Effects of ocean warming on the behaviours of an invasive predator and native keystone prey

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A Thesis in

The Department of Biology

Presented in Partial Fulfillment of the Requirements

for the Degree of Master of Science (Biology) at

Concordia University

Montréal, Québec, Canada

July 2025

This is to certify that the thesis prepared

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Entitled: Effects of ocean warming on the behaviours of an invasive predator and native keystone prey

And submitted in partial fulfillment of the requirements for the degree of

Master of Science (Biology)

complies with the regulations of the University and meets the accepted standards with respect to originality and quality.

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GENERAL ABSTRACT

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Katelyn Tessa Moffat

Both climate change and invasive species are threatening coral reef ecosystems globally. These two stressors are often studied singularly despite co-occurring in nature. For reef fishes, ocean warming due to climate change leads to elevated metabolic rates, which can increase feeding rates. Invasive species can also cause major declines in abundance and even extinctions in native prey through predation. Here, we examine the effects of ocean warming on the behaviours of an effective invasive predator, the Indo-Pacific lionfish (*Pterois spp*.), and their prey, native parrotfish (*Scarus iseri* and *S. taeniopterus*), which are keystone herbivores on Caribbean coral reefs. We hypothesized that warming would increase both lionfish predatory behaviours and parrotfish foraging behaviours but would decrease parrotfish anti-predator behaviours. To test this, lionfish and parrotfish were placed in experimental mesocosms heated to 32 °C or 29 °C. Lionfish hunted significantly more at 32 °C than those at 29 °C, but only at midday. Lionfish at 32 °C also rested less and spent more time near parrotfish at midday. Although some parrotfish anti-predator behaviours like sheltering did not differ between temperature treatments, parrotfish activity levels (i.e., feeding, hovering, and swimming behaviours) increased at elevated temperatures. We also examined the effect of temperature on various growth metrics in lionfish and parrotfish but found no difference between treatments. Our findings suggest that climate change can potentially exacerbate the negative, predatory effects of invasive lionfish on native keystone prey, through warming effects on both predator and prey, which could lead to cascading impacts in coral reef ecosystems.

Acknowledgements

I would first like to thank my supervisor, Dr. Nicola Smith, for providing me with the incredible opportunity to conduct this project. It may not have always been smooth sailing, but, as you often said, a smooth sea never made a skilled sailor. Thank you so much for your guidance and support. I would also like to thank the members of my committee, Dr. Eric Pedersen and Dr. Lauren Chapman, for their help and feedback in every step of the process, and Dr. Grant Brown, who I consider an honorary committee member, for your help with understanding fish behaviour. This work was funded by Concordia University's Faculty of Arts and Sciences, the Department of Biology, and the Natural Sciences and Engineering Research Council of Canada (Discovery Grant) to Dr. Nicola S. Smith. A special thank you to the Cape Eleuthera Institute and its staff for allowing us to use its facilities and tools and for three long months. What an amazing location for fieldwork, and what amazing staff helping us collect this data.

This project would not have been possible without the assistance of the friends I made at Concordia. Iris, Sofia, Félixe, and Alex, your support throughout my MSc has been invaluable. Thank you for your patience while I complained, the fun both in and out of the office, and generally being so wonderful. I will miss seeing you all at happy hour. I would also like to thank all the friends I made at CEI: Sam, Che, Sonnee, Kristin, Sarontaa, Marco, Isabelle, Laurens, Isaiah, and so many more, for comforting us when could not catch fish and celebrating with us when we did. Thank you for advocating for us, helping us on the water and in the lab, and making our disastrous field season so much better (mostly with ice cream). This was truly a team effort, and I'm so grateful for all those who put their time and energy into making this project happen.

A special thank you to TJ, for being such a trooper. Your tenacity inspires me, and your help was invaluable in the field. Thank you for spending hours staring at fish with me. I couldn't have done this without you! Iris, I'm certain I would have died (or at least come home with no data) without you there. Thank you for keeping me sane in the field, I really couldn't have chosen a more wonderful person to spend the summer suffering with. To my amazing friends, Morgan, Piper, Becca, Flora, and Justine, thank you for letting me rant and rave about the fishes even though I know you don't actually care. I hope you still think I'm cool. To Pepper, thank you for always managing to cheer me up. Finally, I would like to thank my family, who I know would drop everything to help me if I needed. Thank you for your love, endless support, and for cheering me on. I hope I make you proud!

Contribution of Authors

A version of this thesis has been submitted for peer-review in the Proceedings of the National Academy of Sciences of the United States (PNAS).

Study concept and experimental design: Moffat, Smith
Acquisition of data: Moffat, George
Analysis and interpretation of data: Moffat, Pedersen, Smith
Drafting of manuscript: Moffat
Critical revision: Moffat, Smith

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Introduction

Rising ocean temperatures caused by human-driven climate change have many detrimental consequences in marine ecosystems, particularly in the Caribbean (Altieri et al., 2021; IPCC, 2022; Moree et al., 2023; Taylor et al., 2018). Caribbean mean ocean temperatures are predicted to rise by 1.5 degrees Celsius by the year 2100 (Bove et al., 2022; Taylor et al., 2018) while Caribbean marine heatwaves (i.e., abnormally warm ocean temperatures lasting at least five days) are now five times as frequent and last for twice as long as they did relative to the 1980s (Bove et al., 2022). Warming waters are concerning for marine ectotherms like fishes because external heat sources modulate body temperature and increase basal metabolic rates (Koenigstein et al., 2016). Changes in metabolism can, in turn, affect fitness by altering behaviour, life cycles, and physiological limitations (Koenigstein et al., 2016).

One important fitness related behaviour affected by rising temperatures in ectotherms is predation (Allan et al., 2015, 2017; Volkoff & Rønnestad, 2020; Albins, 2015; Côté & Green, 2012; Jutfelt, 2020). In warm waters, both marine and freshwater fishes increase attack and predation rates to meet the elevated energy demand caused by increased metabolism (Albins, 2015; Allan et al., 2015, 2017; Côté & Green, 2012; Johansen et al., 2015; Jutfelt, 2020; McInturf et al., 2022; Volkoff & Rønnestad, 2020). For example, the dottyback *Pseudochromis fuscus* acclimated to 29 °C for seven days increased their predation rate and capture success compared to those held at 26 °C (Allan et al., 2015). Likewise, predation rate was higher in the largemouth bass *Micropterus salmoides* in fish acclimated for seven days at 22 and 25 °C than fish held at 11, 14 and 18 °C (McInturf et al., 2022).

The effects ocean warming can be even more consequential in prey species. Prey fish can increase foraging time to compensate for increased metabolic demands at the expense of anti-predator behaviours such as shoaling and shelter-seeking (Basford et al., 2015; Nowicki et al., 2012). Tropical Australian surgeonfishes *Acanthurus triostegus* and *A.dussumieri* fed more at 25 °C than at 20 °C after a 7-to-24-day acclimation period (Basford et al., 2015). Similarly, prey fish may engage in riskier behaviours to feed more at higher temperatures, potentially increasing mortality rates, as seen with juvenile rainbow trout *Oncorhynchus mykiss* (Biro et al., 2006, 2007). Prey behaviours such as responsiveness and directionality to stimuli are also altered in warmer waters (Warren et al., 2017). Further, ocean warming can alter prey fish physiology (Abrahams et al., 2007; Allan et al., 2015, 2017). Prey fish may become more vulnerable in a warmer environment due to reduced escape distances and swimming speeds (Allan et al., 2015). However, these changes are not uniform, and differ between species, life stages, and previous exposure to warm temperatures (Allan et al., 2015, 2017).

If feeding rates cannot keep up with increased energetic demands in warming waters, fish growth rates are also altered (Domenici et al., 2019; Fenkes et al., 2016). Increased activity caused by warming has been shown to reduce the growth rate of fish, since active fish tend to grow slower despite compensatory feeding (Bartolini et al., 2015; Biro et al., 2010; D'Agostino, Jimenez, et al., 2020; Rennie et al., 2005). For example, a fast-growing population of yellow perch *Perca flavescens* was found to have lower rates of activity than a slow-growing population, while feeding less (Rennie et al., 2005). Growth is also limited by oxygen availability, and because higher metabolic rates demand more oxygen and warmer waters contain less of it, fish size is decreasing with climate change (Breitburg et al., 2018; Clarke & Johnston, 1999; Ikpewe et al., 2021). While smaller body sizes may help cope with warming (Ohlberger, 2013), this can increase their vulnerability to predators, as predatory fish are often gape-limited, especially on coral reefs (Hambright, 1991; Holmes & McCormick, 2010; Mihalitsis & Bellwood, 2017;

Nilsson & Brönmark, 2000). Other ecological consequences of body size reduction in fish include changes in nutrient cycling, increased sensitivity to other stressors like pollutants, and reduced ecosystem services for humans like food provisioning (Martins et al., 2023; Sentis et al., 2024; Campillay-Llanos et al., 2021; Ikpewe et al., 2021; Ohlberger, 2013).

Along with climate change, the spread of invasive species, i.e., non-native species that have negative impacts on novel environments where they have established and spread, is also adversely affecting ecosystems (IPBES, 2019). Invasive species pose a significant threat to native biodiversity, contributing to 60% of extinctions globally, alongside other factors (IPBES, 2019). The United States alone spend billions of USD annually to control invasive populations and prevent damage to native environments and human health (Poland et al., 2021). Invasive species can introduce new diseases to native species and humans, alter environmental conditions, and damage infrastructure (Diez et al., 2012; Poland et al., 2021; Simberloff et al., 2013). Moreover, biological invasions are expected to increase with climate change (Diez et al., 2012).

Although usually studied singularly (Kindinger & Albins, 2017; Sarmiento et al., 2004), invasive species and climate change often co-occur in aquatic and terrestrial systems where they can potentially interact (Jaureguiberry et al., 2022). For example, climate change allows some invasive species to spread and establish in previously inaccessible areas, applying further pressure to environments already experiencing the adverse effects of a changing climate (Frank & Just, 2020; IPBES, 2019). Climate-change driven intensification of storms, surges, winds, and more can transport invasive species to a novel environment (Diez et al., 2012). Additionally, reduced biotic resistance of communities due to major disturbances caused by climate change (e.g., hurricane or forest fire) allow invaders to more easily establish, spread, and further harm native biodiversity (Diez et al., 2012).

The invasion of Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) in the Caribbean is a notable system to investigate the effects of climate change on invasive species (Côté & Green, 2012). Lionfish are effective, mid-level, generalist predators of fish and invertebrates on coral reefs and are currently invading the Western Atlantic Ocean (Green et al., 2011; Schofield, 2009). Since 2012, *P. miles* is also invading the Eastern Mediterranean (Kletou et al., 2016). Lionfish were first introduced off the east coast of Florida, USA, in 1985, via intentional or unintentional releases from the aquarium pet trade (Carballo-Cárdenas, 2015; Côté & Smith, 2018; Schofield, 2009; Whitfield et al., 2002). Since then, lionfish have spread as far north as North Carolina, USA, and as far south as Brazil in the Western Atlantic (Soares et al., 2023; Schofield, 2009). In their invaded range of the Bahamas, lionfish are having detrimental effects on native biodiversity, where they have reduced native prey fish biomass by 65% on natural reefs (Côté & Smith, 2018; Green et al., 2012).

Lionfish can substantially reduce prey fish populations in the Caribbean partly because of little population control from native predators or competitors. In both their invaded and native ranges, lionfish have few natural predators (Côté & Smith, 2018; Albins & Hixon, 2013; Maljković et al., 2008). While a select few native predators like large-bodied groupers provide some biotic resistance to lionfish invasion (Smith & Côté, 2021), lionfish grow faster and have higher predation rates than small-bodied, ecologically similar native groupers like coney grouper *Cephalopholis fulva* and graysby grouper *C. cruentata* in the Caribbean (Albins, 2013; Albins & Hixon, 2013; Secord, 2015).

Importantly, in the Caribbean, many native prey species do not recognize lionfish as a predator due to its recent arrival in the Caribbean Ocean, cryptic colouration, and novel hunting strategy (Anton et al., 2016; Black et al., 2014; Green et al., 2019). Lionfish prey include native juvenile princess *Scarus taeniopterus* and striped *S. iseri* parrotfishes (Anton et al., 2016; Berchtold & Côté, 2020; Morris et al., 2008) - both keystone herbivores on Caribbean coral reefs that keep macroalgae, which inhibits coral growth, in check (Bellwood & Choat, 1990; Hughes et al., 2003; Jh et al., 1996). Currently, it is uncertain whether Caribbean parrotfish recognize lionfish as a predator as it seems to vary by species and pre-exposure to lionfish at varying densities (Anton et al., 2016; Berchtold & Côté, 2020; Eaton et al., 2016). For example, a field study found that princess parrotfish approach closer to lionfish than to native predators, suggesting that they do not fully recognize lionfish as a predator (Anton et al., 2016). However, a study on striped parrotfish showed that juveniles from reefs with high lionfish densities performed anti-predator behaviours in response to cues of both native predators and lionfish, but those from reefs with low lionfish densities only responded to the native predator, implying that predator recognition in striped parrotfish varies with exposure to lionfish (Berchtold & Côté, 2020).

Given the numerous effects of temperature on predator-prey dynamics and the detrimental effects of invasive lionfish on native prey, an important question is whether future ocean warming will exacerbate the negative effects of invasive lionfish on native prey fish populations through increased predation, as inferred by increased predatory behaviours, and a decrease in prey anti-predator behaviours. To our knowledge, no study has empirically examined predator-prey interactions under a changing climate in the Caribbean with an extremely effective invasive predator like lionfish and native, keystone prey. To accomplish this, we observed the behaviours of wild-caught lionfish and parrotfishes at two temperatures (29 °C versus 32 °C) under laboratory conditions. We hypothesized that under ocean warming, lionfish will increase their predatory behaviours while parrotfish will increase their feeding behaviours and decrease their anti-predator behaviours. We also hypothesized that both lionfish and parrotfish would grow slower under elevated ocean temperatures.

Methods

Ethics statement

All fishes were caught and handled with permission from The Bahamas Department of Environmental Planning and Protection (BS-2024-691719) and in accordance with Concordia animal care protocol (30019689).

Study site and fish collection

Our study took place at the Cape Eleuthera Institute on Eleuthera Island, The Bahamas, from July to September 2024. Twelve lionfish and 35 juvenile parrotfishes were collected from shallow, natural coral patch reefs (~3 m deep) near the Institute between July and August 2024 (Table S1). Lionfish and parrotfish were collected from nearby patch reefs, which were sometimes the same reef (Figure S1). Lionfish were collected on SCUBA and by free diving while all juvenile parrotfishes were collected on SCUBA. We used both princess and striped parrotfishes because they fill similar ecological roles, shoal together, and are almost visually indistinguishable as juveniles (Bellwood et al., 2012; Humann & DeLoach, 2014). All fishes were carefully transported to the Cape Eleuthera Institute by boat in individual coolers, where they were immediately transferred to holding tanks.

Housing and animal care

Lionfish were held in a 1700 L outdoor holding tank for 1-14 days prior to the start of the experiment and were periodically fed frozen tilapia fish filets and freeze-dried bloodworms. At the start of the experiment, lionfish were measured and weighed (Table S1), then moved indoors into 280 L (123.19 cm x 46.99 cm x 53.85 cm; length x width x height) glass tanks that were separated into ¼ and ¾ sections by an opaque divider (sponge filter media) lodged between two transparent dividers (corrugated board and plastic mesh; Figure 1). One lionfish was placed into the larger section of a tank while two to four parrotfishes were measured and weighed, then transferred into the smaller sections of the tank (Table S2). We used a total of 12 tanks: nine tanks had three parrotfish, two tanks had two parrotfish, and one tank had four parrotfish. Because we only had ten tanks, we reused two tanks in the experiment. Unlike lionfish, parrotfish were held indoors in the 280 L glass tanks immediately upon arrival at the Institute. Each tank was equipped with two sponge filters (one on either side of the barriers). The side of the tank containing lionfish had one large rock as shelter, a mesh bag of ammonia remover rocks, a submersible heater, and either a chiller pump to keep the water from overheating or a mock chiller pump made from sponge filter media (for warming treatment tanks). The side of the tank containing parrotfishes had a small algae-covered rock for shelter, and a 10 cm long PVC pipe for shelter. Lionfish and parrotfish were only separated visually, as water exchange occurred between the two sides of the tank.

Fishes were held for a total of 17 days in experimental tanks (Figure 2). All fishes were acclimated to captivity under ambient/current summer (29 °C) conditions for five days before warming treatment tanks underwent a ramping period in which temperature was increased at a rate of 1 °C per day (Lapointe et al., 2018; Penny & Pavey, 2021) for three days to reach the target temperature of 32 °C. This target temperature is based on average projections of Caribbean Ocean surface temperature under a business-as-usual emissions scenario in the year 2100 from three Earth Systems models (GFDL, IPSL, and MPI; Dunne et al., 2020; Boucher et al., 2020, Gutjahr et al., 2019). Fishes were then acclimated under experimental conditions for seven days, after which experimental trials occurred for two days. Lionfish were fed snapper and tilapia filets when first moved into experimental tanks and then once every six days afterwards. Specifically, lionfish were fed at the start of the experimental period and twice more during the 17 days (Figure 2). Parrotfishes were fed approximately similar amounts of algal flakes (TetraColor®) at dawn and at midday every day during the 17 days.

Experimental trials

All trials were recorded using a GoPro Hero11™ and the video footage was analysed after the experiment. Daily observations of the 12 lionfish and 35 parrotfish behaviours took place at dawn (when lionfish are most active; Cornic, 1987) and midday (when parrotfish are active; Ogden & Buckman, 1973) during the ramping and treatment acclimation periods (day six to 15; Figure 2). Parrotfish were fed five to ten minutes before dawn and midday trials. However, these daily observations were not analyzed in this study.

Daily observations for lionfish included a 20-minute scan technique, recording behaviours every 30 seconds (Martin & Bateson, 2007). These behaviours included swimming (actively moving in the water column), hovering (floating in the water column, not moving), resting (laying on the floor or against shelter, not moving), and threat/hunting displays (splaying out spines, head down, angled towards prey). Time spent near or far from the parrotfishes/the barrier shown by demarcated zones was also measured. To ensure inter- and intra-observer reliability, observers were trained on lionfish and parrotfish behaviour footage prior to collecting data. Observers had at least 95% agreement between each other, and each observer also rewatched the same video footage and quantified behaviours numerous times until they had a repeatability score of at least 95%.

Daily observations for parrotfishes consisted of a 20-minutre scan technique, where the number of parrotfish out of shelter, their behaviours, and whether they were near or far from the barrier was recorded every 30 seconds. Behaviours were classified as swimming, sheltering (immobile, under/behind shelter), hovering, resting (immobile, not in shelter), feeding (pecking at the floor/rock/filter or feeding in the water column), and aggression (biting and chasing conspecifics). We also looked at colouration since juvenile princess and striped parrotfish change colour in response to predators or other threats (Berchtold & Côté, 2020; Crook, 1999; Wisenden, 2003). Specifically, princess and striped parrotfish can appear striped (black with three white stripes) while unstressed, pale colouration (silvery) while moderately stressed, or mottled colouration (brown with white specks) while extremely stressed (Figure S2).

During experimental trials, which occurred over two days post treatment acclimation (on days 16 and 17; Figure 2), the opaque divider was removed at the start of the trial for 30 minutes so that the predator and the prey could see each other. In addition to the lionfish behaviours described above (swimming, hovering, resting, and hunting), we also recorded the number of times lionfish approached the barrier. For parrotfish, the same behaviours were recorded during the experimental trials as during the daily observations (swimming, sheltering, hovering, resting, feeding, aggression, and near/far). After 30 minutes, the opaque divider was replaced. At the end of the experiment, parrotfishes were measured, weighed, and returned to natural reefs while invasive lionfish were humanely euthanized by submersion in eugenol (Green et al., 2012), then measured and weighed.

Statistical analyses

All statistical analyses were conducted in RStudio version 4.4.1 (R Core Team, 2024) with the following packages: mgcv version 1.9.1 (Woods, 2017), marginal effects version 0.25.0 (Arel-Bundock et al, 2024), glmmTMB version 1.1.10 (Brooks et al., 2017), effect size version 0.8.9 (Ben-Shachar et al., 2020), lme4 version 1.1.35.5 (Bates et al., 2015), and emmeans version 1.10.4 (Lenth, 2024).

To quantify the effects of temperature and time of day on lionfish behaviours, we used a general additive model (GAM) with a multinomial distribution. Lionfish behaviours (resting, hovering, swimming, and hunting) were the response variables while treatment temperature (29 °C versus 32 °C) and time of day (dawn versus midday) were the explanatory variables. Tank number (1 to 10) was used as a random effect. Model assumptions of convergence and overfitting were checked using the gam.check() function. Collinearity was checked using a correlation matrix. To check model accuracy, we compared predicted and observed behaviours using a confusion matrix (Table S4). The confusion matrix summarizes the proportion of observations that were correctly classified (diagonal values) versus those that were misclassified (off-diagonal values); Kuhn & Johnson, 2013; Stehman, 1997). We generated predicted probabilities using the multinomial GAM output to examine the effects of temperature and time of day on all four behaviours (resting included). Contrasts between treatment and time of day for predictions were calculated using the comparisons() function from the marginal effects package.

We used a generalized linear mixed effects model (GLMM) with a binomial distribution to examine the effect of treatment temperature (29 °C versus 32 °C), time of day (dawn versus midday), and their interaction on lionfish proximity to the barriers in the tank. The binary response variable was dummy coded as 1 (Near) and 0 (Far). Tank was included as a random intercept to account for repeated measures within experimental tanks.

Lastly, we looked at the approach behaviour of lionfish. For number of approaches, we used a negative binomial GLMM with temperature, time of day, and their interaction as fixed effects, while tank was included as a random intercept. All model assumptions were checked and met. For all GLMMs, percent change was calculated using rate ratios:

$$Rate\ Ratio = e^{coefficient}$$

$$Percent\ change = (Rate\ ratio - 1) \times 100$$

We quantified parrotfish behaviours (swimming, sheltering, hovering, feeding, aggression, and resting) using a GLMM with a negative binomial distribution to account for overdispersion in the count data. Temperature and time of day were included as fixed effects, while tank number was a random intercept. The log transformed number of parrotfish in the tank (2 to 4 fish) was used as an offset variable to account for tanks having different numbers of parrotfish. All assumptions of a negative binomial GLMM were tested and met.

Parrotfish colouration was similarly quantified. We first examined changes in parrotfish colouration between temperature and time of day using a negative binomial GLMM. We tested only pale and striped colourations, as the mottled colouration appeared too infrequently to test statistically. Temperature and time of day were included as fixed effects, while tank number was a random intercept. The log transformed number of parrotfish in the tank was again used as an offset variable. We then used Spearman’s rank correlation to assess the association between colouration (mottled colouration included) and parrotfish behaviours. To correct for multiple comparisons, we applied the Holm-Bonferroni adjustments to p-values.

We also quantified different growth metrics for lionfish and parrotfish. Specifically, we calculated how absolute growth rate (absolute change in weight or length), relative growth rate (change in weight or length taking the initial size of the fish into account), and condition factor (*K*; nutritional state of the fish) changed between treatments during captivity (Busacker et al., 1990). We used the Fulton formula to calculate *K*:

$$K = 100 \times weight/length^3$$

For lionfish, we looked at both weight (g) and total length (cm) and used linear models with temperature as a fixed effect. For parrotfish, we only looked at weight (g) and used linear mixed effects models with temperature as a fixed effect and tank number as a random intercept.

Results

Lionfish behaviours

The change from the baseline (resting) behaviour to hovering, swimming, and hunting was not significantly affected by the individual effects of temperature or time of day (Table 1). However, the interaction between temperature and time of day was significant for the three behaviours ($p \leq 0.001$, Table 1). Specifically, hot temperatures during midday decreased the amount of time spent resting and increased the amount of time spent hovering, swimming, and hunting (Figure 3).

We used the predicted probabilities from the multinomial GAM to further interpret the difference in lionfish behaviours between temperature and time of day. At midday, lionfish were predicted to spend 14% ± 7% (mean ± SE) of the time resting in control tanks, but this value dropped to 2% ± 1% (mean ± SE) in hot tanks ($p = 0.040$, $z = -2.052$, Table 3, Table S3, Figure 3a). Hovering behaviour followed the same trend, with a slight but nonsignificant increase in hovering at midday (from ~15% to ~18% for both treatments, Table 3, Table S3, Figure 3b). Lionfish were predicted to swim slightly more at midday for both temperature treatments (15% ± 11% to 17% ± 13% for control tanks and 10% ± 9% to 16% ± 13% for hot tanks); however, the effect was not significant (Table 3, Table S3, Figure 3c). Lionfish appeared to display hunting behaviour most often in both temperature treatments, with probabilities ranging from 50–65% of the trial time spent hunting (Table S3). At midday, lionfish in hot tanks were predicted to spend approximately 65% ± 22% of their time hunting, compared to 50% ± 23% in control tanks ($p = 0.002$, $z = 3.103$ Table 3, Table S3, Figure 3d).

Lionfish tank position and approaches

Temperature alone did not have a significant effect on lionfish position in the tank; however, its interaction with time of day was significant. Lionfish spent 35% less time near the prey fish at midday in control tanks ($p = 0.004$, $z = -2.879$, Table 4, Figure 4) but spent about 158% more time near the prey fish at midday in hot tanks ($p < 0.001$, $z = 4.056$, Table 4, Figure 4). There was no effect of treatment, time of day, or their interaction on the number of approaches to parrotfish (Table 5, Figure 5).

Parrotfish behaviours

Temperature had a significant effect on swimming, hovering, and feeding behaviours in parrotfish (Figure 6a, 6d, 6e). Parrotfish in hot tanks increased feeding by 215% ($p = 0.004$, $z = 2.914$), hovering by 112% ($p = 0.041$, $z = 2.046$), and swimming by 178% ($p = 0.004$, $z = 2.846$) compared to those in control tanks (Table 6). There was weak statistical evidence for an effect of temperature on resting behaviour in parrotfish ($p = 0.06$, $z = -1.854$), with parrotfish resting 39% less in hot tanks than in control tanks (Table 6, Figure 6c). Time of day had a significant effect on swimming, resting, feeding, and aggressive behaviours (Figure 6a, 6c, 6e, 6f). At midday, parrotfish rested 48% less ($p = 0.009$, $z = -2.578$), were about 232% more aggressive ($p = 0.020$, $z = 2.324$), fed 182% more ($p = 0.006$, $z = 2.738$), and swam 356% more ($p < 0.001$, $z = 4.362$) than at dawn (Table 6). The interaction between treatment and time of day had a significant effect on only swimming behaviour (Figure 6a). Parrotfish swam 71% less at midday in hot tanks than in control tanks ($p = 0.014$, $z = -2.453$, Table 6). There was no effect of treatment, time of day, or the interaction between the two on the sheltering behaviour in parrotfish (Table 6, Figure 6b). Time of day alone was significant for parrotfish positioning relative to the lionfish (Figure 7, Table 7). Parrotfish spent 275% more time near the divider than far from the divider at midday than at dawn ($p = 0.0004$, $z = 3.538$).

Parrotfish colouration

There was no effect of treatment, time of day, or the interaction between the two on parrotfish colouration (Table 8, Figure 8). After adjusting the p-value to account for multiple comparisons, we found that the pale colouration was strongly and significantly associated with sheltering behaviour ($\rho = 0.873$, $p < 0.001$, Table 9, Figure 9). Striped colouration was significantly associated with hovering ($p = 0.011$, Table 9, Figure 9), although the association was moderate ($\rho = 0.479$). Striped colouration was marginally non-significantly ($p = 0.058$) associated with feeding, and again the association was moderate ($\rho = 0.415$, Table 9, Figure 9). Mottled colouration appeared too infrequently to be analyzed statistically.

Growth metrics

There was no effect of temperature on the absolute growth rate in weight (g) and total length (cm; Table 10, Figure 10a, b), relative growth rate in weight (g) and total length (cm; Table 11, Figure 10c, d), and condition factor (*k*; Table 12, Figure 10e) for lionfish. Similarly, there was no effect of temperature on the absolute growth rate in weight (g; Table 13, Figure 11a), relative growth rate in weight (g; Table 14, Figure 11b), and condition factor (*k*; Table 15, Figure 11c) for parrotfish. For both lionfish and parrotfish, weight and length did not change significantly throughout the 17 days and did not differ between treatments (Figures 12 and 13).

Discussion

Lionfish acclimated to 32 °C conditions showed more hunting behaviours and spent more time near prey fish at midday than lionfish acclimated to 29 °C. They also showed increased hovering, swimming, and hunting behaviours at midday when compared to the baseline conditions (resting at dawn in 29 °C tanks). Parrotfish acclimated to 32 °C tanks showed increased feeding, hovering, and swimming behaviours than those acclimated to 29 °C. Parrotfish also spent more time near the divider separating them from the lionfish than far from the divider at midday than at dawn, regardless of temperature. Parrotfish often showed the pale colouration when sheltering, but the striped colouration when hovering or feeding. Temperature had no discernible effect on various metrics of growth in both lionfish and parrotfish.

In ectotherms, feeding behaviours such as hunting generally increases with warming, until temperatures exceed the species' optimal thermal range (Volkoff & Rønnestad, 2020). As predicted, lionfish spent more time hunting in hot tanks than in control tanks, but this effect was tempered by time of day. Increased predatory behaviours under warming have been predicted and empirically observed in lionfish (Côté & Green, 2012; South et al., 2017; Steell et al., 2019), and in other coral reef and freshwater fish species such as the dottyback (Allan et al., 2015), coral trout *Plectropomus leopardus* (Johansen et al., 2015), largemouth bass, and striped bass *Morone saxatilis* (McInturf et al., 2022). However, the effect of time of day on predatory behaviour was not explored in any of these studies. It is important to note that increased hunting behaviours may not necessarily result in increased prey capture success and mortality. Nonetheless, under current temperature conditions, lionfish predation has substantial, negative impacts on their invaded ecosystem (Côté & Smith, 2018; Green et al., 2012), and these predatory impacts on native prey fish, if increased hunting behaviours lead to increased prey capture success and mortality, have the potential to be exacerbated under warming scenarios as predicted here.

This is concerning, as lionfish physiology may allow them to fare better in warming waters than native competitors and prey, despite lionfish having slightly lower upper thermal tolerance compared to ecologically similar native species (Barker et al., 2018; Steell et al., 2019). Lionfish digestion was more efficient for fish acclimated to 32 °C than 26 °C, indicating that they might accrue further benefits from increased temperatures predicted by climate change (Barker et al., 2018). Additionally, lionfish defensive spines allow them to spend more time feeding instead of engaging in anti-predator behaviours like predator avoidance (Steell et al., 2019). While the long-term effects of increased temperatures on the digestive and energetic physiologies of the lionfish are unknown, prioritizing hunting over other activities, if successful, allows lionfish to put more energy into fitness-related processes like reproduction and growth (Steell et al., 2019). Increased hunting behaviours with warming, combined with their already demonstrated faster growth and consumption rates than native competitors at ambient conditions (Albins, 2013), may put lionfish at a serious advantage over native competitors and prey.

As expected, juvenile parrotfish spent more time feeding in hot tanks than in control tanks. They also spent more time near the divider separating them from lionfish and feeding at midday than at dawn, which is consistent with their diurnal behaviour (Ogden & Buckman, 1973). When feeding, parrotfish cannot perform anti-predator behaviours like sheltering or shoaling, elevating exposure to predators. Similar increases in risky behaviour and/or mortality rates under warming were seen in juvenile rainbow trout *Oncorhynchus mykiss* (Biro et al., 2006, 2007), juvenile whitetail damselfish *Pomacentrus chrysurus* (Lienart et al., 2014), the guppy *Poecilia reticulata* (Weetman et al., 1998), and even in shrimps *Palaemon spp.* (Marangon et al., 2020). Increased foraging to compensate for the rise in metabolic rate could result in longer time being exposed to potential lionfish predation. Increased susceptibility to predation is particularly concerning in parrotfish because they are keystone prey on Caribbean coral reefs, being the only significant herbivore on reefs after the collapse of diadema populations in the 1980s (Burkepile & Hay, 2010; Carpenter, 1986; Hughes et al., 2003, 2007; Spiers & Frazer, 2023). Elevated parrotfish mortality rates can potentially cascade down marine food webs, affecting primary productivity and coral cover (Arnold et al., 2010; Comeros-Raynal et al., 2012; Mumby et al., 2007).

Parrotfish were more active (i.e., hovered and swam more) in hot tanks than in control tanks. This result was seen in several other fish species with different acclimation times, such as lemon damselfish *Pomacentrus moluccensis* (Biro et al., 2010), pale-tail damselfish *Pomacentrus trichrourus* (D'Agostino et al., 2020), bluntnose minnow *Pimephales notatus* (Moffat et al., 2025), and giant danio *Devario aequipinnatus* (Bartolini et al., 2015). Fish tend to be more active under warming to increase feeding rates and ensure growth despite the higher metabolism caused by temperature and increased movement (Biro et al., 2007). However, when a fish reaches their thermal optimum, activity (and feeding) declines, possibly to reduce energy spent and mitigate the effects of heat stress on their bodies (D'Agostino et al., 2020; Nowicki et al., 2012). Importantly, while increasing activity benefits the fish during warm periods, it also elevates their exposure to predators, leading to potential adverse consequences described above (Biro et al., 2007).

Increased activity due to warming can also have a social cost by increasing aggressive encounters between fish (Kochhann et al., 2021). We did not observe an increase in parrotfish aggression with warming in our study. However, this lack of aggression may be due to the low density of parrotfish (2-4 juvenile fish per tank) in our experiment. Indeed, hotter temperatures have affected aggressive behaviours in many other fish species (Biro et al., 2010; Francispillai et al., 2024; Kochhann et al., 2015; McDonnell et al., 2019). Increasing activity and aggressive behaviours could have both positive and negative effects on fish fitness. While activity increases feeding rate, aggression could promote boldness in juvenile parrotfishes by encouraging them to fight for better territory and access to food and mates, which could give them a competitive edge over less aggressive conspecifics during periods of intense warming (Biro et al., 2010; Sih et al., 2004; Smith & Blumstein, 2008). However, increased activity and aggression also reduce the amount of energy available for growth and reproduction (Rennie et al., 2005). Active fish under warming may stay further apart, decreasing school cohesion and elevating vulnerability to predators (Bartolini et al., 2015; Matthews & Wong, 2015). Higher levels of activity and aggression may also prevent fish from performing anti-predator behaviours, again increasing risk of predation and lowering body condition (Biro & Stamps, 2010; Kochhann et al., 2021).

Contrary to our predictions, some parrotfish anti-predator responses (i.e., sheltering and resting) did not change between hot and control tanks. Usually, in response to predator cues, prey species reduce their activity and perform anti-predator behaviours such as sheltering, freezing, and shoaling (Kelley & Magurran, 2003; Lehtiniemi, 2005). However, rising temperatures can affect these behaviours, as seen in juvenile Trinidadian guppies *Poecilia reticulata* that reduced their time spent freezing in response to an alarm cue (Breedveld et al., 2025), increased their activity, and decreased distance from predators (Zanghi et al., 2023). Reduced escape performance with rising temperatures was also seen in the lemon damselfish and the Ambon damselfish *Pomacentrus amboinensis* (Warren et al., 2017). Nevertheless, some studies found no effect of temperature on anti-predator behaviours (Vicente et al., 2024), while other studies found that prey responses improved due to negative effects of temperature on the predator (Grigaltchik et al., 2012). In our experiment, parrotfish spent most of their time sheltering in the presence of lionfish regardless of tank temperature. We could have unintentionally selected for a specific behavioural type while catching juvenile parrotfish due to a low capture success rate (often only two to three fish out of schools of ten to 15 individuals).

Furthermore, the chronic exposure to a predator through chemical cues throughout the duration of this study could have affected the anti-predator behaviours of parrotfish. Prey use chemical cues to gain information about their surroundings and potentially avoid threats (Abreu et al., 2016; Chivers & Smith, 1998; Korpi & Wisenden, 2001). Predator odour has been shown to induce anti-predator behaviours such as increased sheltering and stress responses in many prey species such as tilapia *Oreochromis niloticus* (Miyai et al., 2016), cichlid *Neolamprologus pulcher* (Fischer et al., 2017), and glowlight tetras *Hemigrammus erythrozonus* (Brown & Dreier, 2002). However, little is known about how chronic exposure to predator odour affects fish anti-predator behaviours. Parrotfish in our experiment exhibited some change in prey behaviours under warming in the form of increased activity. However, whether increased activity in parrotfish is an anti-predator behaviour is unclear. Unfortunately, we did not have a lionfish absence control to examine whether increased parrotfish activity is also an anti-predator response, although increased inspection activity as an anti-predator behaviour has been observed in some fish (Brown & Godin, 1999; Brusseau et al., 2024).

Colour changing is another useful tactic to avoid predator detection (Stuart-Fox & Moussalli, 2009). Juvenile parrotfish colour patterns were not significantly affected by treatment conditions or time of day. This is surprising, as juvenile parrotfish tend to appear pale or mottled when extremely stressed or during the night (Bellwood & Choat, 1989). However, when looking at how parrotfish colourations correlated with their behaviour in our study, sheltering fish usually appeared pale, indicating some level of stress. In general, the juvenile parrotfish in our experiment would usually show the pale colour pattern, implying that they were experiencing a constant baseline level of stress possibly due to constant proximity to lionfish. Striped colouration was only significantly correlated with hovering, although the correlation was moderate (~0.5). In another study, striped colour pattern in parrotfish was associated with increased movement and foraging (Berchtold & Côté, 2020). The hovering fish in our experiment may have felt safe enough to leave shelter in these instances, despite being visible to the lionfish, which could indicate risky behaviour.

Most effects of temperature on various lionfish and parrotfish behaviours were tempered by the time of day when the trials were performed (i.e., dawn or midday). Princess and striped parrotfish are diurnal species and generally are more active during the day, only beginning to feed after dawn (Ogden & Buckman, 1973). Increased activity at midday is likely their normal diel pattern. On the other hand, lionfish are crepuscular and are generally more active at dawn and dusk than at midday (Green et al., 2011). However, lionfish can often be seen hunting during the day with relatively high predation rates (Côté & Maljković, 2010). It is possible that the increased temperature in the treatment tanks prompted the lionfish to hunt more often at unnatural times in an attempt to compensate for a higher metabolic rate. Additionally, parrotfish swam, hovered, and fed significantly more at midday than at dawn, and in general spent more time near than far from lionfish at midday, possibly causing lionfish to hunt more at midday in response to prey activity. Finally, the room where we conducted our observations had fluorescent lighting with only two settings: on or off. This meant relatively similar light levels at dawn and at midday, which could have affected lionfish behaviours.

Despite increased activity in parrotfish and hunting in lionfish at 32 °C, there was no effect of temperature on growth rate in any of the metrics examined in this study (absolute growth rate, relative growth rate, and condition factor). This is surprising as a warming of 3 °C was predicted to directly affect growth rates of coral reef fishes, especially those of predators (Millington et al., 2022). Reduced body size in response to warming has been seen across many species, though fish in particular show the most extreme examples (Gardner et al., 2011; Martins et al., 2023; Sheridan & Bickford, 2011). A decrease in growth rate or body condition when exposed to increased temperatures was seen in marine and freshwater fish such as damselfish *Acanthochromis polyacanthus* (Donelson et al., 2010; Munday et al., 2008), common carp *Cyprinus carpio* (Oyugi et al., 2012), burbot *Lota lota*, and northern pike *Esox lucius* (Gerasimov et al., 2024). Moreover, shrinkage in response to extreme ocean temperatures during marine heatwaves can occur in some species, as seen in clown anemonefish *Amphiprion percula* (Versteeg et al., 2025).

Our nonsignificant growth rate findings could be due to the relatively short seven-day period of elevated temperature exposure within the full 17 days of captivity. The species listed above were held for a minimum of 20 days, which could have allowed for sufficient time to detect a difference in growth. However, effects of temperature on growth were seen in bridled leatherjacket *Acanthaluteres spilomelanurus* held for only seven days (Booth et al., 2014). Lionfish are robust against starvation, especially at larger sizes, only losing between 5 and 16 percent of their body weight after three months (Fishelson, 1997). Lionfish growth responses to stressors may therefore be less sensitive than other species. In contrast, the parrotfish in our study were fed a non-standardized number of flakes twice a day, which, in addition to the short acclimation time, may have compensated for any loss of growth that might typically be seen in hot treatment tanks.

One important caveat to our study is that a seven-day acclimation period may not fully represent how these fishes will respond under prolonged warming. Thermal acclimation influences physiology and behaviour, and while some traits (e.g., thermal tolerance limits) can adjust within days, metabolic rate in some species often requires longer times to stabilize (Chabot et al., 2016; Manciocco et al., 2015; Pörtner, 2010). Increasing thermal acclimation time has been found to cause compensatory changes in metabolic and cardiorespiratory performances in many freshwater and marine species (Johansen et al., 2021; Nyboer & Chapman, 2017, 2018; Sandblom et al., 2014). Our findings may therefore more closely reflect the behavioural consequences of heatwave-like conditions. It is unclear whether longer acclimation times might alter the magnitude and/or direction of the observed behavioural responses (Chabot et al, 2016; Sentis et al., 2022).

Overall, increases in lionfish hunting behaviours with warming in our study suggests that lionfish predatory impacts on Caribbean coral reefs might be exacerbated in future. This negative, predatory impact may be magnified by co-occurring increases in parrotfish activity levels with warming, which could make them more vulnerable to elevated lionfish predation. If these behaviours lead to subsequent declines in parrotfish populations, this could disrupt Caribbean reef food webs by increasing primary productivity and decreasing coral cover (Albins & Hixon, 2013). While not currently endangered in The Bahamas, parrotfishes are threatened by climate change and other anthropogenic factors, like habitat degradation, overfishing, and invasive species (Comeros-Raynal et al., 2012; Rasher & Hay, 2010; Paddack et al., 2009). As keystone herbivores on coral reefs, increased actions in future to safeguard parrotfish from these many stressors, including an elevated threat from invasive lionfish, may be necessary.

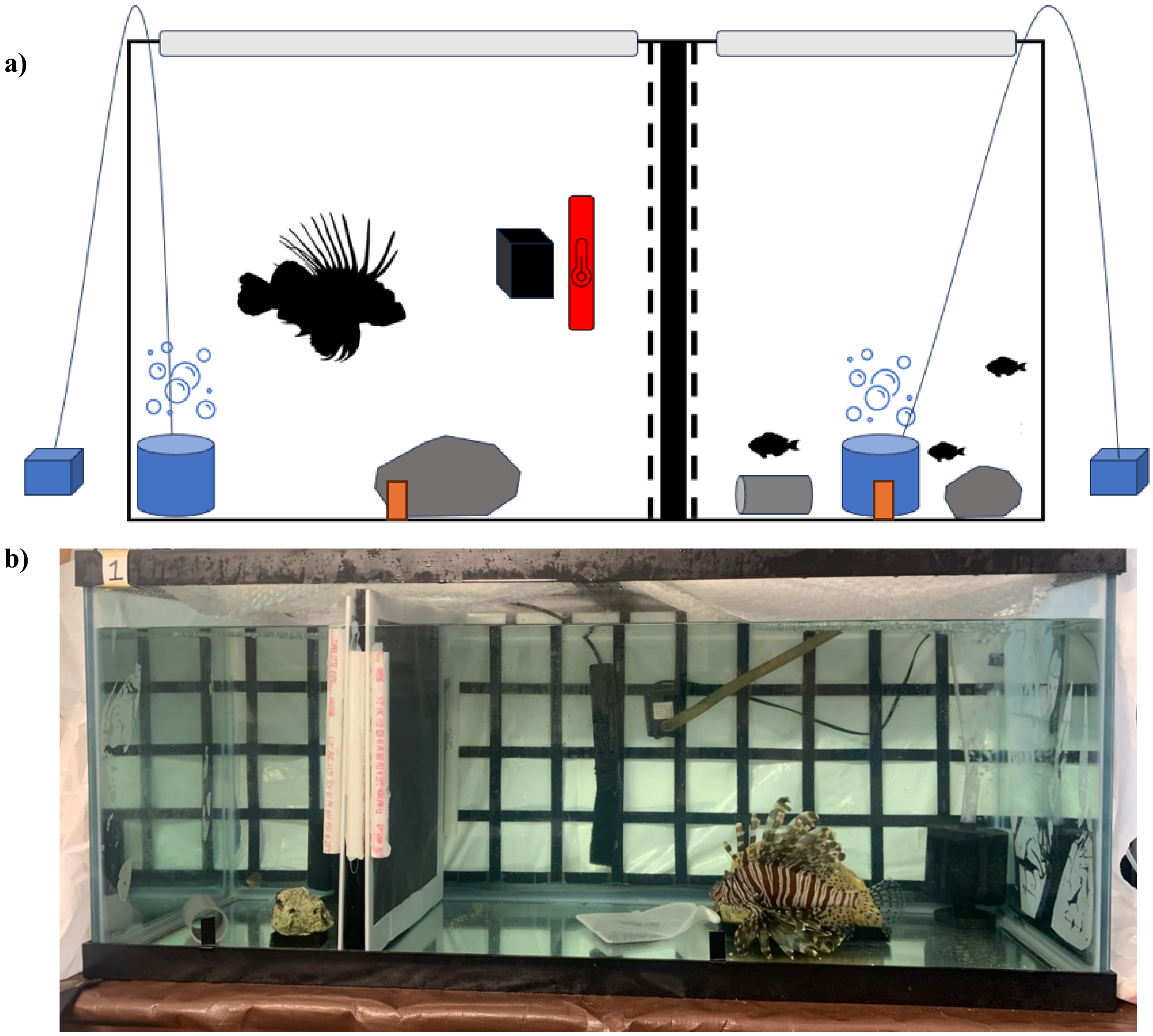

Figure 1. *a)* Schematic of experimental tank. Predators are separated from prey by a transparent divider (screen mesh; dotted bar) and an opaque divider (filter sponge media; black bar). Each tank had a submersible heater (HiTauing Aquarium Heater; red rectangle) placed at the centre of the tank to ensure that heated water was evenly distributed throughout the tank. Control tanks had a water pump connected to a chiller (BAOSHISHAN Aquarium Chiller; black box) to keep the tanks at 29 °C, while hot treatment tanks had a mock chiller pump (filter sponge media; black box). Tanks also had sponge filters with built-in airstones (small blue cylinders). Lionfish and parrotfish sides of the tank were separated in two by black electrical tape (orange rectangles). At

the start of the experiment, the opaque divider was removed, and lionfish predatory behaviours were recorded while parrotfish foraging and anti-predator behaviours were recorded. *b)* Photo of experimental tank setup.

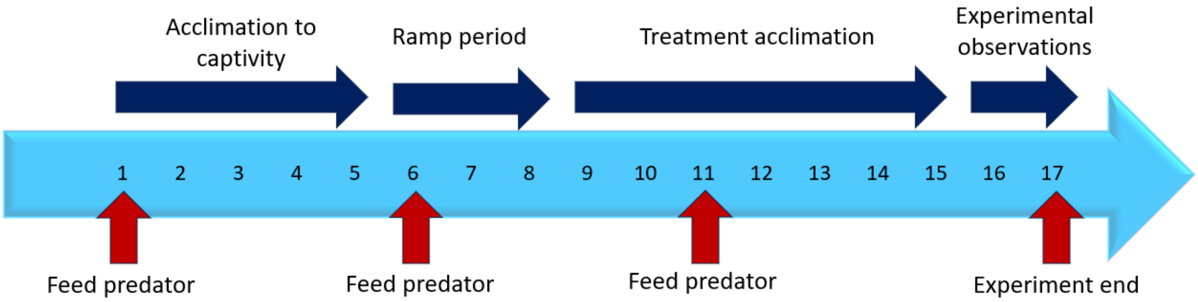

Figure 2. Experiment timeline. Fish were captured from natural coral patch reefs surrounding the field station and kept in captivity for 17 days. Predators were fed three times during captivity and prey were fed throughout the study. At the end of the experiment, invasive lionfish were humanely euthanized while native parrotfishes were returned to natural reefs.

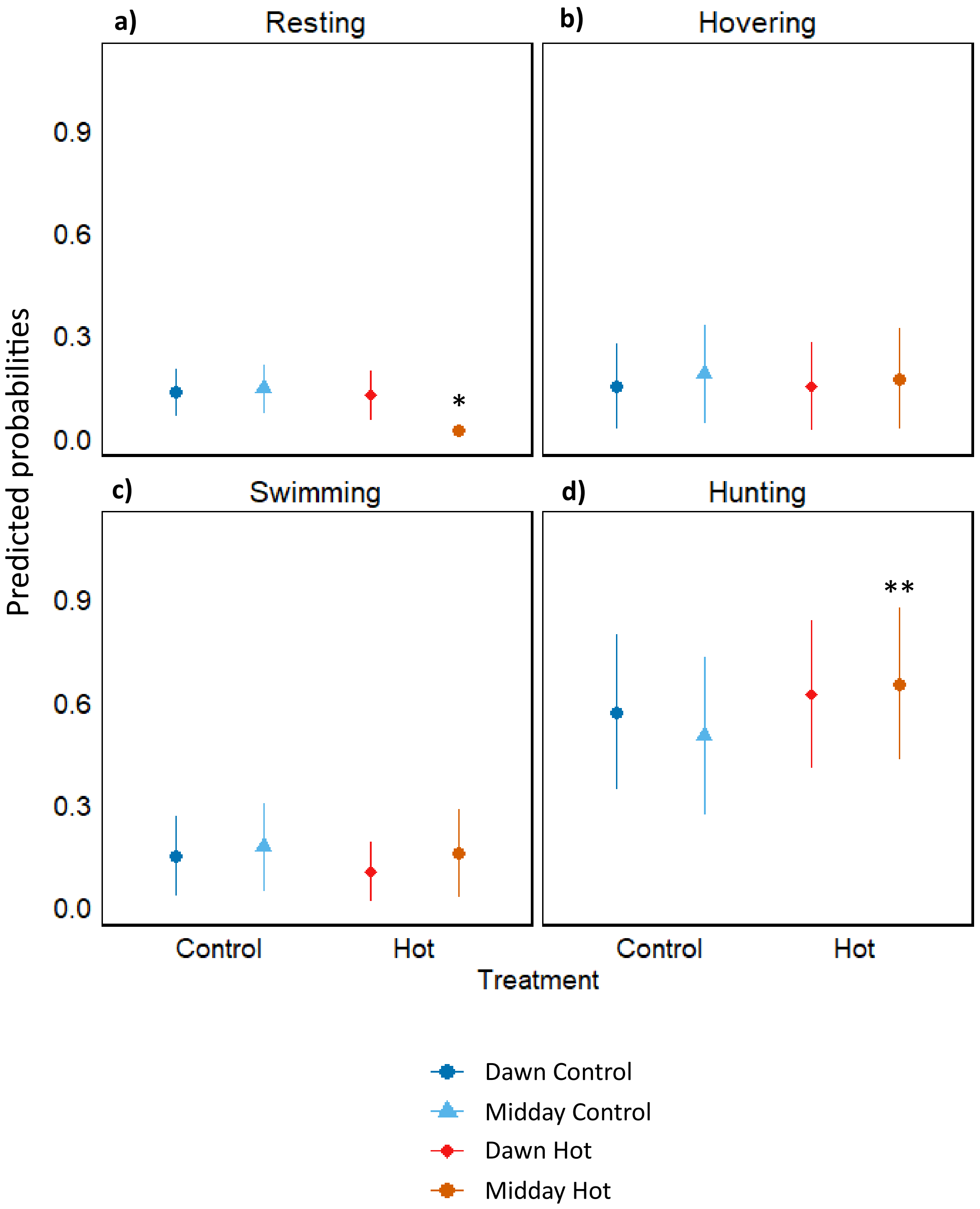

Figure 3. Predicted probabilities of lionfish (*Pterois spp.*) behaviours under two different treatment conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday). Figure 3*a* shows resting, defined as being immobile at the bottom of the tank or against a form of cover. *b)* Hovering; immobile in the water column. *c)* Swimming; actively moving in any

direction. *d)* Hunting; angled towards the prey fish with pectoral fins fully splayed. Points represent the estimated mean probability of each behaviour based on generalized additive model (GAM) predictions, with error bars showing standard error. *p <0.05, **p < 0.01, ***p < 0.001.

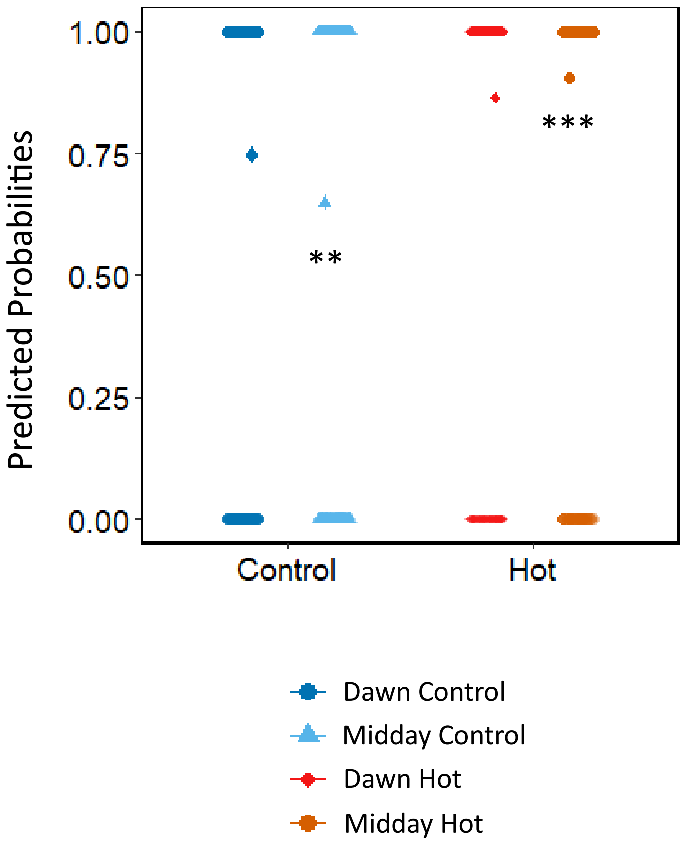

Figure 4. Predicted probabilities of lionfish (*Pterois spp.*) being near (1) versus far (0) from parrotfish (*Scarus spp.*) across treatments conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday). Points represent the mean with standard error. Individual data points are present at 0 and 1. *p <0.05, **p < 0.01, ***p < 0.001.

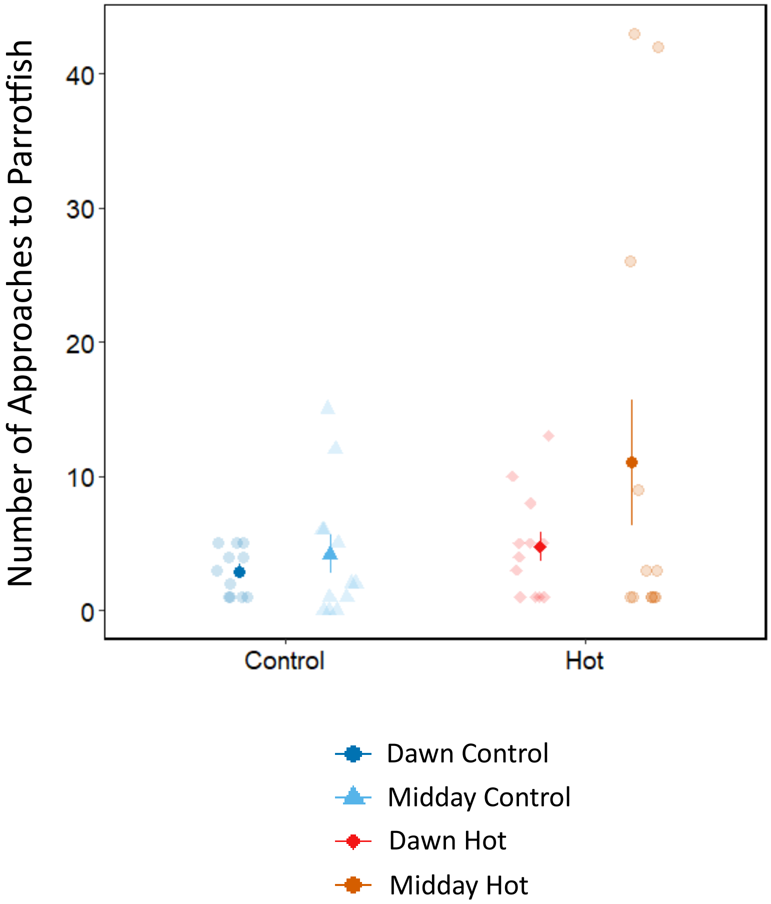

Figure 5. Number of lionfish (*Pterois spp.*) approaches to parrotfish (*Scarus spp.*) across two different treatment conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday). Points represent the mean with standard error. *p <0.05, **p < 0.01, ***p < 0.001.

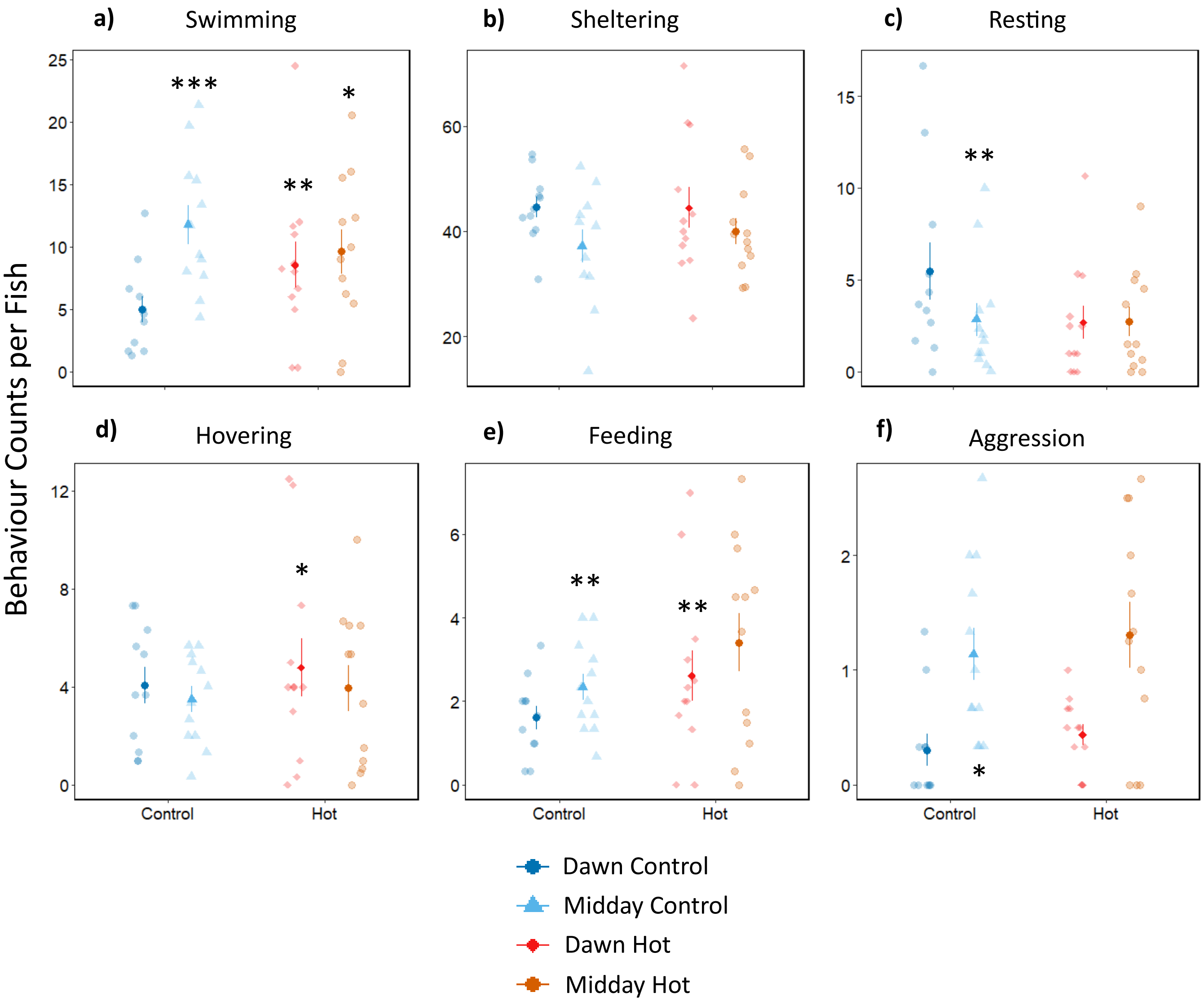

Figure 6. Observed parrotfish (*Scarus iseri* and *S. taeniopterus*) behaviours measured per fish in response to exposure to an invasive lionfish (*Pterois spp.*) under two different treatment conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday). Note the different scales on the y axes. Points represent the mean with standard error, while individual datapoints are overlaid. Figure 6*a* shows swimming behaviour, defined as calmly swimming around. *b)* Sheltering; hiding behind or under objects in the tank. *c)* Resting; immobile against the bottom of the tank, but not behind or under shelter. *d)* Hovering; immobile in the water

column. *e)* Feeding; pecking at the bottom of the tank, objects in the tank, or at the surface of the water for food. *f)* Aggression; chasing or biting other fish in the tank. *$p < 0.05$, **$p < 0.01$, ***$p < 0.001$.

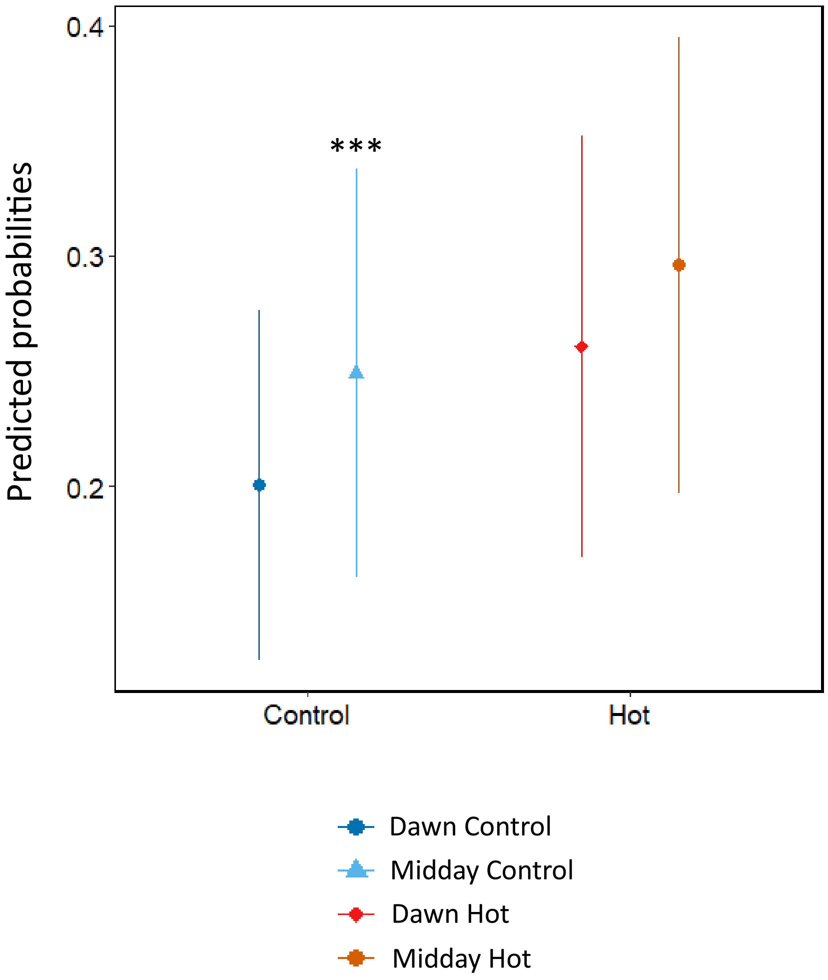

Figure 7. Predicted probabilities of parrotfish (*Scarus iseri* and *S. taeniopterus*) being near versus far from lionfish (*Pterois spp.*) across treatments conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday). Probabilities were estimated for each combination of temperature treatment and time of day. Points represent the model-predicted mean probability of being near, and error bars represent the standard error. *p <0.05, **p < 0.01, ***p < 0.001.

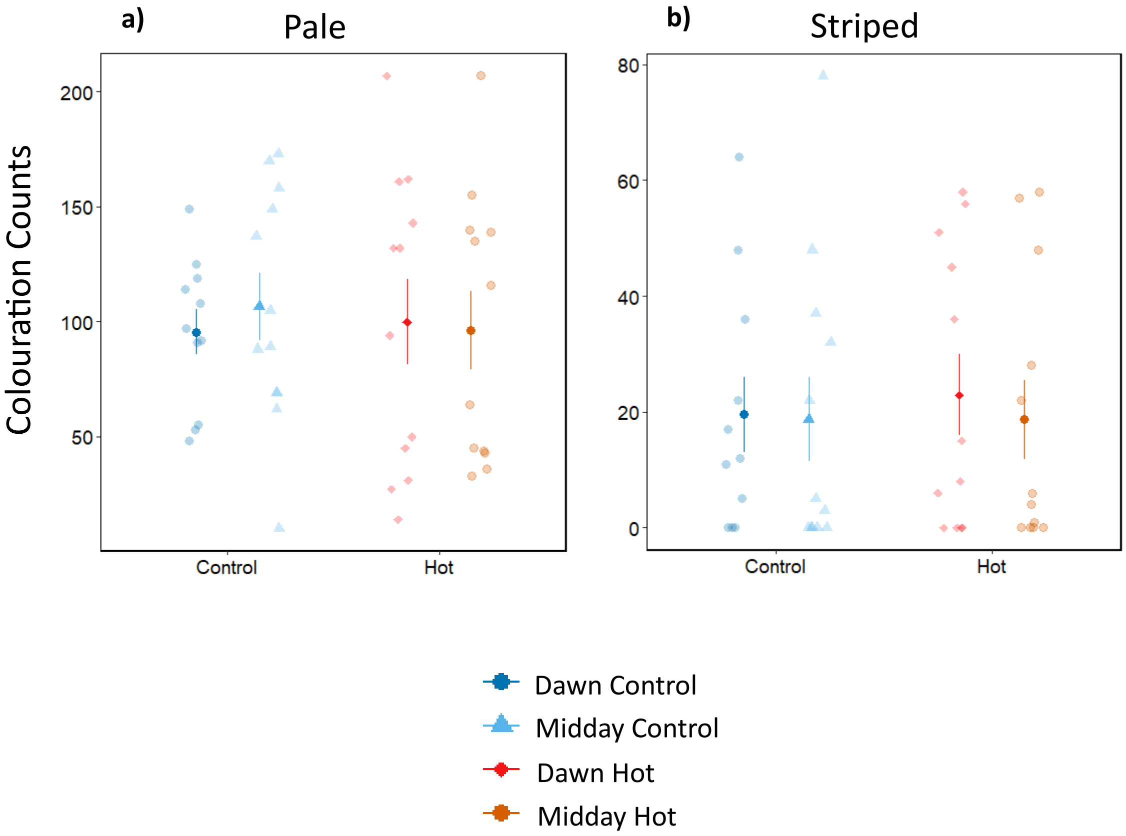

Figure 8. Observed parrotfish (*Scarus iseri* and *S. taeniopterus*) colourations measured per fish in response to exposure to an invasive lionfish (*Pterois spp.*) under two different treatment conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday). Note the different scales of the y axes. Points represent the mean with standard error, while individual datapoints are overlaid. Figure 8*a* shows pale colouration, while Figure 8*b* shows striped colouration.

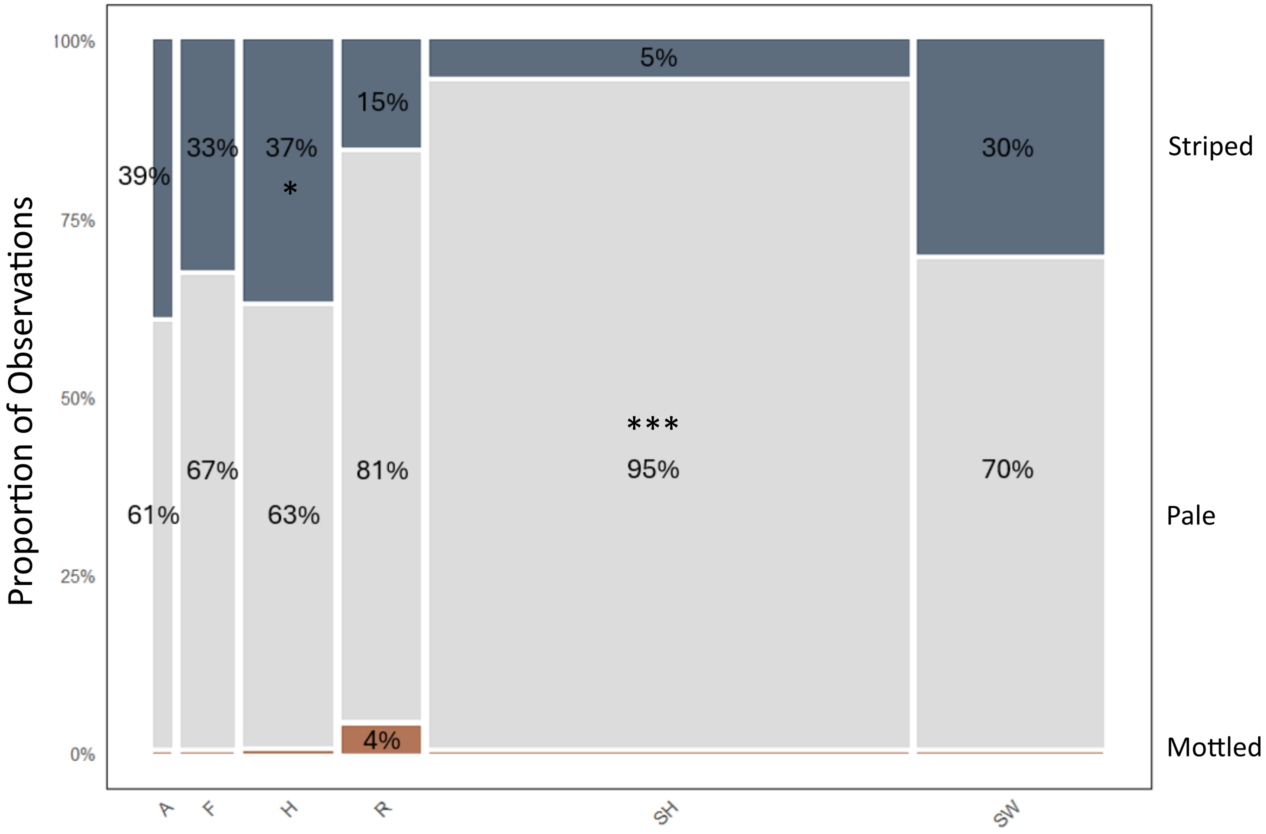

Figure 9. Proportion of observations for each behaviour showing parrotfish colourations (*Scarus iseri* and *S. taeniopterus*). Behaviours include aggression (A), feeding (F), hovering (H), resting (R), sheltering (SH), and swimming (SW), and colourations include pale (gray), striped (dark gray), and mottled (brown). $*p < 0.05$, $**p < 0.01$, $***p < 0.001$.

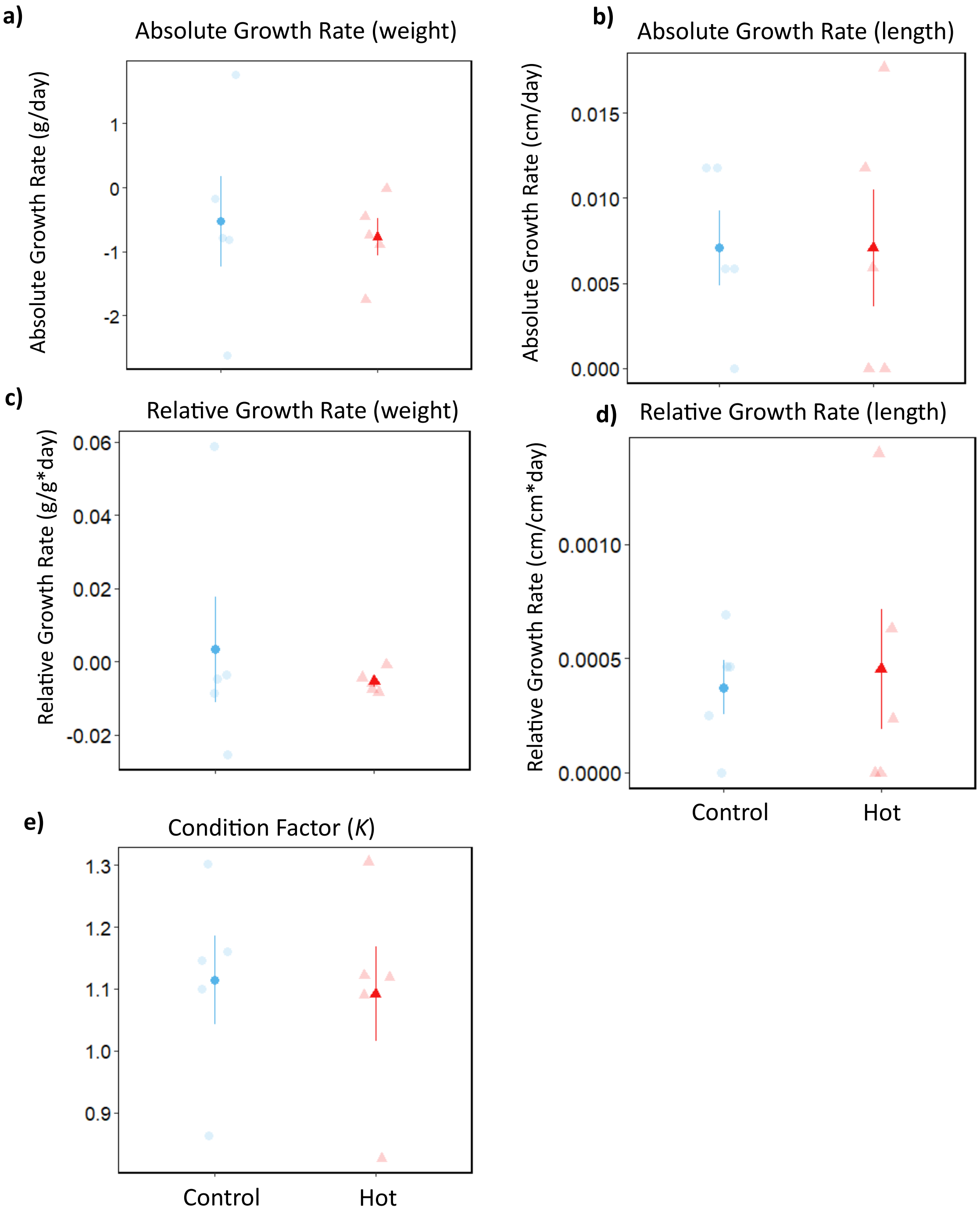

Figure 10. Lionfish (*Pterois spp.*) growth metrics after being held under two different treatment conditions (control, 29 °C versus hot, 32 °C) for 17 days. Note the different scales of the y axes. Points represent the mean with standard error, while individual datapoints are overlaid. Figure

10*a* shows absolute growth rate for weight. *b)* Absolute growth rate for total length. *c)* Relative growth rate for weight. *d)* Relative growth rate for total length. *e)* Fulton’s condition factor (*K*).

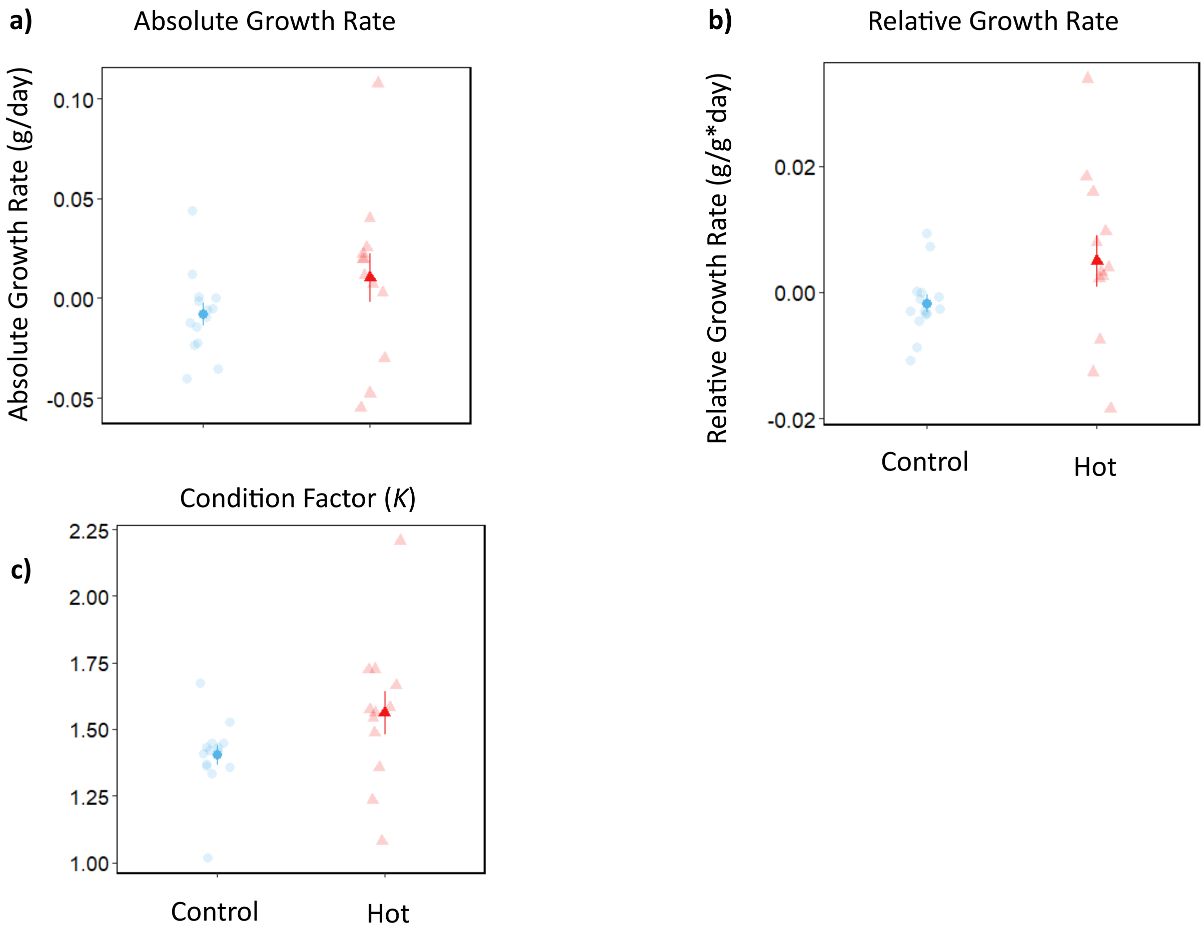

Figure 11. Parrotfish (*Scarus iseri* and *S. taeniopterus*) growth metrics after being held under two different treatment conditions (control, 29 °C versus hot, 32 °C) for 17 days. Note the different scales of the y axes. Points represent the mean with standard error, while individual datapoints are overlaid. Figure 11*a* shows absolute growth rate of parrotfish weight. *b)* Relative growth rate of parrotfish weight. *c)* Fulton's condition factor (*K*).

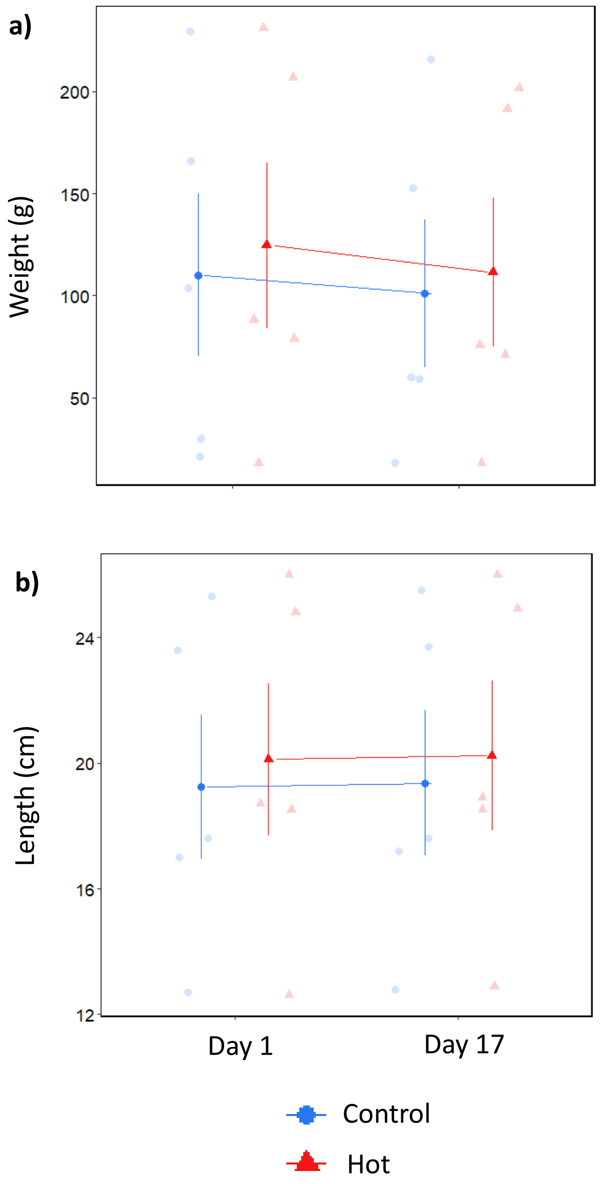

Figure 12. Lionfish (*Pterois spp.*) growth after being held under two different treatment conditions (control, 29 °C versus hot, 32 °C) for 17 days. Note the different scale of the y axes. Points represent the means and bars show the standard error, while individual datapoints are overlaid. Figure 12*a* shows change in weight (g) over time, while *b)* shows the change in total length (cm) over time.

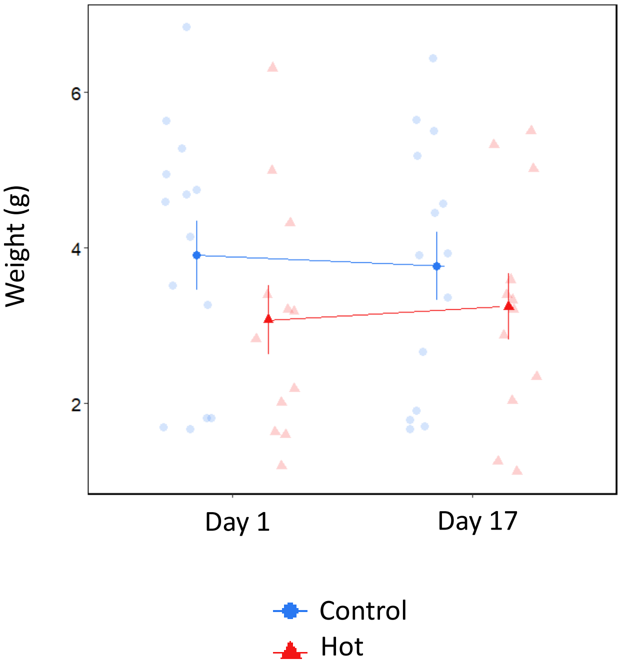

Figure 13. Change in weight (g) for juvenile parrotfish (*Scarus iseri* and *S. taeniopterus*) held under two different treatment conditions (control, 29 °C versus hot, 32 °C) for 17 days. Note the different scale of the y axes. Points represent the means and bars show the standard error, while individual datapoints are overlaid.

Table 1. Summary of a multinomial generalized additive model (GAM) examining the effects of treatment (control, 29 °C versus hot, 32 °C), time of day (dawn versus midday), and their interaction on observed lionfish behaviours. The response variables were the categorical behaviours resting, hovering, swimming, and hunting. Resting behaviour at dawn in control tanks were the baselines for the model. The model includes a random effect for tank specified as a smooth term. The table reports estimate on the log-odds scale relative to the baseline behaviour (resting), along with standard error (SE), z-statistic, and p-value.

Behaviours	Effect	Estimate	SE	z-statistic	p-value
Hovering	Intercept	0.134	0.809	0.166	0.868
	Hot Treatment	0.074	0.338	0.220	0.826
	Midday Trial	0.123	0.193	0.635	0.526
	Hot Treatment * Midday Trial	1.745	0.539	3.239	**0.001**
Swimming	Intercept	0.124	0.746	0.166	0.868
	Hot Treatment	-0.313	0.361	-0.866	0.387
	Midday Trial	0.078	0.217	0.360	0.719
	Hot Treatment * Midday Trial	2.087	0.551	3.787	**0.0002**
Hunting	Intercept	1.463	0.861	1.699	0.089
	Hot Treatment	0.158	0.299	0.528	0.597
	Midday Trial	-0.209	0.163	-1.287	0.198
	Hot Treatment * Midday Trial	1.994	0.519	3.845	**0.0001**

Table 2. Approximate significance of smooth terms for the random effect of tank in the multinomial generalized additive model (GAM). Effective degrees of freedom (edf), reference degrees of freedom (ref. df), Chi-squared statistics, and p-values are shown for each behavioural comparison relative to the baseline behaviour (resting). The model explains 29.2% of the deviance, with a restricted maximum likelihood (REML) score of 1964, based on n = 2828.

Behaviours	Smoothers	Edf	Ref. df	Chi-square	P-value
Hovering	s(Tank)	8.554	9	4747	0.487
Swimming	s.1(Tank)	8.496	9	1214	0.694
Hunting	s.2(Tank)	8.692	9	14773	0.167

Table 3. Pairwise comparisons of predicted probabilities for lionfish behaviours (resting, hovering, swimming, and hunting) between treatments (control, 29 °C and hot, 32 °C), and time of day (dawn or midday), based on a multinomial generalized additive model (GAM). Hot-control contrast estimates are presented on the probability scale, with corresponding standard errors (SE), z-statistics, p-values, and 95% confidence intervals (conf. low, conf. high). Significant p-values are in bold.

Time of day	Behaviour	Estimate	SE	Z-statistic	p-value	Conf. low	Conf. high
Dawn	Resting	-0.008	0.032	-0.259	0.796	-0.073	0.056
	Hovering	0.001	0.029	0.0400	0.968	-0.055	0.058
	Swimming	-0.047	0.041	-1.137	0.256	-0.128	0.034
	Hunting	0.054	0.046	1.193	0.233	-0.035	0.144
Midday	Resting	-0.121	0.059	-2.052	**0.040**	-0.236	-0.005
	Hovering	-0.012	0.035	-0.339	0.734	-0.081	0.057
	Swimming	-0.019	0.036	-0.521	0.602	-0.089	0.051
	Hunting	0.151	0.049	3.103	**0.002**	0.0558	0.247

Table 4. Summary of a generalized linear mixed effects model (GLMM) examining the effects of treatment (control, 29 °C and hot, 32 °C), and time of day (dawn or midday) on the position (near or far) of lionfish (*Pterois spp.*) in a tank in relation to prey (*Scarus iseri and S. taeniopterus*). The model used a binomial distribution and had tank as a random intercept. Significant fixed effects are shown in bold. Random effect variance for tank is 4.303 ± 2.074.

	Estimate	SE	Z-statistic	P-value
(Intercept)	2.172	0.684	3.174	**0.002**
Hot Treatment	-0.187	0.208	-0.901	0.368
Midday Trial	-0.426	0.148	-2.879	**0.004**
Hot Treatment * Midday Trial	0.947	0.233	4.056	**4.99E-05**

Table 5. Summary of a generalized linear mixed effects model (GLMM) examining the effects of treatment (control, 29 °C and hot, 32 °C), and time of day (dawn or midday) on the approach behaviour of lionfish (*Pterois spp.*) towards prey fish (*Scarus iseri and S. taeniopterus*) in a tank. The model used a negative binomial distribution and has tank as a random intercept. Significant fixed effects are shown in bold. Random effect variance for tank is 0.1874 ± 0.4329.

	Estimate	SE	Z-statistic	P-value
(Intercept)	1.190	0.392	3.031	**0.002**
Hot Treatment	0.194	0.508	0.332	0.703
Midday Trial	0.233	0.435	0.535	0.592
Hot Treatment * Midday Trial	0.190	0.597	0.318	0.751

Table 6. Summary of a generalized linear mixed effects model (GLMM) examining the effects of treatment (control, 29 °C and hot, 32 °C), and time of day (dawn or midday) on the behaviours of striped (*Scarus iseri*) and princess parrotfish (*S. taeniopterus*). Behaviours include resting, aggression, feeding, hovering, sheltering, and swimming. Resting behaviour, control treatment, and dawn trial were used as the baseline conditions. The model used a negative binomial distribution and included an offset for number of fish in the tank and tank as a random intercept. Significant fixed effects are shown in bold. Random effect variance for tank is 4.816e-10 ± 2.195e-05.

Behaviours	Effect	Estimate	SE	z-statistic	p-value
Resting (Baseline)	(Intercept)	1.792	0.179	9.985	**1.77E-23**
	Hot Treatment	-0.499	0.269	-1.854	0.064
	Midday Trial	-0.663	0.257	-2.578	**0.009**
	Hot Treatment * Midday Trial	0.586	0.378	1.551	0.121
Aggression	Aggressive Behaviour	-2.197	0.431	-5.102	**3.37E-07**
	Hot Treatment	0.356	0.569	0.626	0.531
	Midday Trial	1.199	0.516	2.324	**0.020**
	Hot Treatment * Midday Trial	-0.040	0.703	-0.057	0.955
Feeding	Feeding Behaviour	-1.312	0.274	-4.803	**1.56E-06**
	Hot Treatment	1.147	0.394	2.914	**0.004**
	Midday Trial	1.037	0.379	2.738	**0.006**
	Hot Treatment * Midday Trial	-0.764	0.541	-1.413	0.158
Hovering	Hovering Behaviour	-0.390	0.253	-1.545	0.122
	Hot Treatment	0.751	0.367	2.046	**0.041**
	Midday Trial	0.515	0.358	1.438	0.150
	Hot Treatment * Midday Trial	-0.634	0.517	-1.226	0.220
Sheltering	Sheltering Behaviour	2.005	0.239	8.392	**4.76E-17**
	Hot Treatment	0.497	0.347	1.433	0.152
	Midday Trial	0.481	0.338	1.423	0.155
	Hot Treatment * Midday Trial	-0.509	0.486	-1.046	0.296
Swimming	Swimming Behaviour	-0.182	0.250	-0.729	0.466
	Hot Treatment	1.022	0.359	2.846	**0.004**
	Midday Trial	1.518	0.348	4.362	**1.29E-05**
	Hot Treatment * Midday Trial	-1.230	0.502	-2.453	**0.014**

Table 7. Summary of a generalized linear mixed effects model (GLMM) examining the effects of treatment (control, 29 °C and hot, 32 °C), and time of day (dawn or midday) on the position (near or far) of parrotfish (*Scarus iseri and S. taeniopterus*) in a tank in relation to lionfish (*Pterois spp.*). The model used a binomial distribution and had tank as a random intercept. Significant fixed effects are shown in bold. Random effect variance for tank is 1.323 ± 1.150.

	Estimate	SE	Z-statistic	P-value
(Intercept)	-1.384	0.474	-2.917	**0.004**
Hot Treatment	0.338	0.671	0.504	0.615
Midday Trial	0.280	0.0791	3.538	**0.0004**
Hot Treatment * Midday Trial	-0.104	0.111	-0.937	0.349

Table 8. Summary of a generalized linear mixed effects model (GLMM) examining the effects of treatment (control, 29 °C and hot, 32 °C), and time of day (dawn or midday) on the different colourations of striped (*Scarus iseri*) and princess parrotfish (*S. taeniopterus*). Colourations include pale and striped. Pale colouration, control treatment, and dawn trial were used as the baseline conditions. The model used a negative binomial distribution and included an offset for number of fish in the tank and tank as a random intercept. Random effect variance for tank is 2.377e-09 ± 4.876e-05.

Colouration	Effect	Estimate	SE	z-statistic	p-value
Pale	(Intercept)	3.461	0.209	16.582	**9.42E-62**
	Hot Treatment	0.078	0.289	0.268	0.788
	Midday Trial	0.109	0.289	0.379	0.705
	Hot Treatment * Midday Trial	-0.186	0.404	-0.461	0.643
Striped	(Intercept)	-1.268	0.327	-3.881	**0.0001**
	Hot Treatment	0.385	0.457	0.841	0.400
	Midday Trial	0.070	0.467	0.149	0.881
	Hot Treatment * Midday Trial	-0.140	0.651	-0.214	0.830

Table 9. Spearman's rank correlations (r_s) between colourations (pale, striped, mottled) and behaviours (swimming, sheltering, resting, hovering, feeding, aggression) of striped (*Scarus iseri*) and princess parrotfish (*S. taeniopterus*). Correlations are based on frequencies summarized by trial across treatments (control, 29 °C and hot, 32 °C) and time of day (dawn or midday). Adjusted p-values account for multiple comparisons using the Holm-Bonferroni method. Statistically significant correlations (adjusted $p < 0.05$) are in bold.

Behaviour	Colouration	Correlation	p-value	Adjusted p-value
Swimming	Pale	0.343	0.018	0.274
	Striped	0.328	0.024	0.315
	Mottled	-0.107	0.473	1
Sheltering	Pale	0.873	1.23E-15	**2.21e-14**
	Striped	-0.322	0.027	0.325
	Mottled	-0.105	0.481	1
Resting	Pale	0.311	0.033	0.365
	Striped	-0.084	0.576	1
	Mottled	0.243	0.099	0.992
Hovering	Pale	0.2189	0.140	1
	Striped	0.479	0.001	**0.011**
	Mottled	-0.121	0.418	1
Feeding	Pale	0.158	0.288	1
	Striped	0.416	0.004	0.058
	Mottled	0.046	0.759	1
Aggression	Pale	0.336	0.021	0.291
	Striped	0.181	0.223	1
	Mottled	-0.203	0.172	1

Table 10. Summary of a linear model (LM) examining the effects of treatment (control, 29 °C and hot, 32 °C), on the absolute growth rate (weight (g) and total length (cm)) of lionfish (*Pterois spp.*) held in captivity for 17 days.

Metric	Effect	Estimate	SE	t-value	p-value
Weight (g)	(Intercept)	-8.962	9.134	-0.981	0.355
	Hot Treatment	-4.176	12.918	-0.323	0.755
Length (cm)	(Intercept)	0.120	0.049	0.449	**0.04**
	Hot Treatment	-1.755E-14	0.069	0.000	1.00

Table 11. Summary of a linear model (LM) examining the effects of treatment (control, 29 °C and hot, 32 °C), on the relative growth rate (weight (g) and total length (cm)) of lionfish (*Pterois spp.*) held in captivity for 17 days.

Metric	Effect	Estimate	SE	t-value	p-value
Weight (g)	(Intercept)	0.057	0.174	0.329	0.750
	Hot Treatment	-0.149	0.246	-0.606	0.561
Length (cm)	(Intercept)	0.006	0.003	1.836	0.104
	Hot Treatment	0.001	0.005	0.276	0.790

Table 12. Summary of a linear model (LM) examining the effects of treatment (control, 29 °C and hot, 32 °C), on the condition factor (*k*) of lionfish (*Pterois spp.*) held in captivity for 17 days.

	Estimate	SE	t-value	P-value
(Intercept)	0.011	0.0007	15.029	**3.8e-07**
Hot Treatment	0.0002	0.001	0.211	0.838

Table 13. Summary of a linear mixed-effects model (LMM) examining the effects of treatment (control, 29 °C and hot, 32 °C), on the absolute growth rate (weight (g)) of striped (*Scarus iseri*) and princess parrotfish (*S. taeniopterus*) held in captivity for 17 days. Tank was included as a random intercept.

	Effect	Estimate	SE	df	t-value	p-value
Fixed effects	(Intercept)	-0.1375	0.1946	8.858	-0.707	0.498
	Hot Treatment	0.3300	0.2802	9.424	1.178	0.268
Random effects	Tank	0.1455	0.3814			
	Residual	0.1860	0.4313			

Table 14. Summary of a linear mixed-effects model (LMM) examining the effects of treatment (control, 29 °C and hot, 32 °C), on the relative growth (weight (g)) of striped (*Scarus iseri*) and princess parrotfish (*S. taeniopterus*) held in captivity for 17 days. Tank was included as a random intercept.

	Effect	Estimate	SE	df	t-value	p-value
Fixed effects	(Intercept)	-0.290	0.053	7.317	-0.547	0.601
	Hot Treatment	0.116	0.077	8.095	1.502	0.171
Random effects	Tank	0.006	0.075			
	Residual	0.026	0.161			

Table 15 Summary of a linear mixed-effects model (LMM) examining the effects of treatment (control, 29 °C and hot, 32 °C), on the condition factor (*k*) of striped (*Scarus iseri*) and princess parrotfish (*S. taeniopterus*) held in captivity for 17 days. Tank was included as a random intercept.

	Effect	Estimate	SE	df	t-value	p-value
Fixed effects	(Intercept)	0.014	0.001	8.141	23.008	**1.07e-08**
	Hot Treatment	0.002	0.001	9.096	1.777	0.1090
Random effects	Tank	3.486e-07	0.001			
	Residual	4.370e-06	0.002			

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Supplementary materials

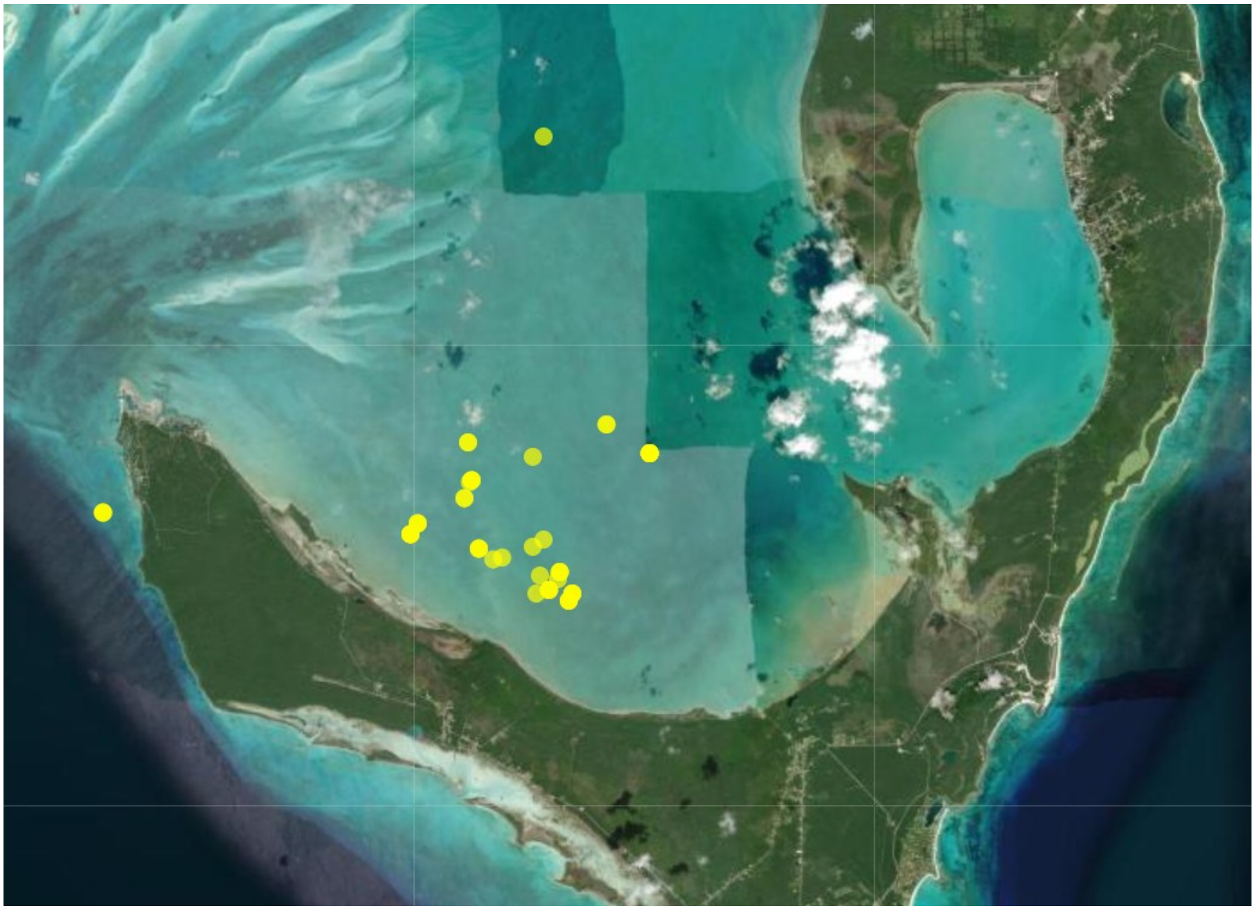

Figure S1. Map of lionfish and parrotfish capture sites off Cape Eleuthera, Eleuthera Island, The Bahamas. Yellow points represent the sites of successful fish capture.

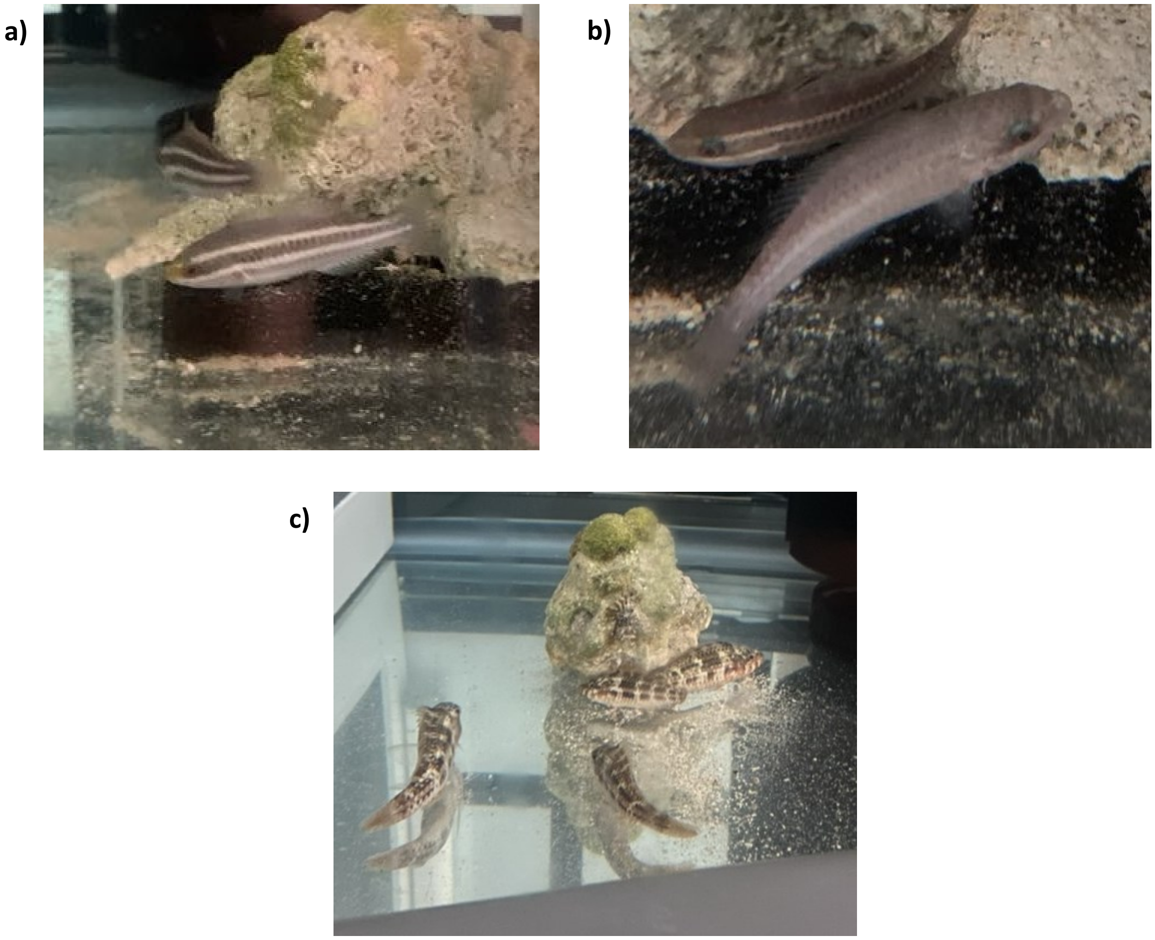

Figure S2. Three colourations of princess (*Scarus taeniopterus*) and striped (*S. iseri*) parrotfish. Figure S2*a* shows the striped colouration (black with two white stripes, sometimes with a yellow splotch on the nose). *b)* Pale colouration (all silvery). *c)* Mottled colouration (brown speckles, camouflage). Juvenile princess and striped parrotfish change colour as a response to predators or other threats (Berchtold & Côté, 2020; Crook, 1999; Wisenden, 2003). They often appear striped while unstressed, pale while moderately stressed, or mottled colouration while extremely stressed.

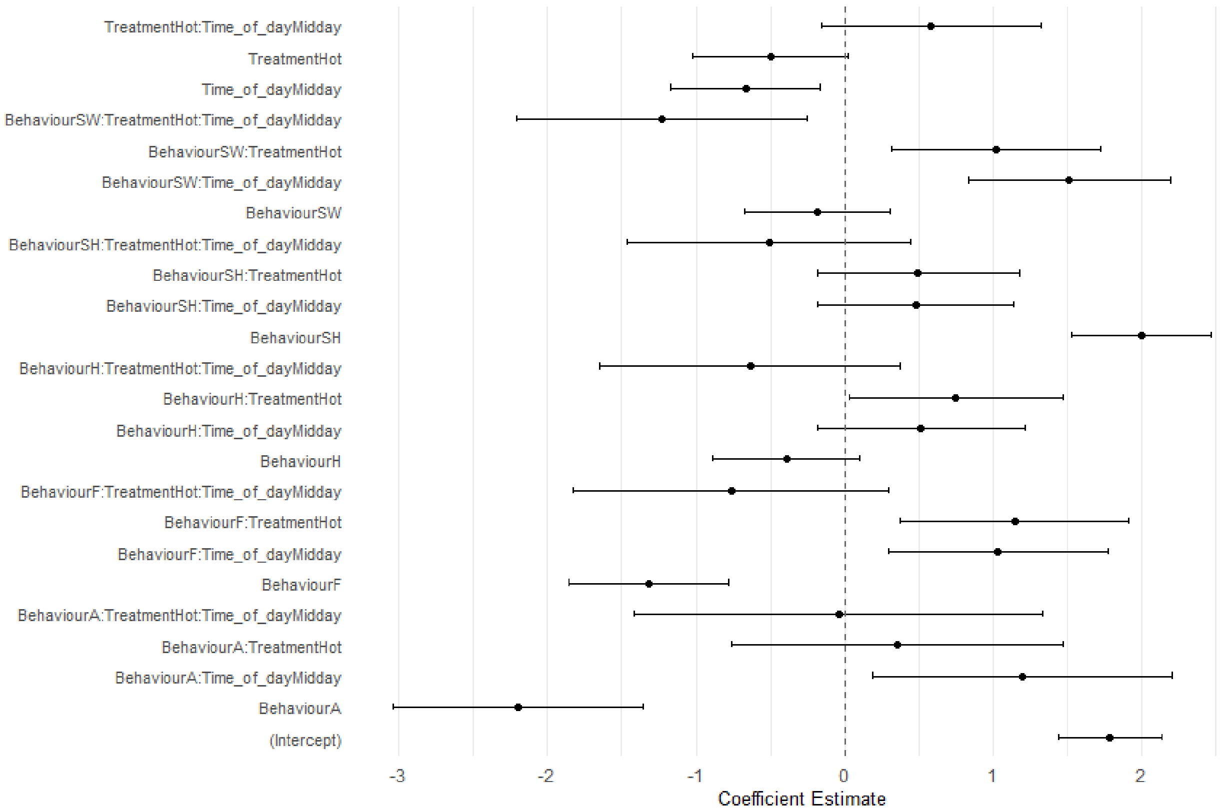

Figure S3. Standardized effect sizes ± 95% confidence intervals for pairwise contrasts from a generalized linear mixed effects model (GLMM) with a negative binomial distribution examining the effects of treatment conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday) on the behaviour of striped (*Scarus iseri*) and princess (*S. taeniopterus*) parrotfish, measured per fish. Behaviours include aggression, feeding, hovering, resting, sheltering, and swimming. Resting behaviour, control treatment, and dawn trials were used as the baseline conditions for the GLMM. Positive values indicate greater expression of the behaviour per fish in the first condition listed in each contrast. Significant effects are indicated by non-overlapping confidence intervals with zero.

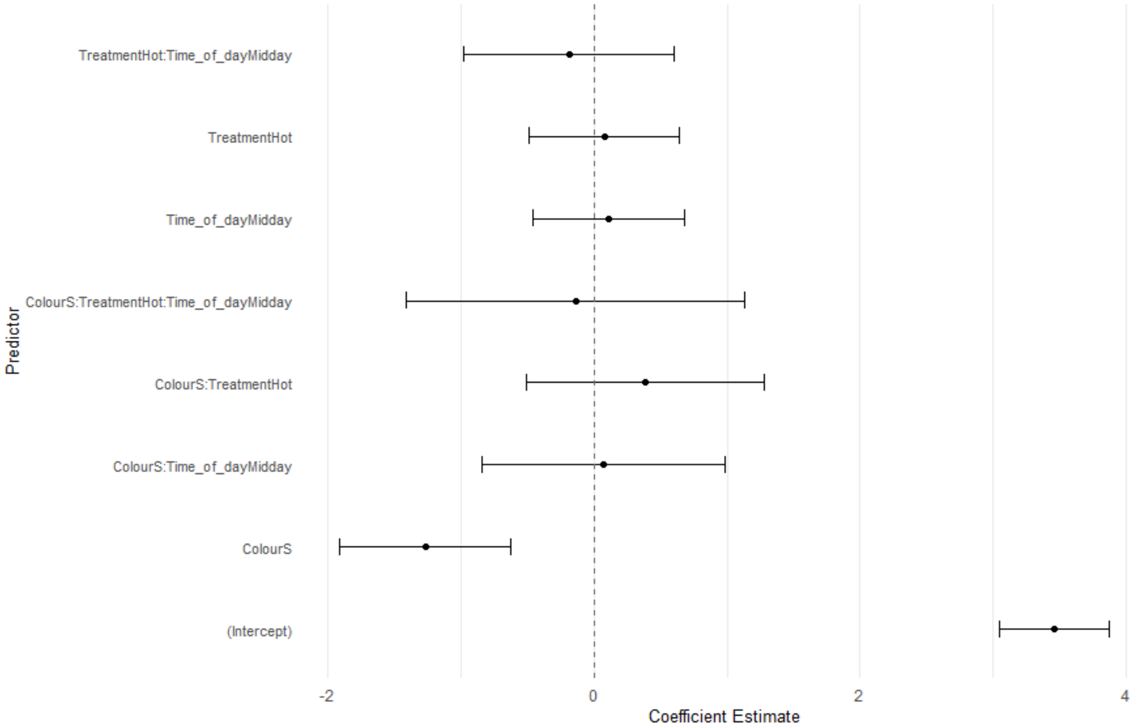

Figure S4. Standardized effect sizes ± 95% confidence intervals for pairwise contrasts from a generalized linear mixed effects model (GLMM) with a negative binomial distribution examining the effects of treatment conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday) on the colouration in striped (*Scarus iseri*) and princess (*S. taeniopterus*) parrotfish, measured per fish. Colourations include pale and striped. Pale colouration, control treatment, and dawn trials were used as the baseline conditions for the GLMM. Positive values indicate greater expression of the colouration per fish in the first condition listed in each contrast. Significant effects are indicated by non-overlapping confidence intervals with zero.

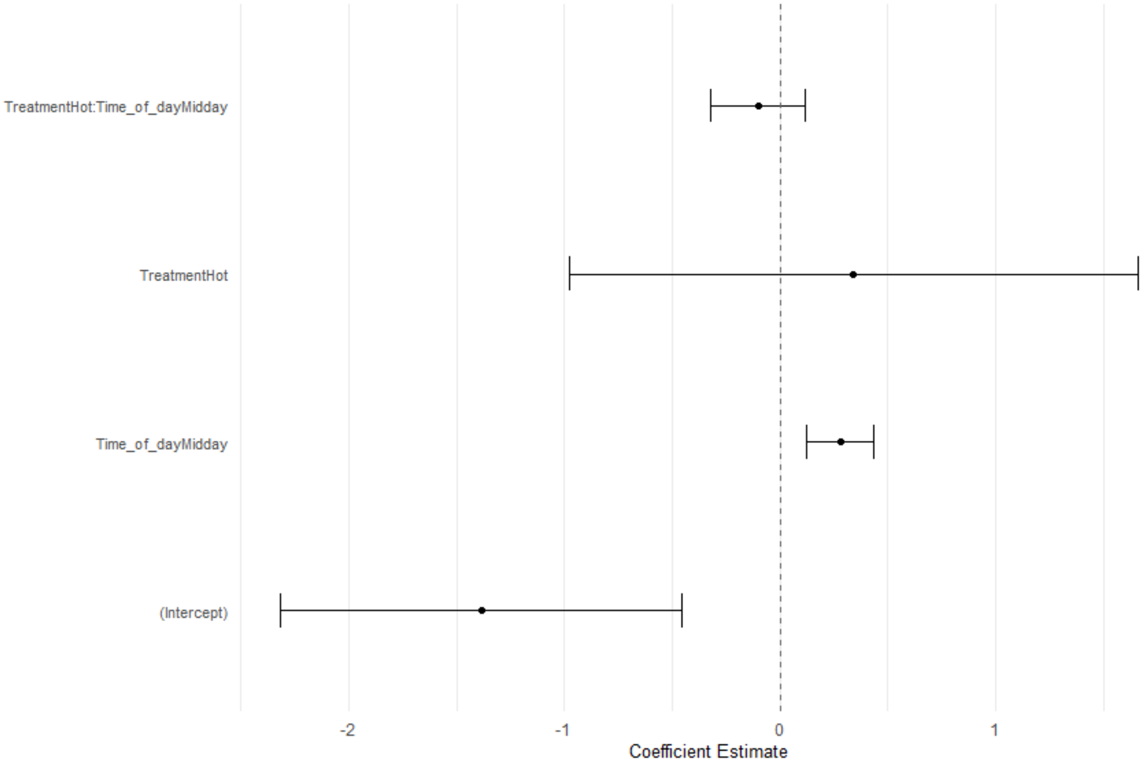

Figure S5. Standardized effect sizes ± 95% confidence intervals for pairwise contrasts from a generalized linear mixed effects model (GLMM) with a binomial distribution examining the effects of treatment conditions (control, 29 °C versus hot, 32 °C) and time of day (dawn versus midday) on the position of striped (*Scarus iseri*) and princess (*S. taeniopterus*) parrotfish in relation to lionfish (*Pterois spp.*).

Table S1. Start and end weights (g) and total lengths (cm) of lionfish in the study. Lionfish were weighed and measured at the start of the experiment and after the experiment finished.

Tank	Treatment	Start weight (g)	Start length (cm)	End weight (g)	End length (cm)
1	Hot	123.38	21.2	NA	NA
1b	Control	229.75	25.3	215.89	25.5
2	Hot	206.67	26.0	191.5	26.0
3	Control	103.60	17.0	59.06	17.2
4	Control	172.40	26.5	NA	NA
4b	Hot	231.31	24.8	201.55	24.9
5	Hot	17.99	12.6	17.74	12.9
6	Control	21.10	12.7	18.08	12.8
7	Hot	88.35	18.7	75.71	18.9
8	Hot	78.66	18.5	70.79	18.5
9	Control	165.98	23.6	152.59	23.7
10	Control	29.99	17.6	59.99	17.6

Table S2. Mean start and end weights (g) and total lengths (cm) ± standard error (SE) for striped (*Scarus iseri*) and princess parrotfish (*S. taeniopterus*) used in this project. Parrotfishes were weighed and measured at the start of the experiment and after the experiment finished. Control tanks were set to 29 °C, while hot tanks were set to 32 °C.

Tank	Treatment	Mean start weight (g) ± SE	Mean end weight (g) ± SE	Mean start length (cm) ± SE	Mean end length (cm) ± SE
1	Hot	4.76 ± 0.80	3.81 ± 0.88	6.5 ± 0.4	6.5 ± 0.5
1b	Control	4.13 ± 1.24	4.20 ± 1.23	6.5 ± 0.8	6.5 ± 0.7
2	Hot	3.03 ± 0.74	2.76 ± 0.45	5.3 ± 0.4	5.4 ± 0.4
3	Control	6.32 ± 0.74	6.19 ± 1.81	7.4 ± 0.8	7.4 ± 0.7
4	Control	3.18 ± 0.84	2.75 ± 0.65	5.8 ± 0.5	6.0 ± 0.5
4b	Hot	4.38 ± 1.10	4.45 ± 0.82	6.6 ± 0.6	6.7 ± 0.6
5	Hot	1.82 ± 0.19	1.73 ± 0.61	4.9 ± 0.3	5.0 ± 0.3
6	Control	3.43 ± 1.01	3.24 ± 1.03	5.9 ± 0.7	6.0 ± 0.6
7	Hot	2.41 ± 0.62	2.60 ± 0.67	5.3 ± 0.6	5.4 ± 0.6
8	Hot	4.09 ± 0.91	5.17 ± 0.16	6.4 ± 0.4	6.6 ± 0.5
9	Control	5.77 ± 1.08	6.45 ± 1.00	7.2 ± 0.5	7.3 ± 0.5
10	Control	3.57 ± 0.90	3.74 ± 1.08	6.1 ± 0.6	6.1 ± 0.6

Table S3. Predicted probabilities from a multinomial generalized additive model (GAM), with estimates, standard errors (SE), z-statistics, p-values, and 95% confidence intervals (conf. low, conf. high). Random effects for tank were excluded. Each row corresponds to a specific combination of the observed behaviours (resting, hovering, swimming, and hunting), treatment (control, 29 °C and hot, 32 °C), and time of day (dawn or midday). Significant p-values are in bold and represent the probability that a given behaviour under a specific combination of treatment and time of day is statistically different from zero.

Behaviour	Treatment	Time of day	Estimate	SE	Z-statistic	p-value	Conf. Low	Conf. High
Resting	Control	Dawn	0.132	0.070	1.885	0.059	-0.005	0.269
		Midday	0.142	0.070	2.047	**0.041**	0.006	0.279
	Hot	Dawn	0.123	0.071	1.738	0.082	-0.0157	0.262
		Midday	0.022	0.016	1.367	0.172	-0.009	0.053
Hovering	Control	Dawn	0.151	0.125	1.208	0.227	-0.094	0.395
		Midday	0.184	0.143	1.291	0.197	-0.096	0.464
	Hot	Dawn	0.152	0.129	1.178	0.239	-0.101	0.404
		Midday	0.172	0.147	1.171	0.242	-0.116	0.461
Swimming	Control	Dawn	0.149	0.117	1.273	0.203	-0.081	0.379
		Midday	0.174	0.129	1.351	0.177	-0.077	0.427
	Hot	Dawn	0.102	0.086	1.191	0.234	-0.066	0.270
		Midday	0.156	0.129	1.211	0.226	-0.096	0.408
Hunting	Control	Dawn	0.569	0.225	2.524	**0.012**	0.127	1.010
		Midday	0.499	0.231	2.163	**0.031**	0.047	0.951
	Hot	Dawn	0.623	0.216	2.887	**0.004**	0.200	1.046
		Midday	0.650	0.222	2.930	**0.003**	0.215	1.086

Table S4. Confusion matrix showing the proportion of predicted versus observed lionfish behaviours (resting, hovering, swimming, and hunting) based on a multinomial generalized additive model (GAM). Values represent the percentage of predictions (rows) that matched each observed behaviour (columns). The bold diagonal values indicate correct classifications, with an overall classification accuracy of 66.2%.

	Actual			
Predicted	Resting	Hovering	Swimming	Hunting
Resting	**0.69**	0.12	0.06	0.13
Hovering	0.00	**0.46**	0.10	0.43
Swimming	0.04	0.12	**0.51**	0.32
Hunting	0.05	0.15	0.10	**0.70**