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Temperature influences habitat preference of coral reef fishes: Will generalists become more specialised in a warming ocean?

Running head: Temperature influences habitat preference

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Primary Research Article

Abstract

Climate change is expected to pose a significant risk to species that exhibit strong behavioural preferences for specific habitat types, with generalist species assumed to be less vulnerable. In this study, we conducted habitat choice experiments to determine how water temperature influences habitat preference for three common species of coral reef damselfish (Pomacentridae) that differ in their levels of habitat specialisation. The lemon damselfish *Pomacentrus moluccensis*, a habitat specialist, consistently selected complex coral habitat across all temperature treatments (selected based on local average seasonal temperatures naturally experienced in situ: ambient winter 22˚C; ambient summer 28°C; and elevated 31˚C). Unexpectedly, the neon damselfish *Pomacentrus coelestis* and scissortail sergeant *Abudefduf sexfasciatus*, both of which have more generalist habitat associations, developed strong habitat preferences (for complex coral and boulder habitat, respectively) at the elevated temperature treatment (31˚C) compared to no single preferred habitat at 22°C or 28°C. The observed shifts in habitat preference with temperature suggest that we may be currently underestimating the vulnerability of some habitat generalists to climate change and highlight that the ongoing loss of complex live coral through coral bleaching could further exacerbate resource overlap and species competition in ways not currently considered in climate change models.

Introduction

When environmental conditions remain relatively stable, species with specialised ecological niches are often more effective at competing with generalists for given resources, such as food or habitat (Schoener, 1971; Sorensen, Turnbull, & Dearing, 2004). However, as environmental conditions change, the flexible nature of generalist species may be advantageous, particularly when the resources that specialists rely on are lost or degraded (Biesmeijer et al., 2006; Jones, McCormick, Srinivasan, & Eagle, 2004; Julliard, Jiguet, & Couvet, 2004; McKinney, 1997). Loss of or reduction in availability of preferred resources for specialist species can lead to declines in performance (e.g. locomotion, growth and reproductive output) and consequently mortality if they cannot exhibit flexibility in resource use (reviewed in Clavel, Julliard, & Devictor, 2011). Alternatively, if species exhibit flexibility through more generalist resource use or switch to an alternative resource they can face increased competition with other species for less preferred resources, especially when resources diminish (Clavel, Julliard, & Devictor, 2011). Such competitive interactions are likely to involve costs and benefits to performance and survival (Munday, 2001). However, a trade-off between competitive ability and fitness associated with using alternative habitats may provide a mechanism of coexistence for competing species (Rosenzweig & Abramsky, 1997). Patterns of habitat use consistent with this trade-off have been observed among many species and ecosystems (Colwell & Fuentes, 1975; Martin & Martin, 2001; Munday, 2001; Schoener, 1974).

It has been proposed that specialist species could be used as ecological indicators for impacts of climate change at the community level (Clavel, Julliard, & Devictor, 2011; Devictor & Robert, 2009), just as they have in the monitoring of sustainable development (Gregory et al., 2005). Thus it is of major concern that declines in population numbers of specialist species

have been observed over the last decade, from a broad range of taxa, including plants (Rooney, Wiegmann, Rogers, & Waller, 2004), mammals (Fisher, Blomberg, & Owens, 2003), birds (Julliard, Jiguet, & Couvet, 2004), insects (Stefanescu, Carnicer, & Peñuelas, 2011) and coral reef fishes (Munday, 2004; Pratchett et al., 2008). Predicting the "winners" and "losers" within assemblages is crucial in making accurate forecasts about changes in biodiversity and ecosystem functioning that may occur with continued climate change (Ehrlén & Morris, 2015; Pearman, Guisan, Broennimann, & Randin, 2008). However for this to be possible, increased knowledge of species' ecological requirements (e.g. habitat) and the impacts of environmental change are required, particularly in aquatic ecosystems (Freitas, Olsen, Knutsen, Albretsen, & Moland, 2015).

The first response of individuals to altered environmental conditions is often a change in their behaviour (Tuomainen & Candolin, 2011). Behavioural responses may provide a means to rapidly react to environmental change, allowing improvement or maintenance of individual performance and ultimately population viability (Pigliucci, 2001; Price, Qvarnstrom, & Irwin, 2003). For instance, some species have adjusted the timing of breeding or migration in response to environmental warming (Charmantier et al., 2008; Gordo & Sanz, 2005; Kuczynski, Chevalier, Laffaille, Legrand, & Grenouillet, 2017; Merila & Hendry, 2014). However, not all behavioural responses to climate change will be adaptive, especially as environmental conditions shift beyond what has been experienced during the species' evolutionary history (Gates & Gysel, 1978; Robertson & Chalfoun, 2016; Robertson, Rehage, & Sih, 2013; Schlaepfer, Runge, & Sherman, 2002). For example, with increasing environmental temperature some lizard species have been observed to spend more time sheltering at the expense of other fitness related activities including foraging and reproduction, significantly impacting species persistence (Sinervo et al., 2010). Thus, it is

expected that behaviour will play an important role in how species respond to human-induced rapid environmental change (Tuomainen & Candolin, 2011). At present greater knowledge about the effects of temperature on species behaviour is required to gain insight into how species will be impacted by ongoing climate change.

Behavioural responses of individuals to environmental conditions are driven in part by their underlying physiology. Due to the lack of internal thermal regulation in ectotherms, changes in the ambient thermal conditions result in metabolic and cellular physiological impacts (Fry, 1967; Pörtner, 2002). Moreover, tropical ectotherms are expected to be disproportionally effected by climatic warming as they have evolved in relatively stable thermal environments resulting in narrow thermal performance windows as well as tending to live closer to their thermal maxima (Deutsch et al., 2008; Donelson, Munday, McCormick, Pankhurst, & Pankhurst, 2010; Tewksbury, Huey, & Deutsch, 2008). The physiological performance of tropical ectotherms can be significantly reduced when temperatures approach the edges of their optimal thermal ranges (Pörtner, 2001; Rummer et al., 2014) and species may make behavioural adjustments if they cannot compensate physiologically (Angilletta, Niewiarowski, & Navas, 2002), or individuals may utilise behaviour as a means of maintaining optimal internal temperature (Habary, Johansen, Nay, Steffensen, & Rummer, 2017; Nay, Johansen, Habary, Steffensen, & Rummer, 2015). When temperatures reach the upper or lower thermal limits in tropical fishes this has been shown to affect behavioural traits including levels of aggression (Warren, Donelson, McCormick, Ferrari, & Munday, 2016), boldness (Biro, Beckmann, & Stamps, 2010) and foraging rates (Eme & Bennett, 2008; Nowicki, Miller, & Munday, 2012). Variation in the underlying physiology and thermal sensitivity of animals occupying different ecological niches is therefore likely to be a

critical factor in the behavioural responses of specialists and generalists to climate warming (Martin, Cunningham, & Hockey, 2015).

Climate change also creates pressure on ectothermic species via indirect effects due to reduction or loss of resources. An ecosystem where this is especially evident is coral reefs with recent increases in the incidence and severity of coral bleaching events (Hughes et al., 2017) and the severity of tropical storms (Knutson et al., 2010; Knutson, Sirutis, Garner, Vecchi, & Held, 2008) leading to global declines in coral cover, reductions in habitat complexity, changes in benthic composition and habitat fragmentation (Bonin, 2011; Hoegh-Guldberg, 1999; Nyström, Folke, & Moberg, 2000; Webster, Holland, Curry, & Chang, 2005). While studies have shown the negative impacts of habitat degradation on coral reef fishes (Kerry & Bellwood, 2012; Munday, 2004; Pratchett, Coker, Jones, & Munday, 2012; Pratchett, Hoey, Wilson, Messmer, & Graham, 2011), little research has explored the effects of increasing temperature directly on habitat preference. As ocean temperatures continue to rise and habitats degrade, we can expect to see increasing pressure on species that rely on a particular habitat for survival (e.g. coral habitat specialisation) while those that use a range of habitats (e.g. habitat generalists) may be less impacted (Munday, 2004; Pratchett, 2005). Thus, determining how environmental temperature may influence species' habitat associations will aid our ability to predict which coral reef fishes are likely to be most impacted by future warming and ongoing habitat degradation.

We aimed to investigate the effect of water temperature on habitat preferences of species of coral reef fishes, which differed in habitat specialisation. To do this, we conducted choice experiments to quantify habitat preferences of three model species from the family Pomacentridae (damselfishes). Specifically, we addressed the following questions: (1) do

habitat preferences of coral reef fishes vary among current-day seasonal, and elevated environmental temperatures? (2) how does the response of habitat preference to water temperature differ between habitat specialists compared to generalists?

Materials and Methods

Study species

This study focused on three species of coral-reef damselfish (Pomacentridae): the lemon damselfish, *Pomacentrus moluccensis*, the neon damselfish, *Pomacentrus coelestis* and the scissortail sergeant, *Abudefduf sexfasciatus*. These species were selected because they could be classified as known habitat generalists or specialists, and could be found in abundance at the study location. *Pomacentrus moluccensis* is a habitat specialist, found in small aggregations on live coral, where it primarily occupies branching growth forms, and occasionally in the water column feeding on plankton and algae (Allen, 1991; Coker, Wilson, & Pratchett, 2014; Pratchett, Coker, Jones et al., 2012). *Pomacentrus coelestis* is a moderate habitat generalist, found on a range of habitats from coral rich to rocky and rubble areas, and is an omnivorous species (Bell & Galzin, 1984; Lecchini et al., 2012; Ohman, Munday, Jones, & Caley, 1998; Randall, Allen, & Steene, 1997; Syms, 1998). *Abudefduf sexfasciatus* is also a habitat generalist, associating with a range of habitats from coral reefs to rocky shorelines where they aggregate to feed on plankton and algae (Allen, 1991).

Microhabitat choice experiments

This study was undertaken at One Tree Island, southern Great Barrier Reef, Australia (23°30′30″S, 152°05′30″E). Juvenile *P. moluccensis* (20-25 mm standard length; SL), *P. coelestis* (20-25 mm SL) and *A. sexfasciatus* (25-30 mm SL) were collected from reefs around One Tree Island daily using clove oil and hand nets. It is expected that these fish were

around a few weeks to a month post-settlement (Kingsford, Smith, & Flood, 2011; McCormick & Weaver, 2012; Pearce & Hutchins, 2009). Fish were transported to the laboratory within 1 hr of capture.

To determine the effects of ocean temperatures on habitat preference, individuals were randomly allocated to one of three temperature treatments: ambient winter (22˚C: *P. moluccensis*, n = 12, *P. coelestis*, n = 9, *A. sexfasciatus,* n = 10), ambient summer (28˚C: *P. moluccensis*, n = 12, *P. coelestis*, n = 8, *A. sexfasciatus*, n = 10), and elevated, ambient summer + 3˚C (31˚C: *P. moluccensis*, n = 12, *P. coelestis*, n = 8, *A. sexfasciatus*, n = 10). These temperature treatments were chosen based on the average seasonal range of temperatures naturally experienced at this location (Australian Institute of Marine Science. Weather stations: water temperature at One Tree Island, temperature loggers; http://weather.aims.gov.au/#/station/131) and to reflect projected ocean warming of up to 3˚C likely to be experienced by fishes at this location by 2100 (Collins et al., 2013; Hobday & Lough, 2011; Lough, 2007). Each species was housed in 3-4 replicate 30 L tanks per temperature, at a density of 2-4 individuals. All tanks (both temperature treatment and testing tanks) were provided with a constant flow of seawater and aeration along with independent temperature control in each tank (heater 300-watt). Fish were provided with short lengths of PVC piping (approximately 10 cm in length) for shelter and fed live brine shrimp nauplii *Artemia* spp. once daily. Tanks in the 22˚C treatment group were held in a separate laboratory to all other aquaria, so that air-conditioning could also be used to maintain water temperature. Laboratory conditions included minimal noise from the outside environment and evenly-distributed lighting. Fish were habituated from ambient temperature conditions (~ 28˚C during the collection period) to the temperature treatments by ± 0.5˚C per day until the test temperature was reached, which was within the natural daily temperature change experienced

in situ (Australian Institute of Marine Science. Weather stations: water temperature at One Tree Island, temperature loggers; http://weather.aims.gov.au/#/station/131). Fish were maintained at their treatment temperature for 4 to 6 days prior to behavioural testing.

Habitat choice trials (two habitats presented per trial) were carried out to assess the habitat preferences of the three species. An individual fish was introduced to the centre of a rectangular testing arena (64 cm length x 41 cm width x 27 cm height) containing two similar sized (10 cm diameter x 6 cm height) but distinct habitats (Fig. 1). Habitats were positioned at opposite ends of the arena approximately 15 cm away from each side of the tank and 30 cm from the other habitat. Positions of the two habitats were randomised using paired combinations of the following: complex coral (*Pocillopora damicornis*), non-complex coral (*Porites lobata*), coral rubble (small dead fragments of coral skeletons) and boulder (a larger rounded piece of dead coral), within the arena between trials. Coral health was monitored throughout trials, with corals not exhibiting any signs of stress throughout the experiments. To start each trial, fish were placed in a clear PVC holding tube (10 cm in diameter) for 5 min prior to being released into the testing arena by carefully lifting the tube vertically out of the water (Fig. 1; Pratchett, Berumen, Marnane, Eagle, & Pratchett, 2008).

Each individual fish was run through experimentation of every 2 x 2 habitat combination in a random order. Trials were undertaken during daylight hours and lasted 3 hr, which had previously been found to be a good indicator of habitat preference 14 hr post release (Matis unpublished data), and an individual's habitat choice was recorded every 15 min (total of 12 observations per trial). Fish were considered to have selected a habitat when they were no greater than a body length in distance from the habitat, otherwise the fish was considered to have made no selection.

Statistical analyses

Due to the categorical nature of habitat selection, simple hypothesis testing methods that typically assume that data are continuous such as t-tests and rank tests were not appropriate in this context. Data were therefore modelled using the framework of discrete choice experiments (Street & Burgess, 2007; Train, 2009), which are widely used in transportation (Greene & Hensher, 2003), market research (Revelt & Train, 1998), health economics (Norman, Hall, Street, & Viney, 2013), and habitat selection behaviour (Carter, Brown, Etter, & Visser, 2010; McDonald, Manly, Nielson, & Diller, 2006). This statistical approach allows simultaneous analysis of a number of habitat types, automatically taking into account dependence in the selection process. It can model changes in habitat availability by changing the composition of choice sets and can estimate the probability of a particular habitat unit being selected during one choice rather than at least once after multiple choices. The discrete choice analysis was performed in version 3.2.1 of the R programming language (R Core Team, 2015). The mlogit function from the *mlogit* package was used to build the models (Croissant, 2013). Information from each trial, including all habitat combinations, was combined into a model to allow us to estimate the overall habitat preference of each species at each temperature.

To incorporate the species and temperature information into the model, a mixed logit model was used with Benjamini Yekutieli correction for multiple comparisons (Benjamini & Yekutieli, 2001), where the available habitats were defined at the trial level but species and temperature were defined at the level of an individual fish, since temperature and species were constant for a particular fish. Likelihood ratio tests were used to identify the best fitting set of main effects and interaction terms (Hausman & McFadden, 1984). The best fitting model was the model with both the main effects and two factor interaction for species and

temperature (p < 0.001), determined via a backward selection process. In order to summarise the preference of different habitats, or no selection, across species and temperatures, the model was used to calculate the probability that a particular species would choose a particular habitat at a particular temperature. This allowed the effect of temperature on habitat preferences to be determined and establish the significance of these differences using two-proportion z-tests.

Results

Water temperature had a significant effect on habitat choice and differed among the three damselfish species (Fig. 2, Table S1; likelihood ratio test, p < 0.001). The habitat specialist *P. moluccensis* exhibited the most consistency in habitat choice across temperatures, choosing complex coral over all other habitats at all temperatures (Fig. 2a; Table 1a). Although the dominant preference of *P. moluccensis* remained stable across temperatures, there were slight differences in the ranking of subsequent habitat choices. Individuals of this species preferred rubble over remaining habitat choices (boulder, non-complex coral and no selection) at 22°C, but preferred rubble and boulder over non-complex coral and no selection at 28°C and 31°C (Fig. 2a, Table 1a,b).

The habitat generalist, *P. coelestis*, did not exhibit consistent preferences for the same habitat across temperatures (Fig. 2b, Table 1). At 28°C, the only habitat preferences observed were that complex coral was significantly preferred to boulder and all habitats were preferred to making no habitat selection (Table 1a). In contrast, complex coral and boulder were equally preferred at 22°C, while at 31°C a strong preference for complex coral was observed with lower preferences for boulder and rubble (Fig. 2b, Table 1a). Additionally, the proportion of

time no selection was made significantly reduced at 31°C compared to 28°C and 22°C (Fig. 2b, Table 1b).

Preferences of the habitat generalist, *A. sexfasciatus* were similar at 22°C and 28°C, with boulder and complex coral preferred over all other available habitats (Fig. 2c, Table 1a). However, at 31°C a strong preference for boulder emerged over all other available habitats, with a decline in preference for complex coral (Fig. 2c, Table 1a).

Differences observed between species were primarily driven by the consistency in habitat preferences shown by *P. moluccensis* across all temperatures compared to the more variable habitat preferences of *P. coelestis* and *A. sexfasciatus* across temperatures (Fig. 2, Table 1c). Distinctions in habitat preferences between *P. moluccensis* and the other species were greatest at 22°C (Fig. 2, Table 1c) due to the lack of strong preference for one specific habitat by both *P. coelestis* and *A. sexfasciatus* at 22°C. Other differences between species were seen due to *A. sexfasciatus* exhibiting a relatively higher proportion of no selection across all temperatures compared to the other species (Fig. 2, Table 1b).

Discussion

Here we demonstrate how ambient water temperate affects habitat preferences of coral reef fishes. We found the effect of water temperature differed among species, with habitat generalists *P. coelestis* and *A. sexfasciatus* modifying their habitat preferences in response to water temperature, whereas the habitat specialist *P. moluccensis*, retained consistent habitat preference for complex coral across all temperature treatments. At elevated water temperature above the current summer average the moderate generalist *P. coelestis* shifted preference to complex coral. This continued preference by *P. moluccensis*, and increased preference by *P.*

coelestis for complex coral could be a concern as less complex coral will be available in the future due to ongoing habitat degradation of coral reefs globally (Graham, Cinner, Norstrom, & Nystrom, 2014; Pratchett, Hoey, & Wilson, 2014).

The increase in strength of preference shown in this study by the habitat generalists *P. coelestis* and *A. sexfasciatus* for a particular habitat at the extreme warm temperature suggests evidence of behavioural plasticity (Wong & Candolin, 2015). *Pomacentrus coelestis* and *A. sexfasciatus* at ambient summer temperatures (28°C) in the current study exhibited the generalist habitat associations typically observed for these species (Allen, 1991; Bell & Galzin, 1984; Lecchini, Carassou, Frederich et al., 2012; Ohman, Munday, Jones et al., 1998; Randall, Allen, & Steene, 1997; Syms, 1998). Tropical ectotherms may make behavioural adjustments when temperatures approach the edges of their thermal performance range, reducing non-essential activities, including swimming, foraging, growth and energy storage (Donelson, Munday, McCormick et al., 2010; Donelson, Munday, McCormick, & Pitcher, 2012; Johansen, Messmer, Coker, Hoey, & Pratchett, 2014; Johansen et al., 2015; Munday, Kingsford, O'Callaghan, & Donelson, 2008; Pörtner, 2002; Pörtner & Peck, 2010). *Pomacentrus coelestis'* shift to select complex coral might be because it provides the greatest refuge (Almany, 2004; Graham & Nash, 2013; Johansen, Bellwood, & Fulton, 2008). This is complimented by both *P. coelestis* and *A. sexfasciatus* indicating non-complex coral was the least preferred habitat, potentially because it provided the least amount of shelter (Almany, 2004; Graham & Nash, 2013; Johansen, Bellwood, & Fulton, 2008). The strong preference of boulder habitat at the warmest temperature treatment for *A. sexfasciatus* may suggest a trade-off between optimal refuge structure with other areas of the reef that provide sufficient food to live (Allen, 1991), although food was not provided and feeding during the behavioural trials was not recorded in this study. However, environmental change can cause a mismatch

between the quality of a habitat and the cues used by individuals to assess that quality (Schlaepfer, Runge, & Sherman, 2002) and this might mean *A. sexfasciatus* is making a poor choice for boulder habitat that doesn't provide the most shelter. These results generally suggest that as water temperature increases, species previously considered to associate with a range of habitats (i.e. generalists) may become more selective in their habitat associations and further research into the consequences of switching from using a broad to narrow range of habitats requires investigation.

While both generalist species exhibited a shift in preference at the warmest testing temperature, only *P. coelestis* demonstrated stronger habitat preferences at 22°C, specifically a preference for complex coral and boulder. The finding that *A. sexfasciatus* only showed a preference for a particular habitat at the warmest temperature suggests this species habitat preference is robust within the seasonal range of temperatures experienced, and may only experience physiological stress at the elevated temperature of 31°C. The lack of thermal sensitivity at 22°C for *A. sexfasciatus* may not be surprising since the critical thermal minimum for *Abudefduf* spp. is expected to be around 17°C, compared to *P. coelestis* at 19°C (Figueira & Booth, 2010). At both 22°C (ambient winter) and 31°C (elevated), *P. coelestis* may experience physiological stress (Johansen & Jones, 2011; Johansen, Steffensen, & Jones, 2015) and therefore prioritise selecting the habitat that provides the greatest amount of shelter, i.e. complex coral and boulder respectively. Indeed, tropical vagrant fishes may survive better in sheltered habitats at temperate latitudes (Feary et al., 2014). Moreover, sheltering may help mediate competitive interactions (Holbrook & Schmitt, 2002; Munday, 2001) or reduce predation (Beukers & Jones, 1998; Caley & St John, 1996; Coker, Pratchett, & Munday, 2009; Hixon & Beets, 1993). However, additional time spent sheltering can also come at a cost through reduced time foraging (as observed for terrestrial ectotherms; Sinervo,

Mendez-de-la-Cruz, Miles et al., 2010), significantly impacting species persistence. Alternatively, the finding that *P. coelestis* exhibited more selective behaviour at 22°C, in addition to 31°C, might be due to *P. coelestis* not being a pure habitat generalist (Bell & Galzin, 1984; Lecchini, Carassou, Frederich et al., 2012; Ohman, Munday, Jones et al., 1998; Randall, Allen, & Steene, 1997; Syms, 1998), since specialisation and generalisation are not discrete choices but a continuum.

Our results confirm the expectation that a habitat specialist maintains the level of specialisation across changes in environmental parameters and are therefore likely to be particularly vulnerable to degradation or decline of specific habitat types (Coker, Wilson, & Pratchett, 2014; Pratchett, Coker, Jones et al., 2012). The habitat specialist tested in this study (*P. moluccensis*) maintained its habitat preference for complex coral across all temperatures, making them particularly vulnerable to continued degradation and loss of coral cover as a result of ocean warming events (Alvarez-Filip, Dulvy, Gill, Cote, & Watkinson, 2009; Bellwood, Hughes, Folke, & Nystrom, 2004; Gardner, Cote, Gill, Grant, & Watkinson, 2003). For species that rely on live coral, especially across life stages, declining complexity and availability of coral habitat will mean substantial negative impacts to populations (Jones, McCormick, Srinivasan et al., 2004; Munday, 2004). For instance, populations of *P. moluccensis* have declined in response to localised loss of complex branching coral (Pratchett, Coker, Jones et al., 2012). Species that rely on specific habitats for survival may be at an increased risk of their niche disappearing completely (McKinney, 1997). Conversely, other species may escape the effects of environmental change if the habitat they rely on, unlike most coral habitat, is resilient to disturbance (Pratchett, Coker, Jones et al., 2012).

If more habitat generalists shift their preferences with ocean warming towards habitats already preferred by other species, it could lead to increased competition for resources as niches start to show greater overlap. The results of this study suggest that while the habitat generalist *P. coelestis* does not currently occupy the same habitat as the coral habitat specialist *P. moluccensis*, under expected ocean warming they could be competing for similar complex coral resources. Alternatively, species may undergo a competitive release if niche breadth declines when they become more selective (Bolnick et al., 2010), as was the case for *A. sexfasciatus* in the current study, where association with complex coral habitat was significantly reduced at the elevated testing temperature and boulder became the preferred habitat. This suggests that *A. sexfasciatus* may represent a resilient generalist species in the future in terms of habitat preferences. Of course, outcomes of habitat preferences and potential competitive interactions in the future are likely to be complex and require direct testing (Warren, Donelson, McCormick et al., 2016).

In common with all laboratory-based experiments, the results of this study cannot fully replicate all factors involved in habitat selection in the wild. In order to isolate the effect of temperature on habitat preference within a controlled experimental setting, other factors likely to influence behaviour (such as competition, predation, resource availability and priori effects) were necessarily excluded. In addition, the temporal scale of our observations does not reveal any plastic responses to temperature with developmental and cross-generational exposure (Donelson, Munday, & McCormick, 2012; Donelson, Munday, McCormick, & Nilsson, 2011; Sorensen, Munday, & Nilsson, 2014). Longer exposure to elevated temperature could therefore potentially lead to different effects on habitat preferences since developmental exposure length has been found to influence both intra- and interspecific competitive interactions for habitat (Warren, Donelson, McCormick et al., 2016). Although

beyond the scope of the current study, these longer-term temporal dimensions would represent interesting extensions of our results and increase our understanding of how thermal environment can influence habitat preference of specialist and generalist reef fishes.

With future reductions in habitat quality, as global temperatures rise, we can expect to see increasing pressure on species that rely on a particular habitat (such as complex coral) for survival (Alvarez-Filip, Dulvy, Gill et al., 2009; Bellwood, Hughes, Folke et al., 2004; Gardner, Cote, Gill et al., 2003). The shifts in habitat preferences observed in this study suggest that we may also see increased pressure on species that currently occupy a variety of habitat niches (habitat generalists), indicating that climatic warming could affect ecological relationships in subtle and unexpected ways. Furthermore, the impacts of rising temperatures on organisms' realised niches should be considered further to better understand and predict ecosystem functioning as environments continue to change.

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Figures and Tables

Figure 1. Example experimental tank set up prior to the start of a habitat-choice trial (a). Habitat preferences were assessed for juvenile *Pomacentrus moluccensis, Pomacentrus coelestis* and *Abudefduf sexfasciatus* at 22°C, 28°C and 31°C for all possible combinations using paired combinations of the following: (b) complex coral, (c) non-complex coral, (d) rubble and (e) boulder.

Figure 2. Percentage of time (mean ± SE) spent at each of four experimental habitat types, (based on the option of no selection and equal availability of habitat types) for juvenile individuals of the species (a) *Pomacentrus moluccensis* (b) *Pomacentrus coelestis* and (c) *Abudefduf sexfasciatus* observed at 22°C, 28°C and 31°C (photo credit P. Matis).

Table 1. Comparisons of habitat preferences (p-values) of juvenile *Pomacentrus moluccensis, Pomacentrus coelestis* and *Abudefduf sexfasciatus* between (a) habitats (rubble, boulder, complex coral, non-complex coral and no selection) (b) temperatures (22°C, 28°C, 31°C) and (c) species.

(a)

Habitat Comparison	Temperature	Species		
		P. moluccensis	*P. coelestis*	*A. sexfasciatus*
Rubble v Boulder	22°C	*< 0.001*	*< 0.001*	*< 0.001*
	28°C	*>0.999*	*0.602*	*0.004*
	31°C	*0.750*	*>0.999*	*< 0.001*
Rubble v Complex	22°C	*< 0.001*	*< 0.001*	*< 0.001*
	28°C	*< 0.001*	*0.516*	*< 0.001*
	31°C	*< 0.001*	*< 0.001*	*0.208*
Rubble v Non-Complex	22°C	*< 0.001*	*>0.999*	*0.002*
	28°C	*< 0.001*	*>0.999*	*>0.999*
	31°C	*< 0.001*	*< 0.001*	*< 0.001*
Rubble v No selection	22°C	*< 0.001*	*< 0.001*	*>0.999*
	28°C	*< 0.001*	*< 0.001*	*>0.999*
	31°C	*< 0.001*	*< 0.001*	*0.024*
Boulder v Complex	22°C	*< 0.001*	*0.637*	*>0.999*
	28°C	*< 0.001*	*0.006*	*0.334*
	31°C	*< 0.001*	*< 0.001*	*< 0.001*
Boulder v Non-Complex	22°C	*0.587*	*< 0.001*	*0.023*
	28°C	*< 0.001*	*0.964*	*0.035*
	31°C	*< 0.001*	*< 0.001*	*< 0.001*
Boulder v No selection	22°C	*< 0.001*	*< 0.001*	*< 0.001*
	28°C	*< 0.001*	*< 0.001*	*< 0.001*
	31°C	*< 0.001*	*< 0.001*	*< 0.001*
Complex v Non-Complex	22°C	*< 0.001*	*< 0.001*	*0.012*
	28°C	*< 0.001*	*0.290*	*< 0.001*
	31°C	*< 0.001*	*< 0.001*	*0.049*

Complex v No selection	22°C	*< 0.001*	*< 0.001*	*< 0.001*
	28°C	*< 0.001*	*< 0.001*	*< 0.001*
	31°C	*< 0.001*	*< 0.001*	*>0.999*
Non-Complex v No selection	22°C	*0.051*	*< 0.001*	*< 0.001*
	28°C	*0.001*	*< 0.001*	*0.863*
	31°C	*0.124*	*< 0.001*	*0.058*

(b)

Temperature Comparison	Habitat Preference	Species		
		P. moluccensis	*P. coelestis*	*A. sexfasciatus*
22°C v 28°C	Rubble	*>0.999*	*< 0.001*	*0.370*
	Boulder	*< 0.001*	*< 0.001*	*0.855*
	Complex	*0.035*	*0.108*	*>0.999*
	Non-Complex	*>0.999*	*0.003*	*>0.999*
	No selection	*0.392*	*>0.999*	*0.574*
28°C v 31°C	Rubble	*0.060*	*>0.999*	*0.613*
	Boulder	*>0.999*	*0.108*	*< 0.001*
	Complex	*0.067*	*< 0.001*	*< 0.001*
	Non-Complex	*>0.999*	*< 0.001*	*0.001*
	No selection	*0.700*	*< 0.001*	*>0.999*
22°C v 31°C	Rubble	*0.042*	*0.002*	*0.005*
	Boulder	*< 0.001*	*0.546*	*< 0.001*
	Complex	*>0.999*	*0.022*	*< 0.001*
	Non-Complex	*>0.999*	*< 0.001*	*< 0.001*
	No selection	*>0.999*	*< 0.001*	*>0.999*

(c)

Species Comparison	Habitat Preference	Temperature		
		22°C	28°C	31°C
P. moluccensis v A. sexfasciatus	Rubble	*< 0.001*	*0.004*	*>0.999*
	Boulder	*< 0.001*	*>0.999*	*< 0.001*
	Complex	*< 0.001*	*0.021*	*< 0.001*
	Non-Complex	*< 0.001*	*< 0.001*	*>0.999*

		< 0.001	< 0.001	< 0.001
	No selection	< 0.001	< 0.001	< 0.001
P. moluccensis v P. coelestis	Rubble	< 0.001	>0.999	0.248
	Boulder	< 0.001	0.485	0.593
	Complex	< 0.001	< 0.001	0.593
	Non-Complex	0.031	< 0.001	0.516
	No selection	0.248	0.001	< 0.001
A. sexfasciatus v P. coelestis	Rubble	0.593	0.010	>0.999
	Boulder	>0.999	0.323	< 0.001
	Complex	0.637	>0.999	< 0.001
	Non-Complex	0.142	0.154	0.516
	No selection	0.021	< 0.001	< 0.001

(a)

(b) Complex coral   (c) Non-complex coral   (d) Rubble   (e) Boulder

(a) *Pomacentrus moluccensis*

(b) *Pomacentrus coelestis*

(c) *Abudefduf sexfasciatus*

Legend:
- rubble
- boulder
- complex coral
- non-complex coral
- no selection

Y-axis: Proportion of Time (%)

X-axis: Temperature — 22°C, 28°C, 31°C