RESEARCH ARTICLE

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Physiological and behavioural effects of anemone bleaching on symbiont anemonefish in the wild

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Abstract

1. Climate change causes extreme heat waves that have induced worldwide mass coral bleaching. The impacts of temperature-induced bleaching events on the loss of algal endosymbionts in both corals and anemones are well documented. However, the cascading impacts of bleaching on animals that live in association with corals and anemones are understudied.

2. We performed a field-based experiment to investigate how host anemone bleaching affected the metabolic rate, growth, behaviour and survival of wild juvenile orange-fin anemonefish *Amphiprion chrysopterus* over 1, 2 and (for survival) 9 months.

3. We found that the standard metabolic rate of anemonefish residing in bleached anemones decreased over time but was unaffected in fish from healthy anemones. Despite the reduced metabolic cost, the growth rate of fish from bleached anemones was significantly lower compared to fish from healthy anemones, suggesting that animals residing in bleached hosts are at an energetic disadvantage. This was corroborated by our finding that fish from bleached anemones spent more time out of their anemones, suggestive of a greater need to forage in the water column. However, fish from bleached anemones were overall less active and used less space around the anemone, resulting in a negative correlation between space use and survival after 4 weeks.

4. Our results provide insight into the physiological and behavioural effects of host bleaching on juvenile fish in the wild, and highlight how relatively short-term thermal anomalies can have long-lasting impacts beyond the bleached anemones or corals themselves.

KEYWORDS

acclimation, climate change, coral reef fish, environmental stressor, growth rate, standard metabolic rate, survival, temperature

1 | INTRODUCTION

Anthropogenic climate change and extreme weather events are global phenomena that impact terrestrial and aquatic organisms. The increasing frequency and duration of global episodes of coral reef bleaching (Hughes et al., 2017) are testament to the severity of climate-driven impacts on coral reef ecosystems. Corals are not alone, as other marine invertebrates, including sea anemones, also bleach in response to environmental stressors (McClanahan et al., 2009). If these organisms survive, the temporary loss of endosymbiotic dinoflagellates can last several months before recovery (Jones, 1997; Lang et al., 1992; Saenz-Agudelo et al., 2011; Beldade et al., 2017). As such, short-term climatic stressors such as transient heat waves lasting from days to weeks (Glynn, 1996; Oliver et al., 2018) are outlived by the ensuing longer-term bleaching episodes. The impacts of these bleaching events may cascade onto other animals associated with corals and anemones for either shelter, foraging, or recruitment (Graham et al., 2007; Jones & Syms, 1998; Wilson et al., 2006). However, the physiological and behavioural impacts of bleaching on associated species, such as coral reef fish, have rarely been tested.

Fishes are essential components of coral reef ecosystems, due to their role in reef health, diversity, resilience and local economy (Bellwood et al., 2004; Graham et al., 2006; Moberg & Folke, 1999). Bleaching-induced coral mortality can drive fish mortality due to the degradation and loss of suitable habitats (Bonin et al., 2009), but recent evidence has shown that temporary bleaching of anemones also impacts the physiology and reproduction of associated anemonefish (Beldade et al., 2017; Norin et al., 2018). To cope with prolonged bleaching, fish may need to adjust their physiology and behaviour through phenotypic plasticity (e.g. acclimation) to enhance fitness while living in a bleached environment. For example, bleaching-associated decreases in anemonefish food sources (e.g. plankton in the water column, anemone waste products and symbiont algae; Piontkovski & Castellani, 2009; Tada et al., 2003; Verde et al., 2015) may require anemonefish to alter their behaviour to maximise foraging, or to adjust their energy expenditure to compensate for reduced food intake (Dill, 1983; Höjesjö et al., 1999). As fish associated with bleached (white) hosts are visually more conspicuous (Coker et al., 2009), the risk of predation potentially increases too, which may reduce foraging and other behaviours outside of the anemone (Lima & Dill, 1990). The previously observed increased metabolic demands of anemonefish after two weeks of bleaching in the laboratory (Norin et al., 2018) may also trade-off with growth due to competition for a finite energy budget (energy allocation trade-off; Weiner, 1992). However, to what extent these behavioural and physiological adjustments occur in nature remains unknown.

Here, we quantify the effects of varying bleaching exposure durations on a suite of life-history traits of anemonefish living in the wild. We conducted an extensive field-based study with wild site-attached juvenile orange-fin anemonefish *Amphiprion chrysopterus* transplanted onto healthy (unbleached) or bleached anemones in the lagoonal reef system of Moorea, French Polynesia. Anemonefishes live in a permanent obligatory mutualistic symbiosis with sea anemones (Fautin, 1991) and remain with the host anemone on which they settled as juveniles (Buston, 2003a; Hattori, 1994), even if it bleaches (Saenz-Agudelo et al., 2011), making them especially vulnerable to bleaching and an ideal model species (Beldade et al., 2017; Mills et al., 2018, 2020). We compared standard (resting) metabolic rate (SMR), behaviour (activity and space use) and growth rate of anemonefish after 4 and 8 weeks of living with unbleached or bleached anemones, and tracked the fish's survival for 9 months. These exposure durations are ecologically relevant both to bleaching and anemone recovery (Jones, 1997; Lang et al., 1992), and sufficient to observe the potential for acclimation (Fangue et al., 2014; Sandblom et al., 2014). We also explored correlations among the measured traits, as environmental disturbances are known to alter the relationship between physiological and behavioural traits (Killen et al., 2013).

2 | MATERIALS AND METHODS

2.1 | Experimental overview

Magnificent sea anemones *Heteractis magnifica* ($n = 53$) and juvenile orange-fin anemonefish *Amphiprion chrysopterus* ($n = 47$) were collected in the northern lagoon of Moorea, French Polynesia (17°32′19.8″S, 149°49′46.3″W) from September to November 2017.

Unbleached anemones were collected 2 to 3 weeks before the fish, during which time about half of the anemones were thermally induced to bleach in the laboratory at the CRIOBE research centre (see 'Host anemones' below). Two days before placing fish onto them, unbleached and bleached anemones of similar size were individually placed back into the field in 47 cylindrical cages (60 × 40 cm) randomly distributed across four sites in Moorea's northern lagoon (Figure 1). Environmental conditions (water flow, water temperature and depth) were measured at the sites (Table S1) consisting of a sandy flat, such that all cages were 5 m away in any direction from any larger coral structures ('bommies'). Cages were used to prevent anemone predation from, for example, turtles, and were placed at least 10 m apart.

Anemonefish were caught from unbleached anemones in the lagoon (there was no bleaching at this time) and placed individually into the 47 cages with either an unbleached ($n = 26$) or a bleached ($n = 21$) anemone.

The metabolic rate, growth rate and behaviour (see individual sections below) of the anemonefish were measured approximately 4 weeks (26–29 days; Table S2A) after residing in unbleached or bleached anemones, and a random subset of individuals ($n = 23$) were measured a second time after approximately 8 weeks (46–65 days; Table S2A), with no difference in exposure time between treatments for either exposure period (Table S3). While the experimental exposures to unbleached or bleached anemones varied around the target 4 and 8 weeks, we will, for simplicity, refer to the two measurement points as 'Week 4' and 'Week 8'. The first day of the experiment, when fish were placed onto anemones, is referred to as 'Week 0'.
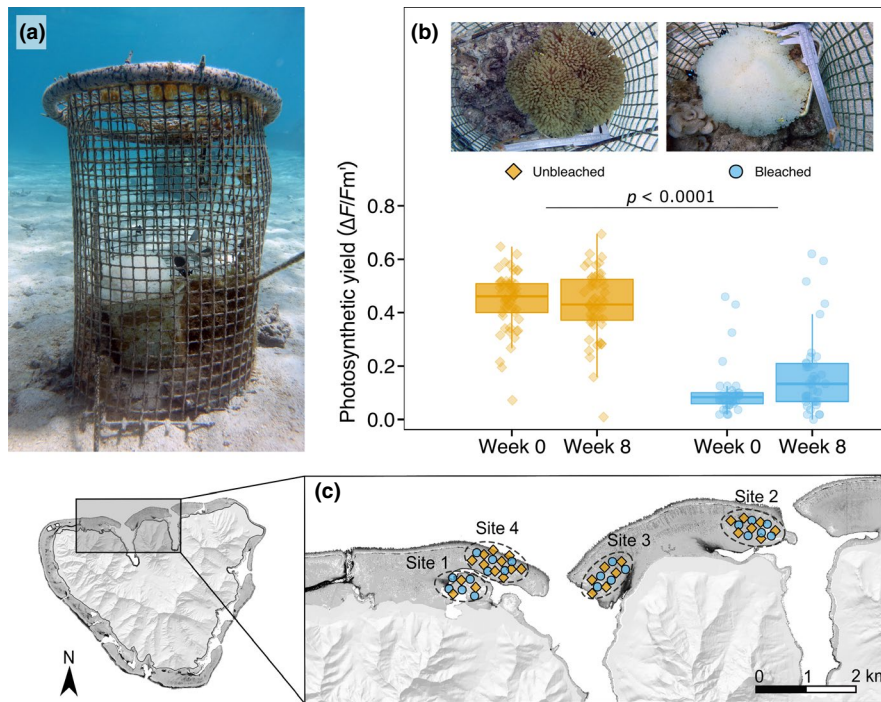
FIGURE 1 In situ experimental photographs and study sites. (a) Experimental set-up with a bleached anemone and a juvenile orange-fin anemonefish *Amphiprion chrysopterus* inside a cage (3 × 3 cm mesh size). The anemonefish could freely swim in and out of the cage through the mesh. The cage was used to prevent anemone predation and secured in place with steel rods. (b) Photosynthetic yield in unbleached and bleached anemones at the start (Week 0) and after 8 weeks (Week 8). Δ*F* is the difference between *F*m′ (maximum fluorescence yield) and *F* (fluorescence yield of a dark reference). The photos show the top-view from within a cage containing an unbleached (left) and a bleached (right) anemone, each with a juvenile anemonefish and 20-cm long callipers included for scale. (c) Map of the island of Moorea with an insert of the northern lagoon (17°32′19.8″S, 149°49′46.3″W) showing the location of the two treatments (unbleached and bleached anemones) distributed across four sites

Anemonefish survival and anemone bleaching status were monitored weekly over the first 8 weeks and then every 2 weeks over a further 7 months. At the end of the ninth month of monitoring, all anemonefish were returned to the un-caged host anemone from which they were originally collected, and anemones were returned to anemone patches in the lagoon.

Ethical approval for the study was granted from The Animal Ethics Committee, Centre National de la Recherche Scientifique (permit number 006725).

2.2 | Host anemones

Anemones (containing no anemonefish) were collected by hand while SCUBA diving at depths of 3–6 m and brought to the CRIOBE laboratory in coolers filled with water from the collection sites. In the laboratory, the anemones were kept in aquaria receiving flow-through water from the lagoon and fed brine shrimp daily. About half were maintained at 28°C for 2 weeks and remained unbleached. The others were bleached by heating the aquaria water to 31°C for 2 weeks.

Once positioned in the field, anemone bleaching status was ascertained visually on a weekly basis and confirmed by measuring photosynthetic activity at Week 0 and Week 8 of the experiment. Photosynthetic activity in the anemones was measured in triplicate using an underwater diving pulse amplitude modulated fluorometer (DIVING-PAM; Heinz Walz GmbH). All the anemones from one site were measured on the same night, and measures were taken from all sites between 17:12 and 17:37. Photosynthetic activity was significantly higher in unbleached than bleached anemones both at the beginning of the experiment and after 8 weeks (linear mixed-effects models, LME: Treatment; $t = 11.793$, $p < 0.0001$; Time; $t = 1.000$, $p = 0.324$, $mR^2 = 0.583$, $cR^2 = 0.712$, Figure 1b; Table S4B). Anemone size (surface area) was measured at Weeks 0, 4 and 8 (details in Supporting Information).

Three out of the 21 bleached anemones started to show signs of recovery after 4 weeks and were replaced with other bleached anemones of approximately the same size. As replacing a recovering bleached anemone may disturb associated anemonefish, to ensure equal disturbance between treatments, we correspondingly replaced a healthy anemone at the same site with another healthy anemone of approximately the same size.

2.3 | Anemonefish

Anemonefish were caught by hand-netting while free or SCUBA diving between September and November 2017 (Table S2), transferred in water-filled coolers to CRIOBE's aquarium facilities, weighed and, on the same day, returned to the lagoon onto one of the caged anemones,

with no significant difference in start date between treatments (Table S3). Fish were released within ~10 cm of the caged anemone and always swam straight to the anemone and hid within its tentacles.

Natural recruitment of *A. chrysopterus* is limited in Moorea (Beldade et al., 2012, 2016; Schmitt & Holbrook, 2000) and post-settlement mortality is high due to intraspecific aggression (Buston, 2003a). We therefore maintained the number of *A. chrysopterus* juveniles at one individual per anemone throughout the experiment, and any natural recruits (smaller in size than our focal fish) were noted and removed. *Dascyllus trimaculatus* also use anemones during a part of their life cycle (O'Donnell et al., 2017), however, they are subjected to heterospecific aggression from *A. chrysopterus* (Mills et al., 2020), which depresses their density and survival (Holbrook & Schmitt, 2004; Schmitt & Holbrook, 1996), but their presence has little to no effect on anemonefish (Schmitt & Holbrook, 2000). Nevertheless, to control for any aggression, growth or density-dependent effects on focal experimental *A. chrysopterus*, all natural recruits of *D. trimaculatus* were removed.

Focal *A. chrysopterus* were monitored weekly. Even though the anemonefish were able to move through the netting of their cages, the distance between cages (>10 m) and high predation risk outside the anemone tentacles (Buston, 2003a; Elliott et al., 1995; Mariscal, 1970), especially for juveniles (Buston & Garcia, 2007), made the chance of fish exchanging anemone host unlikely. Nevertheless, to confirm individual identification during the experiment, focal fish were photographed and identified by colour patterns based on the second and third vertical white stripes (example photos in Figure S1).

2.4 | Metabolic rate

At the end of Week 4 and 8, the anemonefishes were caught and transferred by boat in a water-filled cooler to CRIOBE's aquarium facilities. The fish were initially held with unfed unbleached or bleached anemones (as per their respective treatments in the field) for ~20 hr in aquaria receiving filtered, flow-through water from the lagoon. This was done to ensure that the fish were not digesting during subsequent metabolic rate measurements. Each individual fish was then transferred to an intermittent-closed respirometry setup where its oxygen uptake rate could be recorded as a proxy for its metabolic rate (Svendsen et al., 2016).

The respirometry setup was shielded from surrounding disturbances and comprised a 40 L (water volume) tank receiving flow-through normoxic seawater from the lagoon at $29.16 \pm 0.04°C$ ($M \pm SE$ temperature in the respirometry setup across all experiments), glass respirometry chambers (35 or 110 ml volume, depending on fish size) in which the oxygen uptake rate of the fish could be measured by use of fibre-optic oxygen meters with probes (FireStingO$_2$; Pyro Science GmbH) and accompanying software (Pyro Oxygen Logger; Pyro Science GmbH), a peristaltic pump (Masterflex L/S; Cole-Parmer) with gas-tight tubing that recirculated water through the respirometry chambers and past the oxygen probes and a set of flush pumps (EHEIM Compact; EHEIM GmbH & Co) which intermittently flushed fresh and fully aerated seawater through the respirometry chambers for 5 min in every 9 to 10 min intermittent-closed respirometry cycle (flush and close durations were adjusted based on chamber volumes and fish sizes). The respirometry chambers were supported by two plastic pipes in between which anemones from the respective treatment were placed such that their tentacles touched the bottom and sides of the respirometry chambers (photos in figure 1 in Norin et al., 2018). This allowed the fish to be surrounded by and see (but not touch) the anemones, and also receive olfactory cues from the anemones in the flush water. Fish were introduced to respirometry chambers a few minutes before the first automated oxygen uptake rate recordings were started in the afternoon and remained there for ~17 hr until the following morning. The fish were then removed from the respirometry chambers and their body mass recorded.

Fish oxygen uptake rates were calculated by multiplying the slopes (over 3–4 min) for the decline in oxygen inside the respirometry chambers during the closed phases of the respirometry cycles by the volume of the respirometry chamber after subtracting fish volume and background bacterial respiration (calculated from a respirometry chamber without fish). The SMR of each individual fish was then estimated by first calculating the mean of the lowest 10% of its oxygen uptake rate measurements from the ~17 hr respirometry trial, then excluding any outliers (data points outside the mean ± 2 *SD*s, or data points with r^2 values for the linear regressions of the decline in oxygen over time lower than the mean r^2 − 2 *SD*s), and finally re-calculating the mean of the remaining data points.

Due to electrical problems at the research station, some of the scheduled respirometry trials could not be completed, resulting in a reduced sample size for metabolic rate measurements ($n = 15$ and $n = 14$ fish from unbleached and bleached anemones, respectively, at Week 4, and $n = 12$ and $n = 9$ fish, respectively, at Week 8; Table S2A).

2.5 | Behaviour

A GoPro camera was placed on the top of each cage in the lagoon (~50 cm from the anemone) in the afternoon of an experimental day (between approximately 14:00 and 15:00), and 20 min videos were recorded. The first 10 min of these videos were discarded as the acclimation period (Nanninga et al., 2017), while the following 10 min were used to quantify: (a) *Time spent out of the anemone* – defined as the percentage difference between the total observation time and the time that at least 50% of the fish's body was within the anemone tentacles from observations of a fish's location every 3 s ($n = 200$ observations); (b) *Activity* – the total number of times a gridline was crossed per minute, calculated by digitally separating the video frame into a grid of 10 × 6 sections of equal size (Figure S2) and counting each time the fish crossed a gridline within three haphazardly selected periods of 30 s; and (c) *Space use* – the total number of unique squares a fish occupied per minute, calculated from the number of unique squares on the digital grid (Figure S2) that the fish occupied within three haphazardly selected periods of 30 s.

Due to time restrictions in the field, only a subset of the fish was filmed at Week 4 ($n = 11$ and $n = 12$ in unbleached and bleached treatments, respectively; Table S2A). At Week 8, 23 fish were filmed but three videos were unusable due to poor camera placement on the cage, resulting in $n = 12$ and $n = 8$ in unbleached and bleached anemones, respectively (Table S2A).

2.6 | Growth rate

Anemonefish were weighed to the nearest 0.001 g at the start of the experiment (Table S2A), at which point body masses were not significantly different between treatment groups (Wilcoxon-test; $W = 209$, $p = 0.81$, $n = 40$). Fish were re-weighed at Week 4 ($n = 20$ and $n = 20$ in unbleached and bleached treatments, respectively; Table S2A) and Week 8 ($n = 13$ and $n = 9$ in unbleached and bleached treatments, respectively; Table S2A).

Specific growth rate (SGR) was determined as the percentage increase in individual body mass per day as $SGR = \ln(BM_{t_2}) - \ln(BM_{t_1}) \times t^{-1} \times 100$, where BM is body mass at t_2 (final time) and t_1 (initial time), and t is the time (days) between the two consecutive measures (Hopkins, 1992).

2.7 | Survival

Anemonefish survival (absence/presence) was recorded weekly over the first 8 weeks and every 2 weeks over the following 7 months. Given that juvenile anemonefish are unlikely to voluntarily leave their anemone due to risk of predation (Buston, 2003a; Elliott et al., 1995), the absence of a fish from its anemone was equated to mortality. Despite the use of cages, seven anemones (and thus also the anemonefish) disappeared during the nine months survival study, but these absent fish were not included in the survival analyses. In addition, non-natural mortality linked to electrical problems at the research station was also excluded from survival analyses (final $n = 29$, Table S2B).

2.8 | Statistical analysis

Statistical analyses were performed in R version 3.6.1 (R Core Team, 2019).

Linear mixed-effects models (LMEs) were used to explore the effect of the explanatory variables – anemone treatment (categorical), exposure time (continuous), fish body mass (continuous) and site (categorical) – on fish SMR, growth rate and behaviour. Fish ID (categorical) was included as a random effect to account for non-independence of data (i.e. when fish were measured twice over time). Time was included as a continuous variable since not all measurements were taken at exactly four or eight weeks but spread around these target time points for logistical reasons. All LMEs were fitted using the LMERTEST package (Kuznetsova et al., 2017), while marginal

(mR^2) and conditional (cR^2) R^2 were obtained with the package PIECE-WISESEM (Lefcheck, 2016). The selection of the best-fit model was determined using likelihood ratio tests (LRTs), starting from the most complex model and subsequently removing non-significant interactions and explanatory variables (Tables S6A, S7A, S8A, S9A and S10A) via the LMTEST package (Zeileis & Hothorn, 2002). In addition, SMR and fish body mass were $\log_{10}$-transformed to account for their nonlinear (power) relationship. The 'ns' function in the SPLINES package was used in the growth rate model to account for nonlinear body mass effects on fish growth. Space use was $\log_{10}$-transformed to alleviate non-normality. In each model, residuals were visually inspected to ensure that all assumptions were met. For graphical representation, regressions were fitted on predicted values obtained using the 'ggemmens' function in the GGEFFECT package (Lüdecke, 2018).

The consistency of each individual fish's behaviour across the three haphazardly chosen sections of 30 s video was evaluated by calculating the adjusted repeatability (R_{adj}) of activity and space use using the RPTR package (Stoffel et al., 2017). We calculated overall R_{adj} using the same model structure as for the LMEs (Table S5A), with chronological order of the three 30 s sections added as an additional explanatory variable. We also calculated R_{adj} for each anemone treatment separately by sub-setting the data for each treatment and removing treatment as a fixed effect in these models. Behaviour was significantly repeatable in all cases ($R_{adj} = 0.318$ to 0.464, $p \leq 0.0072$; Table S5B).

We tested for differences in survival between treatments using a Cox proportional hazard model via the 'coxph' function in the SURVIVAL package (Therneau, 2020; Therneau & Grambsch, 2000). Site was used as a covariate. Cox proportional hazard models calculate survival as the probability that an individual survives from the time origin (start of experiment) to a specified future time (end of experiment). To do this, the hazard function (risk of death over time) is used as a response variable.

Correlations among all traits were performed using Pearson's correlation coefficient or Spearman's rank correlation (parametric and nonparametric data, respectively). For each trait where fish body mass had an effect, body-mass-adjusted values were used for correlation analyses. Body-mass-adjusted values were obtained by calculating model partial residuals (i.e. fixing body mass and removing its partial effect) using the 'remef' function from the REMEF package (Hohenstein & Kliegl, 2020).

3 | RESULTS

3.1 | Physiology

The SMR of anemonefish varied over time depending on anemone treatment (bleached or unbleached, Figure 2), as indicated by the significant interaction between treatment and exposure time (LME: Time × Treatment; $t = 2.024$, $df = 45$, $p = 0.049$; $mR^2 = 0.904$, $cR^2 = 0.904$; Table S6B). SMR was the same between treatment
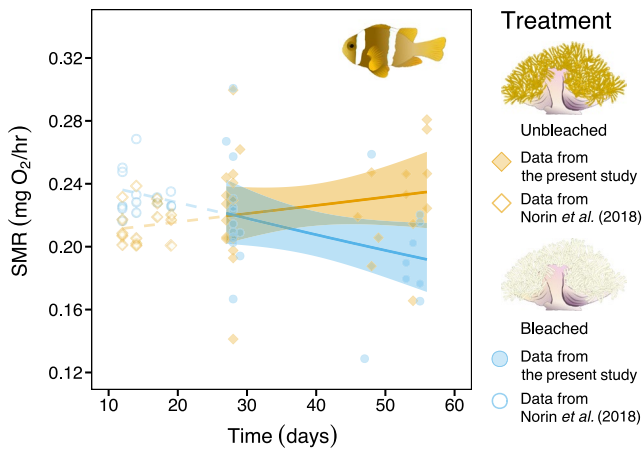
FIGURE 2 Standard metabolic rate (SMR) of *Amphiprion chrysopterus* juveniles residing in unbleached or bleached anemones over time. Solid orange and blue lines are model predicted regression lines fitted to the data from the present study, surrounded by 95% confidence bands. Data shown in open symbols at 12–19 days are from a previous laboratory study by Norin et al. (2018) and the regression lines have been extended to these data (dashed lines) for visual comparison only [i.e. the data from Norin et al. (2018) are not part of the fit]. The presented SMR data, including those from Norin et al. (2018), have all been adjusted (using model residuals) to the overall mean body mass of the fish from the present study (0.59 g), to allow direct comparisons between data [note that the SMR data from Norin et al. (2018) were adjusted to a body mass of 1 g in their figure 3]

groups after approximately 4 weeks of anemone exposure, but decreased in anemonefish from bleached anemones between 4 and 8 weeks of exposure (Figure 2).

3.2 | Behaviour

3.2.1 | Time spent out of the anemone

Anemone treatment had a significant effect on the time fish spent out of the anemone (LME: Treatment; $t = -2.946$, $df = 29.69$, $p = 0.006$; $mR^2 = 0.331$, $cR^2 = 0.592$; Table S7B), with fish from bleached anemones spending 22.7% more time out of the anemone compared to fish from unbleached anemones (Figure 3a). In addition, the amount of time fish spent out of the anemone increased over time by 0.77% each day (LME: Time; $t = -3.893$, $df = 23.61$, $p < 0.001$; Figure 3a; Table S7B).

3.2.2 | Activity

Anemone treatment had a significant effect on fish activity (LME: Treatment; $t = 2.276$, $df = 38$, $p = 0.029$; $mR^2 = 0.339$, $cR^2 = 0.339$; Table S8B), with fish from unbleached anemones being more active than fish from bleached anemones (Figure 3b). Exposure duration did not have a significant effect on fish activity (LME: Time;
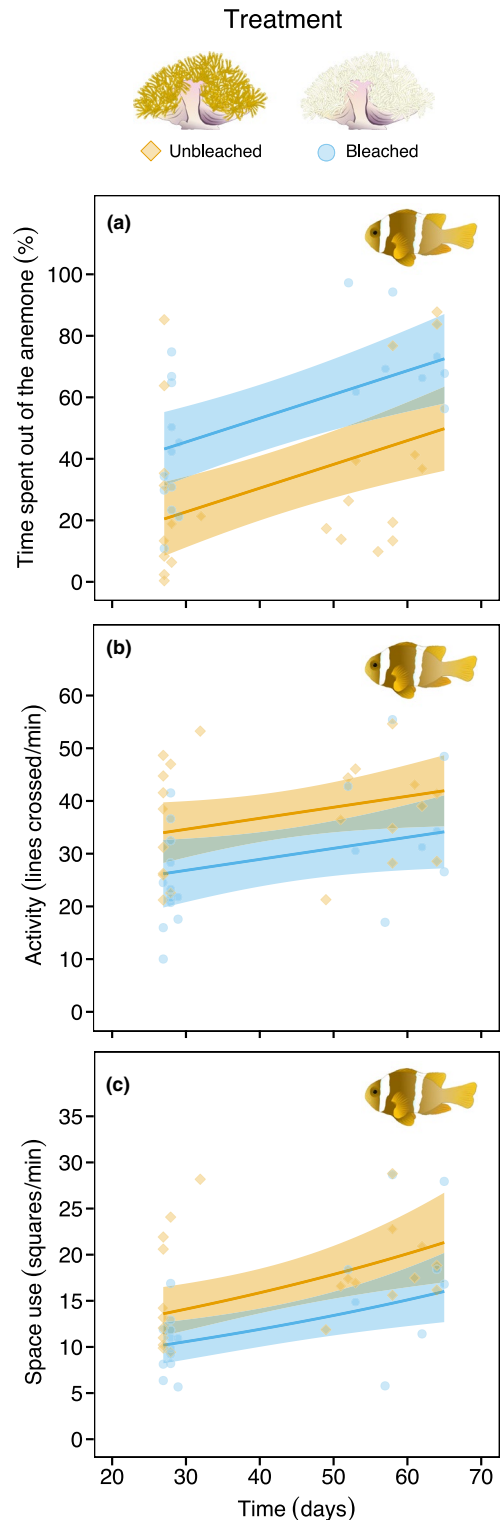

FIGURE 3 Behaviours of *Amphiprion chrysopterus* juveniles residing in unbleached or bleached anemones over time. (a) Time spent out of the host anemone, (b) movement activity and (c) horizontal space use above the anemone. Symbols represent individual raw data points in (a) while in (b) and (c) data points are adjusted (using model residuals) to the overall mean body mass of the fish from the present study (0.59 g), as body mass significantly affected activity and space use but not time spent out of the anemone. Lines are model predicted regression lines surrounded by 95% confidence bands

$t = 1.795$, $df = 38$, $p = 0.081$; Table S8B), but larger fish tended to be more active than smaller fish (LME: Body mass; $t = 1.928$, $df = 38$, $p = 0.061$; Table S8B).

3.2.3 | Space use

Anemone treatment also had a significant effect on fish space use (LME: Treatment; $t = 2.495$, $df = 38$, $p = 0.017$; $mR^2 = 0.492$; $cR^2 = 0.492$; Table S9B), with fish from unbleached anemones using more space over and around the anemone than fish from bleached anemones (Figure 3c). Fish also increased space use over

time by ~1.2% each day (LME: Time; $t = 3.027$, $df = 38$, $p = 0.004$; Table S9B). As expected, larger fish used more space around the anemone (LME: Body mass; $t = 2.627$, $df = 38$, $p = 0.012$; Table S9B).

3.3 | Growth rate

Anemone treatment had a significant effect on fish growth rate (LME: Treatment; $t = 4.047$, $df = 57$, $p < 0.001$; $mR^2 = 0.707$, $cR^2 = 0.707$; Table S10B), with fish of a given mass growing 0.85% per day faster when residing in unbleached than bleached anemones
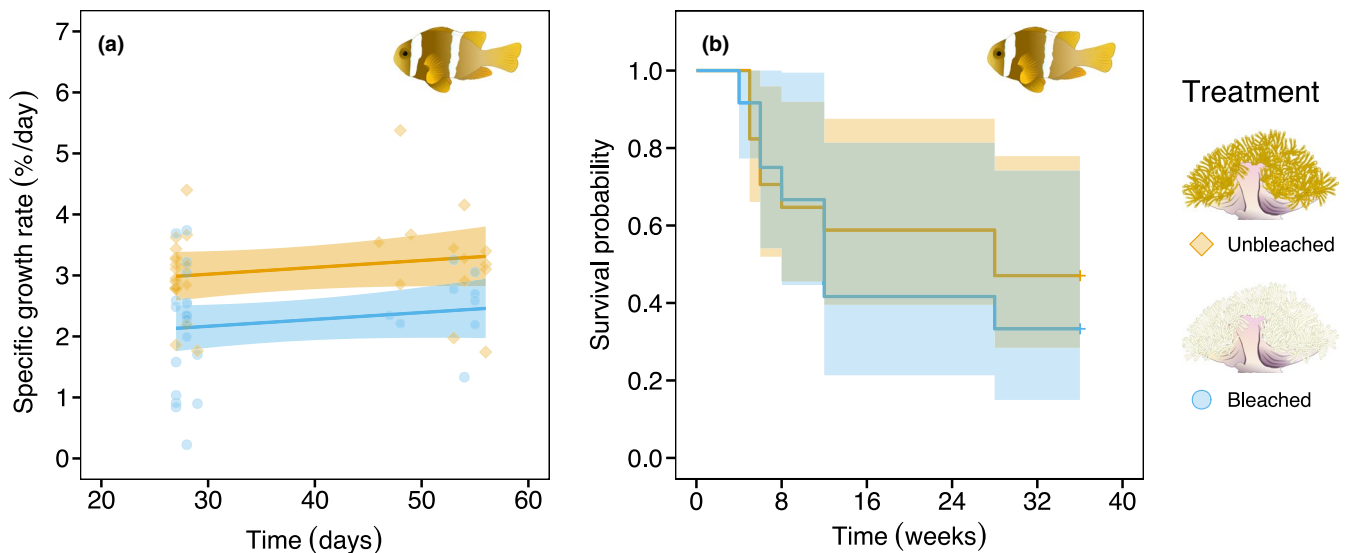

FIGURE 4 Growth and survival of *Amphiprion chrysopterus* juveniles residing in unbleached or bleached anemones over time. (a) Specific growth rate. Symbols represent individual data points adjusted (using model residuals) to the overall mean body mass of the fish used in the growth analyses at the initial time (t_1, 0.23 g). Solid orange and blue lines are model predicted regression lines fitted to the data, surrounded by 95% confidence bands. (b) Survival over 9 months (initial 8 weeks of the main experiment plus an additional 28 weeks of monitoring the fish in the same treatments). Solid orange and blue lines are survival probability curves, surrounded by 95% confidence bands

FIGURE 5 Correlations between all measured traits after 4 and 8 weeks of residing in unbleached or bleached anemones. Correlations (circles and diamonds) where the 95% confidence interval (horizontal error bars) does not cross zero (dashed vertical lines) are significant. Body mass significantly affected standard metabolic rate (SMR), activity, space use and growth rate, so body-mass-adjusted ($_{adj}$) values were used in correlations. For time spent (out of the anemone), raw values were used as fish body mass had no effect on this trait (Figure 3a). All test statistics are summarised in Table S12
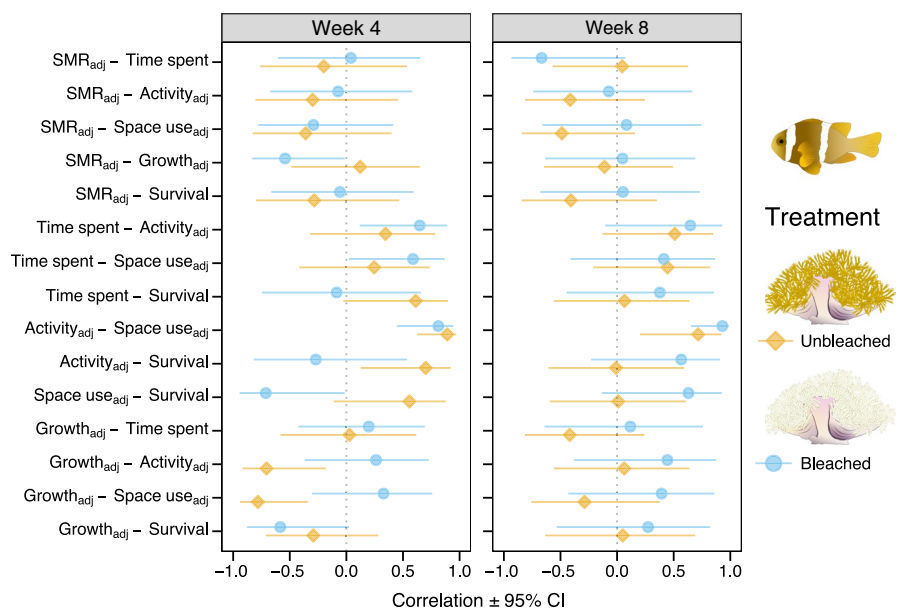
across the entire experiment (Figure 4a). Treatment exposure time had no significant effect on fish growth rate (LME: Time; $t = 1.217$, $df = 57$, $p = 0.229$; Figure 4a; Table S10B).

3.4 | Survival

Although survival appeared to diverge between treatments after 10 weeks (Figure 4b), there was no significant difference in survival between fish from unbleached and bleached anemones throughout the 9 months of treatment exposure (coxph model: Treatment; coef $= -0.56$, $z = -1.11$, $p = 0.268$, Table S11B). However, study site had an impact on fish survival with Site 3 showing higher survival probability compared to Sites 2 and 4 (coxph model: Site 3; coef $= -1.66$, $z = -2.31$, $p = 0.021$; Table S11B).

3.5 | Correlations among traits

Standard metabolic rate correlated negatively with growth rate after 4 weeks in bleached anemones (Figure 5). Behaviours correlated positively with each other: time spent out of the anemone was positively correlated with fish activity and space use after 4 weeks in bleached anemones, and activity and space use were highly positively correlated in both treatments after both 4 and 8 weeks (Figure 5). Activity was also positively correlated with survival in fish inhabiting unbleached anemones after 4 weeks, but did not correlate in fish from bleached anemones at either 4 or 8 weeks (Figure 5). Space use was negatively correlated with survival in bleached anemones after 4 weeks (Figure 5). Growth rate was negatively correlated with activity and space use in unbleached anemones after 4 weeks, but there were no significant correlations among these traits in fish from bleached anemones (Figure 5). All test statistics are summarised in Table S12.

4 | DISCUSSION

Our field-based experiment allowed us to test the indirect effects of climate change and warming-induced bleaching on wild coral reef fish in the absence of elevated temperature, while also exposing fish and anemones to natural variability arising from selection and environmental variables, including water current, food availability, solar radiation and inter- and intra-specific interactions (all small organisms <4 cm body depth could traverse the mesh cages). We found that bleaching induced a reduction in the fish's activity, a reduction in hiding as fish spent more time out of bleached anemones, a decrease in SMR over time and lower growth rates. However, despite these differences in fish behaviour and physiology, after 9 months there was no impact of host anemone bleaching on fish survival.

At first glance, our results for SMR appear to contradict a previous laboratory study showing that bleaching increased the metabolic demands of juvenile anemonefish after two weeks (Norin et al., 2018). However, the increased SMR observed by Norin et al. (2018) fits well

with our SMR results when extrapolated back to a 2-week exposure period (Figure 2), despite the different experimental conditions (laboratory vs. field). Combined, these results suggest that anemonefish initially experience increased SMR in response to the short-term stressor of bleaching, but that metabolic rates decrease over a longer, and more ecologically relevant, exposure to bleaching. Reduced food intake is a likely contributing factor to the observed decrease in SMR, and is known to cause a reduction in SMR in other fish species (Auer et al., 2015; O'Connor et al., 2000; Van Leeuwen et al., 2012). The lower growth rate of anemonefish from bleached anemones further corroborates that reduced food intake is likely causing the decrease in SMR, which is also supported by the negative correlation between SMR and growth in fish from bleached, but not unbleached, anemones after 4 weeks.

The decrease in SMR over time in fish from bleached anemones suggests that individuals with a relatively high SMR were energetically disadvantaged, had little excess capacity for growth, and were forced to down-regulate their SMR. While a down-regulated SMR can be advantageous in food-limited environments (Auer et al., 2015; Metcalfe, 1998; Metcalfe et al., 1995; O'Connor et al., 2000), there is a limit to how much SMR can be reduced without affecting basic physiological functioning, and reduced tissue-level metabolic rates, as a consequence of reduced food intake, carry an oxidative cost in the form of harmful reactive oxygen species (Salin et al., 2018). The indication of a decreasing SMR up to 8 weeks of exposure to bleached anemones provides no evidence for acclimation (stabilisation) in SMR, unlike other studies on coral reef fish that have reported physiological and behavioural acclimation to the thermal stressor itself (Donelson et al., 2011). Therefore, our observed decrease in SMR between 4 and 8 weeks of bleaching is more likely to reflect a deteriorating condition rather than acclimation. An interesting next step would be to investigate if fish are able to back-regulate their metabolic physiology after anemones have recovered from bleaching. Moreover, we conducted our study on bleaching-naïve wild juveniles about 1-month-old and, as such, phenotypically plastic responses over multiple bleaching events remain to be explored.

The negative impact of bleaching is further supported by our behavioural data, as survival correlates positively with space use and activity in unbleached anemones (Figure 5), but negatively in bleached anemones. High activity and space use are likely important for foraging on planktonic prey in the water column and for territorial behaviour and competition with both con- and hetero-specifics (e.g. *D. trimaculatus*), behaviours that are all energetically costly (Barry, 2014; Biro & Stamps, 2010; Koteja, 2000; Schmitz, 2005; Yeates et al., 2007). Anemonefish receive their nutrients from plankton, whose density declines under thermally induced bleaching (Piontkovski & Castellani, 2009; Tada et al., 2003), and from anemone waste products and symbiont algae (Verde et al., 2015); both of these food sources may be reduced or lost entirely when anemones bleach. Under normal, unbleached conditions, the positive correlation between survival and behaviour (space use and activity) indicates that foraging and territoriality are balanced with food intake from the territory. However, during bleaching episodes, even though fish from bleached anemones spent more time out of

their anemone (Figure 3a), they were less active and used less space around the anemone compared to fish from unbleached anemones (Figure 3b,c), with no indication that they maximised foraging or compensated energetically for the diminished food availability. The absence of energetic compensation can have detrimental outcomes (Brown & Kotler, 2004; Werner & Anholt, 1993), emphasised here by the negative correlation between survival and space use in bleached anemones. The energetic cost of spending more time outside the anemones might be balanced with other benefits, such as finding a better, unbleached habitat. However, the anemones were placed 10 m apart in our study and, as anemonefishes are sedentary species (Hattori, 1994), we did not observe any movement between cages.

The loss of symbiont algae and the likely decreased availability of waste products in bleached anemones, coupled with an absence of compensatory foraging, are two likely causes of the lower growth rate observed for fish from bleached anemones (Figure 4a). A third cause may be initially higher metabolic rates, which can occur 2 weeks after the onset of bleaching (Norin et al., 2018; Figure 2). Although fish with a higher SMR can digest and grow faster if enough food is available to cover their increased maintenance costs (Millidine et al., 2009; Reid et al., 2012), in the absence of any compensatory foraging (as our behavioural data suggest), the initially higher SMR may have impacted growth for the remaining 6-week exposure period through competition for a finite energy budget and an inability to catch up on growth later (Metcalfe & Monaghan, 2001). This is supported by the observed negative correlation between SMR and growth after 4 weeks in bleached anemones. In addition, the subsequent decrease in SMR of fish from bleached anemones may have further reduced their growth rate. Growth is an especially important trait in anemonefishes, as they live in size-dependent hierarchies, which determine the timing of sex change and reproductive status (Buston, 2003b; Fricke, 1979). The finding that bleached anemone hosts lower the growth of associated fish is therefore likely to have cascading and life-long consequences for individual anemonefish (in addition to reduced reproduction; Beldade et al., 2017), but also for other fish species associated with hosts that bleach. Indeed, a poor start in life during bleaching episodes, with lower growth and reduced size-at-age, results in smaller fish more likely to lose in competition for space and more vulnerable to predation (Arendt, 1997; Sogard, 1997).

Despite all the indications that host anemone bleaching affects the resident anemonefish negatively, bleaching did not significantly reduce anemonefish survival over 9 months. The use of cages (to reduce anemone predation) could have reduced natural predation on anemonefish by predators larger than the cage mesh size, especially considering that juveniles from bleached anemones spent less time in their anemone, which should render them more vulnerable to predation (Buston, 2003a; Elliott et al., 1995; Mariscal, 1970). Moreover, the bleached, white coloration of anemones enhances the visual contrast between anemone and fish, rendering the fish more visible to predators (Coker et al., 2009). However, our results corroborate those of previous natural field observations in which neither anemonefish densities nor adult survival were affected by bleached anemones (Beldade et al., 2017; Saenz-Agudelo et al., 2011).

Overall, the evidence of detrimental effects of bleaching, together with the strong habitat dependency of coral reef species (~12% of coral reef fishes live in symbiosis with hosts that bleach; Beldade et al., 2017) emphasises the importance of mitigating and regulating human actions that contribute to climate-induced bleaching events.

CONFLICT OF INTEREST
The authors declare no conflicting interests.

AUTHORS' CONTRIBUTIONS
Designed the study: D.C., T.N., R.B., A.C., S.S.K. and S.C.M.; Collected the data: D.C., T.N., R.B., A.C., S.S.K. and S.C.M.; Analysed the data: D.C. and T.N.; Wrote the manuscript: D.C., T.N., R.B. and S.C.M.; Revised the manuscript: all authors.

DATA AVAILABILITY STATEMENT
Data and code are available on Zenodo: https://doi.org/10.5281/zenodo.4167473 (Cortese et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.