthaster* cf. *solaris* ($n = 48$ CoTS, $n = 191$ righting time observations, $n = 188$ average movement rate observations).

Response	Factor	Num *df*, Den *df*	F	*p* value
Righting time (s)*	Temperature	3, 179	0.24	0.871
	Experimental week	3, 164	1.20	0.312
	Wet weight*	1, 47	0.17	0.686
	Mode of righting	2, 181	5.94	**0.003**
Av. Movement rate (cm min^{-1})	Temperature	3, 173	3.42	**0.019**
	Experimental week	3, 162	1.26	0.290
	Wet weight*	1, 55	73.88	**< 0.001**
	Distance travelled*	1, 184	9.24	**0.003**

The influence of the covariates: experimental week, wet weight (g) mode of righting and distance travelled (cm) are also included. Responses and covariates with an asterisk (*) were log-transformed in the models to meet the normality assumption. Significant *p* values are in bold

Fig. 2 The effect of temperature on **a** righting time (s) and **b** average movement rate (cm min^{-1}) in *Acanthaster* cf. *solaris* ($n = 48$ CoTS, $n = 191$ righting time observations, $n = 188$ average movement rate observations). Estimated marginal means are provided ($\pm$ SE). Letters represent significant differences between temperatures (Tukey method, $p < 0.05$)

Table 2 Output of the linear mixed effects model on the effect of temperature (T) treatment, run, and their interaction on the standard metabolic rate (mg O_2 g^{-1} h^{-1}) of *Acanthaster* cf. *solaris* ($n = 42$ CoTS, $n = 76$ observations).

Response	Factor	Num df, Den df	F	p value
Standard metabolic rate (mg O_2 g^{-1} h^{-1})	Temperature treatment	3, 38	11.76	**< 0.001**
	Run	1, 30	0.30	0.587
	T Treatment x run	3, 30	0.34	0.798

The response was log-transformed in the model to meet the normality assumption. Significant p values are in bold
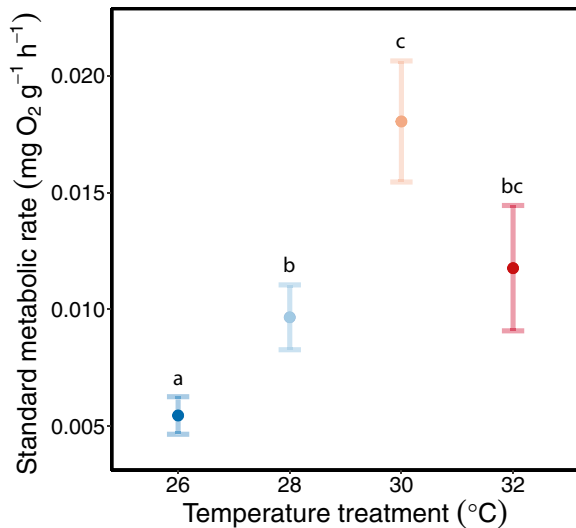
Fig. 3 The estimated marginal means ($\pm$ SE) for the effect of temperature treatment on the standard metabolic rate (mg O_2 g^{-1} h^{-1}) of *Acanthaster* cf. *solaris* ($n = 42$ CoTS, $n = 76$ observations). Letters represent significant differences between treatments (Tukey method, $p < 0.05$)

Fig. 4 Kaplan–Meier survival curve for the effect of the 26 °C (dark blue), 28 °C (light blue), 30 °C (orange) and 32 °C (red) treatments on survival probability (%) in *Acanthaster* cf. *solaris* ($n = 48$) over 59 days. The shaded bands represent the 95% confidence intervals. The survival curve for each temperature treatment began at 100%. The overlapping lines of the four treatments were offset horizontally, in order for their complete survival curve to be visualised. Final temperatures were reached for the 28, 30 and 32 °C treatments on days 5, 12, and 19, respectively. The righting and movement experiments took place on days 1, 8, 15 and 22. Letters represent significant differences between temperature treatments (Benjamini–Hochberg method, $p < 0.05$)

the SMR of starfish in the 32 °C treatment was 33% (Q_{10}: 0.1) lower than those in the 30 °C treatment (Fig. 3, see S3 in Online Resource). The run did not significantly impact the SMR, and there was no interaction between temperature treatment and run (Table 2). The positive correlation between the weight of the starfish and the SMR was similar in the majority of the treatments ($b = 0.96$, 1.02 and 0.97 for the 26, 28 and 32 °C treatments, respectively), but was lower in the 30 °C treatment ($b = 0.70$, see S4 in Online Resource).

Survival

We found an overall significant effect of temperature treatment on the probability of survival (Log-rank, $\chi^2 = 25.30$, $df = 3$, $p < 0.001$). The difference in survival between treatment pairs was only significant for the 32 °C (75% mortality) treatment compared to the 26 °C ($p < 0.001$, 0% mortality), 28 °C ($p = 0.008$, 17% mortality) and 30 °C ($p = 0.012$, 25% mortality) treatments, respectively (Fig. 4). The Cox proportional hazards model further supports this result (Likelihood
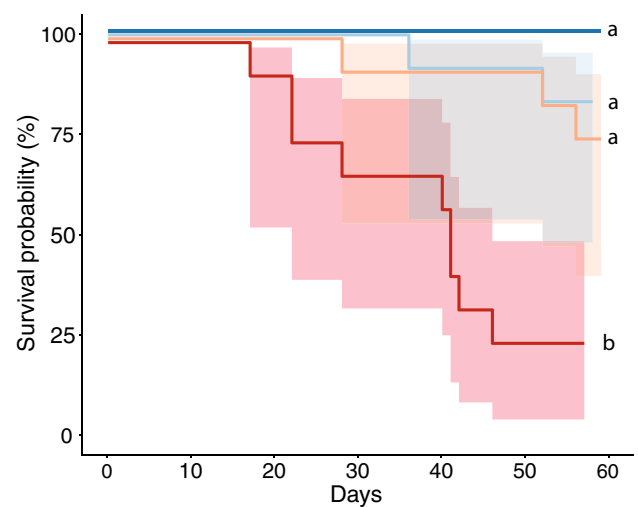
ratio test $= 11.66$, $df = 2$, $p = 0.003$), with hazard ratios revealing a sevenfold ($p = 0.007$) and fourfold ($p = 0.012$) lower probability of survival in the 32 °C compared to the 28 °C and 30 °C treatments, respectively (Table 3). We observed the first mortality event on day 17. The deceased starfish was from the highest temperature treatment when the water temperature was approximately 31 °C. All remaining deaths occurred after the final temperatures were reached, with the two subsequent deaths occurring 3 days after 32 °C was reached in the applicable temperature treatment. The first deaths in the 30 °C and 28 °C treatments occurred on days 28 and 36, respectively, 13 and 28 days after these final temperatures were reached. We found no significant effect of starfish wet weight (g) on the probability of survival (Cox

Table 3 Results of the Cox proportional hazards model indicating the probability of survival in *Acanthaster* cf. *solaris* ($n = 48$ CoTS) between temperature treatment pairs.

Treatment comparison	Hazard ratio	Lower 95% CI	Upper 95% CI	*p* value
28–30 °C	1.51	0.25	9.05	0.651
28–32 °C	8.30	1.76	39.07	**0.007**
30–32 °C	5.49	1.46	20.70	**0.012**

The 26 °C control treatment could not be included due to the lack of 'events'. The hazard ratios, lower and upper 95% confidence intervals and *p* values (significant values in bold) are provided. The hazard ratios − 1 reveals the -fold difference in the probability of survival between treatments

proportional hazards model, Likelihood ratio test = 1.45, $df = 1$, $p = 0.228$).

Discussion

Establishing the thermal sensitivity of the corallivorous Pacific crown-of-thorns starfish is an essential step forward in understanding how future shifts in environmental temperature may alter the impact of this asteroid on the reef. In the present study, we found that seawater temperatures of 32 °C had negative effects on the performance and survival of CoTS. Average movement rates and SMR increased from 26 °C to 30 °C, and over this thermal range survival was, for the most part, maintained. However, starfish at 32 °C had a lower SMR, reduced movement rate and a lower probability of survival, than those at 30 °C. This temperature is approximately 4 °C above the average, and 2 °C and above the maximal summer temperatures commonly experienced on the central mid-shelf of the GBR (AIMS 2021a, b), but it is predicted that temperatures of 32 °C will be frequently exceeded under near future climate change (IPCC 2013, 2021; Hoegh-Guldberg et al. 2018).

In nature it is expected that activity rates of organisms will decline when thermally stressed (Peck et al. 2008; Kidawa et al. 2010; Pörtner et al. 2017; Sun et al. 2018; Lang et al. 2021). In the present study, we observed that average movement rate increased with temperature until 30 °C, but slowed at 32 °C (14% decrease compared to 30 °C), indicating that starfish may experience thermal stress at this degree of ocean warming. In contrast, water temperature had little effect on righting time. This lack of thermal sensitivity is not uncommon (Wood et al. 2010; Zhang et al. 2017) and could be a consequence of the importance of this behaviour to avoid injury and predation, such that CoTS have evolved to invest a great deal of energy in maintaining their natural orientation (Lawrence 1984; Wood et al. 2010; Deaker et al. 2021). The differing responses between the two activities

may, however, be a product of the methodological design. Because movement rate was assessed directly after righting time, the latter response may be impacted by the energy investment in the prior activity (Lawrence 1984). Whatever the exact cause of our observations, the additional costs of activity seem to be limited at 32 °C, due to reduced aerobic metabolism, and therefore energy production of CoTS at this temperature. Constraints in energy production at high temperatures appears particularly relevant to larger (adult) individuals, highlighted by the lower value of *b* for average movement rate at 32 °C, compared to cooler temperatures (Lawrence 1984; Pörtner 2001; 2002; Doyle et al. 2012; Pörtner et al. 2017). It is currently unknown how the activity of CoTS will be influenced by warmer temperatures in nature. Environmental signals from predators, prey and conspecifics have a substantial impact on this asteroid, and provide a strong impetus to move away or towards such signals (Hall et al. 2017; Pratchett et al. 2017). This may result in the starfish maintaining high activity levels during marine heatwaves, potentially at the expense of other biological processes and behaviours (Lawrence 1984).

Reductions in aerobic capacity and associated energy reserves is expected to be a major contributor to compromised performance (including activity levels) in a warmer ocean (Pörtner et al. 2017; Lang et al. 2021). In this study, starfish in the 32 °C temperature treatment had a 33% slower SMR, compared to those in the 30 °C treatment, similar to the decline in movement rate observed between the same temperatures. The lower SMR in the highest temperature treatment is likely a result of the depression of aerobic metabolism, and an increased reliance on energy deficient, and unsustainable anaerobic metabolism (Pörtner 2001, 2002; Pörtner et al. 2017; Lang et al. 2021). In the present study, aerobic metabolic decline occurred at temperatures which were at least 1 °C cooler than observed in acute ramping trials (24–36 °C over 12 h) in CoTS that were collected from the same location and at the same time of the year. Although for smaller CoTS, metabolic depression was not observed even at temperatures as high as 36 °C when acutely exposed (Lang et al. 2021). The differing observations between these two studies is likely a result of factors that generally lead to compromised performance only after prolonged exposure to sub-optimal temperatures, such as mitochondrial failure (Pörtner 2002; Schulte et al. 2011), protein denaturation (Pörtner 2001, 2002; Pörtner et al. 2017) and oxidative damage (Pörtner 2002; Pörtner et al. 2017).

Aside from the lower SMR of CoTS at 32 °C, we observed a 260% higher SMR of individuals in the 30 °C compared to the 26 °C treatment (Q_{10}: 24.6). This is likely a result of the inherent increased rate of chemical reactions and cellular processes at higher temperatures (Peck and Prothero-Thomas 2002; Clarke and Fraser 2004; Schulte 2015; Harianto et al. 2018). The high Q_{10} coefficient indicates that CoTS have a

very high physiological thermal sensitivity across this testing range, which is far greater than observed in temperate echinoderms (Q_{10}: ~ 1.0–3.0; Christensen et al. 2011; Weber et al. 2013; Harianto et al. 2018). It is not surprising that tropical species, such as CoTS may be more thermosensitive than temperate species, considering that they evolved in a stable thermal environment, and are therefore less equipped to cope with extreme temperature fluctuations (Peck et al. 2010; Nguyen et al. 2011). Such a substantial increase in SMR with temperature is concerning because this would mean that CoTS would need to consume more coral prey to meet increased energetic demands, potentially resulting in greater impacts on coral communities (Barbeau and Scheibling 1994; McBride et al. 1997; Siikavuopio et al. 2008; Kamya et al. 2018; Haywood et al. 2019; Keesing et al. 2019; Kühnhold et al. 2019). Although, a smaller *b* in the 30 °C treatment (that has the highest mean SMR), highlights lower relative upper limits to SMR in the larger individuals, which naturally consume more coral, compared to smaller conspecifics (Lawrence 1984; Pörtner 2001; 2002; Doyle et al. 2012; Pörtner et al. 2017).

While CoTS are able to withstand temperatures exceeding 36 °C acutely (Lang et al. 2021), we observed that the ecological thermal limits of this asteroid are likely between 30 and 32 °C, which appears conserved between starfish across the tested weight distribution (10–1556 g). Here, starfish in the 32 °C temperature treatment exhibited a four- and sevenfold lower probability of survival than those in the 30 °C and 28 °C treatments, respectively. Mortality occurred within a couple of days of the water temperature reaching ~ 31–32 °C, indicating that even brief marine heatwaves that reach these temperatures may induce mortality in CoTS. Yet, 25% of starfish were able to survive extended exposure to 32 °C, suggesting that thermally tolerant individuals may persist in a warmer ocean (Binyon 1972; Johnson and Babcock 1994; Pörtner 2002). The present aquarium study may, however, overestimate survival that would occur in nature, due to a higher risk of disease at higher temperatures, either due to the greater pathogen virulence or lower host defences (Bates et al. 2009; Kohl et al. 2016; Hewson et al. 2018; Uthicke et al. 2021). Even if some CoTS are able to survive future extreme heating events, a greater amount of energy required for maintaining homeostasis may result in a lower energy investment in reproduction (Brockington and Clarke 2001; Siikavuopio et al. 2006, 2008; Uthicke et al. 2014; Delorme and Sewell 2016; Hue et al. 2020). CoTS from New Caledonia, for instance, produced significantly smaller eggs, had poorer fertilisation success and a reduced gonado-somatic index with only 2 °C warming above the ambient summertime seawater temperature (Hue et al. 2020). Furthermore, a recent cross-generational study on the sea urchin *Echinometra* sp. A from the GBR

found that there were negative carry-over effects from parents to offspring reared in predicted near-future ocean conditions (+ 1 °C, 685 ppm; + 2 °C, 940 ppm), providing uncertainty regarding the adaptive capacity of echinoderms (Uthicke et al. 2021).

In the current study, we present evidence for thermal effects on the performance and survival of CoTS. An increased performance of CoTS when exposed to current maximal summertime temperatures (~ 30 °C), which may become more commonly experienced prior to the end of the century (AIMS 2021a, b; IPCC 2021; Hoegh-Guldberg et al. 2018), could result in a higher incidence and severity of population irruptions. Considering the faster metabolic rates (260%), movement rates (27%) and probably feeding rates of CoTS at this optimal temperature, these irruptions may result in increased coral loss on the GBR (De'ath et al. 2012; Mellin et al. 2019). Elevated coral predation will reduce the likelihood of recovery for corals already suffering from cumulative disturbance effects caused by temperature-induced bleaching and cyclones, among other stressors (De'ath et al. 2012; Vercelloni et al. 2017; Mellin et al. 2019).

While moderate increases in temperature (up to 30 °C) may increase the incidence and impacts of population irruptions of CoTS, the performance and survival of coral-feeding CoTS is expected to be greatly compromised at 32 °C, corresponding with projected end of century temperatures (IPCC 2013, 2021; Kamya et al. 2014; Hoegh-Guldberg et al. 2018; Lough et al. 2018; AIMS 2021a, b). However, at these temperatures, increased coral bleaching and mortality will more than offset benefits accrued from reduced incidence of population irruptions of CoTS (Eisenlord et al. 2016; van Hooidonk et al. 2016; GBRMPA 2019; Castro-Sanguino et al. 2021). Moreover, CoTS may have some capacity to acclimate or adapt to a warmer environment (Schulte et al. 2011; Schulte 2015; Pörtner et al. 2017; but see Uthicke et al. 2021). If CoTS are able to adjust their metabolism and oxygen requirements, and activity levels at supra-optimal temperatures, they may be able to conserve more energy, reducing their nutritional requirements (Pörtner et al. 2017). As a consequence, CoTS may switch their feeding preferences to feed more readily on partially bleached corals, which have lower nutritional value, but will be more common in a warmer ocean (MacArthur and Pianka 1966; Glynn 1985; Rodrigues and Grottoli 2007; Keesing et al. 2019). If unable to acclimate or adapt to warmer conditions, CoTS populations may persist by redistributing to cooler, more southerly reefs (Sill and Dawson 2021), facilitated by larval dispersal (Dight et al. 1990). However, population redistributions may be constrained by the dispersal capacity of CoTS larvae in a warmer ocean (Dight et al. 1990) and the availability of suitable settlement substrate (Britton et al. 2021). Acclimation and adaptation capacity, as well as range shifts may result in CoTS continuing to be a significant

threat on the reef for years to come (De'ath et al. 2012; Mellin et al. 2019). For this reason, it is axiomatic that these possibilities are investigated.

Declarations

Conflict of interest All authors declare no conflicts of interest.

Ethical approval Starfish were collected under the Great Barrier Marine Park permit G15/37535.1. Echinoderms are exempt from animal ethics approvals in Australia.

Consent to participate Consent to participate was obtained from all authors.

Consent for publication Consent for publication was obtained from all authors.

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