BRIEF COMMUNICATION

Diurnal foraging of a wild coral-reef fish *Parapercis australis* in relation to late-summer temperatures

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In situ observations of diurnal foraging behaviour of a common site-attached shallow reef mesopredator *Parapercis australis* during late summer, revealed that although diet composition was unaffected by seawater temperature (range 28.3–32.4° C), feeding strikes and distance moved increased with temperature up to 30.5° C, beyond which they sharply declined, indicative of currently living beyond their thermal optimum. Diel feeding strikes and distance moved were however, tightly linked to ambient temperature as it related to the population's apparent thermal optimum, peaking at times when it was approached (1230 and 1700 hours) and declining up to four fold at times deviating from this. These findings suggest that although this population may be currently living beyond its thermal optimum, it copes by down regulating energetically costly foraging movement and consumption and under future oceanic temperatures, these behavioural modifications are probably insufficient to avoid deleterious effects on population viability without the aid of long-term acclimation or adaptation.

KEYWORDS

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Optimal foraging theory predicts that under certain environmental constraints and opportunities, individuals make adaptive foraging decisions (*e.g.* choice of diet, activity or food consumption level) to optimize their fitness (MacArthur & Pianka, 1966; Zemke-White *et al.*, 2002). Consequently, animals display predictable diel cycles of movement, foraging and predation risk, which are influenced by environmental interactions (*e.g.* seasons and global climate change, see Avgar *et al.*, 2013) and the processes dependent upon them (*i.e.* prey distribution, see Metcalfe *et al.*, 1999).

For water-breathing ectotherms, such as fishes, aerobic behaviour is believed to be governed by an oxygen-limited thermal tolerance (Pörtner & Farrell, 2008). Specifically, an optimal ambient temperature range is believed to permit optimal performance of the cardiovascular system and hence, aerobically-supported processes (Angilletta *et al.*, 2002; Pörtner *et al.*, 2005; Farrell, 2009). If temperatures exceed this thermal optimum, the capacity to direct energy toward tasks beyond that required for basic maintenance (*i.e.* aerobic scope) declines, most abruptly for highly aerobic tasks essential for fitness (*e.g.* growth, digestion, feeding and motor activity) (Pörtner *et al.*, 2005; Pörtner & Farrell, 2008). Hence, a temperature-induced reduction of aerobic scope may have far-reaching consequences on populations, species and community structure (Pörtner *et al.*, 2005; Pörtner & Peck, 2010). Because the thermal optimum range for aerobic scope of coral-reef fishes appears to be relatively narrow and approached during current late-summer periods, it is expected to be exceeded by late-century (Rummer *et al.*, 2014), when up to a 3° C increase in ambient tropical sea surface temperature (SST) is projected due to climate change (Poloczanska *et al.*, 2007; IPCC, 2014).

Conceivably, populations might behaviourally respond to temperatures beyond their thermal optimum *via* two principal pathways, depending upon their mobility. Mobile species may thermoregulate by re-locating to a more favourable thermal niche (small-scale: cooler refugia within the local environment; large-scale: range-shift; Parmesan 2006; Feary *et al.* 2013; Nay *et al.* 2015). By contrast, site-attached species may be less capable of re-locating and hence, more inclined to cope by minimizing aerobically-costly behaviours (*i.e.* exhibit behavioural plasticity; Johansen *et al.*, 2014; Abram *et al.*, 2017) during ecological processes. This idea is supported by preliminary field (Scott *et al.* 2017) and laboratory (Nowicki *et al.*, 2012) findings. In laboratory, for example, the anemonefish *Amphiprion melanopus* Bleeker 1852 decreases food consumption by 22% when reared at 3° C above current day SST (31.5° C), compared with being reared at only 1.5° C above current day SST (30° C) (Nowicki *et al.*, 2012). Similarly, a 3° C increase in water temperature significantly reduces energy efficiency and maximum swimming speeds of site-attached reef damselfishes (Pomacentridae) (Johansen and Jones, 2011). However, whether and how coral-reef fishes may behaviourally adapt to temperatures exceeding their thermal optimum remains uncertain, partially because few relevant studies have been conducted on wild populations in their natural habitat (Scott *et al.*, 2017).

We investigated *in situ* the diurnal feeding ecology of a wild population of a site-attached coral-reef fish, the sandperch *Parapercis australis* Randall 2003, family Pinguipedidae, in relation to fluctuating northern Great Barrier Reef (GBR) current-day late-summer ambient SST. *Parapercis australis*, is a small (maximum 23cm total length; L_T) elongate fish, widely distributed throughout the Indo-Pacific Oceans (Stroud, 1982;

Randall *et al.*, 1997; Sano, 1993). Populations inhabiting shallow-reef areas probably experience relatively wide temperature fluctuations over short (*e.g.* within-day) time-frames (McCabe *et al.* 2010; Schoepf *et al.* 2015). Within the Pinguipedidae family, diet composition has been previously examined (Stroud, 1982), but modification of foraging ecology in response to temperature remains unexplored. This study aims to broadly characterize diet composition (through *in-situ* feeding observations and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ stable-isotope analysis), movement rate and feeding strike rate and to determine whether and how these change in relation to ambient SST fluctuation during late-summer.

The study was conducted at Lizard Island (14° 40' S; 145° 27' E), located on the northern GBR, Australia, during the late-summer (February–March 2012). A sub-population (≥ 50 individuals) inhabiting a patchy rubble, sand and seagrass area, located approximately 50 m offshore on the western side of the island was chosen for the study. This species represents a shallow-water, site-attached reef species on reefs currently experiencing increased SST due to climate change. To facilitate recording the distance moved by fishes, a large grid of nylon string was overlaid on top of the study site to produce multiple 5 m² quadrats (total area: 35 × 25 m); this method provides a best-estimate for distance moved based on individual size and movement range. Water temperature was recorded within the study site by two Vemco-II Minilog temperature loggers (www.vemco.com; accuracy 0.1° C) secured to metal stakes *c.* 13cm above the substratum.

Behavioural snorkel-based observations were conducted within the gridded study site between 0800 and 1800 hours; for consistency, all observations were performed by the same observer. To avoid repeatedly recording the same individual within a sampling

period, 15 individuals (adults and sub-adults, mean L_T 76 mm $\pm$ 3 S.E.) within the sampling area were tagged with a unique elastomer tag combination (Northwest Marine Technologies Inc.; www.nmt.us) at least 24 h prior to observations. Tagged individuals were then encountered, approached from a distance of > 1 m and given 3 min to adjust to observer presence. Individuals were only observed if they displayed a lack of responsiveness to the observer. Time of day was recorded and individuals were then observed for 15 min. Distance moved (activity rate) was recorded by drawing the fish movement path on a scaled-down grid printed on underwater paper, measuring the total distance of the movement path and scaling the mapped total distance to the actual value (nearest m) using the appropriate conversion ratio.

Total feeding strikes were recorded and grouped according to three broad categories: invertebrates (crustaceans and worms), turf algae and small fish. Predation tactics on visually-detectable invertebrates were distinct and characterized by a stalking approach, followed by a swift ram capture of prey on sand, rubble, or seagrass substratum. Strikes on visually-detectable turf algae were also distinct and characterized by a relatively slow approach towards algae and ripping it off the substratum with the side of the mouth. All predation events on small fish were visible and the tactic was characterized by chase (or rarely, ambush) approach, followed by ram feeding capture. While behavioural observations are commonly used for diet characterization, they are susceptible to inaccuracies, due to their limited ability to account for prey items that are struck, but not consumed or assimilated (Fry, 2006). Therefore, diet inferred by behavioural observations was verified using stable-isotope analysis (Fry, 2006). Immediately after the behavioural study, fish ($n = 12$) and putative prey specimens were

collected within the study area using hand-nets and clove oil. All samples were processed at West Australian Biogeochemistry Centre (WABC) and analysed for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ using a continuous-flow system, consisting of a Delta V Plus mass spectrometer (Thermo Scientific; www.thermofisher.com; Supporting Information Material and Methods). These stable isotopes are commonly used to determine food web variables and diet signatures (Hobson, 1999; Sotiropoulos *et al.*, 2004; Fry, 2006), specifically in fish diet studies (McCutchan *et al.*, 2003; Binning *et al.*, 2009).

To explore the relationship between mean distance moved and mean feeding strikes (dependent variables) and time of day (parametric) and ambient water temperature (non-parametric) (predictor variables), a generalized additive model (GAM) was employed in R (www.r-project.org) with family set as Gaussian and smoothing term *s* applied to temperature (R package mgcv; Hastie & Tibshirani, 1987). Both predictor variables were transformed ($\ln n + 1$) prior to analysis to address assumptions of normality and constant variance. To uncouple the influence of temperature and time of day, separate models were produced for each behavioural and each environmental variable. Akaike information criterion (AIC) was employed to compare models and identify if temperature or time of day was a better estimate of feeding and distance moved.

In *P. australis*, distance moved (mean $0.5 \text{ m min}^{-1} \pm 0.03 \text{ S.E.}$) was highly correlated with feeding strikes (mean $1.1 \text{ min}^{-1} \pm 0.07 \text{ S.E.}$, Pearson's correlation $R^2=0.37$, $F_{1,20}=11.97$, $P < 0.01$; Supporting Information Figure S1), suggesting that it represents foraging movement. This is further supported by *P. australis*' diet, which comprises prey items that are patchy in space and mobile, necessitating pursuit for

capture. There was notable variation in this relationship among individuals, which may reflect sex-specific foraging strategies previously reported for the species (Sano, 1993).

Visual observations revealed that feeding strikes taken were primarily directed towards benthic invertebrates (97.5%) and only rarely towards juvenile fishes (2.3%) or turf algae (0.2%) (Supporting Information Figure S2). During late-summer (February–March), SSTs ranged from 28.3 to 32.4° C between 0800 and 1800 h [Figure 1(a)]. Diet composition did not appear to vary with time of day or SST, but this needs to be interpreted cautiously due to few observations of fish and algae strikes. Although diet composition did not appear to change in response to acute increases in SST within this study, it is possible that under prolonged temperature stress associated with future climate change scenarios, prey availability may change, resulting in an altered diet for *P.*

australis, further affecting the species' foraging strategies and behaviour. Stable-isotope (time-averaged) analysis corroborated relatively well with feeding observations (point-in-time) and provided a more accurate, extended-time period representation of the population's actualized and assimilated diet (Fry, 2006). On the sampled reef, algae was the richest in $\delta^{13}\text{C}$ (-11.83 ± 0.1 s.d.), while worms were the poorest (-13.62 ± 0.1 s.d.). Crustaceans and worms had similar $\delta^{15}\text{N}$ (6.7 ± 0.1 s.d. and 5.8 ± 0.1 s.d., respectively), while algae was lighter and fish was heavier (3.5 ± 0.1 s.d. and 9.5 ± 0.1 s.d., respectively). Based on the average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of muscle tissue, the mean isotopic value of *P. australis*'s diet was estimated to be $\delta^{13}\text{C} = -12.4 \pm 0.08\text{‰}$ Vienna pee-dee belemnite, $\delta^{15}\text{N} = 6.93 \pm 0.12\text{‰}$ air (mean $\pm$ s.e.) (Figure 2), assuming an isotopic fractionation of 1‰ for carbon and 3.4‰ for nitrogen (Wyatt *et al.*, 2010). $\delta^{15}\text{N}$ levels of *P. australis* fall between 6.4 and 7.6, suggesting a trophic level with that of an

invertivore (Binning *et al.*, 2009; Ashworth *et al.* 2014). Indeed, based on *P. australis* ^{13}C levels, crustaceans appear to dominate their diet. The rich $\delta^{13}\text{C}$ levels moreover suggest, that unlike feeding observations, algae are also a considerable dietary component. While this may be consequent of targeted algal grazing, it may also be an inadvertent bi-product of targeting invertebrates residing on algal substrata, which might explain discrepancies in estimated algal diet found between visual and isotopic analyses. The variation in $\delta^{13}\text{C}$ observed among individuals further supports previous findings that *P. australis* is a generalist omnivore (Stroud 1982). Analysis of gut contents have shown other members of the Pinguipedidae family feed mainly on crustaceans (including copepods and stomatopods, 40%), polychaetes (12%), algae (22%), echinoderms (6%), molluscs (5%) and other benthic invertebrates and Teleostei (see Stroud, 1982; Sano, 1993).

Mean distance moved and feeding strikes were significantly related to time of day (distance: GAM; $t = 2.79$, $P < 0.001$; feeding: GAM; $t = 7.09$, $P < 0.001$) and temperature (distance: GAM; s (temperature): $F_{3,3} = 5.3$, $P < 0.001$; feeding: GAM; s (temperature): $F_{3,5} = 18.2$, $P < 0.001$). Distance moved was equally explained by time of day and temperature; however, feeding as a function of temperature fit the data better than time of day (AIC -20.9, 5.188, respectively) however the two variables may influence feeding behaviour together or separately at different times of day. Separating the effects of time of day and temperature on *in situ* wild populations is difficult and controlled aquaria experiments such as to replicate natural feeding events is also difficult. In support of the temperature theory, there is no evidence that feeding patterns are diurnal for this reef fish (Sano 1993). Specifically, distance-moved and feeding strikes (herein cumulatively referred to as foraging activity) steadily increased by 37% (mean 0.5–0.8 m) and 74%

(mean 0.5–2.0), respectively, with temperature from 28.5 to 30.5° C (Figure 3). As SST rose further from 30.5 to 32° C, foraging activity sharply declined; suggesting a 30.5° C thermal optimum for these behaviours and a thermal optimum of < 30.5° C for aerobic scope. The decline in foraging activity performance at temperatures > 30.5° C may suggest that currently, the population is living beyond its thermal optimum for aerobic scope (Rummer *et al.* 2014) and food consumption (Jobling, 1997) during late-summer. This may have consequences on individual growth and survivorship, which could be exacerbated by the projected SST increase of up to 3° C by late-century.

Throughout the day however, *P. australis* appeared to actively modulate foraging activity in response to exposure to SSTs deviating from their apparent thermal optima (T_{OA}) of 30.5° C (Figure 1). Specifically, distanced moved and feeding strikes began relatively low in the morning (0800 hours at $0.4 \text{ m} \pm 0.1 \text{ S.E.}$ (distance moved); $0.5 \text{ bites m}^{-1} \pm 0.1 \text{ S.E.}$ (strike rate) respectively), when SST was 1.5° C below T_{OA} ; and steadily doubled (increased by 203%) and then tripled (increased by 340%) by mid-day (c. 1230 hours) when SST reached T_{OA} . Subsequently, these behaviours declined by 66% and 51%, respectively, by 1400 hours, when SST increased further to 0.7° C beyond T_{OA} . As SST cooled into the evening, distance moved and strike rate peaked once more (at $0.9 \text{ m} \pm 0.2 \text{ S.E.}$ and at $2.1 \text{ bites min}^{-1} \pm 0.5 \text{ S.E.}$) as SST reached the populations' T_{OA} again by 1700 hours and then declined again as SST fell 0.8° C below their T_{OA} by 1800 hours (Figure 1). Consistently, it has been recently shown in a wild population of coral trout *Plectropomus leopardus* (Lacépède 1802) that individuals reduce feeding and foraging activity at late-summer temperatures > 30° C (Scott *et al.*, 2017). In fishes, appetite and ingestion levels generally decline if temperature deviates from thermal optima for aerobic

scope and conversion efficiency (the % of food converted into growth; Elliott; 1976; Brett, 1971; Jobling, 1997; Johansen *et al.* 2015). Conceivably, active down regulation of foraging activity at temperatures deviating from the thermal optimum for aerobic scope is an energy-saving strategy, placing less physiological demand on the individual (Nowicki *et al.*, 2012; Johansen *et al.*, 2014). Cumulatively, these results suggest that although *P. australis* may be living beyond its thermal optimum during certain times of the day in late-summer (Figure 1), it may mitigate associated costs on net energy budget by down-regulating energetically-costly foraging activity. Given that these results are only correlative however, they should be interpreted cautiously. Indeed, in addition to SST, several other environmental modulators that vary within the day are likely to affect *P. australis* diel foraging patterns, including UV-visible light levels, predator abundance and prey abundance (*e.g. via* vertical migration of benthic crustaceans at sunset, Jacoby & Greenwood, 1989; Yahel *et al.*, 2005). Additionally, diel patterns of foraging may partially be driven by those of social–mating behaviour. For example, *c.*40 min prior to sunset, courting and spawning commences in the species (Stroud, 1982; Walker *et al.*, 2010), which is likely to reduce foraging effort. In order to better understand the independent causal effect of increased temperature on foraging in this species, follow-up studies that control for potential environmental/social confounds are needed.

Although future SSTs are projected to exceed the thermal optima of coral reef fishes, potential behavioural adaptations remain poorly known, partially due to a paucity of research on wild populations in their native habitat. It seems that this is the first study to examine *in situ* foraging modifications of a site-attached coral reef fish in response to increased temperature. We observed that *P. australis* appears to be already living beyond

its thermal optimum for aerobic scope of $c.30.5^{\circ}\text{C}$ during late-summer, to which it responds by actively down-regulating foraging movement and food consumption. Further research is now needed to confirm whether these foraging alterations mitigate bioenergetic inefficiency caused by reduced aerobic scope, by reducing energetic demand. To the extent these modifications do, however, such behavioural plasticity is unlikely to allow full recovery of losses to net energetic budget, with associated declines in foraging regime and fitness potential. Since the population's T_{OA} of $c.30.5^{\circ}\text{C}$ is exceeded for only a few hours per day during late-summer, this scenario may bear little threat to its viability at the current time. In the future oceanic climate however, temperatures $> 30.5^{\circ}\text{C}$ will occur for a longer duration and higher magnitude throughout the year, posing potential threat to the population's fitness that can only be remedied by its capacity for long-term range expansion, long-term acclimation or genetic adaptation (Wong & Candolin 2015). Finally, given the novelty and small-scale of this study, caution should be exercised while broadly generalizing the foraging responses observed here to other site-attached coral-reef fishes. Indeed, we might expect notable variation in response deriving from differences in thermal reaction norms, which can vary considerably among fish species and site-specific populations of coral-reef fishes (Munday *et al.*, 2008). Response variation among fishes may also be expected due to differences in the aerobic demand of utilized foraging tactics (*e.g.* ambush *v.* stalking), dietary assimilation efficiency and caloric content of prey.

Authors' contribution

T.J. Chase & J.P. Nowicki contributed equally to this work.

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SUPPORTING INFORMATION

Supporting information can be found in the online version of this paper.

Material and Methods: stable-isotope analysis.

FIGURE S1 Relationship between average number of predatory strike and distance moved for 22 individual *Parapercis australis*. ■, 95% C.I.

FIGURE S2 Mean ($\pm$ S.E.) strike rate by *Parapercis australis* on varying prey types.

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FIGURE 1 Box plots (—, median; ◁, 25 and 75th percentiles; |, range; O, outliers) of *Parapercis australis* diel foraging activity in association with ambient temperature as it relates to apparent thermal optima of 30.5°C, throughout the day: (a) ambient temperature, (b) distance moved and (c) feeding strikes. ■, Below optimum temperature; ■, above optimum temperature.

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- 1 Change A, B, C to (a), (b), (c).
- 2 After Distance moved insert (m min^{-1}).
- 3 After feeding strikes insert (bites min^{-1}).

FIGURE 2 Box plots (—, median; ◁, 25 and 75th percentiles; |, range; O, outliers) of performance curves for *Parapercis australis* foraging activity in relation to ambient temperature indicate a thermal optimum of 30.5°C: (a) distance moved and (b) feeding strikes.

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- 1 Change A, B, C to (a), (b), (c).
- 2 After Distance moved insert (m min⁻¹).
- 3 After feeding strikes insert (bites min⁻¹).

FIGURE 3 Isotopic bi-plot showing average ($\pm$ S.D.) $\delta^{15}\text{N}$ (trophic position) and $\delta^{13}\text{C}$ (dietary carbon) ratios for potential prey types (fish, crustaceans, worms, algae) and ratios for individual *Parapercis australis* ($\bullet$; $n=12$). Isotopic fractionation has been added to the prey items.

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1 Change *P. australis* to *P. australis*.

FIGURE S1 Relationship between average number of predatory strike and distance moved for 22 individual *Parapercis australis*. ■, 95% C.I.

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1 Add (bites min⁻¹) to y-axis.

FIGURE S2 Mean ($\pm$ S.E.) strike rate by *Parapercis australis* on varying prey types.

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1 Change y-axis to read Number of strikes (bites min⁻¹).

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