REPORT

Impacts of ocean warming on the settlement success and post-settlement survival of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*)

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Abstract Ocean warming and population irruptions of crown-of-thorns starfish (CoTS; *Acanthaster* cf. *solaris*) are two of the greatest threats to coral reefs. As such, there is significant interest in understanding how CoTS may be directly impacted by rising ocean temperatures. Settlement of planktonic larvae and subsequent metamorphosis is purported to be a major population bottleneck in marine invertebrates, yet it is unknown how ocean warming will impact these processes in CoTS. Herein, the effect of temperature (28 °C ambient, 30 °C, 32 °C, 34 °C) on the settlement success, metamorphic success, and post-settlement survival of this corallivore was explored. While larval settlement was robust to elevated temperature, with at least 94% of larvae settling after 48 h across all temperatures, it was observed that settlement success was lower on substrate that had been pre-treated ≥ 32 °C. Metamorphic success was also significantly constrained at temperatures ≥ 32 °C. At 32 °C and 34 °C metamorphic success was 16% and 63% lower than at ambient temperature, respectively. Significant adverse effects of warming on post-settlement survival were observed at even cooler temperatures, with 10% lower survival at 30 °C compared to at ambient temperature, and at 34 °C, survival was 34% lower. Substantial reductions in metamorphic success and early post-settlement survival at elevated temperatures, as well as negative impacts of warming on the settlement substrate and its capacity to induce settlement, may present a bottleneck for recruitment in a warmer ocean.

Keywords Temperature · Metamorphosis · Larvae · Coralline algae · Settlement cue · Great Barrier Reef

Introduction

Climate change is a growing threat to marine ecosystems, and coral reefs are particularly vulnerable (Hoegh-Guldberg et al. 2017; Hughes et al. 2017; IPCC 2019; Mellin et al. 2019; Pratchett et al. 2021a). Ocean warming and the higher prevalence and intensity of marine heatwaves are causing increased severity, frequency, and extent of mass coral bleaching events on reefs (Bahr et al. 2017; Hoegh-Guldberg et al. 2017; Hughes et al. 2017; Mellin et al. 2019; Pratchett et al. 2021a). Moreover, many coral reef ecosystems, such as the Great Barrier Reef (GBR), are facing a multitude of other threats (Vercelloni et al. 2017; Suchley and Alvarez-Filip 2018; Bellwood et al. 2019; Mellin et al. 2019). Crown-of-thorns starfish (*Acanthaster* spp.; CoTS), are causing extensive damage throughout the Indo-Pacific region, due to their tendency to feed on reef-building corals, and their propensity to occur at high densities (Pratchett et al. 2014; Vercelloni et al. 2017; Yasuda 2018; Pratchett et al. 2021b). The future threat of this destructive starfish depends largely upon their tolerance to ocean warming, as

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well as the state of their habitat and prey (Kamya et al. 2016, 2018; Lang et al. 2021, 2022).

Throughout their life cycle, CoTS remain thermally sensitive (Kamya et al. 2014, 2016, 2018; Lamare et al. 2014; Uthicke et al. 2015; Caballes et al. 2017; Hue et al. 2020; Lang et al. 2021, 2022). Like most benthic marine invertebrates, CoTS are broadcast spawners, meaning gametes are released into the water column, where fertilisation occurs (McEdward and Miner 2001; Uthicke et al. 2009; Caballes and Pratchett 2014). Resulting embryos develop into swimming planktonic larvae, which eventually settle on the benthos and develop into juvenile and adult starfish with radial symmetry (Caballes and Pratchett 2014). Prior research has determined that the thermal limit of fertilisation, and the embryonic and larval stages of CoTS, is generally exceeded between 30 and 34 °C, temperatures which are expected to be regularly surpassed on the GBR in the near future (IPCC 2019; AIMS 2022). Temperatures of 30 °C have been shown to have little effect on the performance of algal and coral feeding juvenile CoTS (Kamya et al. 2016, 2018; Lang et al. 2021). At 32 °C, however, the thermal limit is surpassed, with coral-feeding juvenile and adult CoTS exhibiting significant reductions in metabolic performance and survival over ~60 days of thermal exposure (Lang et al. 2022). Coral-feeding CoTS may be able to tolerate short-term marine heatwaves (by definition, when the temperature surpasses the 90th percentile for a minimum of five consecutive days; Hobday et al. 2016) but may be unable to endure prolonged and sustained warming expected to occur as the climate changes (Lang et al. 2021, 2022). Prolonged warming may impact reproductive capacity and the quality of progeny, and the early life stages of CoTS may be further impaired by marine heatwaves that coincide with spawning, and subsequent early development and settlement (Rupp 1973; Kamya et al. 2014; Lamare et al. 2014; Uthicke et al. 2015; Caballes et al. 2017; Hue et al. 2020).

Larval settlement and metamorphosis are essential processes in the life cycle of CoTS and other marine invertebrates (Rodríguez et al. 1993; Hadfield and Paul 2001), and typically involve the planktonic larvae attaining metamorphic competence, active searches for suitable substrate, initial substrate contact, exploration, selection, fixation (i.e. permanent attachment), and subsequent metamorphosis into their juvenile form (Pawlik 1992; Doll et al. 2022). These processes are considered major bottlenecks in the life cycle of marine organisms with planktonic larvae, and the success of settlement and metamorphosis is likely to have a pronounced influence on recruitment and population dynamics (Balch and Scheibling 2001; Uthicke et al. 2009; Wilmes et al. 2018). Few studies have assessed the effect of temperature on settlement and metamorphosis in marine invertebrates (Espinel-Velasco et al. 2018), with the majority of such research focusing on corals (e.g. Nozawa

and Harrison 2007; Putnam et al. 2008; Randall and Szmant 2009). Nevertheless, a field study found that in warmer years, settlement success was higher in the sea urchin *Diadema* aff. *antillarum* from the Canary Islands (Hernandez et al. 2010). It was anticipated that the additive effect of elevated temperature and over-fishing of sea urchin predators would increase their abundance in a warmer ocean, with negative downstream impacts on marine biodiversity (Hernandez et al. 2010; Mos et al. 2011). Conversely, ex situ studies on the sea cucumber *Apostichopus japonicus* and the sea urchin *Tripneustes gratilla* found that at certain critical temperatures, settlement was negatively impacted (Li et al. 2010; Mos et al. 2011). This may be largely a consequence of an increasing energetic demand at higher temperatures, meaning less energy is available for maintaining normal physiological processes and behaviours (Pörtner and Peck 2010; Ross et al. 2011; Pörtner et al. 2017; Espinel-Velasco et al. 2018).

Even if settlement rates remain high in a warmer ocean, this may not necessarily result in successful recruitment (Rowley 1989; Keesing and Halford 1992; Nozawa and Harrison 2007; Hernandez et al. 2010; Vermeij et al. 2010; Mos et al. 2011; Glockner-Fagetti and Phillips 2020). Newly metamorphosed juveniles may have reduced energy reserves in a warmer ocean, interfering with the maintenance of homeostasis, and the growth and development of protective structures, such as spines (Wolfe et al. 2013; Wilmes et al. 2018, 2019). These newly settled juveniles may therefore experience high mortality rates (Nozawa and Harrison 2007; Ross et al. 2011; Pörtner et al. 2017; Espinel-Velasco et al. 2018), particularly on the reef where they are highly vulnerable to predation (Cowan et al. 2017; Keesing et al. 2018; Wilmes et al. 2018, 2019).

Settlement success and early post-settlement survival in marine benthic invertebrates, such as CoTS, may also be hindered by the indirect effect of warming on the settlement substrate (Dworjanyn and Pirozzi 2008; Webster et al. 2011; Mos et al. 2011; Huggett et al. 2018). At a local scale, many marine invertebrate larvae respond to chemical stimuli associated with particular biogenic substrates (mostly marine algae) indicating a suitable environment for their benthic life-history stage (Hadfield and Paul 2001; Huggett et al. 2006; Doll et al. 2022). When tested in isolation from the biogenic substrate, marine biofilms (and associated bacteria or diatoms) are often identified as the harbour of specific chemical components that induce larval settlement in CoTS (Johnson and Sutton 1994), other echinoderms (reviewed by Doll et al. 2022), and a wide range of benthic marine invertebrates (reviewed by Hadfield and Paul 2001; Hadfield 2011). Elevated temperatures can cause shifts in the microbial community structure on the algal surface (Webster et al. 2011; Whalan and Webster 2014; Huggett et al. 2018), but also directly bleach the algae (Webster et al.

2011; Vásquez-Elizondo and Enríquez 2016; Huggett et al. 2018). In a warmer ocean, settlement success and early post-settlement processes in CoTS may thus be indirectly inhibited by the effects of thermal stress on settlement substrates, and their capacity to induce settlement (Hadfield and Paul 2001; Huggett et al. 2018).

The aims of this study were to establish the effect of warming on (1) settlement success (2) metamorphic success, and (3) post-settlement survival of CoTS. This study further aimed to (4) unravel the effect of elevated temperature on the crustose coralline algae (CCA) settlement substrate, and hence settlement and metamorphic success. Based on previous research on the early life-history stages of this species (Rupp 1973; Kamya et al. 2014, 2016; Lamare et al. 2014; Uthicke et al. 2015; Caballes et al. 2017), it was hypothesised that temperatures ≥ 30 °C would reduce the percentage of larvae that successfully settle and metamorphosise, and would increase mortality rates during the early post-settlement stage. It was further hypothesised that settlement success would be constrained by negative effects of warming on settlement substrates (Diaz-Pulido et al. 2012; Webster et al. 2011; Vásquez-Elizondo and Enríquez 2016; Huggett et al. 2018; Muñoz et al. 2018). An inadvertent reduction in recruitment would unequivocally constrain the replenishment of adult CoTS populations, that may themselves be directly affected by warming (Lang et al. 2022).

Materials and methods

Collection and rearing

Adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) were collected from John Brewer Reef (18° 38′ S, 147° 02′ E) and Wheeler Reef (18° 47′ S, 147° 31′ E) in the Central Great Barrier Reef in late-October and early-November 2021. At the time that CoTS were collected, the water temperature was ~ 26–27 °C. CoTS were acclimated at the Australian Institute of Marine Science National SeaSimulator in Townsville, Australia, in filtered seawater (FSW) at 28 ± 0.5 °C. Eggs and sperm were obtained from six females and six males on the 17th November 2021. Ovary lobes were removed from females and placed in a beaker with 200 ml FSW at 28 °C. These ovary lobes were then washed over a 500 μm mesh to remove loose eggs. Ovary lobes were placed in a beaker containing 200 ml FSW with 10^{-5} M 1-methyladenine for 60 min to induce maturation of eggs. Approximately 20 min before the aforementioned step was complete, sperm was removed from males. Dry sperm from each male (2 μL) was mixed with 15 ml FSW at 28 °C, and then 1 ml of the sperm stock solution was added to the egg stock solution. Fertilisation was immediately assessed under a microscope, indicated by the presence of a fertilisation envelope. Fertilisation was determined to be at least 80%. Embryos were then transferred to 70 L vats on low bubbling at a density of approximately 10–15 embryos ml^{-1} (see Fig. 1). Twenty-four hours after fertilisation, 100% water exchanges were conducted to remove undeveloped embryos and dead larvae (which sank to the bottom of the vats when air lines were removed). At 48 h post-fertilisation, 16 L flow through cones (14 L working volume) were stocked with healthy larvae at a density of approximately 1 larvae ml^{-1}, and fed a continuous supply of *Dunaliella* sp. (70%) and *T-Isocrysis* sp. (30%) via an automated feeding system (Uthicke et al. 2018). Larval development was microscopically examined three times per week, and water changes were carried out concurrently.

Experimental setup

At 16 days post-fertilisation, larvae reached the late brachiolaria stage with a well-developed rudiment, indicating that they were competent to settle. Larvae were transported to James Cook University in Townsville and kept in one of twelve plastic bottles containing ~ 500 ml FSW at a density of ~ 1.6 larvae ml^{-1}. These were held within one of four Sanyo MIR-553 incubators (12:12 h light/dark cycle) and maintained at ambient 28 °C (three bottles per incubator; Fig. 1). Air lines connected to the base of each bottle ensured that the water remained oxygenated and prevented the larvae from settling prematurely. A Perspex tub was placed in each incubator, containing crustose coralline algae (*Lithothamnion* sp., CCA) chips with a mean surface area of 0.87 cm^2 (SE $\pm$ 0.03 cm^2). This CCA was collected from various northern and central reefs on the GBR. The tub in one incubator, which was to become the 28 °C control treatment, contained at least 60 chips of CCA. The tub in the other incubators (which were to become the 30, 32, 34 °C treatments) contained at least 12 chips of CCA each. The temperatures in the latter incubators were then set to the desired temperatures, and the larvae and CCA were left to acclimate at these temperatures for 24 h. The temperature range used in the present study represents the approximate current mean (28 °C) and maximum (30 °C) summertime sea surface temperature in the collection vicinity, as well as temperatures similar to those projected to occur under the most optimistic (32 °C) and pessimistic (34 °C) end-of-century (2081–2100) ocean warming scenarios (IPCC 2019; AIMS 2022).

Settlement and metamorphic success

Competent larvae were pipetted into 6-well plates. Four plates were used in each of the four larval temperature treatments (24 replicate wells per temperature, 96 wells total; Fig. 1). Approximately, 10 larvae were added to ~ 10 ml
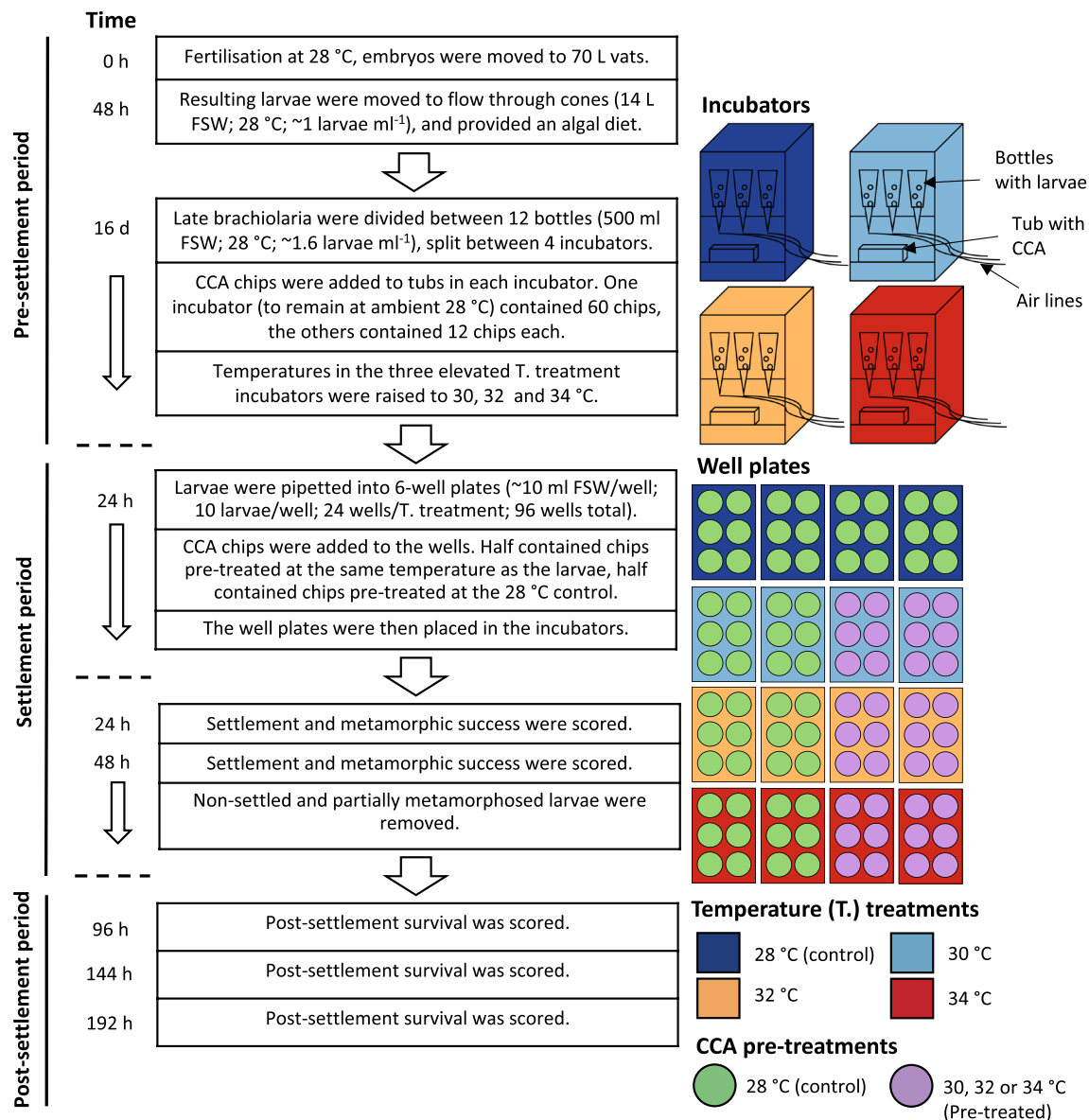
Fig. 1 A flow diagram summarising the methodology, and accompanying diagrams illustrating the set-up of the incubators for the four temperature treatments (28 °C: dark blue; 30 °C: light blue; 32 °C: orange; 34 °C: red), and the well plates containing crown-of-thorns starfish (*Acanthaster* cf. *solaris*) larvae and crustose coralline algae (CCA, *Lithothamnion* sp.; control: green; pre-treated: purple) incubated within them. Dashed lines on the flow diagram indicate time beginning again from zero hours, and arrows indicate a continuation of the methodology at the same point in time as the previous steps

FSW in each well, followed by a CCA fragment. Fragments that had acclimated to the three elevated temperatures for 24 h (pre-treated CCA) were added to 12 wells of the corresponding larval temperature treatment, and fragments acclimated at the 28 °C control temperature (control CCA) were placed in the remaining 12 wells. All wells of the control temperature treatment contained CCA acclimated at the 28 °C control temperature (Fig. 1). Testing settlement using pre-treated and control CCA permitted the observation of whether the quality of CCA, and therefore its relative inductive capacity, may have an impact on settlement success,

and whether this impact is greater at higher magnitude of warming. The four 6-well plates containing larvae for each temperature treatment were placed in the respective incubators and maintained at these temperatures.

Settlement and metamorphic success were scored under a microscope after 24 and 48 h, during which 50% water changes were carried out. Specifically, a single observer (B.J.L.) scored the number of larvae in each well, which had (1) successfully attached to the substrate or bottom of the well and commenced metamorphic transformation (settlement success; Fig. 2a), (2) completed metamorphosis into

juveniles with a radial symmetry (metamorphic success; Fig. 2b). After scoring was complete, non-settled larvae and partially metamorphosed individuals that had not settled on CCA were removed. All other individuals remained in the wells to assess post-settlement survival.

Post-settlement survival

At 96, 144 and 192 h after the commencement of the experiments, the number of post-metamorphic juveniles remaining was counted under a microscope to determine percentage survival in the four temperature treatments. Missing CoTS were presumed to be dead, and thus survival may be underestimated to some degree as a result of detectability limitations. Water changes were carried out daily over this time period.

Statistical analyses

Statistical analyses were carried out in R v.4.1.2 (R Core Team 2021). Generalised linear models were used to establish the effect of temperature, time (24 and 48 h), and their interaction, on the percentage of larvae that settled (settlement success, %) and the percentage of settled individuals that completed metamorphosis (metamorphic success, %). The observations from the control and pre-treated CCA wells were pooled for this analysis. Further generalised linear models were conducted to establish the effect of the CCA treatment on settlement and metamorphic success. For these models, an interaction between CCA treatment and time and CCA treatment and temperature were included. The observations at the 28 °C control temperature were removed from these latter models, because all of the CCA was treated the same for this temperature treatment. All models were conducted using the *glm* function in the *stats* package, with the quasibinomial family (link: logit), which accounted for the overdispersion of the data. The surface area of the CCA was included in initial models as a covariate, but registered no significant effect. Model diagnostics

(using the *check_model* function) were conducted in order to check that the model assumptions were met and to choose the models with superior fit, as such, the surface area of the CCA was excluded from all models. The estimated marginal means for the responses in each of the temperature and CCA treatments were established, and post-hoc analyses using the Tukey method were conducted in order to establish significant pairwise differences between treatments and timepoints.

A log-rank test was conducted, using the *survdiff* function in the *survival* package, in order to compare survival of metamorphosed juveniles in the four temperature treatments. Confidence intervals were established using the *survfit* function (*survival* package), and a Kaplan–Meier survival curve was fitted using the *ggsurvplot* function in the *survminer* package, in order to visualise the data.

Results

Settlement and metamorphic success

Settlement success of CoTS was high at all tested temperatures, with $\geq 83\%$ of larvae settled at 24 h across all temperatures, which increased to $\geq 94\%$ at 48 h (Fig. 3a). Despite high rates of settlement, success did vary significantly among temperature treatments ($F = 6.87$, $df = 188$, $P < 0.001$) and times ($F = 23.36$, $df = 187$, $P < 0.001$), although there was no significant interaction between these variables ($F = 1.67$, $df = 184$, $P = 0.175$). Settlement success was highest at 30 °C (24 h: 97%, 48 h: 100%). At 24 h, settlement success at both the 28 °C control temperature and at 32 °C was 86%, significantly lower than at 30 °C ($P = 0.034$ and $P = 0.041$, respectively), and at 34 °C, settlement success was 83%, again significantly lower than at 30 °C ($P = 0.013$). At 48 h, there was little difference in settlement success between the temperatures tested (28 °C: 95%; 30 °C: 100%; 32 °C: 94%; 34 °C: 99%).

Despite the majority of larvae settling throughout the range of temperatures tested, fewer larvae completed

Fig. 2 Images showing **a** metamorphosing larval crown-of-thorns starfish (*Acanthaster* cf. *solaris*) absorbing the larval body and **b** post-metamorphic juveniles with radial symmetry. Both have settled on crustose coralline algae (CCA, *Lithothamnion* sp.)
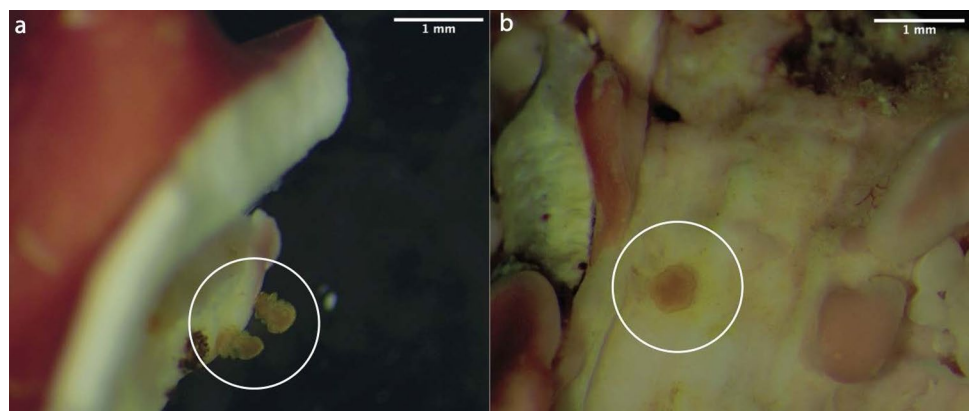
Fig. 3 The effect of temperature (28 °C: dark blue; 30 °C: light blue; 32 °C: orange; 34 °C: red) on crown-of-thorns starfish (*Acanthaster* cf. *solaris*) **a** settlement success at 24 and 48 h (*n* = 24 replicates per temperature treatment at each timepoint), and **b** metamorphic success (*n* = 48 replicates per temperature treatment, replicates for the two timepoints are pooled). The bars are the mean values ± SE
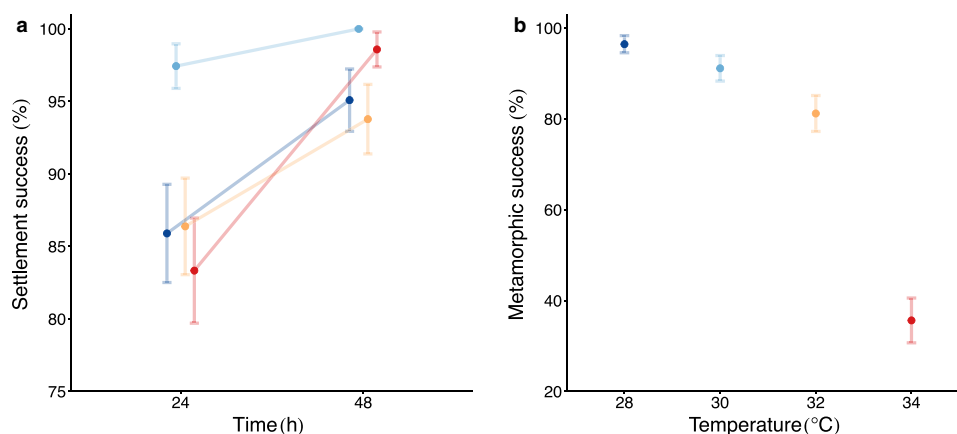
metamorphosis when exposed to warmer temperatures (Fig. 3b). Temperature significantly impacted metamorphic success ($F = 39.51$, $df = 188$, $P < 0.001$), but there was no significant effect of time ($F = 0.07$, $df = 187$, $P = 0.790$) or an interaction between temperature and time ($F = 0.76$, $df = 184$, $P = 0.519$). The percentage of the total number of settled larvae that completed metamorphosis was 96%, 91%, 81% and 36% for the 28 °C, 30 °C, 32 °C and 34 °C treatments, respectively. Metamorphic success was significantly lower at 32 °C than at the 28 °C control temperature ($P = 0.013$), and at 34 °C compared to the three cooler temperatures ($P < 0.001$ for all).

Post-settlement survival

Post-settlement survival remained high ($\geq 62\%$) in all treatments (Fig. 4); however, a significant effect of temperature on post-settlement survival was found (Log-rank test, $\chi^2 = 56.5$, $df = 3$, $P < 0.001$). At 192 h, survival of early juveniles that remained following the 48 h scoring, was 94% (95% CI 91–97%) at 28 °C, 85% (95% CI 80–90%) at 30 °C, 86% (95% CI 81–91%) at 32 °C, and 62% (95% CI 52–72%) at 34 °C. Survival was significantly lower at 30 °C ($P = 0.003$), 32 °C ($P = 0.006$) and 34 °C ($P < 0.001$), compared to the 28 °C control temperature, and was also significantly lower at 34 °C compared to 30 °C and 32 °C ($P < 0.001$ for both).

Ultimately, it was determined that the percentage of the number of individuals that remained at the conclusion of the experiments (192 h), compared to the number of individuals present at the start of experiments (24 h), declined to an even greater extent with temperature. Specifically, at 28 °C, 30 °C, 32 °C and 34 °C there were 83%, 78%, 67% and 27% of all starting individuals remaining at 192 h, respectively.
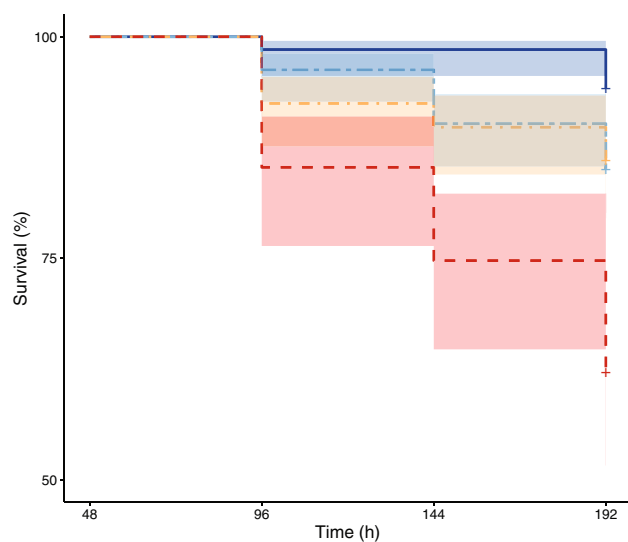

Fig. 4 Kaplan–Meier survival curve illustrating the effect of temperature (28 °C: dark blue solid line; 30 °C: light blue twodash line; 32 °C: orange dotdash line; 34 °C: red dashed line) on the probability of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) surviving post-settlement (%) from 48 to 192 h (*n* = 24 replicates per temperature treatment at each timepoint). The ribbons represent the 95% confidence intervals

Settlement substrate

Exposure of CCA to elevated temperature for an additional 24 h prior to the commencement of settlement experiments impacted settlement success. Settlement success was significantly lower in the pre-treated CCA wells, compared to the control CCA ($F = 41.14$, $df = 142$, $P < 0.001$). At 24 h, settlement success was 89% on pre-treated CCA and 96% on control CCA ($P = 0.007$). At 48 h, settlement success was high (98–100%) in both CCA treatments ($P = 0.080$). It was found that there was no significant interaction between CCA pre-treatment and time ($F = 0.73$, $df = 138$, $P = 0.396$; Fig. 5a), but there was a significant interaction between CCA

Fig. 5 The effect of crustose coralline algae (CCA; *Lithothamnion* sp.) treatment (control: green; pre-treated: purple) on crown-of-thorns starfish (*Acanthaster* cf. *solaris*) settlement success over **a** time (30, 32 and 34 °C treatments pooled; $n = 36$ replicates per CCA treatment at each timepoint) and across **b** the temperature (timepoints pooled; $n = 24$ replicates per CCA treatment at each temperature treatment). The bars are the mean values ± SE
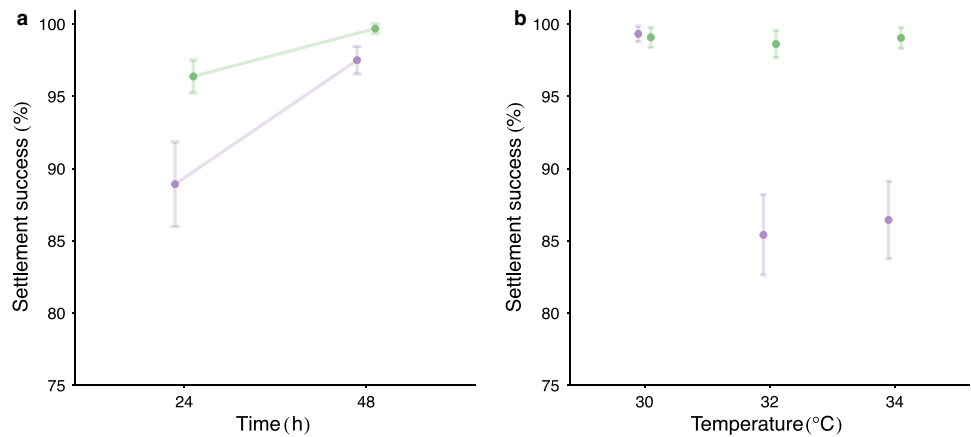
pre-treatment and temperature ($F = 3.95$, $df = 136$, $P = 0.021$; Fig. 5b). At 30 °C there was little difference in settlement success between CCA pre-treatments, given the high (99%) settlement success at this optimal temperature ($P = 0.783$). However, at 32 °C and 34 °C settlement success was 85–87% on pre-treated CCA, but 99% on control CCA ($P < 0.001$ at both temperatures).

There was no impact of CCA pre-treatment on metamorphic success ($F = 0.34$, $df = 142$, $P = 0.562$), and no significant interaction between CCA pre-treatment and time ($F = 0.62$, $df = 138$, $P = 0.433$) or temperature ($F = 1.39$, $df = 136$, $P = 0.253$). Some loss of pigmentation (bleaching) on the CCA was observed at 32 °C, and significant bleaching was observed at 34 °C (192 h, Fig. 6).

Discussion

This study provides evidence that larval settlement rates of *Acanthaster* cf. *solaris* will be largely insensitive to ocean warming. However, the cumulative effects of temperatures ≥ 30 °C will limit metamorphic success, and survival of early juveniles. Such effects may be further exacerbated by negative effects of warming on the settlement substrate (i.e. CCA) and its capacity to induce settlement. These results indicate that recruitment and thus population replenishment of this corallivorous starfish may be constrained at elevated temperatures. Further, these findings add to the growing body of evidence suggesting that CoTS will be highly vulnerable to near-future ocean warming and may experience population declines (Table 1).

The robustness of CoTS settlement to elevated temperatures (up to at least 34 °C) is surprising, especially considering that pre-settlement embryonic and larval development appear very sensitive to elevated temperatures (Table 1). However, there is similar evidence from tropical
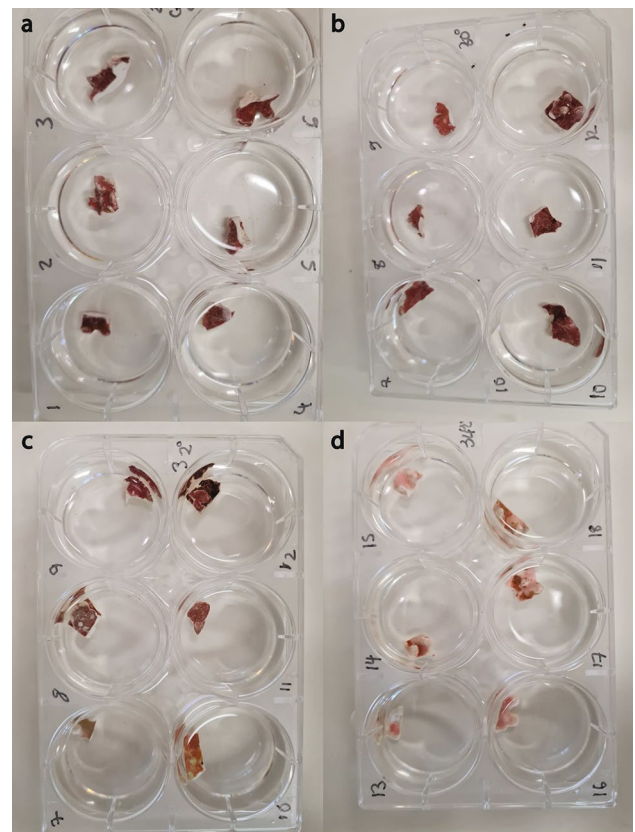

Fig. 6 Photographs of the crustose coralline algae (CCA; *Lithothamnion* sp.) in six-well plates from the **a** 28 °C, **b** 30 °C, **c** 32 °C and **d** 34 °C temperature treatments at 192 h, indicating loss of pigment (bleaching). The well plates contain the pre-treated rather than the control CCA

scleractinian corals that larval settlement may be unaffected by or even benefit from acute exposure to elevated temperatures (Edmunds et al. 2001; Nozawa and Harrison 2007). For instance, larval settlement in the coral *Favites chinensis* was found to be ~ 62% higher at 34 °C (ca. ambient + 7 °C)

Table 1 Studies on the impacts of elevated temperature on crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at different ontogenetic life stages

Study	Collection location (latitude)	Measure	Thermal range tested (Ambient temperature, °C)	Temperature at which significant negative (↓) effect occurs (°C)
Gametes				
Caballes et al. (2017)	Guam (13°N)	Sperm speed (µm s^{-1})	20–36 (28)	Nil
		Sperm motility (%)		↓ 36
		Fertilisation (%)		↓ 32
Hue et al. (2020)	New Caledonia (22°S)	Egg volume (mm^3)	27–29 (27)	↓ 29
		Fertilisation success (%)		↓ 29
Kamya et al. (2014)	GBR (16°S)	Fertilisation success (%)	26–30 (26)	Nil
Rupp (1973)	Guam (13°N)	Fertilisation success (%)	28–36 (28)	↓ 34
Embryos				
Caballes et al. (2017)	Guam (13°N)	Cleavage (%)	20–36 (28)	↓ 32
		Gastrulation (%)		↓ 32
Lamare et al. (2014)	GBR (16°S)	Cleavage (%)	19–37 (27.5)	↓ 32
		Hatching (%)		↓ 32
		Gastrulation (%)		↓ 29
		Abnormality (%)		↓ 30
Rupp (1973)	Guam (13°N)	Cleavage success (%)	28–36 (28)	↓ 34
Larvae				
Kamya et al. (2014)	GBR (16°S)	Normal development (%)	26–30 (26)	↓30
		Length (mm)		↓ 28
		Width (mm)		↓ 28
Lamare et al. (2014)	GBR (16°S)	Bipinnaria (%)	19.4–37 (27.5)	↓33.2
		Abnormality (%)		↓30.2
		Length (µm)		↓30.2
		Width (µm)		↓31.6
Uthicke et al. (2015)	GBR (16°S)	Mid-late brachiolaria (%)	28–30 (28)	Nil
Settlement				
Lang et al. (this study)	GBR (18°S)	Settlement success (%)	28–34 (28)	Nil
		Metamorphic success (%)		↓32
		Post-settlement survival (%)		↓30
Juveniles				
Kamya et al. (2016)	GBR (16°S)	Growth (% day^{-1})	26–30 (26)	Nil
		Arm number		Nil
		Spine number		Nil
		Food consumption (mm^2)		Nil
Kamya et al. (2018)	GBR (16°S)	Growth (mg week^{-1})	26–30 (26)	Nil
		Arm number		Nil
		Spine number		Nil
		Food consumption (mm^2)		Nil
Adults				
Hue et al. (2020)	New Caledonia (22°S)	Gonado-somatic index (%)	27–29 (27)	↓ 29
Lang et al. (2022)	GBR (18°S)	Righting time (s)	26–32 (26)	Nil
		Movement rate (cm min^{-1})		Nil
		Metabolic rate (mg O$_2$ g^{-1} h^{-1})		↓ 32
		Survival probability (%)		↓ 32

Caballes et al. (2017), Hue et al. (2020), Kamya et al. (2014, 2016, 2018) Rupp (1973), Lamare et al. (2014), Uthicke et al. (2015) and Lang et al. (2022)

when exposed to the temperature treatments for 1 h prior to the introduction of settlement substrate, and 24 h after (Nozawa and Harrison 2007). However, the short exposure time in these studies may not be sufficient to instigate negative effects on settlement (Nozawa and Harrison 2007; Randall and Szmant 2009; Conaco and Cabaitan 2020). Li et al. (2010) assessed the settlement success of the sea cucumber *Apostichopus japonicus* after 5 d of exposure to the temperature regimes and settlement substrate, and observed a 22% decline at 24 °C (ca. ambient + 6 °C). However, exposure of larvae to warmer conditions prior to larval competence in experimental studies, as in Li et al. (2010), may lead to difficulties in disentangling direct effects of temperature on settlement capacity from the indirect effects of warming induced constraints on normal larval development, as has been observed in CoTS (Table 1). As a corollary, persistent warming during the larval stage of CoTS in nature may exacerbate effects of warming on settlement success, and lead to detrimental effects at temperatures lower than observed in the present study. Yet, if the species can take advantage of natural thermal heterogeneity on the reef, then CoTS may not be as dramatically affected as these numbers suggest (Johnson et al. 1991; Nozawa and Harrison 2007).

Even if larvae are able to settle effectively at higher temperatures, they may have reduced capacity to complete metamorphosis (Nozawa and Harrison 2007; Mos et al. 2020). A significant decline in metamorphic success at elevated temperatures was recorded from 32 °C (ca. ambient + 4 °C) in the present study. Likewise, a study on the tropical sand dollar *Arachnoides placenta* found that although larval development rate increased with temperature from ambient 28 °C to 34 °C, the incidence of metamorphosis declined by almost 40% over this range (Chen and Chen 1992). The resulting post-metamorphic juveniles were also smaller at higher temperatures (Chen and Chen 1992). These observations may be largely due to the greater oxygen demands and metabolic rates of larvae and juveniles at elevated temperatures, whereby energy reserves may be insufficient for successful metamorphosis, which has been determined to be a particularly energetically costly process in other marine invertebrate taxa, such as Bugula and Abalone (Shilling et al. 1996; Wendt 2000; Randall and Szmant 2009; Pörtner et al. 2017; Espinel-Velasco et al. 2018).

Diminished energy reserves may lead to increased mortality of post-metamorphic juveniles (Randall and Szmant 2009; Pörtner et al. 2017). The present study revealed that for the most part, survival of post-metamorphic juveniles declined with warming. The thermosensitivity observed in our study is similar to that observed in the coral *Porites astreoides*, where the survival of coral recruits exposed to temperatures of 30 °C was 1%, compared to 10% at ambient 27 °C (Ross et al. 2013). However, survival of post-metamorphic juveniles of the sea urchin *Heliocidaris*

erythrogramma appeared unchanged by 4 °C of warming above ambient temperature (Wolfe et al. 2013). In this latter study, organisms were not exposed prior to the juvenile stage being reached, and it therefore did not account for potential carry-over effects from thermal effects on settlement-stage larvae (Ross et al. 2011; Wangensteen et al. 2013; Pörtner et al. 2017; Espinel-Velasco et al. 2018). Yet, a study on the sea urchin *Arbacia lixula* found no carry-over effects of temperature from the larval to the juvenile stages (Wangensteen et al. 2013). In nature, mortality directly resulting from elevated temperature may be secondary to high mortality resulting from predation (Wolfe et al. 2013). Constraints on growth and development of protective structures (*e.g.* spines) for instance, may increase the vulnerability of juvenile CoTS to benthic predators (Cowan et al. 2017).

Elevated ocean temperatures may also reduce the availability of thermosensitive settlement substrate (i.e. CCA) and inhibit their capacity to induce settlement (Webster et al. 2011; Vásquez-Elizondo and Enríquez 2016; Huggett et al. 2018), with subsequent downstream impacts on settlement and metamorphic success and early post-settlement survival. In the present study a reduction in settlement success in response to the presence of CCA that had been exposed to ≥ 32 °C for an additional 24 h was observed. There was clear evidence of CCA bleaching from 32 °C. Bleaching likely reduces the nutritional quality of the algal food, with impacts on juvenile survival (Webster et al. 2011; Huggett et al. 2018). In addition to bleaching, high temperatures can modify the bacterial communities of biofilms on the algal surface, alter the production of inductive metabolites and chemicals, promote pathogenic bacteria which may be harmful to the larvae, and increase the abundance of bacteria, diminishing oxygen levels (Li et al. 2010; Huggett et al. 2018).

On the reef, there may be further biotic and abiotic factors that may exacerbate (or alleviate) the negative effects of warming on the processes of settlement and metamorphosis, and ultimately survival of CoTS. Potential changes to larval food availability in a warmer ocean may affect the condition of the larvae at competence, impacting settlement and subsequent processes (Uthicke et al. 2013, 2018; Pörtner et al. 2017). Uthicke et al. (2018) for instance, showed that settlement rates of CoTS were greater when larvae were provisioned with higher concentrations of algae, thus nourished larvae may be better able to settle at supra-optimal temperatures than malnourished larvae. Ocean acidification, a further consequence of climate change (IPCC 2019), may also have significant impacts on these processes (Kamya et al. 2016, 2017). Kamya et al. (2016) demonstrated that growth and feeding rates of post-metamorphic juvenile CoTS on CCA were in fact higher under acidified conditions. A later study found that the carbon to nitrogen ratio and carbonate levels were lower under ocean acidification, likely increasing

the palatability of the CCA (Kamya et al. 2017). Considering the significant effects of these factors, exploring the additive and interactive effects of these stressors combined with temperature on the processes discussed herein, is an important next step (Uthicke et al. 2013; Wangensteen et al. 2013; Kamya et al. 2016).

Conclusion

While larval settlement appears relatively robust to near-future ocean warming, metamorphic success and post-settlement survival of CoTS is lower at ≥ 32 and ≥ 30 °C, respectively, and at ≥ 32 °C the quality and inductive capacity of CCA is reduced. These observations suggest that the cumulative effects of warming, which may be more pronounced under parental and early larval exposure, will seemingly limit recruitment in the near-future (Ross et al. 2011; IPCC 2019; AIMS 2022). Sea surface temperatures of ~ 30 °C are already experienced during marine heatwaves in the central GBR (AIMS 2022), and by 2081–2100 sea surface temperatures are expected to increase by 1.64–3.51 °C (5–95% model range, relative to 1986–2005, RCP8.5; IPCC 2019). The observations presented herein add to the growing body of evidence indicating that near-future ocean warming will ultimately lead to an abatement in the incidence or severity of population irruptions of CoTS (Table 1), which could alleviate predation pressure on important reef-building corals (Pratchett et al. 2021b; Song et al. 2021). Adaptation or acclimation of CoTS to warmer conditions may be possible; however, e.g. via transgenerational plasticity that may improve the hardiness of the early life stages, yet there is a growing consensus that the oceans may be warming too fast, and marine heatwaves may be too intense for these responses to keep pace with climate change (Munday et al. 2008; Morley et al. 2019; Radchuk et al. 2019). Furthermore, other direct and indirect stressors, both relating to and independent of climate change, may add additional pressures on CoTS populations at different stages of their life cycle (Kamya et al. 2016, 2017; Cowan et al. 2017; Uthicke et al. 2018). Notably, the increasing frequency and intensity of coral bleaching and mortality events, and the corresponding reduction in the availability of coral prey, may further undermine the viability of CoTS populations (Caballes et al. 2016; Hoegh-Guldberg et al. 2017; Hughes et al. 2017; Mellin et al. 2019; Pratchett et al. 2021a, b).

Finally, we acknowledge the Traditional Owners of the land where this works was conducted and pay our respects to their Elders, past and present.

Declarations

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