# Phenotypic responses of coral reef fishes to extreme and novel environments

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# ABSTRACT

In an increasingly variable and rapidly warming global environment, there is still little consensus as to the biological mechanisms that may facilitate population persistence of coral reef fishes. While a range of studies have shown substantial losses of coral reef fishes with environmental impacts, there are an increasing number of studies which have shown the importance of plasticity in behavioural, demographic and life-history traits in sustaining coral reef fish populations. As such, the main goal of this thesis was to investigate whether phenotypic plasticity plays an important role in determining coral reef species survival in an increasingly challenging environment. To do so, I focused on three phylogenetically and ecologically diverse coral reef fish species that thrive in the extreme environment of the Arabian/Persian Gulf (hereafter 'Arabian Gulf'). Within the Arabian Gulf summer temperatures are in line with those projected for the tropical oceans by 2100, while winter condition can be so severe as to induce cold water coral bleaching. Moreover, the Arabian Gulf's waters are characterized by hypersaline conditions that are the highest reported for coral reefs. These conditions provide an ideal setting to investigate the traits which allow resident coral reef fish populations to cope with predicted extremes and high variability in environmental conditions. In parallel, as many Red Sea coral reef fishes have recently invaded and established populations in the Mediterranean Sea (i.e. Lessepsian migration), I focused on the potential role of phenotypic plasticity in facilitating marine fish invasion within a temperate rocky reef ecosystem, as well as investigating the ecological

interaction between invasive species and the wider native and non-native fish community.

As behavioural change is the first response of an organism to environmental stressors, in Chapter 2 I investigated the role of behavioural plasticity in the reef-associated fish *Pomacentrus trichrourus* in mediating seasonal extremes in temperature (winter low: SST = 21 °C; summer high: SST > 34 °C) in the Arabian Gulf. Through *in situ* and *ex situ* observations, I found that this species downregulates metabolically costly activity during winter and summer while upregulating activity and increasing energy stores in spring. Seasonal changes in the level of activity may represent a mechanism to reduce metabolic stress when temperatures are extreme, while accumulation of energy stores during the benign season for activity (i.e. spring, SST = 27°C) will provide such stores to be utilised during environmentally extreme seasons.

One of the most important factors which may determine species success within an extreme environment is how population demography is impacted by environmental change. Therefore, in Chapter 3 I investigated whether fish populations in the Arabian Gulf, compared to populations from the less variable and less extreme Oman Sea, would follow the generalised pattern for ectotherms of size reduction at a higher temperature (i.e. temperature size rule – TSR). Furthermore, I investigated whether the extreme and highly variable water temperature and salinity (i.e. mean annual salinity 42 psu) within the Arabian Gulf, would be the driver of expected body size reduction. Contrary to the prediction of the TSR, I found that salinity was the best environmental predictor of interannual growth across species and regions, with low growth corresponding to more saline conditions. These results highlight the importance of osmoregulation cost in impacting growth, as well as suggesting that future studies will need to consider the effect of multiple stressors when investigating the consequences of future climate change on fish demography.

Invasive species commonly show a high degree of phenotypic plasticity which may facilitate their acclimation to novel introduced environments. Despite this, there is still debate as to the particular traits which may enhance invasion success. Therefore, in Chapter 4 I investigated the key behavioural and ecological traits of Lessepsian lionfish and the resident fish community in the Mediterranean Sea that may contribute to lionfish invasion success, as well as investigating the potential impact on the recipient native fish community. My findings suggest that Mediterranean lionfish are crepuscular generalist predators, though that feed more substantially on solitary, small-bodied benthic or bentho-pelagic associated species. Such trophic behaviour is expected to increase the likelihood of better dealing with the environmental stochasticity of a novel environment. Additionally, native prey fishes show greater naiveté towards lionfish than Lessepsian prey species. Naiveté of resident fishes towards a novel predator may enhance the population success of the invasive species through increased feeding rate and reduced competition with native predators, potentially mitigating any metabolic costs associated with invasion into a new environment.

Overall, the results of this thesis have important implications for understanding how coral reef fishes may respond to environmental variability that is expected to increase under future climate change or to be met during shift in species distribution. Particularly, plasticity in behaviour is likely to play a major role in dealing with extreme and novel environments, while trade-off between body size and metabolic costs are also expected.

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# SUMMARY OF PUBLICATIONS

## Publications from PhD thesis

**D'Agostino D**, Jimenez C, Reader T, Heyworth S, Hadjioannou L, Josephides M and Feary DA (2020) Behavioural traits and feeding ecology of Mediterranean lionfish and naiveté of native species to lionfish predation. *Marine Ecology Progress Series* 638, 123-135. https://doi.org/10.3354/meps13256. **[Thesis chapter 4]**

**D'Agostino D**, Chapman B, Burt JA, Reader T, Santinelli V, Cavalcante G, and Feary DA (2019) The influence of thermal extremes on coral reef fish behaviour in the Arabian/Persian Gulf. *Coral Reef* https://doi.org/10.1007/s00338-019-01847-z. **[Thesis chapter 2]**

## Manuscript from PhD thesis ready to submit

**D'Agostino D**, Burt JA, Santinelli V, Vaughan GO, Fowler A, Reader T, Taylor B, Hoey AS, Cavalcante GH, Baumam AG and Feary DA. Growth impacts for coral reef fishes living in an extreme environment. Submitted to *Coral reefs.* **[Thesis chapter 3]**

## Additional publications

Dean L, Magalhaes IS, Foote A, **D'Agostino D**, McGowan S and MacColl A (2019) Admixture between ancient lineages, selection, and the formation of sympatric stickleback species-pairs. *Molecular Biology and Evolution* 36 (11), 2481-2497 https://doi.org/10.1093/molbev/msz161.

Torquato F, Range P, Ben-Hamadou R, Sigsgaard E, Thomsen P, Riera R, Berumen M, Burt J, Feary DA, **D'Agostino D**, Marshell A, DiBattista J and Møller P (2019). Consequences of marine barriers on genetic diversity of the coral-specialist yellow-bar angelfish from the Western Indian Ocean. *Ecology and Evolution* 9 (19), 11215-11226.

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Gordon TA, Harding HR, Clever FK, Davidson IK, Davison W, Montgomery DW, Weatherhead RC, Windsor FM, Armstrong JD, Bardonnet A, Bergman E, Britton JR, Côté IM, **D'Agostino D**, Greenberg LA, Harborne AR, Kahilainen KK, Metcalfe NB, Mills SC, Milner NJ, Mittermayer FH, Montorio L, Nedelec SL, Prokkola JM, Rutterford LA, Salvanes AG, Simpson SD, Vainikka A, Pinnegar JK, and Santos EM (2018), Fishes in a changing world: learning from the past to promote sustainability of fish populations. *Journal of Fish Biology* 92 (3), 804-827*.*

Magalhaes IS, **D'Agostino D**, Hohenlohe P, MacColl ADCM. The ecology of an adaptive radiation of three-spined sticklebacks from North Uist, Scotland (2016). *Molecular Ecology* 25 (3), 4319-4336.

## Additional manuscripts in review

Magalhaes IS*, Whiting J*, **D'Agostino D**, Hohenlohe P and MacColl ADCM. Intercontinental genomic parallelism in multiple adaptive radiations. Submitted to *Nature Ecology and Evolution* (*joint first authors).

Griffiths G, Wade C, **D'Agostino D**, Burt J and Feary DA. Phylogeography of a commercially important reef fish, *Lutjanus* ehrenbergii, from the coastal waters of the Arabian Peninsula. In review in *Coral Reefs.*

## Additional manuscripts in preparation/close to submission

Magalhaes IS, **D'Agostino D**, Hohenlohe P and MacColl ADCM. Ancestral variation does not explain phenotypic and genomic variation in freshwater three-spined stickleback. In preparation to be submitted to *Molecular Ecology* or *Evolution***.**

Dean LL., Magalhaes IS, **D'Agostino D** and MacColl ADCM. Phylogenetic niche conservatism in an ecological adaptive radiation. In preparation to be submitted to *Current Biology.*

Heyworth S, Wade C, **D'Agostino D,** Azzurro E, and Feary DA. Population genetics and growth of the rabbitfishes *Siganus luridus* and *Siganus rivulatus*: investigating factors structuring successful invasion of the Mediterranean Sea. In preparation.

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# CHAPTER 1

## General introduction

Naturally occurring extreme environments can be regarded as evolutionary experiments, that provide the ability to study how species and their populations may acclimate and/or adapt to stressors and altered ecological conditions. Such work may allow us to test predictions regarding how such species may then acclimate and/or adapt to rapid human-induced environmental change (Riesch et al. 2015). Globally, species can live in starkly different environmental conditions and what constitutes the optimum environment for one species can be extreme or prohibitive for the survival of another. Hence, the definition of an extreme environment is relative to the organism being observed (Rothschild and Mancinelli 2001). In my thesis, I focus on coral reef fish and consider an environment as ‘extreme’ when some physicochemical (e.g. temperature, pH, oxygen, salinity etc.) or biological factor (e.g. high/low population density, low prey/food availability) fall at the very edge of the normal range of a typical environmentally stable coral reef ecosystem (Rothschild and Mancinelli 2001; Lindgren et al. 2016). As such, my work has been based in the Arabian Gulf, which represents the hottest sea in the world with summer temperature above the mortality threshold for many Indo-Pacific species (i.e. > 34 °C) (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers et al. 2018), and that has been extensively used as proxy for end-of-the-century tropical ocean warming (Riegl and Purkis 2012) (see paragraph 1.4 for details).

## 1.1 Human-induced rapid environmental change

Human activities are having a profound impact on the natural world – from climate change, habitat loss and chemical release, to overharvesting and introduction/transport of invasive species (Walther et al. 2002; Parmesan and Yohe 2003; Perry 2005; Burke et al. 2012). Such impacts can have significantly negative consequences on global biodiversity, involving rapid changes in abundance, diversity and composition of species (Bellard et al. 2012; McCauley et al. 2015; Webb and Mindel 2015; Hughes et al. 2018).

Over the last century, average global sea surface temperature (SST) has increased by 0.6 °C, with the prediction of further 4 °C rises by the end of the century (IPCC 2014; Hoegh-Guldberg 2018). This increase in temperature reflects the general global warming trend caused by the anthropogenically increased $CO_2$ and other greenhouse gases concentration in the atmosphere (Hoegh-Guldberg 2018). Atmospheric $CO_2$ concentrations, for example, have risen from ~280 ppm in the 18$^{th}$ centuries to 413 ppm as today (NOAA, February 2020), an increment rate 100 times faster than that experienced in the past 65,000 years (Siegenthaler et al. 2005).

Among ocean acidification and increases in weather extreme events (i.e. heatwaves, storms), ocean warming is one of the most pervasive manifestation of climate change in the marine realm, as it is expected to have major impacts on the biodiversity, functional structure and productivity of marine ecosystems (Folguera et al. 2011; Doney et al. 2012; Bellard et al. 2012; Pecl et al. 2017). For example, alterations have already been recorded along the west coast of Australia – a hotspot of biodiversity and endemism (Wernberg et al. 2013). Here, marine heatwaves have drastically reduced the abundance of habitat-forming temperate seaweeds, with subsequent loss in sessile invertebrates and demersal fish biodiversity, and shifts in community structure towards a depauperate state and tropicalization of the resident fish community (Wernberg et al. 2013). Similarly, in the temperate Mediterranean Sea, the Lessepsian herbivorous fish *Siganus rivulatus* and S. *luridus* have expanded their habitat range and increased their grazing activity due to increasing water temperature (i.e. tropicalization of the Mediterranean Sea), resulting in a dramatic community phase shift where the habitat-forming algal forest has been transformed to 'barrens' (Vergés et al. 2014). In the tropics, global warming and heat waves are transforming coral reef assemblages via mass bleaching and mortality of corals, with subsequent loss of populations that depend on such resources (Hughes et al. 2018).

### 1.1.2 Ocean warming and coral reef fish

Coral reefs cover only 0.1% of the ocean surface yet they hold the highest biodiversity of any marine ecosystems, and provide ecosystem services (e.g. food, coastal protection from natural hazards, tourism, etc.) to more than 500 million people (Roberts 2002; Burke et al. 2012; Beck et al. 2018). However, despite their global importance, coral reefs are subject to a range of local (i.e. overfishing, pollution, habitat loss) and global anthropogenic stressors (i.e. ocean warming and acidification) that have resulted in recent degradation and loss of coral on a global scale (i.e. 20% of coral reefs loss in the past 30 years and > 75% threatened) (Wilkinson 1999; Burke et al. 2012; Cheal et al. 2017; Hughes et al. 2018).

While climate warming that degrades coral reef communities may have indirect impacts on coral reef fishes (i.e. ~11% of fish depending upon living corals and up to 60-70% indirectly affected by coral cover declines) (Sano 1987; Jones et al. 2004; Pratchett et al. 2011, 2018), ocean warming and heatwaves can also have direct impacts to individual fishes as well (Munday et al. 2008b, 2012). Tropical coral reef fish, indeed, have evolved in an thermally stable environment and to minimize energetic costs their molecular and cellular processes are optimized to work in a narrow thermal window (Pörtner and Farrell 2008). Additionally, as they live close to their upper thermal maximum, their tolerance to temperatures outside their thermal optimum is limited (Tewksbury et al. 2008; Sunday et al. 2011; Rummer et al. 2014). Therefore, even small increments in temperature are expected to have serious consequences on reef fish's performance (Nilsson et al. 2009), behaviour (Nagelkerken and Munday 2016), reproduction (Pankhurst and Munday 2011), growth (Munday et al. 2008b; Spinks et al. 2019), and survival (Rodgers et al. 2018).

### 1.1.3 The role of phenotypic plasticity in coping with extreme and novel environments

As coral reef fish species may not be adapted to fast-changing or novel environmental conditions (e.g. warming waters, relocation to temperate seas) (reviewed by Donelson et al. 2019), they will have to respond to the new environmental stressors in order to survive (Bellard et al. 2012). For example, in the context of climate warming species can respond along three main axes: (i) acclimate and/or adapt their physiology or behaviour to extend their *in situ* thermal niche (i.e. survival limits, *sensu* [Connel 1961]) (Parmesan 2006; Wong and Candolin 2015); (ii) relocate to new areas that become available within their thermal niche by shifting geographical distribution (i.e. poleward expansion for tropical species) (Feary et al. 2014; Bates et al. 2014); or (iii) experience range contractions and local extinction where temperature exceeds their thermal niche, therefore preventing survival (Barnosky et al. 2011; Donelson et al. 2019).

While adaptation requires time for natural selection to take place (especially in long-lived organisms) and is therefore thought of not being a suitable response to rapid environmental change (Reznick and Ghalambor 2001; Parmesan 2006), phenotypic plasticity can occur over relatively rapid timescales and is often considered as the first response to environmental stressors (Gienapp et al. 2008; Munday et al. 2013; Donelson et al. 2019). In the context of climate change, phenotypic plasticity is broadly considered as changes in physiology, morphology and behaviour that can improve individuals performance under altered or novel environmental conditions (Angilletta 2009; van Baaren and Candolin 2018; Donelson et al. 2019).

As behaviour mediates the interaction between an individual and the environment (Chapple et al. 2012), behavioural plasticity is considered as one of the primary responses to environmental change, with the speed and scope of behavioural adjustment potentially determining survival (Tuomainen and Candolin 2011; Wong and Candolin 2015). For example, in the context of ocean warming species can change microhabitat use or move to deeper waters to seek more favourable environmental conditions within their normal environment (i.e. thermal refugia) (Dulvy et al. 2008; Breau et al. 2011; Donelson et al. 2019). Alternatively, species can reduce feeding and other energetically costly activities to decrease the metabolic demands that may be intensified by higher temperature (i.e. basal metabolism and oxygen demands increase with temperature in ectotherms) (Nowicki et al. 2012; Johansen et al. 2014; Jutfelt et al. 2020). However, is still not clear to what extent behavioural plasticity can mitigate extremes in temperature in species which are believed to have evolved in habitats that have been highly stable in the past (such as coral reef fish) (Candolin 2018; Donelson et al. 2019). Similarly, when shifting distribution to track their thermal niche and/or invading a new habitat when favourable conditions arise (e.g. the opening of the Suez Canal), species will have to cope with new environmental conditions (Blackburn et al. 2011; Chapple et al. 2012). In this context, invasive species commonly show a high degree of phenotypic plasticity which facilitate their acclimation to novel habitats (Davidson et al. 2011; Hôrková and Kovácˇ 2014; van Baaren and Candolin 2018), and can be studied to identify the traits that may allow species to acclimate and persist in a changing environment (Tuomainen and Candolin 2011; Wong and Candolin 2015).

## 1.3 Thesis outline and data chapters description

### 1.3.1 Chapter 2: The influence of thermal extremes on coral reef fish behaviour and biology in the Arabian/Persian Gulf

While the effect of temperature increase on coral reef fishes has been studied extensively on laboratory-based experiments during the past two decades (reviewed by Nagelkerken and Munday 2016), only recently scientist have started addressing the question of whether behavioural plasticity may play a role in mitigating temperature increase (Nowicki et al. 2012; Johansen et al 2014; Jutfelt et al. 2020). Additionally, laboratory-based experiments may exclude the ecological and biogeochemical complexities inherent in natural reef systems, and fail to completely address the consequences of climate change on coral reef ecosystems (Nagelkerken and Munday 2016). Hence, the importance of assessing the degree of behavioural plasticity within wild organisms observed *in situ* has recently gained more recognition (Nagelkerken and Munday 2016; Scott et al. 2017; Chase et al. 2018). Scott et al (2017) and Chase et al (2018), by carrying *in situ* behavioural observations of coral reef fishes of the Great Barrier Reef in Australia, showed that fish can reduce aerobically costly behaviours (i.e. swimming and feeding) when exposed to above-average temperature, to mitigate temporary bioenergetic inefficiency. However, while novel and insightful, these studies were only able to investigate brief changes in fish behaviour with short-term temperature stress. Such temporally short observations may then be unsuitable to examine whether coral reef fishes will be able to tolerate projected end-of-the-century temperature.

To date, no studies have investigated the potential for phenotypic plasticity in mitigating seasonal extremes in temperature that are in line with climate change projection for the tropical ocean by 2100 (IPCC 2014; Hoegh-Guldberg 2018). Hence, in Chapter 2 I examined whether behavioural plasticity is one of the mechanisms that may allow coral reef fishes living in the Arabian Gulf to cope with its extreme environment. Building from the observed potential for behavioural and feeding plasticity in coral reef fish previously investigated within laboratory experiments (Nowicki et al. 2012; Johansen et al. 2014) and in the field (Scott et al. 2017; Chase et al. 2018), I used field observation and laboratory experiments to examine the behavioural responses of the common pale-tail damselfish (*Pomacentrus trichrourus*) to thermal extremes (Fig. 1.1). Specifically, I hypothesized that (i) fish would minimize aerobically-costly behaviours (i.e. swimming, feeding etc.) when exposed to sub-optimal temperatures for activity in winter (21 °C) and summer (> 34 °C) (Scott et al. 2017; Chase et al. 2018) while compensating for energy losses and building up energetic stores by increasing activity and feeding rate in spring (28 °C) (Armstrong and Bond 2013). I also hypothesized (ii) that *P. trichrourus* would exhibit flexibility in diet by shifting from a predominately planktonic diet during optimal conditions (i.e. spring) to one encompassing both planktonic and benthic prey, when exposed to suboptimal temperature (i.e. winter and summer) (Shraim et al. 2017), with concomitant changes in energetic stores (Armstrong and Bond 2013). Such change in diet was expected to be due to restrictions in foraging movements in suboptimal conditions, with individuals becoming generalist in their feeding habits, exploiting more easily accessible resources. Finally (iii), I tested the hypothesis that variation in behaviour observed in the field was directly mediated by temperature by exposing *P. trichrourus* individuals to temperatures typical of winter (21 °C) and spring (28 °C) in a controlled aquarium-based experiment.

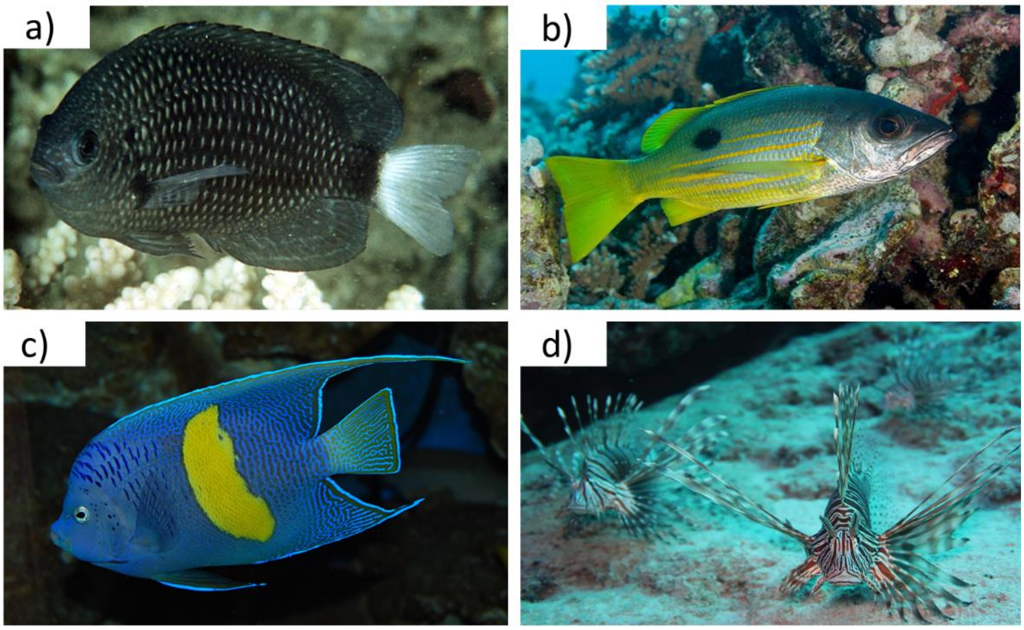

**Fig. 1.1** (**a**) *Pomacentrus trichrourus* (pale-tail damselfish), (**b**) *Lutjanus ehrenbergii* (black-spot snapper), (**c**) *Pomacanthus maculosus* (yellow-bar angelfish), (**d**) *Pterois miles* (common lionfish or devil firefish). Photo credit: a, b, c: FishBase, d: Louis Hadjioannou. Fishes not to scale.

### 1.3.2 Chapter 3: Growth impacts in a changing ocean: insights from two coral reef fishes in an extreme environment

Reduction in average individual body size is recognised as a universal ecological response of ectotherms to global warming (Daufresne et al. 2009; Cheung et al. 2013). In marine environments, particularly, the growth rate and adult body size of fishes are known to vary systematically with variation in water temperature (Pörtner et al. 2001; Audzijonyte et al. 2016; van Rijn et al. 2017), reflecting the potentially pervasive effect of temperature on individual metabolic rate (i.e. the mismatch between oxygen demand, which strongly increase with temperature, and supply, which is limited by physical constraint) (Daufresne et al. 2009; Neuheimer et al. 2011; Pörtner et al. 2017; Pauly and Cheung 2018). The direction and magnitude of this variation may be reliably predicted by the Temperature-Size Rule (TSR), where higher environmental temperatures result in higher initial (juvenile) growth rate, an earlier asymptote in somatic growth rate and reduction in maximum body size (Atkinson 1994; Kingsolver and Huey 2008; Ohlberger 2013; Horne et al. 2017; Huss et al. 2019). However, where the predictive power of the TSR may be important is in understanding the repercussions of changes to environmental factors that structure fish populations. Indeed, a dominance of smaller sized mature fishes will impact fisheries productivity (i.e. reproductive output increases disproportionally with body size) (Baudron et al. 2014; Barneche et al. 2018), prey-predator interactions (Barnes et al. 2010; Audzijonyte et al. 2013), and overall ecosystem function and services (Sheridan and Bickford 2011; Edeline et al. 2013). Hence, understanding what drives reductions in fish body size is essential in predicting how populations will be impacted by projected climate change.

As warming temperatures increase anabolic oxygen demand while decreasing oxygen solubility, imbalances between oxygen demand and supply will constrain aerobic scope, thereby impairing individual performance (Pörtner and Knust 2007). Smaller-sized individuals, however, can better balance oxygen demand/uptake due to their larger surface area to volume ratio (i.e. gill-oxygen limitation theory, Pauly and Cheung 2018a,b). Hence, size reduction at warmer temperature may be a mechanism to retain sufficient aerobic capacity to sustain ecological task (i.e. swimming, feeding, etc.) (Messmer et al. 2017; Pauly and Cheung 2018a). However, despite the ubiquity of the TSR in explaining size reduction in a range of taxa, the underlying mechanisms of body size reduction with increasing temperature are still debated (reviewed by Audzijonyte et al. 2019). Moreover, shrinking cannot only be ascribed to temperature increases, as the interplay of other changing environmental factors (i.e. salinity and productivity) may play an important role.

One approach to understanding how marine fish demography may be impacted by environmental variance and extremes is to study contemporary communities that exist within naturally extreme and variable environments. On this regard, the Arabian Gulf provides fish populations already living in an environment with fluctuating and extreme temperature and salinity, which can be readily contrasted with the populations of the Oman Sea, where conditions are comparably more stable. Hence, in Chapter 3 I examined the possibility of a life-history trade-off between fish body size and metabolic demands in the populations of two ecologically and phylogenetically diverse coral reef fish species: the blackspot snapper (*Lutjanus ehrenbergii*) and the yellow-bar angelfish (*Pomacanthus maculosus*) (Fig. 1.4). Given the differences in environment between the two systems, I hypothesise that in line with the TSR, (i) fishes in the Arabian Gulf would exhibit lower growth rates, as well as smaller size-at-age and maximum body size than conspecifics from the less extreme and variable environment of the Oman Sea. Additionally (ii), I further hypothesise that predicted differences in growth would be driven interannually by local environmental conditions. Therefore, I investigated the role of temperature, salinity and productivity in structuring fish demography between regions by using otolith increment width profiles, and predicted that low growth rate and small body size would be the results of extreme temperature ranges in the Arabian Gulf, exacerbated by high salinity and lower primary productivity.

### 1.3.3 Chapter 4: Behavioural traits and feeding ecology of Mediterranean lionfish and native species naiveté to lionfish predation

Invasive species often show a high degree of phenotypic plasticity, which may facilitate acclimation to novel environments (Davidson et al. 2011; Hôrková and Kovácˇ 2014; Chapple et al. 2012; van Baaren and Candolin 2018). Thus, understanding the ecological, behavioural and life-history traits that enable coral reef species to succeed in environments that differ from their natal environment may be valuable to identify the traits that may allow species to acclimate and persist in a changing environment (Tuomainen and Candolin 2011; Wong and Candolin 2015). Additionally, it may facilitate the identification of species that may withstand human-induced rapid environmental change by being able to effectively shift their geographical distribution (Chapple et al. 2012; Feary et al. 2014).

As the Red Sea and Mediterranean Sea fauna are well characterised (Golani and Bogorodsky 2010; Mouillot et al. 2011; Evans et al. 2015), the resulting invasion of Lessepsian species have offered a unique opportunity to investigate the traits associated with successful fish invasion (Belmaker et al. 2013). Studies have related the Lessepsian migrants' rapid invasion and successful residence in the Mediterranean Sea to a vast array of demographic and ecological traits, including having pelagic propagules (Ben Rais Lasram et al. 2008), having a pelagic lifestyle (Samaha et al. 2016), shallow depths within the Mediterranean Sea, large body size (Arndt and Schembri 2015), schooling behaviour (Belmaker et al. 2013), and reduced competitive pressure within the Mediterranean Sea (Azzurro et al. 2014; Givan et al. 2017).

More importantly for the framework of this thesis, success of invasive species has been linked to large home ranges in their native habitat (i.e. Red Sea) and high water temperature affinity (Belmaker et al. 2013; Givan et al. 2018). This indicates that these species may already possess the degree of phenotypic plasticity necessary to successfully colonise a new environment (Belmaker et al. 2013; Chapple et al. 2012; Wong and Candolin 2015). Similarly, adaptation to warm temperature may be a pre-requisite to succeed in a temperate environment where seasonal fluctuations in temperature may be a major factor limiting introduction (Belmaker et al. 2013; Givan et al. 2018). However, despite behavioural plasticity being a key trait for invasive success (reviewed by Chapple et al 2012), at present no studies have directly investigated its role in structuring the invasion of Lessepsian migrants.

In Chapter 4, therefore, I investigate the role of behavioural plasticity in structuring the Lessepsian invasion of the Mediterranean Sea by focusing on the behaviour and feeding ecology of the Lessepsian lionfish (*Pterois miles*, hereafter 'Mediterranean lionfish', to distinguish it from the 'Atlantic lionfish' *Pterois miles/volitans*) (Fig. 1.4), which have established abundant and stable populations in the eastern Mediterranean Sea (Kletou et al. 2016; Azzurro et al. 2017). Lionfish were chosen because the behavioural, ecological and life-history traits leading to their invasive success in the Western Atlantic Ocean (hereafter 'Atlantic') have been well characterised in the past three decades (Albins and Hixon 2013; Côté and Smith 2018). Thus, this work allowed me to undertake a direct comparison between the two invasions and the identification of traits related to invasion success between the Atlantic Ocean and Mediterranean Sea. Additionally, due to substantial negative impacts on native fish biodiversity registered in the Atlantic (Albins and Hixon 2013; Côté and Smith 2018), this study aimed to determine whether similar impacts are to be expected in the Mediterranean Sea.

In Chapter 4, therefore I first quantified the activity patterns of Mediterranean lionfish to test the hypothesis of a crepuscular pattern in hunting activity (i.e. sunrise and sunset) as this has been shown in the Atlantic invasion (Cure et al.

2012; Benkwitt 2016) and referred as one of the behavioural traits facilitating their invasive success (i.e. increased hunting success as well as broader array of preys being available) (Hobson 1973; Potts 1990; Green et al. 2011). Secondly, I characterised the feeding ecology of Mediterranean lionfish and hypothesised that lionfish would broadly be generalist predators by feeding on a diverse array of prey, which increases the likelihood to better deal with the environmental stochasticity of a novel environment (García-Berthou 2007, Peake et al. 2018). Finally, as native species naiveté has been invoked to explain the success of some predators in invading new regions (i.e. competitive advantage compared to native counterparts) (Anton et al. 2016; Haines and Côté 2019), I investigated the levels of behavioural naiveté towards lionfish in native and Lessepsian prey species, predicting that native prey would be more naïve towards hunting lionfish (Anton et al. 2016).

## 1.4 Study systems

In this thesis, I worked within two main study systems: the Arabian Gulf and the Mediterranean Sea (Fig. 1.2). As the data chapters 2, 3 and 4 have been written as manuscripts, the description of the study systems can be found in each relevant chapter. Here, however, I provide a brief introduction of both study systems to allow the reader to better contextualize the rationale behind the framework of my work and the hypotheses tested.

### 1.4.1 The Arabian Gulf – the hottest sea in the world

The Arabian Gulf is a semi-enclosed, shallow basin (mean depth < 36 m) located between Iran and the Arabian Peninsula (Fig 1.2). It formed ~6000 years ago as an extension of the western Indian Ocean, with which it retains a connection through the narrow Strait of Hormuz (Riegl and Purkis 2012). As a consequence of its geographical location, depth and limited exchange of waters, the Arabian Gulf experiences the highest variation in sea surface temperature for coral reefs globally (winter: < 15 °C, summer: > 35 °C) (Fig. 1.3) (Riegl and Purkis 2012;

Vaughan et al. 2019). Fish communities can endure several months of temperature above the mortality threshold of most tropical reef fish (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers et al. 2018), and below the optimal temperature reported for reef fish elsewhere in the Indo-Pacific (Eme and Bennett 2008; Figueira and Booth 2010; Nakamura et al. 2013; Johansen et al. 2015). Most importantly, present summer water temperature is comparable to that expected for tropical oceans by 2100 (Riegl and Purkis 2012; Hoegh-Guldberg 2018), allowing testable hypotheses on how future extremes in water temperature may shape coral reef communities. Additionally, due to restricted exchange with oceanic waters, high evaporation and limited freshwater input (Reynolds 1993; Reynolds 2002), the Arabian Gulf's waters are characterized by hypersaline conditions (average salinity 42 psu, with peak of > 50 psu in the southern bays and > 70 psu in evaporative lagoons) that are the highest reported for coral reef ecosystems (Sheppard 1993, D'Angelo et al. 2015; Vaughan et al. 2019). In contrast, the adjacent Gulf of Oman, by being part of the wider Western Indian Ocean, is characterized by less extreme and variable temperature and salinity (Coles 1997, 2003). However, due to substantial upwelling along the coastal margin off Oman, primary productivity levels are usually higher and more interannually variable (Coles 1997, 2003).

As a likely consequence of extreme environmental conditions, the biodiversity of the Arabian Gulf has been described as a depauperate subset of those found in the Gulf of Oman, with lower coral and fish abundance, richness, and biomass (Coles 2003; Feary et al. 2010; Burt et al. 2011). Nevertheless, relatively abundant and diverse coral reef communities are still present (Feary et al. 2010), and fisheries represent the second most important natural resource in the region after oil (Sale et al. 2011).

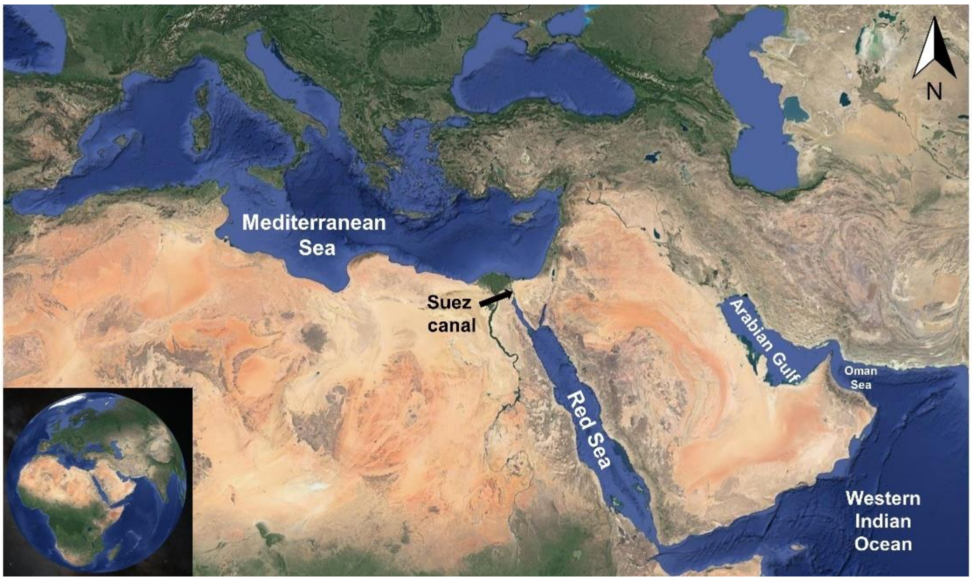


**Fig. 1.2** Satellite view of the biogeographical regions relevant for this study (image source: Google Earth access on February 2020).

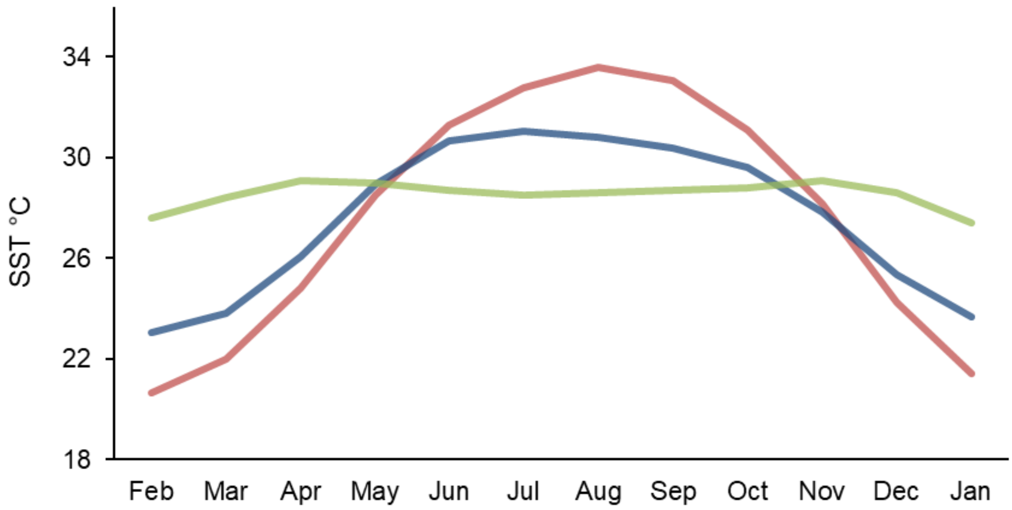


**Fig. 1.3** Monthly mean sea surface temperature (SST) profiles: red indicates the Arabian Gulf (centred Abu-Dhabi, United Arab Emirates), blue indicates the northern Gulf of Oman (Fujairah, Oman), green indicates the Indo-Pacific (Palau Tioman, Malaysia).

### 1.4.2 The Mediterranean Sea and the Lessepsian invasion

The Mediterranean Sea is an inland temperate sea considered a hot spot for biodiversity, containing ~18% of global known marine species while comprising only 0.32% of the global oceans (Bianchi and Morri 2000) (Fig. 1.2). It formed 38–31 million years ago, when the Indian continent and other microplates collided with the modern Eurasian plate (Goffredo and Dubinsky 2014). This tectonic movement resulted in the sealing of the seaway between the current Mediterranean Sea and the Western Indian Ocean with the consequent geographical isolation of marine biodiversity (Goffredo and Dubinsky 2014). However, the two bodies of water were re-connected by the opening of the man-made Suez Canal in 1869, prompting the beginning of the Lessepsian migration (i.e. from the Red Sea to the Mediterranean Sea) (Galil 2009) – the biggest marine invasion witnesses in any other open marine system (Edelist et al. 2013). In addition to substantial movement of tropical animals into the Mediterranean, this sea is also warming at a fast pace (i.e. SST increase of 0.05 °C per year in the eastern basin) (Nykjaer 2009), increasing the thermal affinity of tropical species. This is facilitating the introduction of new Lessepsian migrants, while accelerating the spreading of already settled Lessepsian migrants from the eastern Mediterranean towards the western and northern part of the basin, where the water temperature is usually colder (Fig. 1.4) (Givan et al. 2018).

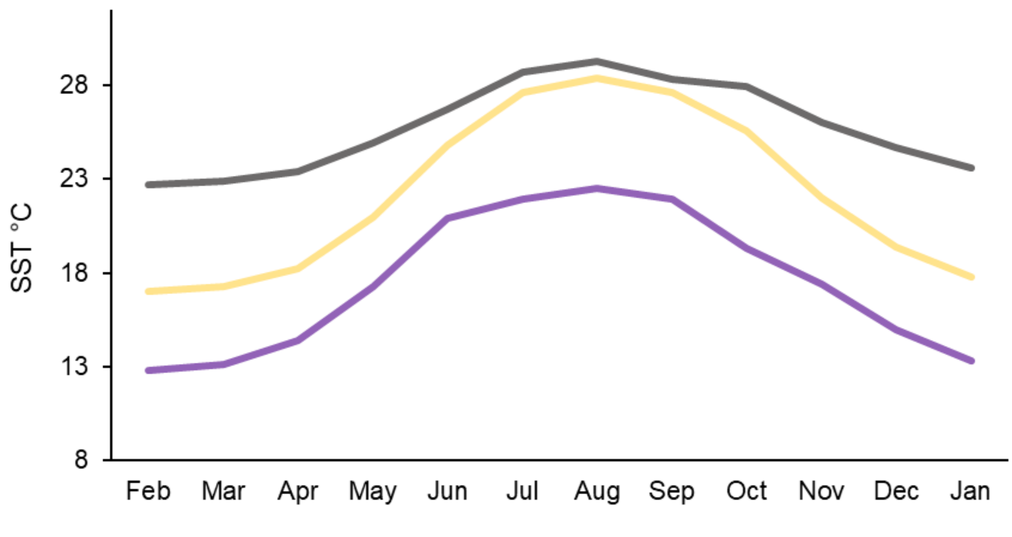

**Fig. 1.4** Monthly mean sea surface temperature (SST) profiles: black indicates the northern Red Sea (centred Sharm el-Sheikh, Egypt), yellow indicates the eastern Mediterranean Sea (Protaras, Cyprus), purple indicates the northern Mediterranean Sea (Marseille, France).

## 1.5 Thesis aims

In this thesis, by using a combination of field observations, laboratory manipulations and statistical modelling, I aim to investigate the role of phenotypic plasticity in determining coral reef species survival in an extreme and challenging environment, as well as its potential role in facilitating coral reef fish invasion in a novel habitat.

Specifically, Chapter 2 and 3 focus on the behavioural and life-history mechanisms that may allow coral reef fishes to cope with living in the extreme environment of the Arabian Gulf, while Chapter 4 focus on the Lessepsian invasion of lionfish, their plasticity in behaviour and how they interact with the native and non-native fish community. Specific research question relevant to each chapter are summarised in Table 1.1.

**Table 1.1**. Summary of questions in this thesis.

| **2. Behavioural plasticity in thermal extremes** | **Main question** | **Relevance** |
|---|---|---|
| **a. *In situ* behavioural plasticity** | i) Is there scope for coral reef fishes living in the extreme environment of the Arabian Gulf (i.e. *Pomacentrus trichrourus*) to show plasticity in behaviour to different environmental conditions?<br><br>(ii) Do individuals minimize aerobically costly behaviours (i.e. swimming, feeding etc.) when exposed to sub-optimal temperatures for activity in winter (21 °C) and summer (> 34 °C)?<br><br>(iii) Are energetic losses during winter and summer compensated by increased activity and feeding rate in spring (28 °C)? | To understand the role of behavioural plasticity in coping with environmental stressors. This is fundamental to understand the potential role of plasticity in sustaining populations. |

| | | |
|---|---|---|
| **b.** ***in situ*** **feeding plasticity** | (i) Can *Pomacentrus trichrourus* adapt their diet when exposed to different environmental conditions? Can individuals become more generalist when required? | To understand the role of feeding plasticity in coping with changing environment conditions. |
| **c.** ***Ex situ*** **behavioural plasticity** | (i) Is variation in individual behaviour, observed *in situ*, directly mediated by temperature?<br>(ii) Do fish exhibit similar degrees of behavioural plasticity when tested in the laboratory? | *In situ* observation could be potentially confounded by other variables that cannot be controlled. Hence, by isolating the environmental stressors in laboratory conditions, findings from *in situ* observations can be strengthened and further investigated. |

| 3. Growth impacts of an extreme environment | Main question | Relevance |
|---|---|---|
| **a. Impacts on growth** | (i) Do fishes in the Arabian Gulf exhibit lower growth rates, smaller size-at-age and smaller maximum body size than conspecifics from the less extreme and variable environment of the Gulf of Oman? | Understanding the demographic traits which may be impacted by an extreme environment can provide insight into how fish populations will be structured by climate change. |
| **b. Role of environmental extremes in size reduction** | (i) Do predicted differences in body size follow the temperature-size-rule?<br>(ii) Which environmental factor drive differences in growth across regions? | Environmental stressors can negatively affect body size with potential negative consequences on population replenishment. Understanding which environmental stressors induce body shrinking is fundamental to predict future impacts on fish populations. |

| **4. Lionfish and traits linked to invasion success** | **Main question** | **Relevance** |
|---|---|---|
| **a. Activity patterns** | (i) What are the activity patterns of Mediterranean lionfish?<br><br>(ii) Are Mediterranean lionfish crepuscular predators? | Activity patterns currently unknown. Crepuscular feeding activity increases hunting success as well as broadening the array of preys being available to predation. Trait linked to invasion success. |
| **b. Feeding ecology** | (i) What is the feeding ecology of Mediterranean lionfish (generalist vs specialist predator)?<br><br>(ii) Which species are the most hunted by Mediterranean lionfish? | Feeding ecology currently unknown. Generalist predators are more likely to better deal with the environmental stochasticity of a novel environment. Trait linked to invasion success. |
| **c. Native prey naiveté** | (i) Are native Mediterranean prey naïve towards lionfish predation? | Naiveté towards an invasive predator offer a competitive advantage compared to native counterparts. Trait linked to invasion success. |

# CHAPTER 2

## The influence of thermal extremes on coral reef fish behaviour and biology in the Arabian/Persian Gulf

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A pdf copy is presented in Appendix (iii)

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Following publication, seasonal changes in biological traits related to energetic stores have been added to the chapter.

This chapter is co-authored by John A. Burt (Center for Genomics and Systems Biology, New-York University Abu-Dhabi, United Arab Emirates), Tom Reader (School of Life Sciences, University of Nottingham, Nottingham, United Kingdom), Grace O. Vaughan (Center for Genomics and Systems Biology, New-York University Abu-Dhabi, United Arab Emirates), Ben B. Chapman (School of Biological Sciences, University of Manchester, United Kingdom), Veronica Santinelli (Department of Earth and Marine Sciences, University of Palermo, Palermo, Italy), Geórgenes H. Cavalcante (Instituto de Ciências Atmosféricas, Universidade Federal de Alagoas, Alagoas, Brazil) and David A. Feary (MRAG Ltd, London, United Kingdom).

DD, BC, TR and DF conceived and designed the study. DD and VS recorded *in situ* fish behaviour and laboratory dissections, while GV, BC and JB provided fieldwork and logistic support. DD conceived and carried out the laboratory

experiment. DD extracted data from videos and dissected the biological samples in Nottingham. DD carried out the statistical analysis with support from TR. GC provided the oceanographic raw data. DD wrote the manuscript with contribution and revision from DF and TR. All authors contributed in the final revision of the manuscript.

All research was carried out under approval of the NYU–AD Institutional Animal Care and Use Committee (IACUC protocol No. 16-0005) and according to the University’s animal ethics guidelines. Fish collection was carried with permission of the Environment Agency, Abu Dhabi (protocol No. EAD-TMBS-RP-0). Thanks to the University of Nottingham for support thought the whole study. The authors acknowledge the support of the NYU Abu Dhabi Marine Biology Core Technology Platform in making this research possible.

## ABSTRACT

Despite increasing environmental variability within marine ecosystems, little is known about how coral reef fish species will cope with future climate scenarios. The Arabian/Persian Gulf is an extreme environment, providing an opportunity to study fish behaviour on reefs with seasonal temperature ranges which include both values above the mortality threshold of Indo-Pacific reef fish, and values below the optimum temperature for growth. Summer temperatures in the Gulf are comparable to those predicted for the tropical ocean by 2090-2099. Using field observations in winter, spring and summer, and laboratory experiments, we examined the foraging activity, distance from refugia and resting time of *Pomacentrus trichrourus* (pale-tail damselfish). Observations of fish behaviour in natural conditions showed that individuals substantially reduced distance from refugia and feeding rate and increased resting time at sub-optimal environmental temperatures in winter (average SST = 21°C) and summer (average SST = 34°C), while showing high movement, feeding activity and increases in somatic energy stores (i.e. visceral fat) in spring (average SST= 27°C). Diet was dominated by plankton in winter and spring, while fish used both plankton and benthic trophic resources in summer. These findings were corroborated under laboratory conditions: in a replicated aquarium experiment, time away from refugia and activity were significantly higher at 28°C (i.e. spring temperature conditions) compared to 21 °C (i.e. winter temperature conditions). Our findings suggest that *P. trichrourus* may have adapted to the Arabian/Persian Gulf environment by downregulating costly

activity during winter and summer and upregulating activity and increasing energy stores in spring. Such adaptive behavioural plasticity may be an important factor in the persistence of populations within increasing environmentally variable coral reef ecosystems.

## 2.1 INTRODUCTION

Over the last century sustained climate change has resulted in average global sea surface temperature increasing by 0.6°C, with predictions of further 4.0°C rises by 2100 (Collins et al. 2013; IPCC 2014). As the planet warms, climate and weather variability, as well as the occurrence of extreme weather events, will also increase (IPCC 2012; Thornton et al. 2014). As the world's oceans absorb 93% of excess heat trapped by greenhouse gases (Laffoley and Baxter 2016), such warming is expected to have major consequences for the biodiversity, functional structure and productivity of marine ecosystems (Folguera et al. 2011; Doney et al. 2012; Bellard et al. 2012; Pecl et al. 2017). Alterations have already been documented in the diversity and assemblage structure in temperate seaweed and seagrass ecosystems (Wernberg et al. 2013; Vergés et al. 2014), coral reefs (Hughes et al. 2018) and coastal temperate rocky reefs (Lejeusne et al. 2010; Albouy et al. 2014). Despite this, our understanding of the capacity for marine ecosystems to resist or show resilience to climate change is limited (Côté and Darling 2010).

Coral reefs are particularly susceptible to a range of natural and anthropogenic disturbances that have resulted in recent degradation and loss of coral on a global scale (Wilkinson 1999; Cheal et al. 2017; Hughes et al. 2018). While these disturbances are clearly significant for the corals that serve as the biogenic engineers of these ecosystems, diverse and ecologically important reef-associated fish assemblages also often exhibit dramatic changes in composition and abundance with increasing environmental variation (Day et al. 2018;

Richardson et al. 2018; Gordon et al. 2018). Indeed, in addition to susceptibility to habitat loss (Pratchett et al. 2018), coral reef fishes are also directly threatened by ocean warming, sea surface temperature anomalies and intense pulse heat stress events (such as the warm phase of El Niño Southern Oscillation – ENSO) (Claar et al. 2018; Cai et al. 2018), due to their narrow thermal tolerance range (Tewksbury et al. 2008; Sunday et al. 2011). Experimental evidence suggests that coral reef fish may already be living close to their upper thermal limits (Rummer et al. 2014) and that their population structure may be directly impacted by increased variability in water temperature (Folguera et al. 2011; Pratchett et al. 2015; Rodgers et al. 2018).

One of the primary responses to environmental temperature change is modification of behaviour, with the speed and scope of behavioural adjustment potentially determining survival (Tuomainen and Candolin 2011; Wong and Candolin 2015). Despite this, tropical reef fishes having evolved in relatively thermally stable environments, are expected to show little ability to adjust behaviour adaptively with changing environmental temperatures (Candolin 2018). Furthermore, as the metabolism and neurophysiology of fishes are directly influenced by temperature (Pörtner and Farrell 2008; Pörtner et al. 2010), environmental temperatures outside an individual's optimum range may then have a substantially negative effect on ecological performance and survival via non-adaptive (dysfunctional) modification of behaviour, resulting in altered feeding rate, increased risk-taking behaviour, and reduced activity levels and habitat use (Figueira et al. 2009; Nagelkerken and Munday

2016). Despite this, there is a growing body of research suggesting that coral reef fishes may show adaptive behavioural plasticity in response to temperature increases, predominantly associated with temporary reductions in aerobically-costly behaviours with acute increased environmental variance (Johansen et al. 2014; Scott et al. 2017; Chase et al. 2018). For example, feeding is associated with substantial metabolic costs due to the high energy expenditure needed for digestion and nutrient uptake (McLean et al. 2018), and has been shown to be downregulated in some fish species to reduce energy costs (Nowicki et al. 2012; Fu et al. 2018). Nevertheless, how well and by what mechanisms coral reef fishes will cope with ocean warming scenarios and increased thermal variability (Thornton et al. 2014; IPCC 2014; Cai et al. 2018), is still poorly understood.

One approach to understanding how individuals may behaviourally respond to environmental variance is to study contemporary communities that exist within naturally variable environments. The fauna associated with the high latitude reefs of the southern Arabian/Persian Gulf (hereafter 'Arabian Gulf') provide a natural test of the impact of extreme water temperature variation on coral reef fish behaviour (Feary et al. 2010; Burt et al. 2011a). The Arabian Gulf experiences the highest annual change in water temperature for coral reefs globally (winter: < 15 °C, summer: > 35 °C), with fishes persisting for several months in conditions that would be considered lethal to reef fishes in other parts of the world (Riegl and Purkis 2012; Vaughan et al. 2019). Summer temperatures in the Arabian Gulf exceed the upper thermal limits of most tropical reef fishes (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers et al. 2018), while winter temperatures are well below the optimum temperatures reported for reef fish elsewhere in the Indo-Pacific (Eme and Bennett 2008; Figueira and Booth 2010; Nakamura et al. 2013). Indeed, contemporary summer water temperatures in the Arabian Gulf are comparable to those predicted for tropical oceans at the end of this century (Riegl and Purkis 2012; IPCC 2014), while winter conditions can be so severe as to induce cold water coral bleaching (Shinn 1976; Coles et al. 1991).

Using a combination of *in situ* field observations and *ex situ* experimental manipulations, this study examined the influence of extreme thermal variability on reef fish behaviour in the southern Arabian Gulf. Using the locally abundant *Pomacentrus trichrourus* (pale-tail damselfish; Günther, 1867) we performed field-based observations of behaviour across three thermally distinct seasons separated by a 13 °C sea surface temperature (SST) range (winter: SST = 21 °C, spring: 27 °C, and summer: 34 °C), monitoring replicate individual’s distance from refugia, resting times, feeding rate and diet between three sites in the southern Arabian Gulf. Additionally, across the dates and sites of all behavioural observations, we collected *P. trichrourus* individuals and examined whether there were seasonal differences in gut, liver and visceral fat weight (i.e. biological traits related to increases in energetic stores).

We predicted (i) that fish would respond to low and high-water temperature extremes by modifying their behaviour (i.e. exhibit behavioural plasticity). Specifically, we hypothesized that fish would minimize aerobically-costly behaviours (i.e. reduced distance from refugia and feeding rate, whilst increasing resting time) when exposed to sub-optimal temperatures for growth and locomotion in winter and summer, while compensating for energy losses and building up energetic stores by increasing activity and feeding rate in spring. We also hypothesized (ii) that *P. trichrourus* would exhibit flexibility in diet by shifting from a predominately planktonic diet during optimal conditions to one encompassing both planktonic and benthic prey, when exposed to suboptimal temperature, with concomitant changes in energetic stores. Such change in diet was expected to be due to restrictions in foraging movements in suboptimal conditions, with individuals becoming generalist in their feeding habits, exploiting more easily accessible resources. Finally (iii), we performed an aquarium-based experiment exposing *P. trichrourus* to temperatures typical of winter (21 °C) and spring (28 °C) in order to examine the hypothesis that variation in behaviour observed in the field was directly mediated by temperature. Overall, the results of this study have important implications for understanding how coral reef fishes may use behavioural modification to respond to the environmental variability that is expected to increase under future climate change.

## 2.2 MATERIAL AND METHODS

The pale-tail damselfish is a small omnivorous damselfish common in southern Arabian Gulf coral communities, often living in association with a single ‘home’ coral head (Allen 1991; Shraim et al. 2017). Within the Arabian Gulf this species shows high abundance, a benthic lifestyle with diurnal behaviour, a strong association with the reef, and high territoriality to a small area (territory size of 0.5 to 1.5 $m^2$). It has a small body size (max 6 cm standard length [SL]) and distinct differences in colour pattern between juvenile and adults (Randall 1995; Feary et al. 2010). All individuals within the *in situ* and *ex situ* behavioural observation were adults (~4–6 cm SL), while individuals collected *in situ* were both juvenile and adults (~2.5–6 cm SL). The optimum temperature for growth for this species is modelled to be between 24.7 °C and 29.3 °C (mean 27.2 °C) (Kaschner et al 2016, based on 258 cells from the Western Indian Ocean, including the Red Sea and the Arabian Gulf).

### 2.2.1 *In situ* behavioural quantification of *P. trichrourus*

To determine the effect of seasonal changes in temperature on behaviour of *P. trichrourus* in the Arabian Gulf, behavioural observations were replicated across three seasons: spring (April/May 2016, average SST = 27°C), summer (August/September 2016, average SST = 34°C), and winter (February/March 2017, average SST = 21°C). Observations were undertaken at three reef sites spaced ca. 40 km apart along the Abu Dhabi coastline (United Arab Emirates – southern Arabian Gulf): Dhabiya (24°21'55.8"N, 54°06'02.9"E), Saadiyat (24°35'56.4"N, 54°25'17.4"E) and Ras Ghanada (24°50'53.4"N, 54°41'25.1"E)

(Fig. 2.1). Sites were located at similar distances from shore (between 5.8 and 3.8 km), with available habitat dominated by hard-coral communities (ca. 40–55% live coral cover, Burt et al. 2011a) with all sites 6–7 m in depth (Grizzle et al. 2015).

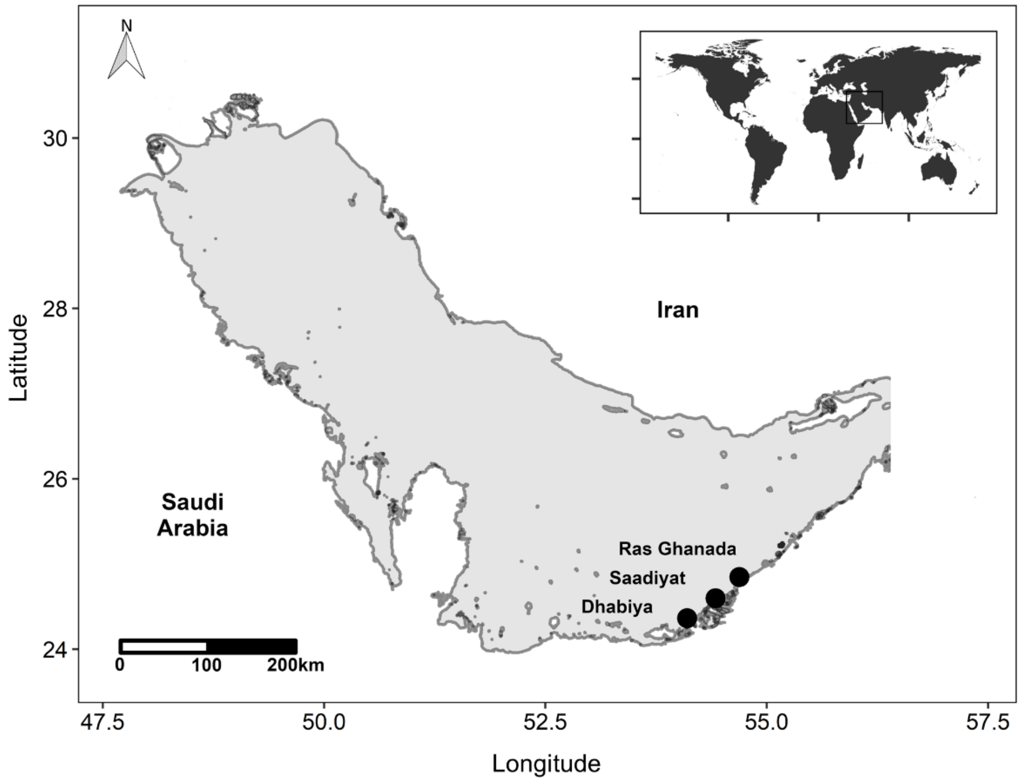


**Fig. 2.1** Study area and sampling locations in the southern Arabian Gulf.

### 2.2.1.1 *In situ* behavioural observation

Observations were undertaken by scuba diving on cloudless days between 1000 and 1400 hrs, reducing any influence of changing light levels on behaviour (Layton and Fulton 2014). In each site, across seasons, replicate coral heads holding *P. trichrourus* individuals were identified by visual searches made whilst swimming along haphazardly located transects of the reef. Coral heads held one (56% of coral heads examined), two (34%), three (7%) or four (2%)

adult *P. trichrourus*. Individual *P. trichrourus* were haphazardly selected during each season and their territory identified and marked using numbered flags (Magalhaes et al. 2013). When several adults shared the same coral head, in order to minimize the developmental variability among individuals being sampled, the individual with the largest body size was selected. Following marking of the territory, focal fish were allowed to acclimate for 4 min, and then filmed for 2 minutes (using DBPOWER HD 1080P). A minimum distance of 3 m was maintained between observer and subject. Observations were aborted if fish displayed any adverse reactions to diver's presence (i.e. increased wariness, hiding after staring at diver etc.; observed in < 5% of individuals). Across sites and seasons, a total of 226 individual behavioural observations were recorded (winter: Dhabiya n = 26, Saadiyat n = 32, Ras Ghanada n = 25; spring: Dhabiya n = 26, Saadiyat n = 32, Ras Ghanada n = 25; summer: Dhabiya n = 23, Saadiyat n = 31, Ras Ghanada n = 29).

#### 2.2.1.2 Analyses of video quantifying in situ individual behaviour

Mean distance from refugia was defined as the distance from the 'home' coral every ten seconds (Beck et al. 2016) and estimated to the nearest 5 cm referenced against the territory marking flag's length (25 cm) and the individual's body size (assumed as 5 cm SL). Resting was taken as total time (seconds) spent immobile (i.e. not active swimming, foraging or chasing behaviour) across each 2-min video. Feeding rate was the total number of bites during the observation period, while diet was identified by classifying each food bite as either on pelagic or benthic substrates. Benthic food bites were further classified as being on live coral, coral rubble, turf or sand. Behavioural data were initially extracted from 15% of videos and independently analysed and validated by two observers. As results differed by < 5 % between observers, all remaining video analyses were carried out by one observer (DD).

To estimate the relative frequency of predation or competition across seasons and sites, the abundance of predators (i.e. piscivorous fish with SL ≥ 15 cm observed interacting with *P. trichrourus*) and competitors (i.e. fishes with comparable ecology/body size to *P. trichrourus* observed chasing/being chased by *P. trichrourus*) entering each individual territory was quantified for each 2-min video observation.

### 2.2.1.3 In situ environmental measurements

To assess seasonal changes in abiotic variables in the Arabian Gulf, across the dates of all behavioural observations, daily *in situ* SST (°C) and dissolved oxygen (DO, mg $l^{-1}$) measurements were taken at 1200 hrs at each site using a YSI Professional Plus multi-parameter probe, while underwater visibility (in m) was visually estimated *in situ* by swimming over a belt transect and measuring the distance at which the diver waiting at the beginning of the transect was not visible anymore. Chlorophyll-a (chl-a, mg $l^{-1}$) measurements were downloaded as monthly composite data at 0.05 resolution from the MODIS-aqua satellite (NASA, Ocean Ecology Laboratory), while salinity (psu), wind (m $s^{-1}$) and currents (m $s^{-1}$) were obtained from the NCEP climate forecast system version 2 (CFSv2, Saha et al 2011). Salinity and current data were accessible as daily means (resolution 0.25-deg x 0.25-deg), while wind data were taken at 1200 hrs (0.205-deg x ~0.204-deg) across all experimental days.

### 2.2.2 Seasonal changes in biological traits related to energetic stores

To determine whether *P. trichrourus*' energetic stores change with seasons, *P. trichrourus* specimens were haphazardly collected across the dates of all behavioural observations (total 126 individuals; winter: Dhabiya n = 10, Saadiyat n = 9, Ras Ghanada n = 11; spring: Dhabiya n = 20, Saadiyat n = 20, Ras Ghanada n = 15; summer: Dhabiya n = 12, Saadiyat n = 11, Ras Ghanada n = 18). Sample collection was performed *in situ* using clove oil and hand nets on SCUBA. Once on the boat, fish were immediately euthanized using an ice slurry and stored on ice. Fish were then brought to the laboratory and processed: body length (standard length [SL], to the nearest mm) was measured first, secondly all organs and tissues in the peritoneal cavity were removed and placed in individual tubes with 10% buffered formalin, finally wet somatic weight of the gutted specimen was measured (SW, nearest 0.001 g). Tissues and organs were fixed in 10% buffered formalin for 24 hours and then stored in 70% ethanol; care was taken to change ethanol after 24 hours. Once transported from Abu Dhabi to Nottingham, all samples had their preservative replaced with fresh 70% ethanol, and then the gut, liver and visceral fat weight was measured (nearest 0.001 g). Raw weight measurements were divided by the somatic weight and multiplied by 10 to calculate the corresponding gut-somatic index (hereafter, GutSI), hepato-somatic index (HepatoSI) and visceral fat-somatic index (FatSI).

### 2.2.3 Aquarium-based behavioural quantification

To experimentally determine the impact of water temperature on behaviour, we examined time away from refugia and distance moved of replicate *P. trichrourus* in controlled conditions in the laboratory. Sixteen adults (mean body size 4.78 [± 0.13 SE] cm SL) were collected from Saadiyat during winter. Eight individuals were randomly allocated to separate pierced 6L bottles within either of two 900L holding tanks (control and experimental group, i.e. one holding tank per treatment). Each bottle had a 10-cm-long plastic pipe provided for shelter. All tanks were kept at 21°C, 40 psu, 8.15 pH, 6.5 mg $l^{-1}$ DO and 12 hours dark/light cycle reflecting *in situ* winter condition. 25% water changes were performed weekly, with ammonia, nitrite and nitrate kept at 0 ppt. Fish were fed *ad libitum* twice daily with commercial pellets.

After a week for acclimation, refuge use and movement of all individuals was tested at 21°C (Fig. 2.2). To do this a randomly chosen individual had its holding container submerged in an experimental tank (80 L * 50 W *40 H [cm], filled to 20 cm H) and was left to acclimate for 10 minutes. The tank's base had been divided into 40 squares (10 * 10 cm grid), a 10-cm-long segment of plastic pipe was provided as shelter, and a DBPOWER HD 1080P video camera was placed one metre above the tank. Following acclimation, the individual was released and led to the shelter; a transparent bottomless bottle was used to confine the individual which was then left for a further 20 minutes. Subsequently the bottle was removed and behaviour videoed for 16 minutes. All videoing occurred between 1000 hrs and 1400 hrs, with a 25% water change between individuals.

Water temperature within the experimental holding tank was then increased to 28°C (~0.5°C/6 h) across four days, while the temperature within the control remained constant (21 °C) (Fig. 2.2). Fish were then left for 7 days. As described above, all individuals were then retested for behaviours within either the experimental or control tank, using individual videoing.

Within all videos, the first 5 minutes were discarded to allow time of acclimation after activation of the video camera. Time away from refuge was quantified (in seconds) when individuals moved 10 cm from the shelter. Distance moved was quantified (in cm) by counting the number of grid-lines crossed over 11 min with one cross being assumed to equal to 10 cm movement, independently of the distance from refuge.

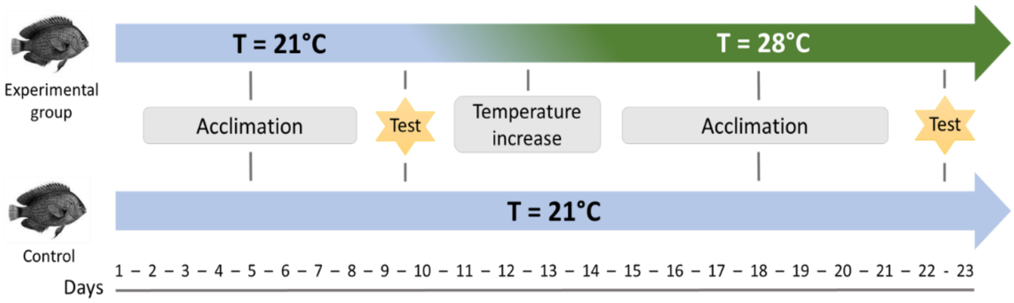


**Fig. 2. 2** Experimental design of the laboratory behavioural experiment. Bottom (days) represent the timeline of the experiment; bottom arrow represents the control group; middle boxes represent the different activities to which the fish in the two different groups were exposed; top arrow represents the experimental group.

### 2.2.4 Statistical Analysis

To determine whether abiotic and/or biotic factors significantly differed among seasons, Kruskal-Wallis test was undertaken. Abiotic factors were then combined using Principal Components Analysis (based on the correlation matrix with centring and scaling of all variables), to identify the main axes of environmental variation among observations; axes that explained more than 15% of the total variance (PC1 to PC3, hereafter 'environmental PCs') were retained and used in further analyses (Magalhaes et al. 2016).

#### 2.2.4.1 *In situ* behavioural analysis

To determine the impact of season, site, predator/competitor abundance and environmental PCs on distance from refugia and resting time, a generalised linear mixed model (GLMM) with Gaussian errors was used, while feeding rate against all predictor variables (as above) was examined using a GLMM with Poisson error distribution and log link function. Both distance from refugia and resting were not normally distributed and were, respectively, log and log (X + 1) transformed prior to testing. In all tests, date of sampling was fitted as a random effect and backwards model selection followed, using likelihood ratio tests to examine the significance of each term removed from the model. To determine whether food preference significantly differed between seasons, individual bites on substrate were analysed using Kruskal-Wallis test.

#### 2.2.4.2 Seasonal changes in biological traits related to energetic stores

To determine whether biological traits (i.e. SL, SW, GutSI, HepatoSI and FatSI) significantly differed among seasons, Kruskal-Wallis test was undertaken.

### 2.2.4.3 Laboratory behavioural assays

To determine the effect of experimental change in temperature on time away from refugia and distance moved, behavioural data before and after temperature manipulation from the control and experimental groups were tested using a GLMM with binomial error distribution and logit link function. As time away from refuge and distance moved were bimodal with a high proportion of zeros, and data transformation did not result in either normality or homoscedasticity, data were converted to binary; an individual was considered 'far from refugia' or 'moving' when time away from refugia or distance moved (respectively) were more than the median and vice versa. In all tests, 'test order' was included as a fixed factor to determine whether the order in which individual fish were tested had any influence on the result, while individual was fitted as a random effect; backwards model selection followed, using likelihood ratio tests to examine the significance of each term removed from the model. All data were analysed in R (R core development team 3.5.1, 2019).

## 2.3 RESULTS

### 2.3.1 *In situ* environmental variation

Significant differences among seasons in SST, DO, chl-a, salinity and visibility were apparent (Kruskal-Wallis test: $p < 0.05$ in all cases; Table S2.1). SST was highest in summer and lowest in winter, while DO showed the opposite trend. Chl-a concentration was higher in summer than the other seasons. PCA showed that 82% of the variation in the raw abiotic variables was captured by the first three principal components, with a high score in PC1 (39%) being associated with low SST and chl-a, and high DO. A high score in PC2 (25%) was associated with high salinity and low visibility, and a high score in PC3 (18%) was associated with high water current (Table 2.1).

**Table 2.1** Loadings of each environmental variables on the first three PC axes and the percent variance explained by each axis. The highest loadings on each of the first three PCs are showed in bold.

| Factors | PC1 | PC2 | PC3 |
|---|---|---|---|
| **Temperature** | **-0.58** | -0.06 | -0.04 |
| **Dissolved Oxygen** | **0.58** | 0.11 | 0.06 |
| **Chl-a** | **-0.49** | 0.25 | 0.03 |
| **Salinity** | -0.10 | **0.70** | 0.14 |
| **Wind speed** | -0.25 | -0.22 | -0.26 |
| **Water current** | 0.06 | -0.14 | **-0.83** |
| **Visibility** | -0.08 | **-0.60** | **0.47** |

Across all sites and seasons, predator abundance was dominated by *Lutjanus ehrenbergii*, comprising 97% of counts (Table S2.2). Predator abundance significantly differed among seasons (Kruskal-Wallis test, H = 73.790, $df = 2$, $p < 0.001$), with predators being more abundant in summer than spring or winter, while among sites predators were more abundant in Dhabiya than Saadiyat or Ras Ghanada (Fig. 2.3). The predominant competitors were other *P. trichrourus* and *Pomacentrus aquilis* individuals (Table S2.2). Competitor abundance significantly differing among seasons (H = 7.191, $df = 2$, $p = 0.027$), with slightly higher abundance in spring than winter (Table S2.2).

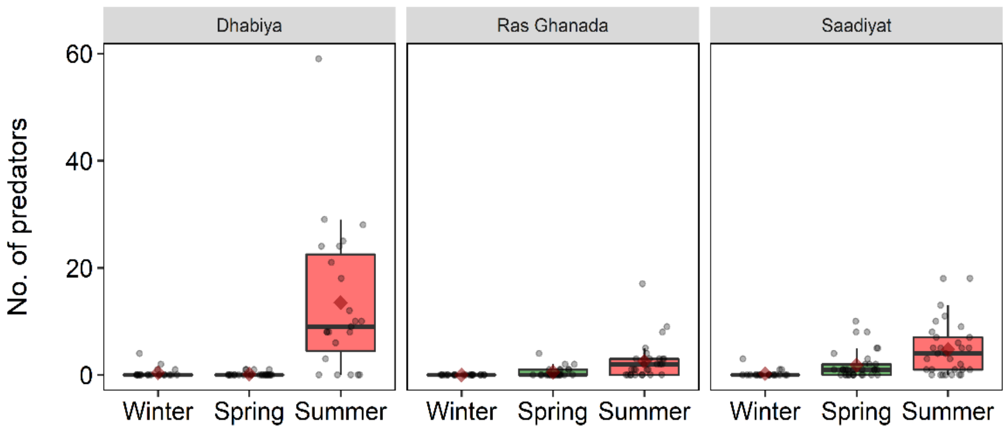


**Fig. 2.3** Changes in abundance of *Pomacentrus trichrourus'* potential predators with seasons (winter = blue, spring = green, summer = red) and locations (Dhabiya, Ras Ghanada and Saadiyat). Solid black line represents the median, with the box indicating the upper and lower quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points, and red diamond show the mean.

### 2.3.2 *In situ* behavioural analysis

Season, and the interaction between site and season, had a significant effect on *P. trichrourus* behaviour (Table 2.2), with individual from Ras Ghanada and Saadiyat showing higher distance from refuge and higher feeding rate in spring than in either winter or summer, while significantly reducing the time spent resting (Fig. 2.4). On the contrary, individuals from Dhabiya showed similar behavioural patterns across seasons in feeding rate only, but not in distance from refuge nor time spent resting (Fig. 2.4).

Significant differences in diet were apparent among seasons, with planktonic prey representing 93% and 96% of food bites in winter and spring, respectively, while only accounting for 73% in summer (Kruskal-Wallis, $H = 139.04$, $df = 2$, $p < 0.001$). Where selected, benthic food bites were predominantly taken from live corals (5 and 4% of total food bites in winter and spring, 17% in summer), with bites on coral rubble, turf and sand accounting for less than 1% of total food bites in winter and spring, and ≤ 4% in summer.

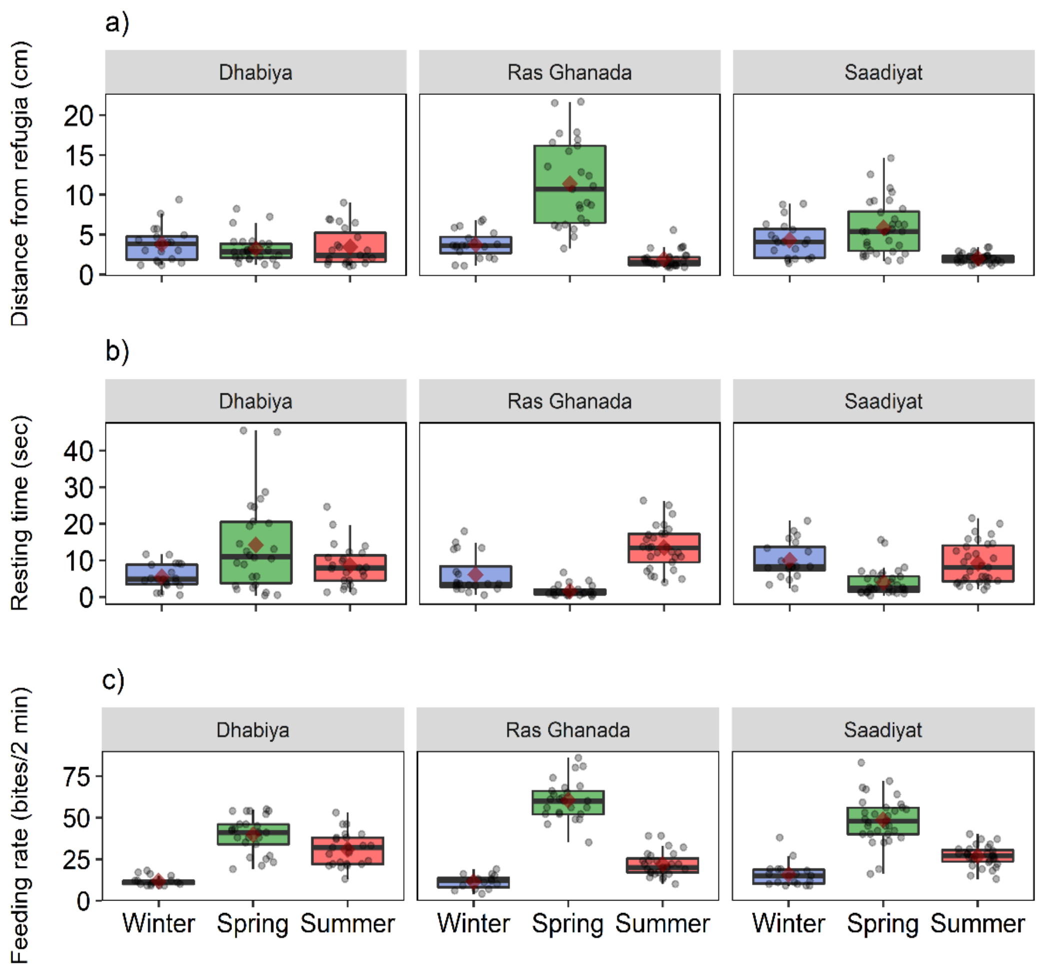


**Fig. 2.4** Changes in *Pomacentrus trichrourus in situ* behaviour among seasons (winter = blue, spring = green, summer = red) and locations (Dhabiya, Ras Ghanada, Saadiyat): **(a)** mean distance from refugia (cm); **(b)** time spent resting (s/120 s) and **(c)** number of feeding bites in 120 s. Solid black line represents the median, with the box indicating the upper and lower quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points, and red diamond show the mean.

**Table 2.2** Results of GLMM analysis of effects of biotic/abiotic factors on *Pomacentrus trichrourus' in situ* behaviour. Gaussian error structure for distance from refugia and resting time; Poisson error distribution and with log link function for feeding rate. Significant *p* values are highlighted in bold.

| Response | Predictor | Residual deviance$_{(df)}$ | Change in deviance$_{(df)}$ | *p* |
|---|---|---|---|---|
| **Distance from refugia** | Season | $8.298_{(5)}$ | $10.925_{(2)}$ | **0.004** |
| | Site | $-1.1050_{(5)}$ | $1.522_{(2)}$ | 0.467 |
| | Site x season | $-2.627_{(7)}$ | $30.565_{(4)}$ | **< 0.001** |
| | PC1 | $-37.767_{(14)}$ | $0.430_{(1)}$ | 0.512 |
| | PC2 | $-33.192_{(11)}$ | $3.690_{(1)}$ | 0.055 |
| | PC3 | $-37.390_{(13)}$ | $0.377_{(1)}$ | 0.539 |
| | Predators | $-36.882_{(12)}$ | $0.508_{(1)}$ | 0.476 |
| | Competitors | $-38.197_{(15)}$ | $0.176_{(1)}$ | 0.674 |
| **Resting time** | Season | $89.580_{(5)}$ | $4.384_{(2)}$ | 0.112 |
| | Site | $86.431_{(5)}$ | $0.539_{(6)}$ | 0.539 |
| | Site x season | $85.196_{(7)}$ | $29.556_{(4)}$ | **< 0.001** |
| | PC1 | $54.937_{(12)}$ | $1.013_{(1)}$ | 0.314 |
| | PC2 | $55.640_{(11)}$ | $0.703_{(1)}$ | 0.408 |
| | PC3 | $53.924_{(13)}$ | $1.324_{(1)}$ | 0.25 |
| | Predators | $52.042_{(15)}$ | $0.015_{(1)}$ | 0.908 |
| | Competitors | $52.601_{(14)}$ | $0.558_{(1)}$ | 0.455 |
| **Feeding rate** | Season | $1730.2_{(4)}$ | $31.427_{(2)}$ | **< 0.001** |
| | Site | $1700.7_{(4)}$ | $1.883_{(2)}$ | 0.39 |
| | Site x season | $1698.8_{(6)}$ | $17.959_{(4)}$ | **0.001** |
| | PC1 | $1674.6_{(12)}$ | $1.459_{(1)}$ | 0.227 |
| | PC2 | $1680.8_{(10)}$ | $3.805_{(1)}$ | 0.051 |
| | PC3 | $1677.0_{(11)}$ | $2.487_{(1)}$ | 0.115 |
| | Predators | $1672.9_{(14)}$ | $0.137_{(1)}$ | 0.137 |
| | Competitors | $1673.1_{(13)}$ | $0.165_{(1)}$ | 0.685 |

### 2.3.4 Seasonal changes in biological traits related to energetic stores

While there were no significant differences in standard length (H = 1.4379, *df* = 2, *p* = 0.066) and somatic weight (H = 2.0775, *df* = 2, *p* = 0.223) in *P. trichrourus* individuals among seasons (Fig. 2.5), the differences between GutSI (H = 50.01, *df* = 2, *p* < 0.001), HepatoSI (H = 33.957, *df* = 2, *p* < 0.001) and FatSI (H = 55.916, *df* = 2, *p* < 0.001) were significant (Fig. 2.6). Particularly, GutSI and HepatoSI were higher in spring compared to winter and summer, while FatSI was lowest in winter, increased in spring and was highest in summer (Fig. 2.6 and Fig. 2.7).

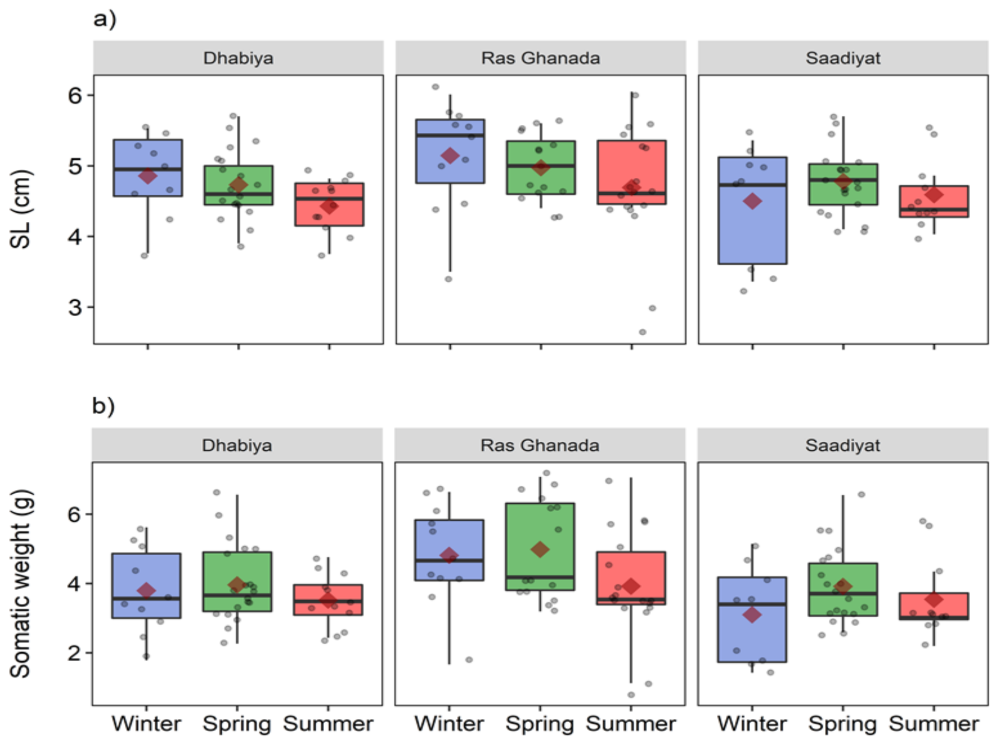


**Fig. 2.5** Changes in *Pomacentrus trichrourus* biological traits among seasons (winter = blue, spring = green, summer = red) and locations (Dhabiya, Ras Ghanada, Saadiyat): **(a)** standard length (cm); **(b)** somatic weight (g). Thick horizontal lines show the median, boxes show inter-quartile (IQR). Solid black line represents the median, with the box indicating the upper and lower

quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points, and red diamond show the mean.

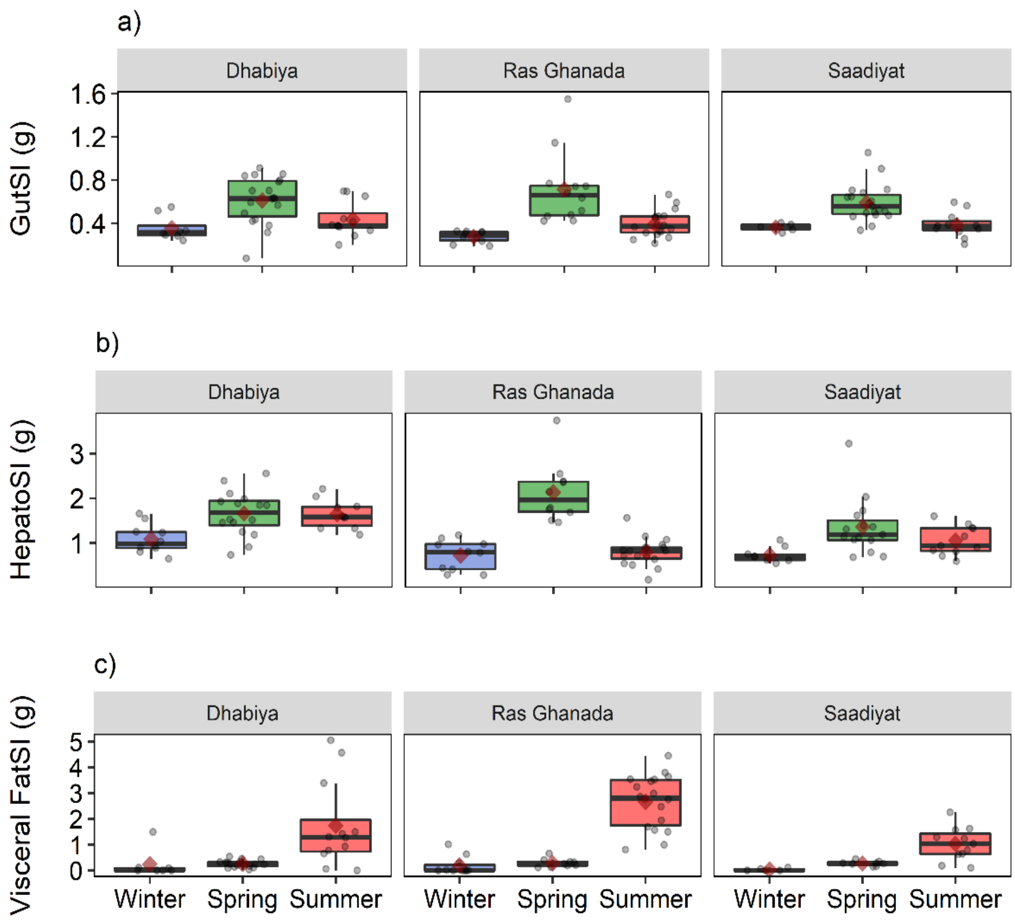


**Fig. 2.6** Changes in *Pomacentrus trichrourus* biological traits among seasons (winter = blue, spring = green, summer = red) and locations (Dhabiya, Ras Ghanada, Saadiyat): **(a)** gut-somatic index (g); **(b)** hepato-somatic index (g) and **(c)** visceral fat-somatic index (g). Thick horizontal lines show the median, boxes show inter-quartile (IQR). Solid black line represents the median, with the box indicating the upper and lower quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points, and red diamond show the mean.

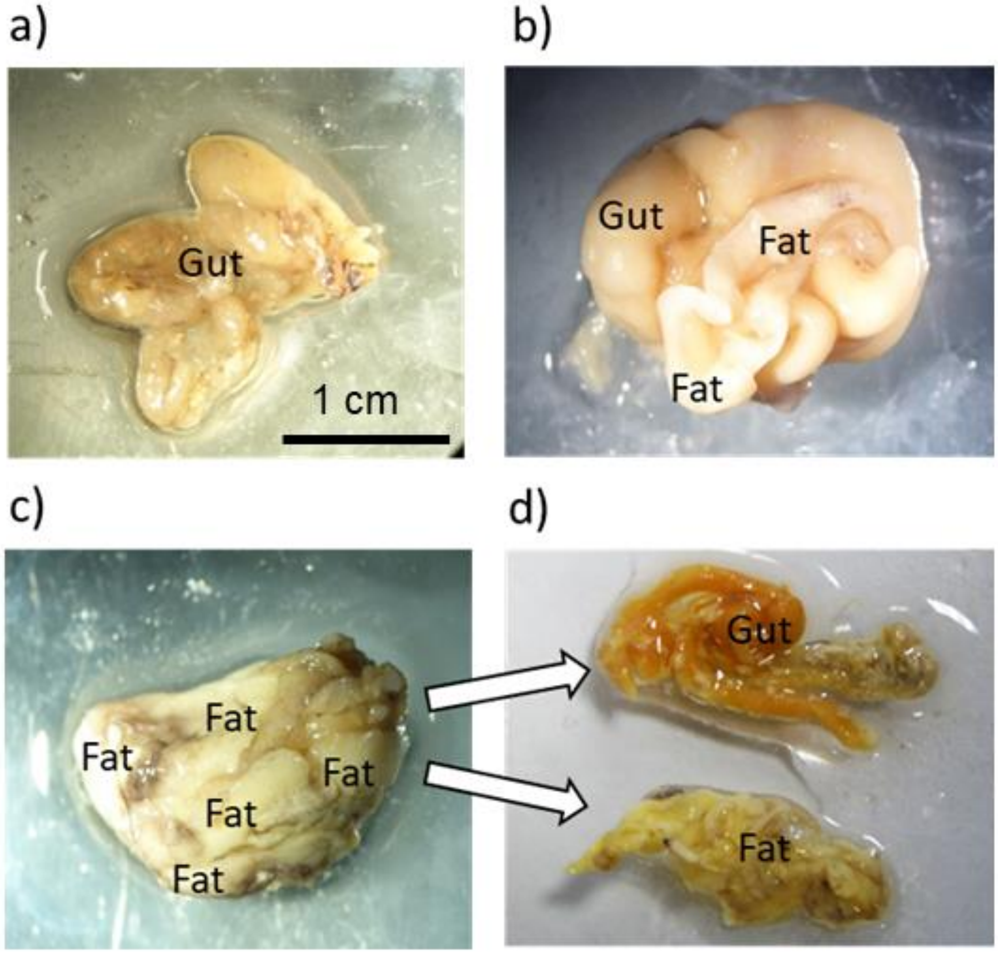


**Fig. 2.7** Example of gut and visceral fat extracted from *Pomacentrus trichrourus* individuals sampled in **(a)** winter, **(b)** spring and **(c)** summer. Note the differences between the lack of fat around the gut in winter and the fat surrounding the gut in summer (c and d).

### 2.3.3 Laboratory behavioural assays

While there was no difference between the control and the experimental group prior to temperature manipulation (i.e. both groups exposed to cold temperature), temperature had a significant effect on fish behaviour after manipulation, with fish spending more time far from the refuge and moving longer distances in the warm experimental treatment than the control (Fig. 2.8 a, b; Table 2.3). Test order had no effect on fish behaviour.

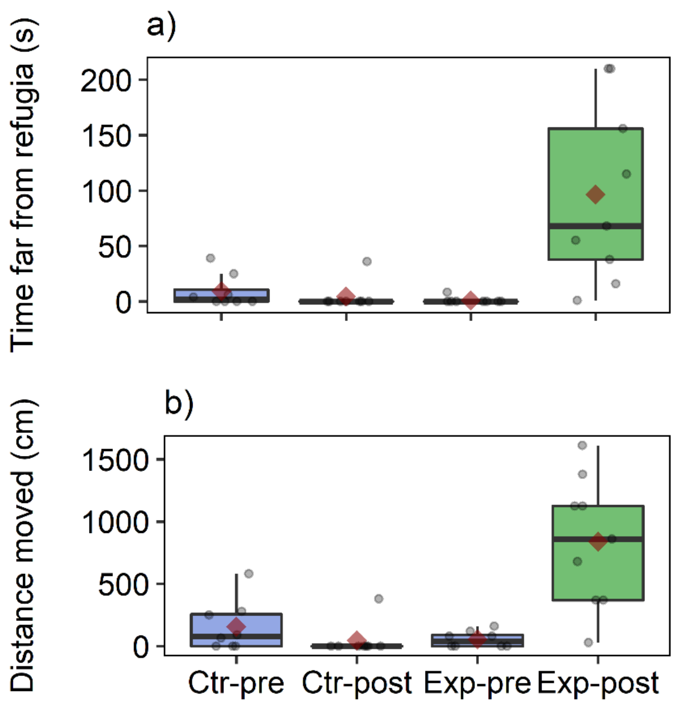


**Fig. 2.8** Changes in *Pomacentrus trichrourus ex situ* behaviour among temperature treatment: (a) mean time spent far from refugia (s), and (b) total distance moved (cm). Colours indicate temperature (blue = 21 °C, green = 28 °C). Solid black line represents the median, with the box indicating the upper and lower quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points, and red diamond show the mean.

**Table 2.3** Results of GLMM analysis of effects of experimental change in temperature on *Pomacentrus trichrourus'* behaviour.

| **Temperature manipulation** | **Response** | **Predictor** | **Residual deviance$_{(df)}$** | **Change in deviance$_{(df)}$** | ***p*** |
|---|---|---|---|---|---|
| **Pre -** | **Time far from refuge** | Treatment | $17.119_{(3)}$ | $2.7561_{(1)}$ | 0.097 |
| | | Test order | $11.945_{(8)}$ | $5.1733_{(5)}$ | 0.395 |
| | **Distance moved** | Treatment | $20.088_{(3)}$ | $1.0823_{(1)}$ | 0.298 |
| | | Test order | $18.56_{(8)}$ | $1.5277_{(5)}$ | 0.910 |
| **Post -** | **Time far from refuge** | Treatment | $6.2268_{(3)}$ | $17.194_{(1)}$ | **<0.001** |
| | | Test order | $4.1307_{(10)}$ | $2.0961_{(7)}$ | 0.954 |
| | **Distance moved** | Treatment | $6.2268_{(3)}$ | $17.194_{(1)}$ | **<0.001** |
| | | Test order | $4.1307_{(10)}$ | $2.0961_{(7)}$ | 0.954 |

'Treatment' denotes whether fish belonged to the control or experimental group. Significant *p* values are highlighted in bold.

## 2.4 DISCUSSION

Although increasing variance in global SSTs may directly impact coral reef fish community biodiversity (Pratchett et al. 2015; Day et al. 2018; Buchanan et al. 2019); coral reef fish populations might be able to mitigate the effect of rapidly changing environments through behavioural plasticity (Nagelkerken and Munday 2016; Scott et al. 2017; Chase et al. 2018). We examined the impact of seasonal changes in biotic and abiotic conditions on distance from refugia, activity and feeding ecology of the pale-tail damselfish *P. trichrourus* within the southern Arabian Gulf. We found that *P. trichrourus* substantially increased resting time and reduced distance from refugia and feeding rate at sub-optimal environmental temperatures (both high and low) when observed *in situ* and when tested in the laboratory. Individuals were also observed to shift from a planktonic-based diet to a mixed planktonic and benthic diet during the Arabian Gulf's extreme summer season. Our results show considerable scope for behavioural and trophic plasticity in *P. trichrourus*, which may allow this species to cope with seasonal variance in environmental conditions, including those that are above the mortality thresholds (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers et al. 2018) and below the optimum temperature of Indo-Pacific reef fish (Eme and Bennett 2008; Figueira and Booth 2010; Nakamura et al. 2013).

We observed substantial behavioural and trophic plasticity in *P. trichrourus'* populations among seasons. In particular, *P. trichrourus* were observed to reduce distance from refugia and feeding rate and increase resting time in winter and summer compared to spring. These seasonal changes are plausibly related to variation in water temperature, as changes in environmental temperature are known to have a direct effect on fish physiology (Angilletta 2009; Abram et al. 2017). In ectothermic animals, environmental temperatures departing from the optimum are associated with reductions in the capacity to deliver oxygen to aerobic processes and, therefore, reduction in energy for costly activities (i.e. swimming, feeding, chasing, etc.) (Pörtner and Knust, 2007; Pörtner and Farrell 2008; Munday 2012). The reduction in activity observed in *P. trichrourus,* is also in line with recent work suggesting that, when exposed to short-term higher than average SSTs, coral reef fish may temporarily mitigate bioenergetic inefficiency through reduction in energetically costly activities, as well as through changes in diet (Nowicki et al. 2012; Johansen et al. 2014; Scott et al. 2017; Chase et al. 2018). However, further research is now needed to confirm whether *P. trichrourus* actively reduce energetically costly behaviour to minimise energetic demand and mitigate bioenergetic inefficacy, or whether fish are being forced to change their behaviour due to being compromised at a lower level of organization (i.e. physiological constraints). Nevertheless, even if fish are able to modulate their activity to reduce the degree of stress they are experiencing, such strategies may not be sufficient to sustain prolonged periods (i.e. months) of extreme temperature (Rummer et al. 2014; Rodgers et al. 2018). For example, reductions in food intake and quality, coupled with low aerobic scope under extreme temperatures, can disrupt an ectothermic organism's energy balance, with substantially less energy available for long-term maintenance, growth and reproduction (Gillooly et al. 2001; Pörtner et al.

2010; Neuheimer et al. 2011), impacting individual fitness and potentially survival (Chase et al. 2018).

*Pomacentrus trichrourus'* persistence within the Arabian Gulf implies that they may have adapted over the long-term to the extreme temperature conditions experienced there (Rummer and Munday 2017). Our results potentially show that a part of their survival may be their ability to undertake seasonal energy recovery in spring, compensating for energy loss during winter by building up energetic stores to endure the upcoming summer season (Armstrong and Bond 2013). Many studies on temperate fishes have highlighted the ability to compensate energetic and growth losses during periods of adverse temperatures or food scarcity through increased feeding rate and feeding activity when conditions become favourable again (Sevgili et al. 2013; Armstrong and Bond 2013; Furey et al. 2016; Peng et al. 2017). For *P. trichrourus* such periods of recovery, where it can access highly nutritious food resources (Shraim et al. 2017) under optimal environmental temperatures (Kaschner et al 2016), may be vital for mitigating energy loss during winter and summer, and hence ultimately permit the persistence of abundant populations within the southern Arabian Gulf throughout the year.

Our lab experiments are consistent with the idea that the seasonal differences in behaviour observed in the field were the result of changes in temperature. However, other potentially important environmental variables also changed with the seasons, including predators and primary productivity. These variables could plausibly be directly responsible for changes in fish behaviour. For example, predators might have had a negative effect on *P. trichrourus* movement (i.e. reduced distance from refugia) and feeding rate (Dill and Fraser 1984; Beck et al. 2016; Catano et al. 2016), potentially leading to the shift to mixed planktonic and benthic diet observed in summer, when *P. trichrourus* may have to rely more on safer benthic food resources (i.e. live corals), despite the loss of nutritional value (Shraim et al. 2017). Similarly, the higher abundance in predatory fish in Dhabiya compared to other sites (Burt JA and Vaughan GO, unpublished data) may explain why fish were seldom observed moving long distances from the refuge, even in spring. On the contrary, we did not observe any correlation between changes in primary productivity and changes in feeding activity, suggesting that shifts in diet may not be related to primary productivity (measured as chlorophyll-a concentration) (Rueda et al. 2015; Zhou et al. 2016) but the result of temperature-related differences in food preference (Shraim et al. 2017). Ultimately, manipulative experiments would be needed to confirm the potential for predators or other drivers to produce similar behavioural changes to those seen in our temperature manipulation.

The Arabian Gulf's average SST is increasing twice as fast as the global average (Al-Rashidi et al. 2009), with predictions of further increases of 0.5 °C–1.4 °C by 2050, associated with hot salt brine discharge derived from local desalinisation plants (AGEDI 2016; Vaughan et al. 2019). As *P. trichrourus* populations live for five months of the year above their predicted thermal optimum (Jun–Oct, mean SST > 30 °C) (Kaschner et al. 2016), of which two months encompass temperatures above the mortality threshold of low latitude Indo-Pacific damselfish (July and August, mean SST ≥ 33 °C) (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers et al. 2018), Arabian Gulf populations may already be living close to their upper thermal limits; further increases in temperature are expected to pose a serious threat to population persistence. In addition, *P. trichrourus* populations in the Arabian Gulf are already considered endangered, associated with a fragmented distribution and with a strong dependence on diminishing coral habitat resources (Buchanan et al. 2016; 2019). Indeed, *P. trichrourus* are highly associated with live coral colonies, utilising them for recruitment, shelter and as trophic resources (Buchanan et al. 2016; Shraim et al. 2017). Therefore, any increases in SST that pose a serious threat to local coral communities, where bleaching events and consequent coral mortality are already common (Riegl and Purkis 2015; Riegl et al. 2018), may deprive *P. trichrourus* populations of suitable habitat and food resources in the long-term (Keith et al. 2018; Pratchett et al. 2018).

The Arabian Gulf's marine community encompasses 241 species of coral-associated bony fish, which are considered a biogeographic subset of the Indian Ocean's fauna that re-colonised the region between 6,000 and 9,000 years ago (Riegl and Purkis 2012). The coral reef fish community richness in the Arabian Gulf is thought to be lower than that in the Indian Ocean as a consequence of the Gulf's physical extremes, which fewer Indian Ocean species are able to tolerate (Coles 2003; Feary et al. 2010). However, despite a range of work examining the reef fish fauna in the region (Burt et al. 2011b; Buchanan et al.

2019), there is still little understanding of how environmental tolerance is achieved in Arabian Gulf-dwelling species. For *P. trichrourus* this study has shown that populations may be able to behaviourally mitigate the high variance in temperature and temperature extremes which are consistent with predictions for the tropical ocean by the end of the century (ICCP 2014). It appears that by reducing movement from shelter and feeding activities within extreme seasons (summer, winter) and showing metabolic compensatory activity behaviour (including feeding) during the environmentally benign spring season, populations of *P. trichrourus* are able to thrive in one of the most thermally extreme marine environments. Such adaptive behavioural plasticity is consistent with current theory regarding how animals deal with extremes and may be an important mechanism for how increases in temperature and temperature variability may be mitigated by fishes on Indo-Pacific reefs by the end of the century.

# CHAPTER 3

## Growth impacts in a changing ocean: insights from two coral reef fishes in an extreme environment

This chapter is co-authored by Tom Reader (School of Life Sciences, University of Nottingham, Nottingham, United Kingdom), John A. Burt (Center for Genomics and Systems Biology, New-York University Abu-Dhabi, United Arab Emirates), Ashley Fowler (University of Technology Sydney, Sydney, Australia), Veronica Santinelli (Department of Earth and Marine Sciences, University of Palermo, Palermo, Italy), Grace O. Vaughan (Center for Genomics and Systems Biology, New-York University Abu-Dhabi, United Arab Emirates), Geórgenes H. Cavalcante (Laboratório de Oceanografia Física, Universidade Federal de Alagoas, Alagoas, Brazil), Andrew S. Hoey (James Cook University, ARC Centre of Excellence for Coral Reef Studies, Townsville, Australia), Andrew G. Bauman (National University of Singapore, Singapore), Brett M. Taylor (Australian Institute of Marine Science, Indian Ocean Marine Research Centre, Crawley, Australia) and David A. Feary (MRAG Ltd, London, United Kingdom).

DD and DF conceived and designed the study. DD, VS, DF, AB, AH, GV collected samples and biometric data. GV, VS and JB provided fieldwork and laboratory support. BT grinded the otoliths and mounted them on slides. DD and BT aged the otolith. DD measured annual increments and built the statistical models, with supervision of TR and AF. GC provided the oceanographic raw data. DD wrote the manuscript with contribution from DF and revision from all co-authors.

# ABSTRACT

Determining the life history consequences for fishes living in extreme and variable environments will be vital in predicting the likely impacts of ongoing climate change on reef fish demography. Here, we compare size-at-age and maximum body size of two common reef fish species (*Lutjanus ehrenbergii* and *Pomacanthus maculosus*) between the environmentally extreme Arabian/Persian Gulf ('Arabian Gulf') and adjacent comparably benign Oman Sea. Additionally, we use otolith increment width profiles to investigate the influence of temperature, salinity and productivity on the individual growth rates. Individuals of both species showed smaller size-at-age and lower maximum size in the Arabian Gulf compared to conspecifics in the less extreme and less variable environment of the Oman Sea, suggesting a life-history trade-off between size and metabolic demands. Salinity was the best environmental predictor of interannual growth across species and regions, with low growth corresponding to more saline conditions. However, salinity had a weaker negative effect on interannual growth of fishes in the Arabian Gulf than in the Oman Sea, indicating Arabian Gulf populations may be better able to acclimate to changing environmental conditions. Temperature had a weak positive effect on the interannual growth of fishes in the Arabian Gulf, suggesting that these populations may still be living within their thermal windows. Our results highlight the potential importance of osmoregulatory cost in impacting growth, and the need to consider the effect of multiple stressors when investigating the consequences of future climate change on fish demography.

## 3.1 INTRODUCTION

Anthropogenic global climate change is having significant biological impacts on individuals, species and ecosystems (e.g. Parmesan and Yohe 2003; Bellard 2012; Hughes et al. 2018; Pratchett et al. 2018; França et al. 2020). Reductions in body size, coupled with geographic shifts in species distribution (Walther et al. 2002; Parmesan and Yohe 2003; Feary et al. 2014) and changes in phenology (Walther et al. 2002; Stenseth 2002; Visser and Both 2005; Taylor 2008), are recognised as common responses to global warming in ectotherms (Daufresne et al. 2009; Gardner et al. 2011; Ohlberger 2013). Such reduction in body size is consistent with the temperature-size-rule (TSR) (i.e. body size decrease at higher temperature) (Atkinson 1994; Kingsolver and Huey 2008; Ohlberger 2013; Horne et al. 2017; Huss et al. 2019) and is particularly evident in aquatic environments (Forster et al. 2012; Horne et al. 2015), where fish and other aquatic organisms' average body size has already declined by 5–20% over the last two decades (Baudron et al. 2014; Audzijonyte et al. 2016; van Rijn et al. 2017). Experimental temperature-size responses, models and meta-analyses suggests that body size will further reduce by 3–5% per degree of warming in aquatic arthropods, while in fishes it may decline by 14–24% by 2050 under a higher green-house gases emission scenario (A2 scenario, IPCC 2007; Cheung et al. 2013; Pauly and Cheung 2018b).

Decreasing fish sizes will impact fecundity and fisheries productivity (Baudron et al. 2014; Barneche et al. 2018), prey-predator interactions (Barnes et al. 2010), and overall ecosystem functioning (Bellwood et al. 2012; Cheung et al.

2013). Understanding what drives reductions in fishes body size will be essential for predicting how populations are impacted by projected climate change. In this regard, despite the ubiquity of the TSR in explaining size reduction in a range of taxa, the underlying mechanisms of body size reduction with increasing temperature are still debated (Audzijonyte et al. 2019) .

Projected increases in mean temperature and temperature variability due to climate change (i.e. 4.0 °C increase by 2100, IPCC 2014; Hoegh-Guldberg 2018) are likely to be particularly challenging for marine fish due to the greater energetic demands for routine metabolic activities (Gillooly et al. 2001; Pörtner and Knust 2007; Neuheimer et al. 2011) with, ultimately, less energy available for somatic growth. Similarly, projected intensification of the global water cycle (4–8% per degree Celsius of increase of surface air temperature change) and consequent increase of water salinity in already dry regions (Durack et al. 2012; Skliris et al. 2014; Zika et al. 2018), will likely increase the osmoregulation costs for many marine species (Boeuf and Payan 2001; Ern et al. 2014), especially those living in hypersaline semi-enclosed seas.

One approach to understanding how marine fish demography may be impacted by future environmental variance and extremes in temperature and salinity is to study contemporary communities that exist within naturally extreme and variable environments. Here, we compare the effect of water temperature, salinity and primary productivity on the size-at-age and growth rate of coral reef fishes between the environmentally extreme southern Arabian/Persian Gulf (hereafter 'Arabian Gulf') and comparatively more benign adjacent Oman

Sea (Fig. 1). The Arabian Gulf has the largest thermal range (> 20 °C) and highest maximum sea surface temperature (SST) experienced by extant coral reef fishes (winter: < 15 °C, summer: > 35 °C), with fishes enduring several months of conditions considered lethal to reef fishes in other parts of the world (Riegl and Purkis 2012; Rummer et al. 2014; Vaughan et al. 2019). In addition, present summer SSTs in the Gulf are comparable to those expected for tropical oceans by 2100 (Riegl and Purkis 2012; Hoegh-Guldberg 2018), while winter temperatures can be so low as to induce cold water coral bleaching (Shinn 1976; Coles and Fadlallah 1991). Additionally, due to restricted water exchange through the narrow Strait of Hormuz, as well as limited freshwater input (Reynolds 2002) and high evaporation (Reynolds 1993), the Arabian Gulf's waters are characterized by hypersaline conditions (annual mean salinity 42 psu) that are the highest reported for coral reefs (Sheppard 1993, Bauman 2013, Vaughan et al. 2019). In contrast, the Oman Sea is subject to less extreme and variable temperature and salinity, but a higher baseline and higher interannual variation of chlorophyll-a concentration (used as a proxy for primary productivity) (Coles 1997, Coles 2003).

Given differences in environment conditions between the Arabian Gulf and the Oman Sea, we hypothesise that, in line with the TSR, (i) fishes in the Arabian Gulf would exhibit lower growth rates, as well as smaller size-at-age and maximum body size than conspecifics from the less extreme and less variable environment of the Oman Sea; and (ii) that predicted differences in growth would be driven interannually by local environmental conditions. We investigated the role of temperature, salinity and productivity in structuring fish demography between regions by using an otolith sclerochronology approach and mixed-effect modelling, and predicted that low growth rate and small body size would be the results of extreme temperature ranges in the Arabian Gulf, exacerbated by high salinity and lower primary productivity.

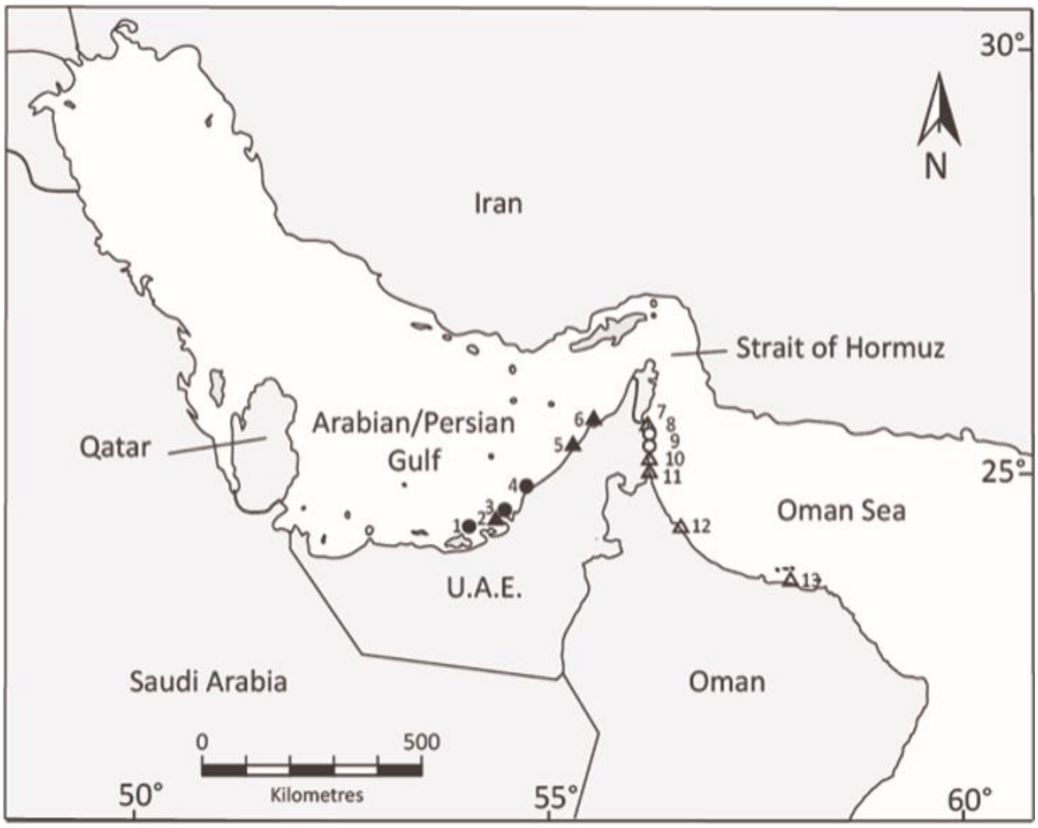


**Fig. 3.1**. Map of the study regions showing collection locations in the southern Arabian/Persian Gulf and northern Gulf of Oman (circles: field collection–reefs, triangles: local fish landing sites; refer to Table S2 for names, coordinates and sampling method).

## 3.2 MATERIAL AND METHODS

### 3.2.1 Study species

To determine whether fish growth is reduced in the Arabian Gulf compared to Oman and whether extreme environmental variables are the drivers of somatic growth differences, we analysed the otolith structure of the blackspot snapper (*Lutjanus ehrenbergii*, F. Lutjanidae [Peters, 1869]) and the yellow-bar angelfish (*Pomacanthus maculosus*, F. Pomacanthidae [Forsskål, 1775]). Both *L. ehrenbergii* and *P. maculosus* are coral-associated species commonly found on nearshore patch and fringing reefs throughout both regions (Feary et al. 2010; Burt et al. 2011b) and are known to have highly determinate growth patterns (Grandcourt et al. 2010; 2011). Furthermore, the two species were chosen because they are phylogenetically and ecologically disparate: *L. ehrenbergii* is a generalist carnivore, feeding on benthic invertebrates associated with turfing algae (i.e. amphipods, isopods) and small fish (Randall 1995; D'Agostino et al. 2019), while *P. maculosus* is a facultative spongivorous/corallivorous (Shraim et al. 2017).

### 3.2.2 Sample collection of focal species for life history comparison

Sample collection encompassed six sites within the Arabian Gulf (three reefs and four local fish landing sites, spanning from Dhabiya to Umm Al Quwain) and seven sites within the Oman Sea (two reefs and five local fish landing sites, spanning from Dibba to As Seeb) (Fig. 1, Table S2). As both species are relatively site attached and the nearest sites between the two regions were separated by more than 300 km (Grizzle et al. 2015), negligible movement between regions was predicted (Buchanan et al.

2019). Individuals collected *in situ* (i.e. from the reefs) were collected using the fish anaesthetic clove oil (juveniles) or spear guns (sub-adults and adults) and euthanized using an ice slurry. Upon collection, all individuals were measured (standard length [SL], nearest mm), weighed (total weight, nearest g) and sagittal otoliths removed, cleaned in ethanol and stored dry.

### 3.2.3 Age determination

To determine age, 1012 and 210 otoliths were sectioned from *L. ehrenbergii* and *P. maculosus* specimens, respectively (Table 3.1). Each otolith was ground to the nucleus to produce a thin transverse section and mounted on a microscope slide using established procedures (i.e. Taylor and McIlwain 2010). Otoliths were examined under transmitted light with a low power microscope and individual ages estimated by counting the number of annual increments, or annuli, along the dorsal antisulcus axis of each otolith (Fig. 3.2). Previous studies have verified the deposition of annual increments for both species (Grandcourt et al. 2010; 2011). Blind reads (for size and collection location) of annual increments were performed on three separate occasions for each specimen. Final age was determined when two or more counts agreed. If agreement was not achieved after three counts, the sample was excluded from the analysis. For individuals < 1 year, otolith sections were further ground with lapping film, polished by hand with 0.3 µm alumina powder and viewed through a compound microscope. For these individuals age was then estimated by counting the number of daily increments, with three blind reads performed for each individual. Final age for juvenile fishes was taken as the median of three counts when all counts were within 10% of the median. Samples with counts > 10% of the median were excluded from the analysis.

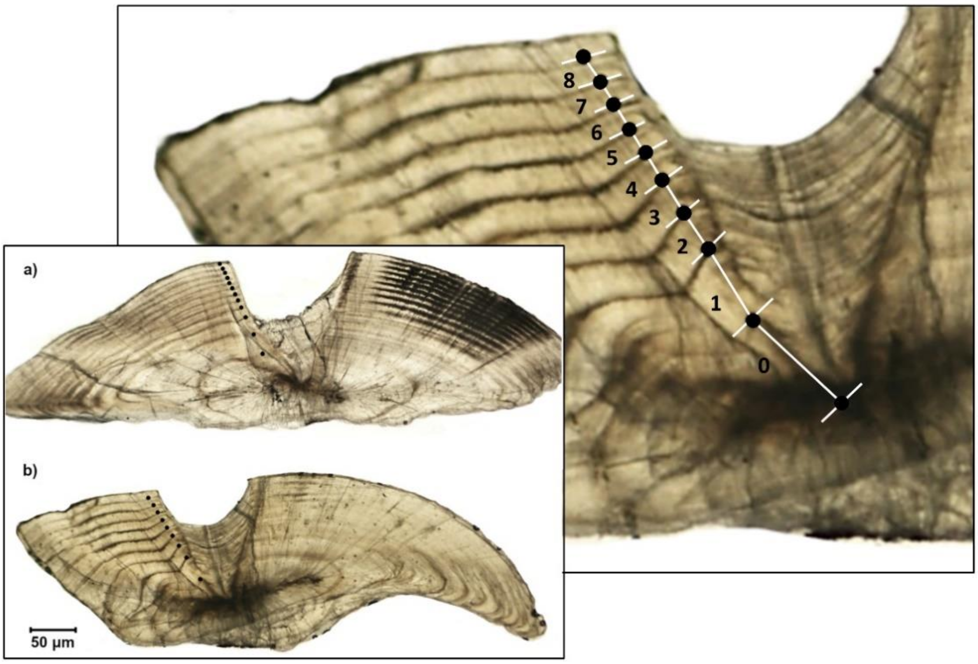


**Fig. 3.2** Annual increment widths follow measurements along transverse sections of otoliths in **(a)** *Lutjanus ehrenbergii*, and **(b)** *Pomacanthus maculosus*. Photographs were taken under a high-power microscope with transmitted light. Inset shows the annotated transverse section of a fish estimated as 8 years old.

**Table 3.1.** Details of *Lutjanus ehrenbergii* and *Pomacanthus maculosus* otolith samples used to investigate differences in growth between the Arabian Gulf and Oman. Site and species-specific growth comparison and best-fit re-parameterised von Bertalanffy growth-function parameters (rVBGF) are shown.

| **Species** | **Area** | ***n*** | **Size range (mm)** | **Age (days–years)** | **Age$_{max}$ (SE)** | **L$_{max}$ (SE)** | **$L_1$** | **$L_3$** | **$L_6$** | **- λ** | **σ** |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Lutjanus ehrenbergii* | Arabian Gulf | 873 | 33–224 | 38–15 | 8.58 (0.41) | 199.52 (1.91) | 132.54 | 186.31 | 189.45 | 4071.80 | 25.53 |
| | Oman | 139 | 18–282 | 27–16 | 11 (0.53) | 246.21 (3.71) | 144.72 | 216.52 | 223.12 | 695.66 | 34.81 |
| *Pomacanthus maculosus* | Arabian Gulf | 168 | 9–262 | 9–31 | 14.62 (1.14) | 197.48 (4.94) | 95.12 | 160.65 | 170.48 | 841.03 | 36.12 |
| | Oman | 42 | 40–264 | 81–22 | 8.55 (1.93) | 227.11 (6.55) | 107.34 | 177.83 | 188.34 | 204.78 | 28.65 |

*n*, sample size; $L_1$, mean size at age one; $L_3$, age three; $L_6$, age six; − λ, negative log-likelihood; σ, standard deviation. All sizes are in mm SL, Ages are in years unless indicated otherwise.

### 3.2.4 Population-level growth, body size and life span

To model and compare the population growth rate of *P. maculosus* and *L. ehrenbergii* between the Arabian Gulf and Oman, the re-parameterised version of the von Bertalanffy growth function (rVBGF, Francis 1988) was used (Visconti et al 2018). The rVBGF describes growth based on modelled body size of individuals at three ages, $L_\tau$, $L_\omega$ and $L_\mu$, allowing a direct comparison of mean size-at-age data between populations. Age $\tau$ represents fast, early growth (i.e. ascending part of the growth trajectory), $\mu$ represents the asymptote of growth (i.e. when growth reaches a plateau), while $\omega$ represents onset of a reduction in growth rate (Trip et al. 2008, 2014). To model species growth based on the trajectory of the region-specific growth curves, ages 1 and 6 years (based on annul increments counts) were taken as $L_\tau$ (hereafter '$L_1$') and $L_\mu$ (hereafter '$L_6$'), respectively, while $L_\omega$ was calculated at 3 years (hereafter '$L_3$'). The rVBGF model was fitted using the age (years) and length data (mm SL) of each sample and by constraining the curve to a length of settlement of 10 mm SL (Grandcourt et al. 2011). The best-fit model parameters, $L_1$, $L_3$ and $L_6$, describing each dataset were determined by minimizing the negative log of the likelihood, given a probability density function with a Poisson distribution (Haddon 2001).

Mean maximum age (hereafter '$Age_{max}$') and mean maximum body size (hereafter '$L_{max}$') were estimated for both species in each region. $Age_{max}$ and $L_{max}$ were taken, respectively, as the average age (years) and body size (SL) of the 25% oldest or largest adult (i.e. ≥ 3 years old) individuals, respectively (Trip et al. 2008, 2014). Differences in mean $Age_{max}$ and $L_{max}$ between populations were analysed using linear models.

### 3.2.5 Individual annual growth estimation

To determine whether yearly growth rate differs within species between regions, annual increment width was measured between individuals. A subset of the total samples (148 and 144 otoliths of *L. ehrenbergii* and *P. maculosus*, respectively; Table 3.2) that showed clear edges between annual increments and with at least one completed annual increment (i.e. individuals ≥ 2 years old) were photographed and examined. As otolith growth is an appropriate representation of fish somatic growth in our species (i.e. significant positive relationship between otolith radius and individual body length, see Fig. S3.1a, b), increment widths were measured (mm) along the dorsal anti-sulcus axis (from core to edge) using MorphoJ (v1.06). Distances between the outer edges of each annual increment were taken to indicate the width of each consecutive growth increment (Fig. 3.2a, b). Through back calculation from age-at-capture (hereafter 'AAC') and year of capture, age ('Age') and calendar growth year ('Year') were respectively assigned to each increment (Table 3.3). The first (core to first annual increment) and last (marginal) increment were not used in the analysis, because they did not represent a full year of growth (Martino et al. 2019). For each region, the sample size was at least five increment measurements per calendar year. In total, increment widths were measured from 148 *L. ehrenbergii* (Arabian Gulf = 58; Oman = 90) and 144 *P. maculosus* (Arabian Gulf = 107; Oman = 37) individuals (Table 3.2). Increment widths encapsulated growth of individuals between 2002 and 2015 in *L. ehrenbergii* and between 1993 and 2016 in *P. maculosus* (Table 3.2).

**Table 3.2.** Summary of *L. ehrenbergii* and *P. maculosus* otolith samples used to develop sclerochronologies.

| Species | Area | No. sampled years | No. fish | No. increment measurements | Age range (yr) | Range of years |
|---|---|---|---|---|---|---|
| *L. ehrenbergii* | Arabian Gulf | 2 | 58 | 211 | 2–15 | 2002–2015 |
| | Oman Sea | 2 | 90 | 368 | 2–16 | 2003–2015 |
| *P. maculosus* | Arabian Gulf | 3 | 107 | 678 | 2–31 | 1993–2016 |
| | Oman Sea | 4 | 37 | 119 | 2–22 | 2002–2016 |

**Table 3.3.** Descriptions of predictor variables used in the mixed-effects modelling of *Lutjanus ehrenbergii* and *Pomacanthus maculosus*'s growth.

| Parameter | Description | Data range |
|---|---|---|
| **Fixed intrinsic effects** | | |
| Age | Age in years when otolith annual increment was formed. | |
| Year | Year in which the annual increment was formed. | |
| AAC | Age in years at time of capture. Measure of potential selectivity on growth. | |
| **Fixed extrinsic effects** | | |
| Mean SST | Mean annual sea surface temperature (°C). | 1993–2016 |
| Max SST | Mean maximum sea surface temperature during the hottest month (Aug) (°C). | 1993–2016 |
| Min SST | Mean minimum sea surface temperature during the coldest month (Feb) (°C). | 1993–2016 |
| Salinity | Mean annual salinity (psu). | 1993–2016 |
| Chl-a | Mean annual chlorophyll-a (mg $m^{-3}$). | 2003–2016 |
| **Random effects** | | |
| 1\|FishID | Unique identifier code for each fish. | |
| 1\|Year | Calendar year in which the increment was formed, quantifies inter-annual growth variability. | |
| Age\|FishID | Random age slope for FishID random intercept, allows for individual-specific differences in the growth−age relationship | |
| Age\|Year | Random age slope for Year random intercept, allows for year-dependent differences in age-specific growth. | |

### 3.2.6 Growth mixed modelling

Sources of annual growth variation in *P. maculosus* and *L. ehrenbergii* were investigated using a series of hierarchical mixed-effects models predicting variation in otolith increment widths (following Morrongiello and Thresher 2015). Growth was modelled separately for the two regions as to avoid the co-variation of multiple environmental factors with regions. All mixed modelling was performed in R (R core development team 3.5.1, 2019), using the packages lme4 (Bates et al. 2015), effects (Fox 2003), and AICcmodavg (Mazerolle 2019). Modelling could not be done for *P. maculosus* in Oman due to insufficient sample sizes.

To explore potential drivers of inter-annual growth variation within the model, we used both intrinsic and extrinsic predictors. Intrinsic predictors (i.e. intra-population drivers) were the fixed effects of Age and AAC, which account for expected age-related trends, bias, and selectivity (Morrongiello et al. 2012), while the random effects of FishID and Year were utilized (Table 3.3 and Supplementary materials Chapter 3 – '[B.1.1] intrinsic predictors' for details). Extrinsic predictors (i.e. environmental predictors) were mean, maximum and minimum annual SST (°C) ('Mean-, Max-  and Min SST', respectively), annual mean salinity ('salinity', psu) and annual mean chlorophyll-a ('chl-a', mg $m^{-3}$) (Table 3.3 and Supplementary materials Chapter 3 – '[B.1.2] Extrinsic predictors' for details). Due to the lack of sex data, sex was not used as growth predictor, nevertheless patterns of sexual dimorphism are known for our species (i.e. female individuals grow larger in *L. ehrenbergii*, while males grow larger in *P. maculosus*) (Grandcourt et al. 2010, 2011), and were taken into account during the interpretation of the results.

### 3.2.6.1 Model selection

Growth, Age, and AAC were log-transformed to meet model assumptions. All variables (intrinsic and extrinsic) were mean centred to facilitate the convergence of the model and the interpretation of the random slopes (Morrongiello and Thresher 2015). Analyses were run with a two-stage approach: in the first stage, we built a base set of linear mixed models that encompassed a series of random effect and fixed intrinsic effect structures in order to identify the optimal intrinsic model (Tables S3.3–S3.6 and Supplementary materials Chapter 3– ' [B.1.3] Models selection' for details of models selection, ranking and fitting). In the second stage of the analysis, we investigated whether environmental factors influenced growth. We extended the optimal intrinsic model for each region to include single or combinations between two environmental variables, which were fitted separately and ranked using Akaike's information criterion corrected for small sample sizes ($AIC_C$) (Burnham and Anderson 2004) and $\Delta AIC_c$ values (Table S3.7, S3.8). Interactions between SST effects and between SST and salinity were not included in the model selection as a high level of correlation was expected. Additionally, collinearity between all the remaining combinations was explored using variance inflation factor (VIF) and models with VIF above 3 were removed from comparison (Hair et al. 1998). Finally, linear temporal growth trends were investigated by adding Year as a fixed effect to the optimal intrinsic model.

## 3.3 RESULTS

### 3.3.1 Population-level growth, body size and life span

The age range of *L. ehrenbergii* individuals was similar between regions, ranging between 38 days to 15 years in the Arabian Gulf and 27 days to 16 years in Oman; instead *P. maculosus* individuals' age range differed between regions comprising younger and older individuals in the Gulf compared to Oman (9 days to 31 years and 81 days to 22 years, respectively) (Table 3.1).

Both *L. ehrenbergii* and *P. maculosus* had consistently smaller asymptotic size and maximum length ($L_{max}$) in the Arabian Gulf than Oman (Fig. 3.3a, b; Table 3.1). Specifically, *L. ehrenbergii* and *P. maculosus* individuals were 19% (linear regression, F = 153.3, *df* = 1,49, $p < 0.001$) and 13% smaller (F = 9.968, *df* = 1,34, $p = 0.003$), respectively. Maximum age ($Age_{max}$) was significantly smaller in the Arabian Gulf compared to Oman for *L. ehrenbergii* (F = 4.362, *df* = 1,49, $p = 0.042$), but did not significantly differ between *P. maculosus* populations (F = 1.859, *df* = 1,34, $p = 0.182$) (Table 3.1).

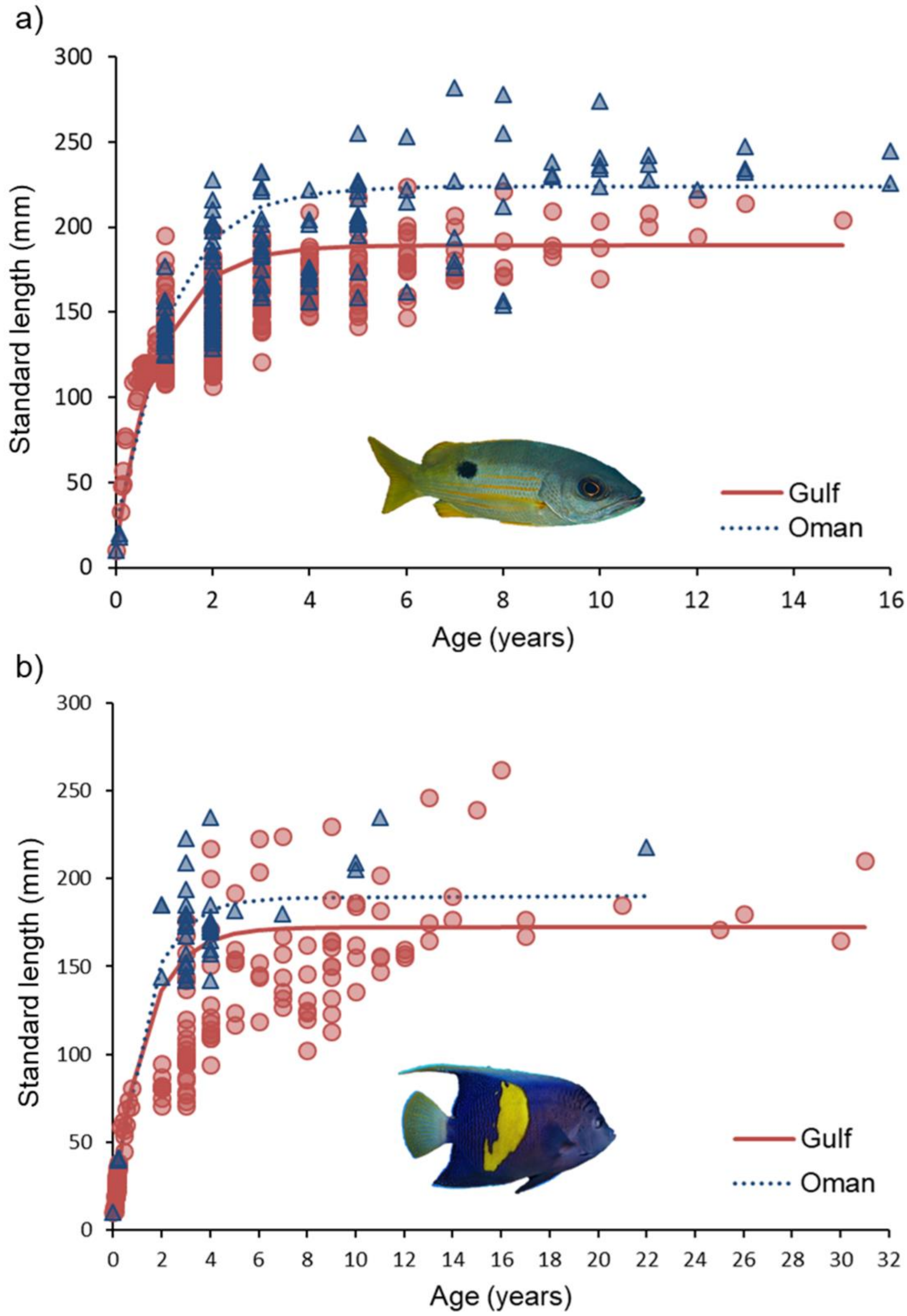


**Fig. 3.3** Comparison of re-parameterised version of the von Bertalanffy growth function (rVBGF) for *Lutjanus ehrenbergii* **(a)** and *Pomacanthus maculosus* **(b)** between the Arabian Gulf ('Gulf') and the Oman Sea ('Oman'). Data points: red circles = Arabian Gulf, blue triangles = Oman Sea. Note different scales on the x-axis.

## 1.3.2 Sources of individual growth variation

### 1.3.2.1. Extrinsic conditions

The magnitude and temporal trends of extrinsic parameters varied significantly between the Arabian Gulf and the Oman Sea (Fig. 3.4, Table S1). Both regions recorded relatively high inter-annual variation in min, mean, and max SST, while inter-annual variation in salinity was high in the Arabian Gulf but minimal in the Oman Sea. In addition, both regions recorded relatively high inter-annual variation in chlorophyll-a concentrations, which was stronger in the Oman Sea than the Arabian Gulf (Fig. 4a). Despite no difference in annual mean SST between regions, the Arabian Gulf had higher intra-annual SST variation, with temperature significantly colder in winter and warmer in summer compared to the Oman Sea, as well as higher annual mean salinities, and lower annual mean chlorophyll-a concentrations (Fig. 4b, Table S3.1).

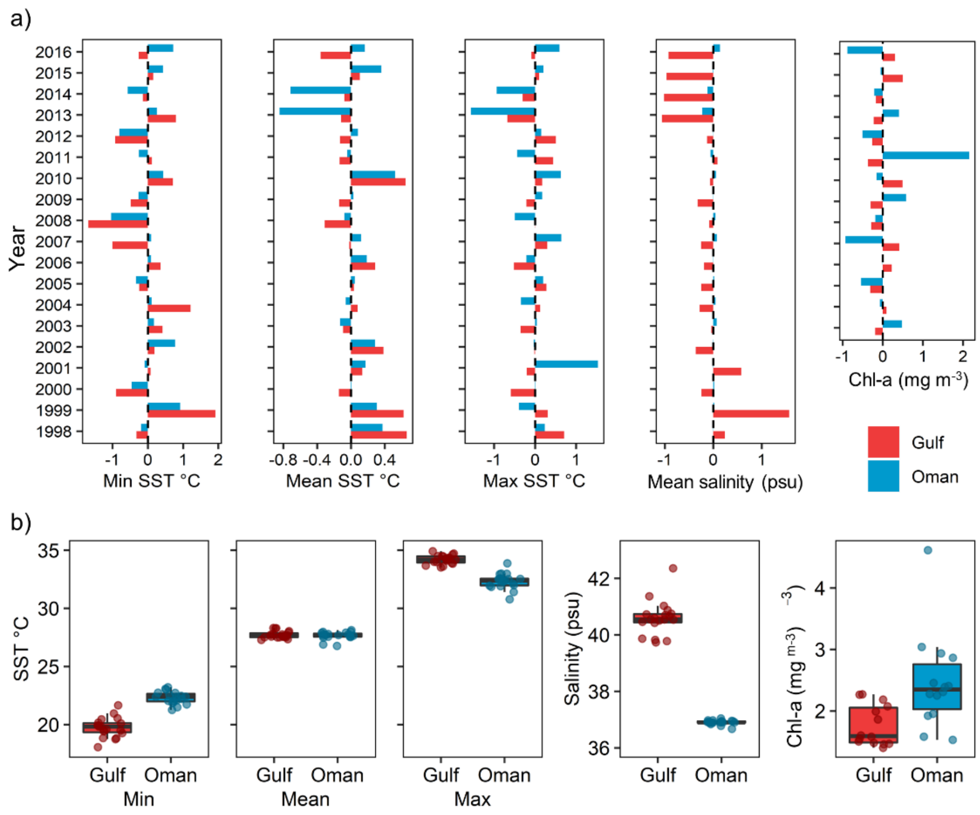


**Fig. 3.4** Intra- **(a)** and inter- **(b)** annual variability in sea surface temperature (min, mean and max), salinity and chlorophyll-a between the Arabian Gulf ('Gulf', red) and the Oman Sea ('Oman', blue). In **(a)** divergent bars quantify the positive/negative annual change of specific environmental variables during a given year from the individual mean (dashed vertical line) across all years. In **(b)** solid black line represents the median, with the box indicating the upper and lower quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points.

### 1.3.2.2 Growth predictors

Across species and regions, growth declined with Age and salinity (Table 3.4 and Table 3.5, see Table 3.4 for random effect structure details). Negative effects of salinity on growth rate were most apparent within the Oman populations of *L. ehrenbergii* (- 107.2% annual growth per unit increase in annual mean salinity [$psu^{-1}$]), while Arabian Gulf populations of *L. ehrenbergii* and *P. maculosus* also showed lower growth with higher levels of salinity (-30.3% and - 5.1% annual growth per unit increase in annual mean salinity [$psu^{-1}$], respectively) (Fig. 3.6a and Table 3.5).

There was little consistent effect of increasing temperature on growth rate between regions, though regional patterns were apparent (Fig. 3.6b and Table 3.5). Water temperature within the Arabian Gulf was positively correlated to growth in both species, with increases in max SST having a predicted effect on *L. ehrenbergii*'s growth rate of + 12.7% per °C*,* and increases in mean SST an effect of + 6.5% per °C in *P. maculosus.* There was no effect of temperature on Oman populations of *L. ehrenbergii*.

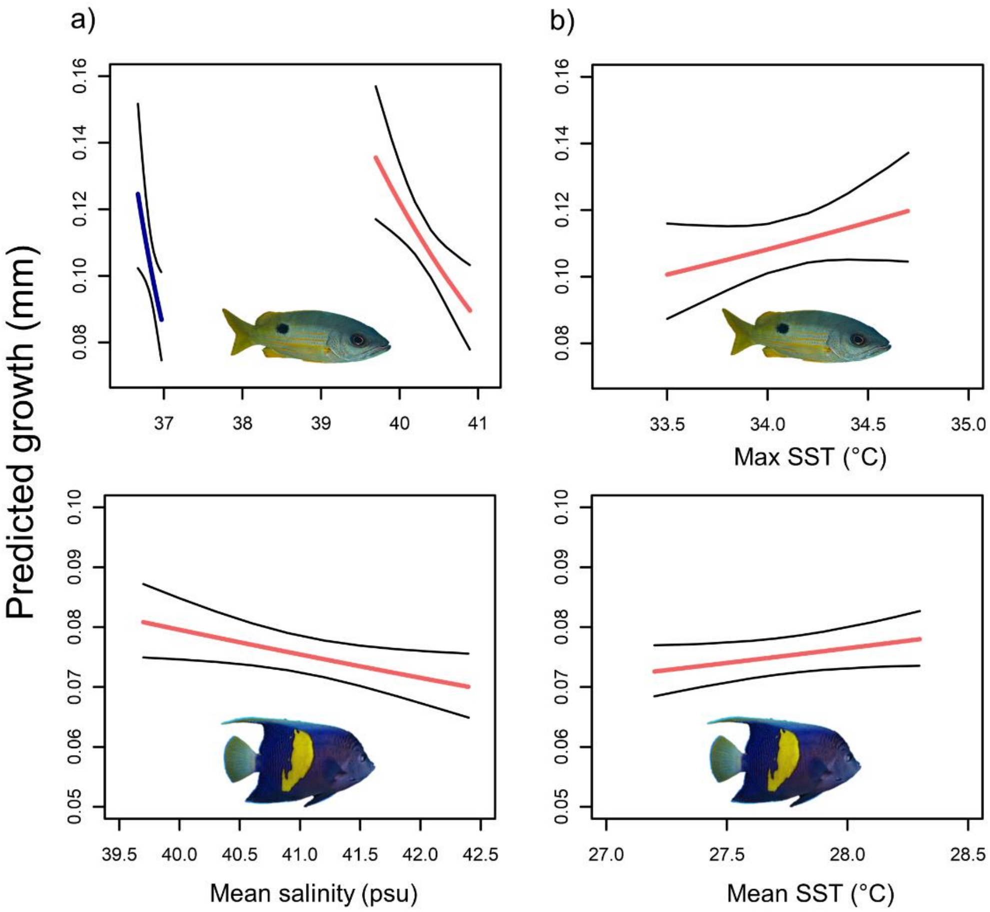


**Fig. 3.6** Predicted effect of annual mean salinity **(a)** and max and mean sea surface temperature (SST) **(b)** on the otolith incremental growth of *Lutjanus ehrenbergii* and *Pomacanthus maculosus* populations between the Arabian Gulf (red lines) and Gulf of Oman (blue lines). Black lines indicate 95 % CI. Note different scales on the y and x-axis. Predicted effects refer to the model outputs described in Table 3.4 and 3.5.

**Table 3.4**. Optimal model structures derived by ranking a series of increasingly complex mixed-effects models.

| Species | Region | Intrinsic model | Fixed effects | Random effects | Best extrinsic covariate structure |
|---|---|---|---|---|---|
| *L. ehrenbergii* | Arabian Gulf | 2a2 | Age + AAC | Age\|FishID + 1\|Year | Salinity + max SST |
| | Oman Sea | 2a2 | Age + AAC | Age\|FishID + 1\|Year | Salinity |
| *P. maculosus* | Arabian Gulf | 3a1 | Age | Age\|FishID + Age\|Year | Salinity + mean SST |
| | Oman Sea | NA | NA | NA | NA |

In *Lutjanus ehrenbergii,* the best intrinsic model was similar across regions and included Age and AAC with a random Age slope for FishID. This indicated that the growth-age relationship differed among individuals, while the random intercept for Year indicated growth varied among years. In *Pomacanthus maculosus* in the Arabian Gulf the best intrinsic model included only Age as fixed intrinsic factor with random Age slope for FishID and random Age slope for Year, indicating the age-growth relationship differed among years.

**Table 3.5.** Fixed effect parameter estimates (± SE) and test statistics for optimal models describing intrinsic, temporal and environmental effects on *Lutjanus ehrenbergii* and *Pomacanthus maculosus*' growth (see Tables S1–8 for model selection and base models' detail).

| | **Arabian Gulf** | | | | **Oman Sea** | | | |
|---|---|---|---|---|---|---|---|---|
| | *L. ehrenbergii* | | *P. maculosus* | | *L. ehrenbergii* | | *P. maculosus* | |
| Fixed effects parameter | Estimate | t value | Estimate | t value | Estimate | t value | Estimate | t value |
| **Intrinsic effects** | | | | | | | | |
| Intercept | - 2.20 (0.02) | - 88.84 | - 2.59 (0.02) | - 130.4 | - 2.26 (0.04) | -56.58 | NA | NA |
| Age | - 1.04 (0.05) | - 19.99 | - 0.82 (0.03) | - 23.61 | -1.06 (0.05) | -23.04 | NA | NA |
| AAC | 0.27 (0.06) | 4.81 | – | – | 0.15 (0.05) | 2.9 | NA | NA |
| **Temporal effect** | | | | | | | | |
| Year | 0.08 (0.01) | 5.59 | 0.01 (0.002) | 6.42 | 0.07 (0.01) | 7.75 | NA | NA |
| **Environmental effects** | | | | | | | | |
| Salinity | -0.3 (0.09) | - 3.51 | - 0.05 (0.02) | - 2.18 | - 1.07 (0.43) | -2.47 | NA | NA |
| SST (mean) | – | – | 0.06 (0.04) | 1.77 | – | – | NA | NA |
| SST (max) | 0.13 (0.08) | 1.58 | – | – | – | – | NA | NA |

## 3.4 DISCUSSION

We compared the growth of two common coral reef fish *L. ehrenbergii* and *P. maculosus* between the environmentally extreme Arabian Gulf and comparably benign Oman Sea, and examined the impact of temperature, salinity and primary productivity on the somatic growth of populations within each region. We found that both species were significantly smaller at age and attained a smaller maximum body size within the Arabian Gulf than within the Oman Sea. However, contrary to the expectation that extremes in temperature would be the main driver of somatic size reduction (i.e. consistent with the TSR), reductions in body size were mainly related to variation in salinity. Such results indicate that salinity may be a vital determinant of both species' growth trajectories. In comparison, temperature had a slightly positive effect on growth rates of Arabian Gulf populations of both species, with no measurable effect on Oman Sea fish populations.

In our study, growth declined with higher mean annual salinity across species and regions, indicating the impacts on demography of a highly saline environment are a reduction and, ultimately, truncation of life history. Indeed, together with temperature, food availability and photoperiod, salinity is known to be a major factor in determining fish development and growth (Boeuf and Payan 2001). Moreover, as osmoregulation is energetically costly (i.e. between 2–30% of daily energy expenditure in marine fish) (Boeuf and Payan 2001; Ern et al. 2014; Kultz 2015), changes in salinity may result in significant energy diversion from growth (Boeuf and Payan 2001). Here, we did not observe the expected crossing of growth curve trajectories between populations living in different thermal regime as predicted by the TSR (i.e. faster juvenile growth but earlier asymptotic growth for fish living in warmer environments) (Trip et al 2014), suggesting that salinity and perhaps even productivity are exhibiting a strong influence on differences in growth between regions. Interestingly, growth rates of populations within the Oman Sea, where salinity conditions are predominantly stable, were impacted more strongly by salinity fluctuations compared to populations within the Arabian Gulf, suggesting Arabian Gulf's populations may have higher capability of acclimation to seasonal and interannual changes in environmental conditions (Rummer and Munday 2017; D'Agostino et al. 2019). While numerous studies have examined the implications of increasing temperature and temperature variability on coral reef fish growth (e.g. Munday et al. 2008; Messmer et al. 2017; Taylor et al. 2019), to our knowledge there has been no investigation of the combined effect of increasing temperature and salinity on coral reef fish demography. This is despite the evidence of synergism between the two stressors (Claireaux and Lagarde 1999; Jian et al. 2003) and the likely occurrence of both stressors in already dry regions and hyper-saline (*sensu* saltier than oceanic salinity) semi-enclosed seas in the near future (such as the Arabian Gulf, Red Sea and Mediterranean Sea) (Durack et al. 2012; Skliris et al. 2014; Zika et al. 2018).

Positive effects of high SST on growth rates of both species within the Arabian Gulf may show that high summer water temperatures do not exceed the population's typical temperature range in this region. For example, there was a positive effect of increased maximum SST on growth rate of *L. ehrenbergii*, potentially indicating that the Arabian Gulf's summer temperature of > 34 °C may not exceed the thermal optimum for this species. Indeed, *L. ehrenbergii* abundance and predatory activity appear to be highest in summer (D'Agostino et al. 2019), suggesting that *L. ehrenbergii* may still have the aerobic capacity to perform ecological tasks (e.g. swimming, feeding) during the Arabian Gulf's extreme summer temperature. Additionally, the positive effect of mean SST on Arabian Gulf populations of *P. maculosus* may suggest that intermediate temperatures experienced during milder winters or slightly warmer springs or autumns may benefit the growth rate of this species (Johansen et al. 2015; Djurichkovic et al. 2019).

The smaller body sizes observed in Arabian Gulf fishes of both species may represent a life-history trade-off between metabolic demands and size, with likely flow-on effects to population structure. Although not universally accepted, the gill-oxygen limitation theory (GOLT) states that as gills function as a two-dimensional surface with growth limited by geometrical constraints, any three-dimensional increases in fish body size, and consequent increases in oxygen demand, may not be met by adequate oxygen supply (Pauly 1981; Pauly and Cheung 2018a, but see Audzijonyte et al. 2019). Consequently, larger-bodied individuals may be unable to compensate for increased metabolic demands associated with high salinity and temperature, due to the incapability of the respiratory system to supply enough oxygen. While we did not observe a strong negative effect of max SST (when dissolved oxygen is at its lowest and the oxygen demand at its highest) on fish growth (Shapiro Goldberg et al. 2019), large-bodied individuals are expected to have limited capacity to increase mass-specific maximum metabolic rate in warmer conditions (Messmer et al. 2017), and to be more likely to approach their maximum physiological capacity (Pauly and Cheung 2018b). Hence, reduced individual body size in the Arabian Gulf may represent a life-history trade-off, whereby survival is enhanced through smaller body size and, therefore, reduced metabolic demands.

Although reductions in body size may play an important role in coping with variable and extreme temperature and salinity, other mechanisms may be involved in facilitating population stability. For example, recent work has highlighted the importance of behavioural and feeding plasticity in coping with the Arabian Gulf's extreme environmental conditions. The pale-tail damselfish (*Pomacentrus trichrourus*) appears able to mitigate bioenergetic inefficiency associated with the fluctuating and extreme water temperature within the Arabian Gulf by downregulating costly activities during winter and summer, while upregulating activity and increasing energy stores in spring (D'Agostino et al. 2019). In this respect, *P. trichrourus*, *P. maculosus* and *Pomacentrus aquilis* all show a degree of feeding plasticity in the Arabian Gulf (Shraim et al. 2017; D'Agostino et al. 2019), suggesting that such plasticity in feeding may be an important factor in understanding growth rate and overall body size of all three species.

Reductions in fish body size, within the magnitude of lowered size reported in the present work, are expected to have substantial consequences for trophic interactions, ecosystem function, fisheries and global protein supply (Shackell et al 2010; Cheung et al. 2013). Fish body sizes are already reducing due to intensive fishing pressure (Stergiou 2002), while there is also evidence to show the potential additive effect of climate change and oxygen limitation on individual (and therefore population) body size spectrum (Cheung et al. 2013; van Rijn et al 2017). Importantly, theoretical models predict that small reductions in individual body size (i.e. 4% over 50 years) may lead to a 50% increase in mortality as well as a 5– 35% reduction in biomass and catch (Audzijonyte 2013). However, most importantly, as fish fecundity is largely correlated with body size, lowered body size is expected to have substantial negative consequences on population reproductive output, replenishment and long-term persistence (Baudron 2014), which will have cascading effects on the wider ecosystem, potentially impacting coastal economies and threatening food security.

Understanding the mechanisms by which fishes endure the Arabian Gulf's extreme and variable environment will be vital to understand how low latitude coral reef fish populations may cope with predicted changes in their environment. The present work shows that sub-tropical fish communities can persist within extreme environmental conditions, albeit with substantial trade-offs to their life history and demographic structure; individuals of both *L. ehrenbergii* and *P. maculosus* showed smaller size-at-age and lower maximum size in the Arabian Gulf compared with conspecifics in the Oman Sea. Our results suggest that, in order to predict the effect of climate change on fish demography, the combined effect of osmoregulatory and thermal stress needs to be considered, especially in regions with limited oceanic exchange and predicted increase SST and evaporation. Ultimately, to tease apart the effect of extreme temperature and salinity on growth of Arabian Gulf fish populations and establish the role of other potential coping mechanisms (i.e. feeding and behavioural plasticity) in mitigating environmental stressors, laboratory-based physiological-behavioural experiments combining multiple stressors and conditions, while assessing detailed energy budget, are needed.

# CHAPTER 4

## Behavioural traits and feeding ecology of Mediterranean lionfish and native species naiveté to lionfish predation

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# ABSTRACT

The detrimental effects of invasion by Indo-Pacific lionfish (*Pterois volitans/miles)* on western Atlantic fishes have spurred concerns for Mediterranean fish biodiversity, where Lessepsian lionfish (*P. miles*) have recently established populations in the eastern basin. In order to assess the potential impact on biodiversity, we examine key behavioural and ecological traits of lionfish, and the resident fish community in the Mediterranean, that may contribute to lionfish invasion success. We focus on Cyprus, where lionfish populations were first sighted in 2012 and have now formed abundant and stable populations. Using field observations, we examine lionfish predatory behaviour and feeding ecology, and resident fish species naiveté to hunting lionfish. Our findings suggest that lionfish in the Mediterranean are crepuscular generalist predators, with prey targeted dominated by small-bodied benthic or bentho-pelagic associated species. Such prey are more likely to be native than introduced (Lessepsian) fishes, with native prey fishes showing greater naiveté towards lionfish than Lessepsian prey species. Notably, one of the Mediterranean's key ecological fish species (the native damselfish *Chromis chromis*), showed the highest level of naiveté and was the most heavily targeted prey. Overall, lionfish in the Mediterranean show similar predatory behaviour and ecology to their western Atlantic counterparts. Although the establishment of Mediterranean lionfish populations is still recent, it may result in a similar disruption to reef fish biomass to that recorded in the Atlantic, with impact on the structure and biodiversity of reef fish communities and the services they provide.

## 4.1 INTRODUCTION

Human activities, such as land-cover change, chemical release, overharvesting, climate change and species transport/invasion, are having a profound impact on global biodiversity (Dirzo et al. 2014; McGill et al. 2015; Gordon et al. 2018), often resulting in rapid changes in the abundance, diversity and composition of species (McCauley et al. 2015; Webb and Mindel 2015; Hughes et al. 2018). Although there has been focus on the numerical response of populations to human-induced rapid environmental change, substantial impacts on the behaviour of individuals may also be apparent (Tuomainen and Candolin 2011; Sih et al. 2011; Wong and Candolin 2015). Such behavioural impacts may be particularly relevant where rapid environmental change results in increases in the abundance of invasive species within habitats (D’Amore et al. 2009; Sih et al. 2010). Indeed, invasive species can generate ecological impacts that propagate along the food-web and may trigger trophic cascades, resulting in a generalised decrease in the abundance and diversity of native communities (Moyle and Light 1996; Strayer 2010; Gallardo et al. 2016). In this respect, a central focus of invasion biology research has been to examine the factors which increase our ability to predict which species may become invasive (Kolar and Lodge 2001; Hayes and Barry 2008). This work has shown that there are a range of life-history, ecological and behavioural traits that are associated with successful invasion, and that can be used to determine the subsequent consequences of an invasion on the invaded ecosystem (Chapple et al. 2012).

The invasion process involves a series of sequential stages (transport, introduction, establishment and spread) that a population has to go through to become a successful invader (Blackburn et al. 2011; Chapple et al. 2012). Each stage presents varied abiotic (i.e. associated with different geography and environment) and biotic barriers (i.e. dispersal, reproduction, feeding, competition) that individuals within an invading population must overcome to succeed (Blackburn et al. 2011); only individuals with certain life-history and behavioural traits may then move forward between steps in the invasion process (Chapple et al. 2012). As a result of such 'filtering' of individuals, the invading population is not a random subset of the native natal population (Felden et al. 2018), while traits 'selected' for in individuals during one stage of the invading process may being maladaptive and lead to invasion failure in following stages (Chapple et al. 2012; Felden et al. 2018). Thus, the introduction or establishment of an invasive species in a novel region will not necessarily lead to the species becoming invasive and to similar impacts on local biodiversity as observed elsewhere.

Substantial negative impacts on native fish biodiversity have been well documented following the invasion of lionfish *Pterois volitans*/*miles* (hereafter 'Atlantic lionfish') in the western Atlantic ocean (Albins and Hixon 2013; Côté and Smith 2018). Such biodiversity loss may mirror that for native biodiversity in the Mediterranean (Galanidi et al. 2018), where a Lessepsian invasion (i.e. from the Suez Canal, Egypt) by lionfish (*P. miles*, [Bennett, 1828], hereafter 'Mediterranean lionfish') has recently begun (Bariche et al. 2013; Jimenez et al.

2016; Kletou et al. 2016; Azzurro et al. 2017). Research on Mediterranean lionfish is still in its infancy, and is still not clear whether Mediterranean lionfish are set for a pan-Mediterranean invasion or whether they will be limited to the Levantine side of the basin (Johnston and Purkis 2014; Azzurro et al. 2014), where the environmental affinity to the Red Sea is higher (i.e. warmer water temperature). Nevertheless, the extensive work on the ecological, behavioural and life-history traits contributing to invasive success of lionfish in the western Atlantic provides a basis for understanding the traits potentially facilitating the Mediterranean invasion (reviewed by Côté and Smith 2018). Such understanding may allow us to predict the impact on local and regional biodiversity of the Mediterranean invasion, and the management decisions needed to effectively mitigate long term changes in community structure (Morris and Whitefield 2009).

Mediterranean lionfish share important life-history and trophic traits with Atlantic lionfish, which may enhance the likelihood of invasion success within the Mediterranean (Kleitou et al. 2019). High growth rates (up to 20 cm total length [TL] in the first year), large body size (up to 37 cm TL at four years) and early maturation (sexual maturity in less than a year) in Mediterranean lionfish (Kleitou et al. 2019), can be expected to translate into rapid rates of population increase (Morris and Whitefield 2009; Edwards et al. 2014; Côté and Smith 2018), which is often an essential prerequisite to outcompete native competitors for spaces and resources during the establishment phase of the invasive process (Holway and Suarez 1999; Chapple et al. 2012). Moreover, early studies on Mediterranean lionfish stomach contents report that they feed on a wide range of crustacean and fish species (Kleitou et al. 2019; Zannaki et al. 2019), suggesting they are generalist predators and that they may be well equipped to deal with environmental stochasticity in the invaded region (Côté and Smith 2018; Peake et al. 2018). However, evidence of dietary specialization on species with particular morphological (i.e. small, elongated body) and behavioural traits (i.e. benthic habitat use, solitary) have been reported for the Atlantic lionfish (Green and Côté 2014; Chappell and Smith 2016), implying stronger predatory pressure on certain species, increasing the risk of localised species extirpation and loss of entire ecological and functional roles (Peake et al. 2018). Lastly, although there is no information on native prey naiveté to Mediterranean lionfish, results from the Atlantic would suggest that naiveté will be an important precursor to Mediterranean lionfish population success (Anton et al. 2016;  Benkwitt 2017; Haines and Côté 2019). In detail, the 'naïve prey' hypothesis postulates that native prey suffer heavy predation by a novel predator due to the lack of recent co-evolutionary history and effective antipredator behaviour (Cox and Lima 2006; Sih et al. 2010; Paolucci et al. 2013). Such prey naiveté may then allow the invasive predator a competitive advantage compared to native counterparts (Anton et al. 2016).

To predict how the structure and biodiversity of Mediterranean fish communities will be impacted, the objective of this study was to document and assess patterns in activity and feeding of Mediterranean lionfish, as well as investigate the potential for native (compared to non-native) prey naiveté. We focus on Cyprus, which is at the forefront of the Mediterranean invasion and holds an abundant and stable population of lionfish in shallow and deep waters (Jimenez et al. 2016, 2019a; Kletou et al. 2016). First (i), we quantified the behaviour of Mediterranean lionfish at three time points (i.e. sunrise, noon and sunset) to test the hypothesis of a crepuscular pattern in hunting activity (i.e. sunrise and sunset) as this has been shown in the Atlantic invasion (Cure et al. 2012; Benkwitt 2016) and invoked as one of the behavioural traits facilitating their invasive success (i.e. increased hunting success and broader array of preys available) (Hobson 1973; Potts 1990; Green et al. 2011). Secondly (ii), we characterised the feeding ecology of Mediterranean lionfish, quantifying the diversity of species preyed upon, and the number of times each species was targeted. We relate this feeding behaviour to fine-scale and broad-scale prey abundance. We predicted that lionfish would broadly be generalist predators by feeding on a diverse array of prey (Peake et al. 2018), but would also show some level of dietary specialization towards species with certain behavioural and morphological traits (Green and Côté 2014; Chappell and Smith 2016). Lastly (iii), we investigated the levels of behavioural naiveté towards lionfish in native and Lessepsian prey species, predicting that native prey would be more naïve towards hunting lionfish (Anton et al. 2016).

## 4.2 MATERIAL AND METHODS

### 4.2.1 Site selection and methodology for recording and quantifying Mediterranean lionfish behaviour

To develop a dataset of Mediterranean lionfish behaviour, in September 2018 we videoed Mediterranean lionfish behaviour at sunrise (between 7:30-8:30), noon (13:30-14:30) and sunset (17:00-18:00) across six rocky reefs (mean area 0.056 $km^2$ ± 0.004 SE) off the eastern coast of Cyprus (Protaras; 35° 0'5.65"N, 34° 4'11.88"E) (Fig. 4.1 for details). A total of 80 individual Mediterranean lionfish were recorded across sites and time of the day. All sites were dominated by rocky reef and ranged in depth between 3.8 and 12.3 m (mean depth 7.5 m ± 0.2 SE). Sites were separated by at least 600 m of sand and deeper waters (up to 30 m). Sites and time of observations were randomised. Within each site where Mediterranean lionfish were identified, care was taken to not video the same individual twice by swimming unidirectionally along each site during the dive, and videoing fish as encountered (Green et al. 2011). Each site was dived only once within a day (~1 hour dive), and if we returned to the same site on a different day, care was taken to observe fish at different time periods from the previous visit (i.e. sunrise, noon or sunset) and in different areas of the site (Côté and Maljkovic 2010; Cure et al. 2012).

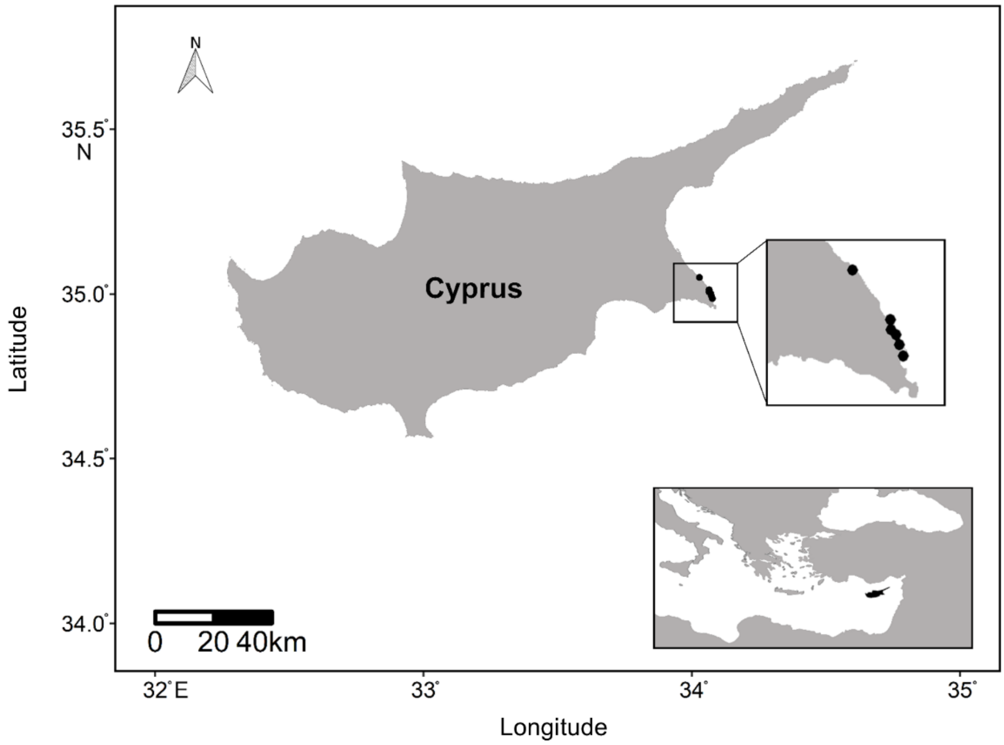


**Fig. 4.1** Study area and sampling locations of the estern part of Cyprus.

Once identified, Mediterranean lionfish were allowed to acclimate for 3 min to the diver, and were then filmed for 5 min, with a minimum distance of 3 m between diver and lionfish (D'Agostino et al. 2019). During the 3 min acclimation period the diver estimated Mediterranean lionfish body size (small [≤ 10 cm TL], medium [11 – 20], large [≥ 21]), group size (number of lionfish within 1 m radius from focal lionfish), water depth (m) and temperature (nearest 0.1 °C), measured using the dive computer RATIO ix3M, visibility (low < 10 m, medium 10 – 20 m, high > 20 m) and current strength (low: diver barely kicking to maintain position, medium: periodic kicking required by diver to maintain position, high: constant kicking by diver required to maintain position); cloud cover was recorded at the beginning of each dive as either clear: 0 – 25%, partly cloudy: 25 – 75% or overcast: > 75% (Côté and Maljkovic

2010; Cure et al. 2012). Underwater data collection and video recording were carried out by three experienced divers (DD, SH and LH); pilot data (not included in the study) where all divers observed the same individuals, were collected on the first day and used to calibrate data collections methodology between observers. Mediterranean lionfish size estimation error was < 10 %.

To quantify activity budget of each Mediterranean lionfish, videoed behaviour was classified into four categories, with each category of behaviour scored every 10 seconds across the 5 min video (Green et al. 2011). Mediterranean lionfish were considered 'resting' when motionless on the substratum, with dorsal spines held flat along the dorsal midline and pectoral fins closed, 'hunting' when approaching/chasing potential prey, with head and flared pectoral fins directed at prey and dorsal spines undulating and erected, 'hovering' when nearly motionless above the substratum, and 'transiting' when swimming from one part of the benthos to another (see supplementary materials Video S4.1-4.4 for examples of lionfish resting and hunting behaviour). In addition, to quantify movement of each Mediterranean lionfish 'distance moved' was quantified (in cm) by estimating the total distance moved (to the nearest 5 cm) every 30 sec interval across each 5 min video, using the lionfish individual size as reference against the background reef. Any videos in which fish displayed an adverse reaction to the diver's presence (i.e. staring at divers or assuming defensive posture, < 5 % of individuals) were excluded from analysis.

### 4.2.2 Quantification of Mediterranean lionfish feeding ecology and fish community structure

To quantify Mediterranean lionfish feeding ecology, across each 5 min video we counted the number of times individuals (hereafter 'prey species') were targeted ('times targeted') across all predation attempts (defined as the action of a lionfish pursuing a single individual). Prey species trophic guild and origin (i.e. native or Lessepsian) were extracted from FishBase (Froese and Pauly 2000).

To characterise the composition of the community with which Mediterranean lionfish associate, either because of shared habitat preferences, or perhaps because of predator-prey relationships, the abundance of all prey species within 1 m radius of focal lionfish was estimated within each video (hereafter 'fine-scale prey abundance'). To characterise the fish community in the broader area to which Mediterranean lionfish could potentially associate or prey upon, 'broad-scale prey abundance' was estimated as the sum of all Mediterranean lionfish prey estimated from underwater visual census surveys conducted on SCUBA during six sampling expeditions (winter, spring, summer and autumn 2017; winter and summer 2018). Such surveys were undertaken at five reef sites (between Protaras and Cape Greco, Fig. S4.1) in the same area as where behavioural observations were quantified. Sites were located at depths ranging between 3.5 and 20 m (average 9.3 m). At each site three replicate transects of 25 x 5 m were surveyed and all fish identified to species, enumerated and their size (cm TL) estimated. Only prey fish ≤ 5 cm TL and from species that had been previously observed to have been targeted by lionfish during the behavioural observations, were selected to estimate fine- and broad-scale prey abundance.

### 4.2.3 Quantification of prey fish naiveté to Mediterranean lionfish predation

To examine and compare naiveté between native Mediterranean and Lessepsian prey species, the 'closest approach distance' (i.e. the distance [cm] at which small prey fish [i.e. ≤ 5 cm TL] stopped approaching or turned away from lionfish) was quantified during each 5 min video (Anton et al*.* 2016). Distance between prey and Mediterranean lionfish was visually estimated by using focal Mediterranean lionfish size (which had been previously estimated *in situ*) as a reference. If the same prey individual approached a Mediterranean lionfish multiple times during the 5 min observation period, only the closest approach was enumerated. The distance of 60 cm was used as minimum starting distance for observation of closest approach distance, as pilot observations showed that prey species predominantly respond to the presence of hunting lionfish within this distance. In order to control for predator behaviour, closest approach distance measures were only calculated from videos where Mediterranean lionfish were identified as hunting (see below) (n = 31).

Mediterranean lionfish behaviour, feeding ecology and native prey naiveté data were initially extracted from 15% of videos and independently quantified by two observers. As results differed by < 5% between observers, all remaining quantification of data from videos analyses were carried out by one observer (DD).

## 4.2.4 Statistical analysis

### 4.2.4.1 Behavioural patterns of Mediterranean lionfish

As there was no significant difference in visibility (always greater than 20 m), currents (always low), cloud cover (always clear) and depth (Kruskal-Wallis test, $H = 3.3323$, $df = 2$, $p = 0.189$) between sampling periods (sunrise, noon, sunset), these environmental variables were not included in further statistical models. Similarly, water temperature was excluded from further analysis because its variation between sampling periods, although statistically significant ($H = 15.328$, $df = 2$, $p < 0.001$), was very limited in magnitude (27.0 to 28.2°C), reflecting normal diel temperature variation during the observational period.

Behavioural analyses only focused on resting and hunting, which represented > 80 % of the behaviours enacted across all videos, as well as total distance moved. To understand the relationship between the response variables of resting, hunting and total distance moved to the independent factors of sampling time (sunrise, noon and sunset), prey availability, Mediterranean lionfish body size (small, medium and large) and group size (one, two or three individuals), separate generalised linear mixed models (GLMMs) were used. A GLMM with binomial error distribution and logit link function was used to model the probability of resting and hunting behaviour being observed in a 5 min video. We took this approach because data for proportion of time spent resting and hunting were bimodal, with a high proportion of ones and zeros, and data transformation did not result in either normality or homoscedasticity within either data sets. An individual was considered as 'resting' if > 50 % of the proportion of time during the 5 min period was spent resting, and 'hunting' if > 50 % of the 5 min period was spent hunting (Cure et al. 2012). To model total distance moved a Gaussian error structure was used. Total distance moved data were log (X + 1) transformed prior to testing to satisfy test assumptions. In both GLMMs, we fitted random intercepts for the factors site (six levels) and date of sampling (five levels), with backwards model selection then followed using likelihood ratio tests to examine the significance of each term removed from each model.

#### 4.2.4.2 Mediterranean lionfish feeding ecology and prey association

To determine whether Mediterranean lionfish were associated with, and predated upon, prey in relation to their abundance in the wider community, two types of test were conducted. First, we used Pearson's correlation tests to look for a relationship between the likelihood of a prey species being targeted, its local (fine-scale) abundance, and its broad-scale abundance in the area. A positive correlation would imply that prey selection is influenced by availability. Second, we used chi-squared tests to determine whether there were significant differences in the relative abundance of prey species targeted by Mediterranean lionfish, and their relative fine- and broad-scale abundance. A significant difference would imply that Mediterranean lionfish are selective about the prey that they attack. In order to meet chi-squared test assumptions, *Thalassoma pavo*, *Coris julis* and *Symphodus* spp. individuals were grouped together by family as 'Labridae'; *Gobius vittatus* (Gobiidae), *Scorpaena notata* (Scorpaenidae) and *Apogon imberbis* (Apogonidae) were grouped as 'rare species'; while *Siganus rivulatus* (Siganidae) and *Sparisoma cretense* (Scaridae) were grouped together because they had relatively high abundance, but were scarce in times targeted (Table S1).

#### 4.2.4.3 Native versus invasive prey naiveté to Mediterranean lionfish predation

To determine whether there was a significant difference in closest approach distance between native and invasive prey species and Mediterranean lionfish, and whether prey species would approach lionfish at different distances in regards of their size, a GLMM with Poisson error distribution and log link function was used. The model had closest approach distance as the response variable and the interaction between origin (native vs invasive) and lionfish size (small, medium, large) as fixed effects, with lionfish ID as random intercept (as multiple observations were conducted on each lionfish). All data were analysed in R (R core development team 3.5.1, 2019) using the nlme package (Pinheiro et al. 2015) for mixed-effects models, and statistical significance was determined at p-values < 0.05.

# 4.3 RESULTS

## 4.3.1 Behavioural patterns of Mediterranean lionfish

We quantified patterns in activity and feeding of 76 Mediterranean lionfish (sunrise n = 27, noon n = 25 and sunset n = 24) ranging in size from 7 to 35 cm TL (mean ± SE: 19 ± 0.8 cm) during a total of 380 min of video. Mediterranean lionfish were observed alone or in groups of up to three individuals. Time of the day had a significant effect on resting, hunting and distance moved (Table 1), with Mediterranean lionfish spending the highest proportion of time hunting, as well as moving longer distances at sunrise and sunset (Fig. 4.2, Fig. 4.3a). At noon Mediterranean lionfish spent the majority of time resting (supplementary materials Video 4.1). Lastly, fine-scale prey abundance and Mediterranean lionfish individual size had a significant effect on resting and hunting behaviour, with hunting behaviour more likely when prey availability was high and lionfish size was small (Table 4.1). Fine-scale prey abundance ranged between 0 to 41 individual prey fishes per Mediterranean lionfish, with highest abundances apparent at sunset (Fig. 4.3 b).

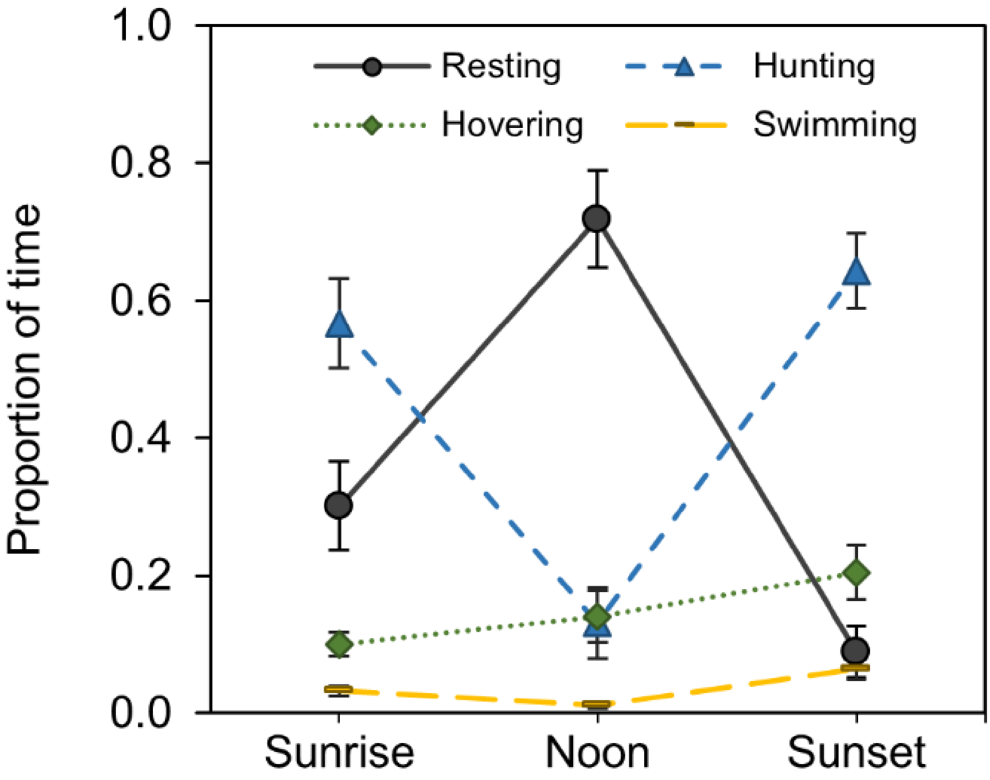


**Fig. 4.2** Time budget of invasive Mediterranean lionfish on Cypriot rocky reefs across time of day for resting, hunting, hovering and swimming. Shown are mean (± SE) proportions of time spent in each behaviour.

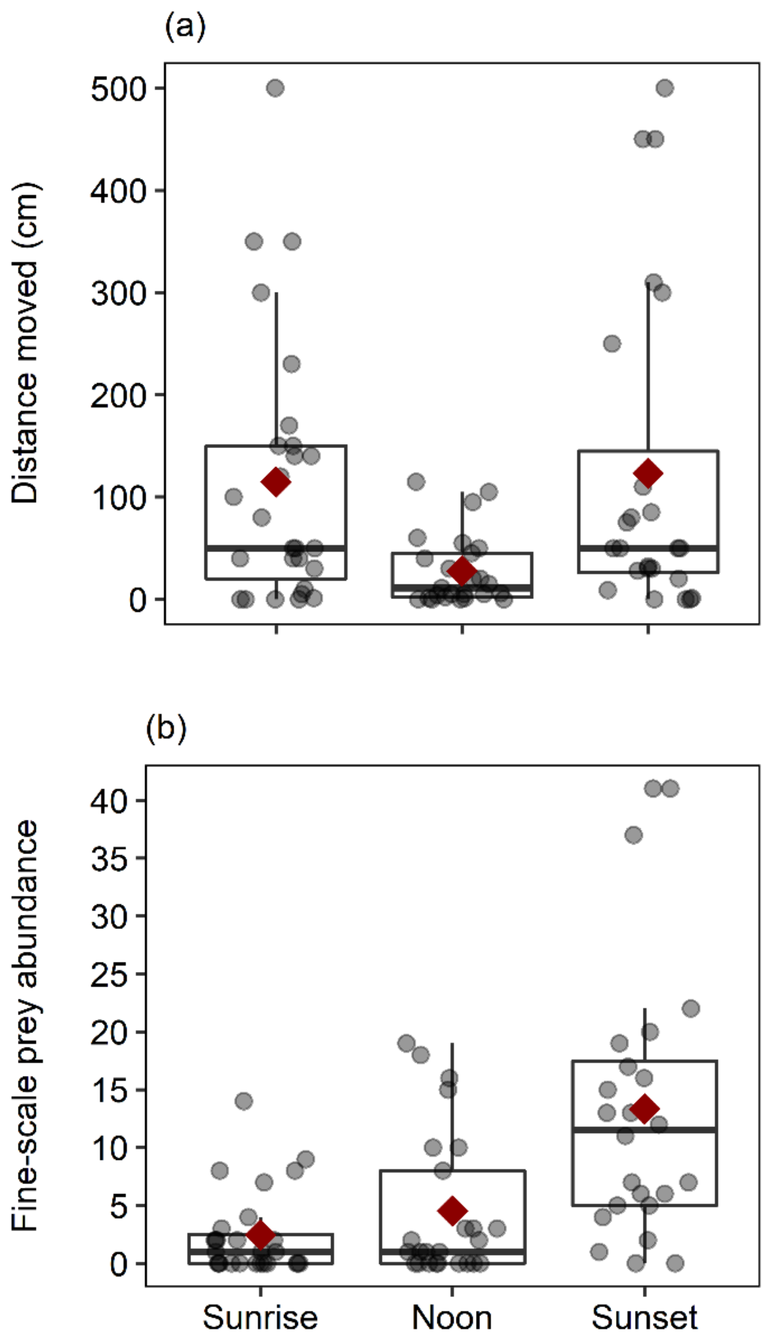


**Fig. 4.3** Changes in Mediterranean lionfish distance moved among time of day **(a)** and changes in fine-scale prey abundance at different time of the day **(b)**. Solid black line represents the median, with the box indicating the upper and lower quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points, and red diamond show the mean.

**Table 4.1** Result of GLMM analysis of the effects of biotic/abiotic factors on Mediterranean lionfish's behaviour. Binomial error distribution with logit link function for resting and hunting behaviour; Gaussian error structure for distance moved. Significant p values highlighted in bold.

| **Response** | **Predictor** | **Residual deviance(*df*)** | **Change in deviance (*df*)** | ***p*** |
|---|---|---|---|---|
| **Resting (inactive)** | Time day | 69.691 (5) | 14.55 (2) | **< 0.001** |
| | Size | 65.163 (6) | 4.5288 (1) | **0.033** |
| | Fine-scale prey abundance | 61.218 (7) | 3.9442 (1) | **0.047** |
| | Time day x fine-scale prey abundance | 59.712 (9) | 1.5062 (2) | 0.471 |
| | Group size | 58.662 (11) | 1.0503 (2) | 0.592 |
| **Hunting** | Time day | 84.570 (5) | 12.894 (2) | **0.002** |
| | Fine-scale prey abundance | 77.258 (6) | 7.3121 (1) | **0.007** |
| | Size | 72.662 (7) | 4.5956 (1) | **0.032** |
| | Time day x fine-scale prey abundance | 71.875 (9) | 0.7874 (2) | 0.675 |
| | Group size | 71.181 (11) | 0.6942 (2) | 0.707 |
| **Distance moved** | Time day | 179.34 (6) | 8.1149 (2) | **0.017** |
| | Fine-scale prey abundance | 178.85 (7) | 0.4872 (1) | 0.485 |
| | Time day x fine-scale prey abundance | 174.28 (9) | 4.5762 (2) | 0.102 |
| | Size | 174.18 (10) | 0.1006 (1) | 0.751 |
| | Group size | 173.54 (12) | 0.6343 (2) | 0.728 |

### 4.3.2 Mediterranean lionfish feeding ecology and prey association

Mediterranean lionfish targeted 10 prey species from seven families, encompassing only grazers and meso-predators (Table 4.2). Prey targeted were predominantly small-bodied benthic or bentho-pelagic associated species; predatory activity was dominated by predation attempts on *Chromis chromis* (Pomacentridae) and juvenile *T. pavo* (Labridae) (supplementary materials Video 4.2 and 4.3, respectively).

Although important, community prey abundance did not completely predict Mediterranean lionfish species-specific targeting rate. Despite the significant positive correlation between the number of times a species was targeted and its fine-scale abundance, and between fine-scale and broad-scale prey abundance, the likelihood of a species being predated upon was not always proportionate to its abundance, either in the immediate vicinity of the lionfish, or in the broader area (Table 4.3). For example, while *C. chromis* broad-scale abundance (64%) reflected its fine-scale abundance (64.8%) and the number of times it was targeted (48.3%), we observed contrasting trends for *S. rivulatus*/*S. cretense* and Labridae. In detail, despite *S. rivulatus*/*S. cretense* being the second most abundant taxa in the area (26.8% broad-scale abundance), fine-scale abundance was intermediate (8.2%) and they were seldom targeted by Mediterranean lionfish (3.4%). In comparison, Labridae individuals had low broad-scale abundance (5.5%), but relatively high fine-scale abundance (15.6%) and were highly targeted (32.2%) (Table 4.2, Table S4.1).

**Table 4.2** Potential prey fish species, the frequency with which they were targeted by Mediterranean lionfish, and their relative abundance in the immediate vicinity of Mediterranean lionfish (fine-scale abundance) and in the broader area (broad-scale abundance). Both absolute (total number of individuals sighted across all samples) and relative (proportion of all individuals sighted) measures of abundance are given.

| Targeted species | Family | Trophic level (± SE) | Origin | Life status | Times targeted | Fine-scale prey abundance | Broad-scale prey abundance | Time targeted index (%) | Fine-scale prey relative abundance (%) | Broad-scale prey relative abundance (%) |
|---|---|---|---|---|---|---|---|---|---|---|
| *Chromis chromis* † | Pomacentridae | 3.8 (0.4) | Native | Adult | 42 | 331 | 6162 | 48.28 | 64.77 | 63.99 |
| *Thalassoma pavo* | Labridae | 3.5 (0.47) | Native | Juvenile | 22 | 64 | 193 | 25.29 | 12.52 | 2 |
| *Parupeneus forsskali* | Mullidae | 3.5 (0.3) | Invasive | Juvenile | 8 | 50 | 336 | 9.2 | 9.78 | 3.49 |
| *Apogon imberbis* | Apogonidae | 3.4 (0.61) | Native | Adult | 4 | 6 | 5 | 4.6 | 1.17 | 0.05 |
| *Coris julis* | Labridae | 3.4 (0.1) | Native | Juvenile | 4 | 13 | 330 | 4.6 | 2.54 | 3.43 |
| *Sparisoma cretense* | Scaridae | 2.9 (0.24) | Native | Juvenile | 2 | 8 | 619 | 2.3 | 1.57 | 6.43 |
| *Gobius vittatus* † | Gobiidae | 2.9 (0.27) | Native | Adult | 1 | 1 | 2 | 1.15 | 0.20 | 0.02 |
| *Siganus rivulatus* | Siganidae | 2.0 (0.0) | Invasive | Juvenile | 1 | 34 | 1966 | 1.15 | 6.65 | 20.42 |
| *Symphodus sp.* | Labridae | - | - | - | 1 | 2 | 5 | 1.15 | 0.39 | 0.05 |
| *Symphodus rostratus* | Labridae | 3.5 (0.0) | Native | Juvenile | 1 | 1 | 2 | 1.15 | 0.2 | 0.02 |
| *Scorpaena notata* | Scorpaenidae | 3.7 (0.2) | Native | Juvenile | 1 | 1 | 9 | 1.15 | 0.2 | 0.09 |

Species ranked by ‘times targeted’. Trophic level 2 indicates herbivorous fish, level 3 indicates meso-predator. Origin: native = Mediterranean Sea, invasive = Red Sea (Lessepsian). Note: † signifies observed capture; ‘–’ indicates no data available.

**Table 4.3** Results of Pearson correlation and chi-squared tests examining patterns of abundance of potential prey species targeted by Mediterranean lionfish, in the immediate vicinity of Mediterranean lionfish (fine-scale abundance), and in the broader area (broad-scale abundance). Correlation tests examine whether the relative abundance of prey targeted or in the vicinity of Mediterranean lionfish reflect (at least partly) the availability of those species in the community. Chi-squared tests examine whether prey species are targeted or associated with Mediterranean lionfish in proportions that are significantly different from what would be expected at random.

| Observation | Pearson correlation test | Chi-squared test |
|---|---|---|
| **Times targeted x fine-scale prey abundance** | t = 3.355, df = 3, **p = 0.043**; cor 0.89 | $\chi^2$ = 22.92, df = 4, **p = 0.00013** |
| **Times targeted x broad-scale prey abundance** | t = 1.581, df = 3, p = 0.212; cor 0.67 | – |
| **Fine-scale prey abundance x broad-scale prey abundance** | t = 3.823, df = 3, **p = 0.031**; cor 0.911 | $\chi^2$ = 238.82, df = 4, **p < 0.001** |

'–' indicates that chi-squared tests was not performed.

### 4.3.3 Native versus invasive prey naiveté to Mediterranean lionfish predation

Origin (i.e. native versus invasive) had a significant effect on closest approach distance, while Mediterranean lionfish size and the interaction between size and origin had no significant effect (Table 4.4). Native fish species approached more closely to Mediterranean lionfish than invasive fish species (Fig. 4.4). Particularly, *C. chromis* (n =182), *T. pavo* (n = 48), *C. julis* (n = 8), *A. imberbis* (n = 3) showed the nearest approach distances ([mean cm ± SE], 25.2 ± 0.9, 32.9 ± 1.6, 23.9 ± 4.2, 23.3 ± 2.4, respectively), while *S. rivulatus* (n = 30) and *S. cretense* (n = 6) showed the furthest approach distances (53.9 ± 0.8 and 51.3 ± 1.8, respectively). 12 instances were recorded in which native prey fishes (11 *C. chromis,* one *T. pavo*) swam within less than 10 cm of a lionfish's mouth (minimum distance 5 cm), while the closest distance recorded by an invasive prey fish species (*P. forsskali,* Mullidae) was 30 cm. In addition, one individual of *G. vittatus* showed nearly no response to approaching Mediterranean lionfish (closest approach distance ≤ 2 cm) and was eventually cornered and predated upon (supplementary materials Video 4.4).

**Table 4.4** Result of GLMM analysis, with Poisson error distribution and log link function, of the effects of origin and Mediterranean lionfish size on prey closest approach distance. Significant p values highlighted in bold.

| Response | Predictor | Residual deviance(df) | Change in deviance (df) | p |
|---|---|---|---|---|
| **Closest approach distance** | Origin | 3171.1 (3) | 238.98 (1) | **< 0.001** |
| | Lionfish size | 2932.1 (5) | 2.6976 (2) | 0.26 |
| | Origin x lionfish size | 2929.4 (7) | 2.4139 (2) | 0.299 |

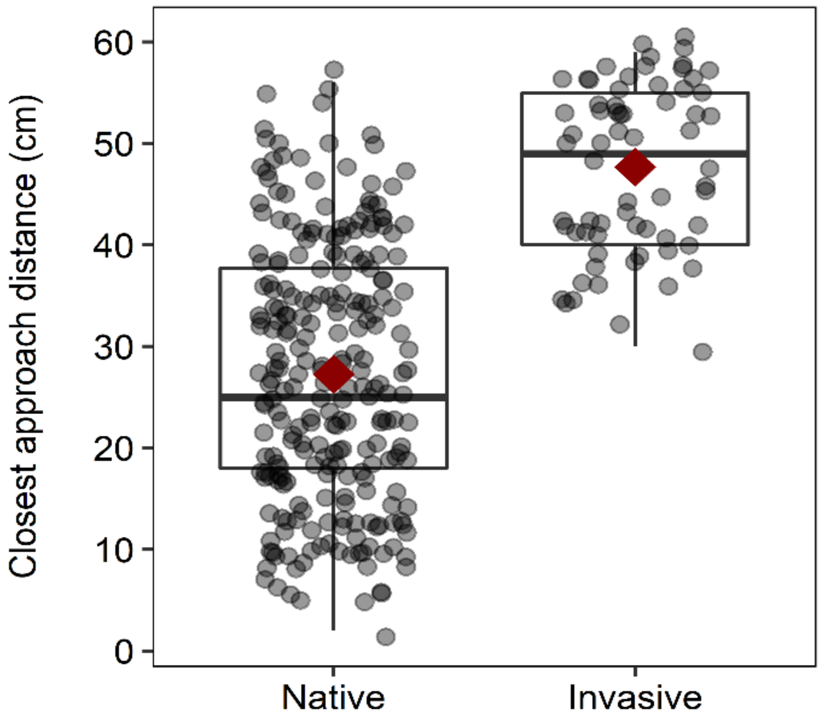


**Fig. 4.4** Box plot of closest approach distance (cm) of native and invasive prey fishes. Solid black line represents the median, with the box indicating the upper and lower quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points, and red diamond show the mean.

## 4.4 DISCUSSION

Given the significant impacts of lionfish invasion on native fish communities in the western Atlantic and Caribbean Sea, the recent establishment of lionfish in the western Mediterranean has created considerable concern amongst conservationists and other sectors of the society (Kletou et al. 2016; Jimenez et al. 2017). Although the extensive array of research on the ecological, behavioural and life-history traits determining the invasive success of Atlantic lionfish may give us an indication of the consequences of the Mediterranean lionfish invasion (Côté and Smith 2018), it is important to establish whether such key traits are similarly present in the Mediterranean invasion. We examined Mediterranean lionfish *in situ* behaviour and feeding ecology, and also investigated whether native Mediterranean prey species are naïve towards the invasive lionfish. We found that Mediterranean lionfish, at least in shallow habitats, are crepuscular, generalist predators with some level of prey specialization. In addition, native fish species show a lower level of predator awareness to Mediterranean lionfish than invasive Lessepsian species. Our results show considerable similarities between Atlantic and Mediterranean lionfish traits and give an indication of the potential scope of impact due to the lionfish invasion, as well as the possible flow-on consequences to the ecosystem and coastal food web.

### 4.4.1 Mediterranean lionfish behaviour, feeding ecology and prey association

Mediterranean lionfish activity varied significantly throughout the day, though with highest activity during sunrise and sunset, with Mediterranean lionfish thus able to be described as active crepuscular predators. Such feeding behaviour is consistent with previous studies on lionfish behaviour in their native (Indo-Pacific) and invaded range (western Atlantic ocean) (Cure et al. 2012; Benkwitt 2016), suggesting that Mediterranean lionfish have maintained their native behaviour, and that activity is influenced by light levels (Côté and Maljkovic 2010). At sunrise and sunset all activities related to foraging (time spent hunting, distance moved) were highest, while around noon most of the Mediterranean lionfish were observed resting or hiding under rock ledges. In lionfish, crepuscular feeding activity may be associated with increased hunting success of lionfish due to their high visual acuity in low light conditions (Green et al. 2011). In the Mediterranean the ability of lionfish to successfully hunt during twilight hours may potentially be an additional trait leading to their invasive success. As prey abundance may increase during twilight, due to the change-over between diurnal and nocturnal species (Hobson 1973; Potts 1990), a crepuscular generalist predator will have access to a broad array of prey species, potentially increasing the likelihood of successfully colonising a new environment. Although we did not systematically quantify nocturnal activity, four active Mediterranean lionfish were observed during a pilot observation taken immediately after sunset, indicating individuals may be hunting at night. This hypothesis may be corroborated by the common findings of nocturnal prey species in Mediterranean lionfish stomach contents (Zannaki et al. 2019; Nir Stern personal communication) and by studies showing nocturnal behaviour in Red Sea lionfish (Fishelson 1975; McTee and Grubich 2014). However, studies on invasive Atlantic lionfish report little or no nocturnal activity (Green et al. 2011; McCallister et al. 2018), suggesting potential differences in nocturnal behaviour between lionfish in natal vs invaded habitats. Further studies are needed to shed light on this potentially important behavioural trait.

The likelihood of hunting behaviour was positively influenced, though not absolutely determined, by fine-scale prey abundance, with such behaviour more prevalent when prey was locally abundant. For example, high levels of predation on *C. chromis* were found, but was also expected, as this prey species was the most abundant both at the fine- and broad-scale level. The Labridae (predominantly juvenile *T. pavo*) were also heavily targeted; although the broad-scale abundance of this group was low, they showed high abundance in the vicinity of Mediterranean lionfish. Such density dependent feeding behaviour may then indicate that Mediterranean lionfish may be associating with habitats where potential prey are more locally abundant. Indeed, Hunt et al. (2019) have recently described how Atlantic lionfish's position on the reef and aggregating behaviour are predominantly driven by large-scale habitat complexity, with such complexity resulting in high prey abundance. Such patterns highlight that lionfish are generalist predators, that may consume available and easily accessible prey (Peake et al. 2018). We can then expect that population expansion of Mediterranean lionfish to be a stepwise progression, with individuals moving with prey abundance, resulting in localised depletion of prey populations proceeded by movement of lionfish populations.

Small body size combined with a shallow body shape, and solitary, demersal behaviour may increase the likelihood of being predated on by Mediterranean lionfish. Such patterns of predation mirror those found for Atlantic lionfish (Green and Côté 2014; Chappell and Smith 2016). For example, in the current study, the heavily predated species *T. pavo* and the other Labridae juveniles fit the description of a small and shallow body shape combined with demersal behaviour, while the most heavily predated on species *C. chromis* are small sized and gather over the rocky substratum to feed on meroplankton at dusk, to shelter during the night and to breed (Aguzzi et al. 2013, Pinnegar 2018). In comparison, despite juveniles of *S. rivulatus* and *S. cretense* being the second and third most abundant species at the broad-scale level, with intermediate fine-scale abundance, both were not an important prey species for Mediterranean lionfish. Both species are relatively deep bodied, showing schooling behaviour and (*S. rivulatus* only) defensive venomous dorsal spines (Popper and Gundermann 1975; De Girolamo et al. 1999), potentially reducing their likelihood of being preferentially preyed upon.

### 4.4.2 Native versus invasive prey naiveté to Mediterranean lionfish predation

Species-specific anti-predatory behaviour may influence predation rates of Mediterranean lionfish, with native Mediterranean fishes (which have been evolutionarily isolated from lionfish) showing closer approach distances (i.e. higher naiveté) to Mediterranean lionfish than co-evolved (Lessepsian) fishes. These results are in line with the native prey naiveté theory, which posits that native prey lack effective anti-predatory responses to a novel predator, due to lack of exposure to the predator archetypes over evolutionary time (Cox and Lima 2006; Sih et al. 2010; Paolucci et al. 2013). This theory has been postulated to explain the predatory advantage of lionfish in the western Atlantic Ocean compared to native predators, and the disproportionate impact that lionfish have exerted on native Atlantic prey populations (Anton et al. 2016; Haines and Côté 2019). These results suggest that, without considerable changes in the behavioural response of prey fishes in the Mediterranean, substantial negative impacts on prey populations may occur (Strauss et al. 2006). For example, a sharp decline in prey populations' abundance will lead to reduced genetic variation, thereby diminishing the potential for adaptation to current environmental change (i.e. topicalization of Mediterranean Sea) (Strauss et al. 2006; Bianchi 2007). However, due to a strong selective predatory pressure, we would expect that prey recognition might eventually evolve in native Mediterranean fish (Strauss et al. 2006), as evolution of prey response to invasive predator has been shown to be possible in just a few generations (Berger 2001). Indeed, negative size-selective mortality (as per the highly targeted Labridae), has been linked to the selection of faster growing phenotypes (Belk et al. 1993; Ellis and Gibson 1995; Sogard 1997) coupled with the selection of shier and less active individuals (Sbragaglia et al. 2019). However, whether larger and more wary fish will be better adapted to cope with Mediterranean lionfish predation in the future is unknown. Nevertheless, to date, there is no evidence of adaptation of western Atlantic prey fish to the threat of Atlantic lionfish, even though lionfish populations have been established for over a decade (Anton et al. 2016; Haines and Côté 2019).

### 4.4.3 Implication for the wider marine community

As both *C. chromis* and *T. pavo* play fundamental roles in the Mediterranean ecosystem (Guidetti and Dulčić 2007; Milazzo et al. 2011; Galasso et al. 2015, Pinnegar 2018), selective predation and localised reduction in populations may have substantial flow-on effects on the wider marine community. For example, *C. chromis* populations channel carbon, phosphorus and nitrogen from the pelagic-zooplankton system to the rocky littoral environment in the form of liquid and solid waste (Bracciali et al. 2012; Pinnegar 2018), subsidising nutrients in one of the most oligotrophic seas in the world (Krom et al. 2014). Furthermore, *C. chromis* is the most abundant prey species of meso-predator fish and seabirds, and a major consumer of zooplankton and fish eggs itself (Pinnegar 2018), meaning that reductions in the abundance of *C. chromis* may have a strong negative impact on the coastal food web. In parallel, *T. pavo* feeds on small molluscs, crustaceans, annelids and echinoderms (Guidetti 2004; Galasso et al. 2015; Sinopoli et al. 2017), with its population abundance having been linked to top-down regulation of sea urchin populations (Guidetti and Dulčić 2007; Galasso et al. 2015). Therefore, reductions in the abundance of this species may accelerate local shifts in community structure from the ubiquitous sea grass bed to predominantly grazed barrens, in an environment already under strong pressure by invasive fish grazers (i.e. *Siganus rivulatus* and *S. luridus*) (Vergés et al. 2014). Lastly, Mediterranean lionfish have been increasingly shown to utilise caves as diurnal refuge habitats in Cyprus and, perhaps, feeding grounds (Jimenez et al. 2019b). Such behaviour may then overlap and, through increased predation, impact the diel migrations of fish and crustacean species between caves and external habitats. Such migration provide an important source of nutrients to the relatively nutrient poor epibenthic communities in caves (Coma et al. 1997; Bussotti et al. 2018). The impact of Mediterranean lionfish preying on diel migrants may then have substantial consequences for the maintenance of such nutrient poor communities, increasing the likelihood of locally mediated losses of cave specific benthic communities.

Our findings show that Mediterranean lionfish possess many of the behavioural and ecological traits that have been key in determining the invasive success of the Atlantic lionfish. Although the Mediterranean lionfish invasion is still at its early stage (first reported established populations in Lebanon and Cyprus in 2015) (Jimenez et al. 2016; Azzurro and Bariche 2017), selective predation and prey naiveté may have substantial population impacts on a range of native prey species (Albins and Hixon 2013; Peake et al. 2018; Côté and Smith 2018). Such impacts are expected to be in line with biodiversity impacts of the western Atlantic lionfish invasion, which has been linked to significant changes in native fish community, including reductions in prey species density, biomass, recruitment, richness (Albins and Hixon 2008; Benkwitt 2015; Albins 2015; Palmer et al. 2016), and even local species extirpation (Ingeman 2016). Ultimately, as the Mediterranean lionfish are at the beginning of the spreading stage of the invasion process (Chapple et al. 2012), is still unknown whether the behavioural and life-history traits measured in this study will be adaptive for a pan-Mediterranean invasion (Candolin 2018), where different thermal-regime and oceanographic conditions occur (Johnston and Purkis 2014). Hence, further studies are needed to track the potential expansion of Mediterranean lionfish distribution, and to evaluate the potential for predator-prey co-evolution of life-history and behavioural traits, by comparing differences in those traits between well-established and recently invaded areas.

# CHAPTER 5

## Thesis summation

With an increasingly changing climate and the threat this poses to coral reef ecosystems (Hughes et al. 2018; Cumming et al. 2020; França et al. 2020), the central focus of my thesis was to experimentally examine and test a range of mechanisms which may sustain coral reef fishes within a challenging environment, as well as potentially facilitating their invasion in a novel ecosystem. As coral reef fishes have evolved in a relatively stable thermal environment (Tewksbury et al. 2008; Sunday et al. 2011; Rummer et al. 2014), a major concern is that there may be little ability to acclimate to rapid changes in environmental conditions associated with ocean warming, increases in extreme weather events, and substantial degradation of habitat, resulting in potential negative population impacts (Sunday et al. 2011; Day et al. 2018; Richardson et al. 2018; Pratchett et al. 2018). In this work therefore, I focused on coral reef fishes that are found in the  extreme and variable environments of the Arabian Gulf, where native species can form abundant and stable communities (Chapters 2 and 3); and the Mediterranean Sea, where coral reef fishes have shown a wide array of success in invading this temperate rocky reef ecosystem (i.e. Lessepsian migrants: species native to the Red Sea who have invaded this sea through the Suez Canal) (Chapter 4). Within these model environments, which are significantly different from an environmentally stable tropical coral reef ecosystem, I examined the behavioural, life-history and demographic traits which may allow coral reef fish populations to sustain and thrive.

Behavioural plasticity is one of the most important factors determining species persistence in an extreme and variable environment (Tuomainen and Candolin 2011; Wong and Candolin 2015). However, is not clear how and to what extent individuals mitigate change in their environment through plasticity in behaviour (Candolin 2018; Donelson et al. 2019). Therefore, in Chapter 2 I focused on how the behaviour of the common pale-tail damselfish (*Pomacentrus trichrourus*) is impacted by temperature variability and extreme temperature in the Arabian Gulf, and experimentally examined the extent to which individuals are able to mitigate seasonal extremes in temperature through behavioural plasticity. Utilising seasonal *in situ* underwater behavioural observations I showed that individuals may mitigate seasonal thermal extremes (both high and low water temperature) in the Arabian Gulf by downregulating energetically costly behaviours during winter and summer, while upregulating activity and increasing energy stores in spring (when water temperatures are within the optimum for activity for this species). Additionally, individuals exhibited flexibility in diet, by shifting from a predominately planktonic (i.e. high nutrition) diet during optimal conditions (i.e. spring) to one encompassing both planktonic and easily accessible benthic food items when exposed to sub-optimal temperature (i.e. winter and summer). Plasticity in behaviour and activity associated with extreme temperature variability was then corroborated within laboratory conditions, where individuals exposed to winter water temperatures significantly reduced their activity compared to fish exposed to spring water temperatures. Finally, I predicted that individuals increase feeding activity in spring to build energetic storage to endure the following extreme summer and winter. Body condition of seasonally caught damselfish corroborated such prediction; somatic weight of the digestive system and liver of individuals were significantly higher in spring compared to winter and summer. Additionally, individuals accumulate visceral fat in spring, with such accumulation reaching its peak in summer, to be then completely depleted by the end of winter, indicating that energy stores are used during the harshest seasons for activity.

One of the most important factors which may determine species success within an extreme environment is how population demography is impacted by environmental change. Therefore, in Chapter 3 I examined whether there is a life-history trade-off between coral reef fish body size and metabolic demands in populations of two different species (i.e. *Lutjanus ehrenbergii* and *Pomacanthus maculosus*). I chose to examine populations living between the thermally extreme and highly saline Arabian Gulf and fish living in the comparably benign environment of the Oman Sea. Using otolith sclerochronology, I found that Arabian Gulf fishes attain a smaller size-at-age and smaller maximum size compared to Oman Sea counterparts, and that differences in environmental factors between regions (i.e. sea surface temperature [SST], salinity and chlorophyll-a) was the main driver of such demographic differences. Particularly, contrary to the expectation that high

SST would be the main factor determining growth reduction in the Arabian Gulf populations (*sensu* temperature-size rule, Atkinson 1994), my analysis showed that high salinity and variability in salinity were highly related with lower growth rates. Overall, these results suggest that osmoregulation can pose a high metabolic cost on coral reef fishes (Boeuf and Payan 2001; Kultz 2015) and may exacerbate the stress put on the organism by extreme environmental temperature (Claireaux and Lagarde 1999; Jian et al. 2003). These findings also suggest that to predict the effect of climate change on fish demography, the combined effect of osmoregulatory and thermal stress need to be considered, especially in regions where thermal and osmoregulatory stresses are expected to increase together. Indeed, although global ocean salinity will be minimally affected by climate change, climatic models predict that salinity will increase in already salty semi-landlocked seas, where evaporation levels are commonly higher than precipitation (Durack et al. 2012; Skliris et al. 2014; Zika et al. 2018). Hence, this result is of interest to other hyperhaline seas (*sensu* saltier than normal oceanic salinity, with evaporation rate higher than precipitation rate), such as the coral reef communities of the Red Sea and the temperate Mediterranean Sea.

Interestingly, this work has also shown for the first time the potential additive effect of increasing salinity and temperature on coral reef fishes' performance and growth, especially in the context of climate change. Indeed, most of the literature looking at the impacts of salinity on growth of fishes is aquaculture-related, with a major focus on temperate euryhaline species; such work has been predominantly structured in examining the role of osmoregulatory costs via reduction (within marine fishes) or increases of water salinity (within freshwater fishes) in determining fish growth (reviewed by Ern et al. 2014). Understanding how fish body size is impacted by changing environmental variables is crucial, as size reductions are expected to have vast consequences for trophic interactions, ecosystem function, fisheries, and global protein supply (Cheung et al. 2013; Sheridan and Bickford 2011; Edeline et al. 2013). Particularly, as fish fecundity is largely correlated with body size, size reduction within populations due to global climate change is expected to have substantial negative consequences on population reproductive output (Baudron et al. 2014; Barneche et al. 2018) and, therefore, long term population persistence.

While most of the studies investigating the effect of climate change on the size of ectotherms are drawn from models, fisheries, and laboratory experiments, this study has been able to show *in situ* size reduction from individuals resident in an environment which is recognised as a proxy for end-of-the-century climate change (Riegl and Purkis 2012; IPCC 2014; Hoegh-Guldberg et al. 2018). Ultimately, the results of this work can be predominantly explained by a life-history trade-off, whereby survival is enhanced through smaller body sizes and the associated reduced metabolic demands, which has flown-on effect to demographic structure. However, to disentangle the effects of extreme temperature and salinity on growth of Arabian Gulf fish populations and establish the role of other potential coping mechanisms (i.e. feeding and behavioural plasticity, see Chapter 2) in mitigating environmental stressors, laboratory-based physiological-behavioural experiments combining multiple stressors and conditions, while assessing detailed energy budget, are needed.

Invasive species commonly show a high degree of phenotypic plasticity, which may facilitate their acclimation to novel environments (Davidson et al. 2011; Hôrková and Kovácˇ 2014; van Baaren and Candolin 2018). Despite this, there is still debate as to the particular traits which may enhance invasion success (Blackburn et al. 2011; Chapple et al. 2012; Feary et al. 2014). Therefore, in Chapter 4 I investigated which behavioural traits allow Lessepsian lionfish (*Pterois miles*) to establish abundant populations in a temperate sea (i.e. the Mediterranean Sea), as well as investigating their predatory interactions with the native and not-native local fish community. By focusing on lionfish daily activities and feeding ecology, I found that lionfish are crepuscular (i.e. sunrise and sunset) generalist predators. Being a generalist predator indicates a predisposition to feed on a broad array of prey, potentially increasing the likelihood of being able to effectively deal with the environmental stochasticity of a novel environment (García-Berthou 2007, Peake et al. 2018). Moreover, as prey abundance may increase during twilight due to the change-over between diurnal and nocturnal species (Hobson 1973; Potts 1990), focusing predatory activity during sunrise and sunset may allow a much broader and more abundant array of prey for lionfish to utilise. Additionally, I showed for the first time in the Mediterranean Sea that native prey fishes show greater naiveté towards lionfish than Lessepsian prey species. Such naiveté of resident fishes towards a 'new' predator may enhance the population success of the invasive species through increased feeding rate and reduced competition with native predators, potentially mitigating any metabolic costs associated with invasion into a new environment (Anton et al. 2016).

While the behavioural traits of invasive Atlantic lionfish have been extensively studied following the substantial negative impacts on native fish biodiversity (Albins and Hixon 2013; Côté and Smith 2018), to date there has been little work investigating the behavioural and feeding ecology of Mediterranean lionfish. As such, Chapter 4 represents novel findings in the understanding of the phenotypic traits that may be adaptive in a novel environment and, potentially, in the acclimation to native ecosystem changes. Indeed, an interesting topic for future research would be to quantify the role of phenotypic plasticity in determining the success of Lessepsian migrants and investigate whether such traits exhibited in the Mediterranean could be adaptive in coral reef ecosystems that are likely to be substantially impacted by end-of-the-century climate change predictions (i.e. shift from a coral-dominated ecosystem to coral rubble, seagrass and turfing algae).

## Conclusion and future of coral reef fish in a changing world

Overall, this thesis examined how coral reef fishes may cope with living in an extreme environment, as well as the phenotypic traits that may facilitate their range expansion into temperate seas, and provides novel results showing that some coral reef fish possess more phenotypic plasticity than previously thought (Candolin 2018; Donelson et al. 2019). Moreover, it shows that some species may be able to acclimate to environments with great seasonal variability in temperature and salinity, as well as end-of-century predicted temperature for tropical oceans due to climate change, and environments where corals are not the main ecosystem engineer (i.e. temperate rocky reefs). Despite this, a high degree of adaptive phenotypic plasticity may not be available in all coral reef fishes. Indeed, the Arabian Gulf's marine community encompasses only 241 species of coral-associated bony fish, which are considered a biogeographic subset of the Indian Ocean's fauna that recolonised the region between 6000 and 9000 years ago (Riegl and Purkis 2012). Indeed, the coral reef fish community richness in the Arabian Gulf is thought to be lower than that in the Western Indian Ocean as a consequence of the Arabian Gulf's physical extremes, which fewer Indian Ocean species can tolerate (Coles 2003; Feary et al. 2010). Similarly, to date, only ~100 fish species have been reported as Lessepsian migrants, none of which are strictly dependent on live coral for food or protection, stressing the point that phenotypic plasticity can be a powerful means to acclimate to a new environment, but that there are habitat constraints which cannot be overcome. Overall, we can expect that there will be a distinct subset of coral reef fishes which may survive, and indeed thrive, in a more environmentally extreme marine ecosystem. Such communities are expected to be those which display adaptive plasticity amongst their ecological traits. Hence, understanding when, and potentially how, individual coral reef fish may adjust their phenotype, and whether such traits are inherent within species when faced with environmental change, will be vital in determining the role and the limits of plasticity in structuring coral reef fishes within an increasingly changing ecosystem (Wong and Candolin 2015; Nagelkerken and Munday 2016).

# SUPPLEMENTARY MATERIALS

## (A) Supplementary materials Chapter 2

### (A.1) Tables

**Table S2.1** Differences in abiotic (a) and biotic (b) environmental variables between seasons (mean ± SE).

| Environmental factor | Winter | Spring | Summer | Kruskal-Wallis |
|---|---|---|---|---|
| **a) Abiotic** | n= 4 | n = 6 | n = 6 | |
| SST | 20.60 (0.12) | 27.45 (0.19) | 33.85 (0.11) | H = 13.294, df = 2, p = **0.001** |
| DO | 6.54 (0.04) | 5.61 (0.02) | 4.86 (0.01) | H = 13.274, df = 2, p = **0.001** |
| Chl-a | 1.38 (0.05) | 1.38 (0.17) | 2.97 (0.62) | H = 10.638, df = 2, p = **0.005** |
| Salinity | 39.93 (0.05) | 38.93 (0.03) | 39.85 (0.13) | H = 10.770, df = 2, p = **0.005** |
| Wind speed | 5.5 (0.70) | 5.91 (0.34) | 5.57 (0.56) | H = 2.592, df = 2, p = 0.274 |
| Water current | 0.03 (0.02) | 0.03 (0.01) | 0.03 (0.01) | H = 1.456, df = 2, p = 0.483 |
| Visibility | 6.00 (1.11) | 11.95 (1.23) | 8.25 (0.66) | H = 6.231, df = 2, p = **0.044** |
| **b) Biotic** | n = 61 | n = 83 | n = 83 | |
| Predators | 0.22 (0.1) | 0.92 (0.2) | 6.41 (1) | H = 73.790, df = 2, p < **0.001** |
| Competitors | 0.38 (0.1) | 0.75 (0.1) | 0.49 (0.1) | H = 7.191, df = 2, p = **0.027** |

**Table S2.2** Comparison of mean (± SE), maximum and total of predators (**a**) and competitors (**b**) that the focal species *Pomacentrus trichrourus* encountered during the 2 minutes behavioural observation in winter (left), spring (middle) and summer (right). Species ranked by order of abundance at the summer season.

| **Species** | **Winter** | | | **Spring** | | | **Summer** | | |
|---|---|---|---|---|---|---|---|---|---|
| | **Mean** | **Max** | **n** | **Mean** | **Max** | **n** | **Mean** | **Max** | **n** |
| a) **Predators** | | | | | | | | | |
| *Lutjanus ehrenbergii* | 0.08 (0.05) | 3 | 5 | 0.89 (0.21) | 10 | 74 | 6.12 (1.00) | 59 | 508 |
| *Scolopsis ghanam* | 0.12 (0.06) | 3 | 7 | 0.01 (0.01) | 1 | 1 | 0.17 (0.06) | 3 | 14 |
| *Epinephelus spp* | 0 | 0 | 0 | 0.02 (0.02) | 1 | 1 | 0.09 (0.05) | 1 | 6 |
| *Lutjanus fulviflamma* | 0 | 0 | 0 | 0.02 (0.02) | 1 | 1 | 0.09 (0.05) | 1 | 3 |
| **Total** | **0.22 (0.10)** | | **12** | **0.92 (0.20)** | | **76** | **6.41 (1.00)** | | **525** |
| **b) Competitors** | | | | | | | | | |
| *Pomacentrus trichrourus* | 0.35 (0.07) | 2 | 21 | 0.75 (0.01) | 4 | 62 | 0.45 (0.06) | 2 | 37 |
| *Pomacentrus aquilis (j)* | 0.05 (0.04) | 2 | 3 | 0.59 (0.07) | 3 | 49 | 0.3 (0.05) | 2 | 25 |
| *Pomacentrus aquilis* | 0.03 (0.02) | 1 | 2 | 0 | 0 | 0 | 0.05 (0.02) | 1 | 4 |
| **Total** | **0.38 (0.10)** | | **26** | **0.75 (0.10)** | | **111** | **0.49 (0.10)** | | **66** |

**Table S2.3** Comparison of *in situ* behaviour (median ± SE, max and min) between seasons.

| | **Winter** (n = 60) | | | **Spring** (n = 83) | | | **Summer** (n = 83) | | |
|---|---|---|---|---|---|---|---|---|---|
| Median | Median | Max | Min | Median | Max | Min | Median | Max | Min |
| **Distance from refugia** | 3.77 (0.3) | 9.38 | 1.08 | 5.38 (0.5) | 21.69 | 1.15 | 1.96 (0.2) | 9 | 0.85 |
| **Resting** | 5.62 (0.6) | 20.74 | 0.48 | 2.48 (1.0) | 45.45 | 0.12 | 10.37 (0.7) | 26.24 | 10.37 |
| **Feeding rate** | 12 (0.7) | 38 | 4 | 49 (0.9) | 86 | 16 | 25 (0.9) | 53 | 25 |

## (A.2) Figures

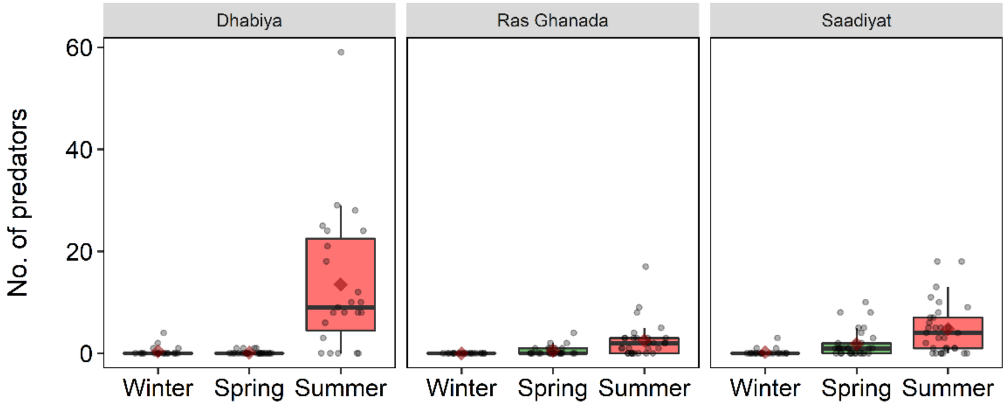


**Figure S2.1** Changes in abundance of *Pomacentrus trichrourus'* potential predators with seasons (winter = blue, spring = green, summer = red) and locations (Dhabiya, Ras Ghanada and Saadiyat). Solid black line represents the median, with the box indicating the upper and lower quartiles, and whiskers representing the maximum or minimum observed value that is within 1.5 times the interquartile range of the upper or lower quartile, respectively. Dots are individual data points, and red diamond show the mean.

# (B) Supplementary materials Chapter 3

## (B.1) Material and methods

### (B.1.1) Intrinsic predictors

A random intercept for FishID was introduced to generate a correlation among increment widths within an individual and allow each individual to have a higher or lower average growth than the model's intercept, accounting for non-independence of the response data (Morrongiello and Thresher 2015). Similarly, a random intercept for Year was included to account for the non-independency of increments formed by different fish in the same year, as the sampled individuals were exposed to the same environment. Finally, we explored whether the model fit would improve when a random age slope for Year (Age|Year) and FishID (Age|FishID) were included (Table 3). Age|Year allowed for year-dependent differences in age-specific growth, while Age|FishID allowed for individual-specific differences in the growth−age relationship (Morrongiello et al. 2015; Barrow et al. 2018).

### (B.1.2) Extrinsic predictors

SST and Salinity were obtained from the NCEP Climate Forecast System Version 2 (CFSv2, Saha et al 2011), while chl-a measurements were obtained from the MODIS-aqua satellite (NASA 2014). For each region, daily mean SST was extracted (resolution 0.25-deg x 0.25-deg), annual mean maximum and minimum were calculated by averaging the daily temperature for the hottest (i.e. August) and coldest (i.e. February) month of the year, respectively; while mean annual SST was the annual average of all daily data. Salinity was downloaded as daily mean (resolution 0.25-deg x 0.25-deg) and calculate as annual average of all daily data, while chl-a was obtained as monthly composite data (resolution 0.05) and calculated as annual average of all monthly data. All environmental variables were centrally located off the cost of Abu-Dhabi (25°25’18.75” N, 51°08’18.44” E) for the Arabian Gulf, and Fujairah (25° 7'17.03"N, 56°24'26.53"E) for the Oman. Satellite data from Abu-Dhabi and Fujairah showed high similarity to the other sampling sites within their region, suggesting that SST, salinity and chl-a variables are consistent across the Gulf and Oman sites (Fig. S3.2).

### (B.1.3) Model selection

The initial base model consisted of a random intercept for FishID, while the second base model consisted of a random Age slope for FishID (Table S3, S4). These models were fitted using restricted maximum likelihood estimation (REML) (Zuur et al. 2009) and ranked using Akaike’s information criterion corrected for small sample sizes ($AIC_C$) (Burnham and Anderson 2004). Random intercepts for Year and random Age slope for Year were added individually to the optimal model, and then fitted and ranked as above (Table S3.3, S3.4). At this stage, all models incorporated the maximum intrinsic fixed effect structure (Age and ACC) (Zurr et al. 2009) (Table S3.3, S3.4). To determine the ‘optimal intrinsic model’ we then re-analyzed the optimal random effects model including and excluding AAC (Table S3.5, S3.6). These models were initially fitted using maximum likelihood estimation (ML) with the best-ranked model refitted with REML to produce unbiased parameter estimates (Zuur et al. 2009).

## (B.2) Tables

**Table S3.1**. Differences in annual mean (± SE) SST (°C), salinity (psu) and chl-a (mg $m^{-3}$) between the southern Arabian Gulf (centrally located off the coast of Abu-Dhabi) and northern Oman (Fujairah).

| Environmental factor | Arabian Gulf | Oman | Range years | Kruskal-Wallis test |
|---|---|---|---|---|
| **Mean SST** | 27.65 (0.06) | 27.6 (0.07) | 1993–2016 | $H = 0.333$, $df = 1$, $p = 0.564$ |
| **Max SST** | 34.21 (0.08) | 32.37 (0.12) | 1993–2016 | **$H = 34.293$, $df = 1$, $p < 0.001$** |
| **Min SST** | 19.73 (0.16) | 22.37 (0.11) | 1993–2016 | **$H = 34.777$, $df = 1$, $p < 0.001$** |
| **Mean salinity** | 40.79 (0.14) | 36.90 (0.02) | 1993–2016 | **$H = 35.265$, $df = 1$, $p < 0.001$** |
| **Max salinity** | 42.01 (0.24) | 37.58 (0.06) | 1993–2016 | **$H = 35.265$, $df = 1$, $p < 0.001$** |
| **Min salinity** | 39.18 (0.13) | 36.45 (0.03) | 1993–2016 | **$H = 35.265$, $df = 1$, $p < 0.001$** |
| **Mean chl-a** | 1.76 (0.33) | 2.31 (0.18) | 2003–2016 | **$H = 10.345$, $df = 1$, $p = 0.013$** |
| **Max chl-a** | 3.26 (0.37) | 8.3 (0.95) | 2003–2016 | **$H = 15.614$, $df = 1$, $p < 0.001$** |
| **Min chl-a** | 1.01 (0.33) | 0.38 (0.04) | 2003–2016 | **$H = 20.276$, $df = 1$, $p < 0.001$** |

**Table S3.2.** Sampling sites, number of specimens collected and relative methods.

| Region | Site | Map Ref no. | Latitude, Longitude | Fishing method | No. LEHR | No. PMAC |
|---|---|---|---|---|---|---|
| **Arabian Gulf** | Dhabiya | 1 | 24°21'55.81" N, 54°06'02.95" E | Field collection | 0 | 10 |
| | Abu - Dhabi | 2 | 24°31'32.47" N, 54°21'35.93" E | Local fishers | 143 | 35 |
| | Abu - Dhabi | 2 | 24°31'32.47" N, 54°21'35.93" E | Local fishers* | 677 | 0 |
| | Saadiyat | 3 | 24°35'56.46" N, 54°25'17.42" E | Field collection | 21 | 109 |
| | Ras Ghanada | 4 | 24°50'53.44" N, 54°41'25.18" E | Field collection | 4 | 2 |
| | Dubai | 5 | 25°17'33.27" N, 55°19'20.61" E | Local fishers | 13 | 5 |
| | Umm Al Quwain | 6 | 25°32'52.22" N, 55°33'38.60" E | Local fishers | 15 | 7 |
| **Oman** | Dibba rock | 7 | 25°36'10.68" N, 56°21'3.73" E | Field collection | 7 | 8 |
| | Dibba | 8 | 25°36'30.12" N, 56°17'34.65" E | Local fishers | 28 | 3 |
| | Al Aqah | 9 | 25°29'32.10" N, 56°21'47.62" E | Field collection | 10 | 19 |
| | Kor Fakkan | 10 | 25°20'52.11" N, 56°21'48.49" E | Local fishers | 3 | 0 |
| | Fujairah | 11 | 25°07'24.41" N, 56°21'29.78" E | Local fishers | 35 | 12 |
| | Sohar | 12 | 24°22'42.69" N, 56°44'24.70" E | Local fishers | 23 | 0 |
| | As Seeb | 13 | 23°41'19.99" N, 58°10'44.17" E | Local fishers | 33 | 0 |

Note: LEHR denote *Lutjanus ehrenbergii*, PMAC denote *Pomacanthus maculosus*; Field collection denote *in situ* collection with hand spear or clove oil; * indicate environmental agency research vessel.

**Table S3.3.** Results of random effect base model selection fitted to *L. ehrenbergii* growth data. Models 1a and 1b were fitted first, followed by model 2a and 3a. All models included the maximum fixed intrinsic effects Age + ACC. Random slope term designated with x|y. Best model highlighted in bold.

| Region | Mod | Random effects structure | df | AICc | ΔAICc | AICc (Wt) | LL | $R^2$(C) | $R^2$(M) |
|---|---|---|---|---|---|---|---|---|---|
| **Arabian Gulf** | 1a | (1\|FishID) | 5 | -96.41 | 11.29 | 0 | 53.35 | 0.890 | 0.835 |
| | **1b** | **(Age\|FishID)** | **7** | **-107.7** | **0** | **1** | **61.12** | **0.910** | **0.878** |
| | **2a** | **(Age\|FishID) + (1\|Year)** | **8** | **-124.56** | **0** | **0.89** | **70.63** | **0.937** | **0.859** |
| | 3a | (Age\|FishID) + (Age\|Year) | 10 | -120.32 | 4.24 | 0.11 | 70.71 | 0.937 | 0.853 |
| **Oman Sea** | 1a | (1\|FishID) | 5 | -145.35 | 13.95 | 0 | 77.76 | 0.894 | 0.857 |
| | **1b** | **(Age\|FishID)** | **7** | **-159.3** | **0** | **1** | **86.81** | **0.927** | **0.891** |
| | **2a** | **(Age\|FishID) + (1\|Year)** | **8** | **-172.83** | **0** | **0.82** | **94.62** | **0.948** | **0.853** |
| | 3a | (Age\|FishID) + (Age\|Year) | 10 | -169.77 | 3.06 | 0.18 | 95.2 | 0.952 | 0.875 |

**Table S3.4.** Results of random effect base model selection fitted to *P. maculosus* growth data. Models 1a and 1b were fitted first, followed by model 2a and 3a. All models included the maximum fixed intrinsic effects Age + ACC. Random slope term designated with x|y. Best model highlighted in bold.

| Region | Mod | Random effects structure | df | AICc | ΔAICc | AICc (Wt) | LL | $R^2$(C) | $R^2$(M) |
|---|---|---|---|---|---|---|---|---|---|
| **Arabian Gulf** | 1a | (1\|FishID) | 5 | -212.06 | 83.5 | 0 | 111.08 | 0.845 | 0.873 |
| | **1b** | **(Age\|FishID)** | **7** | **-295.56** | **0** | **1** | **154.86** | **0.871** | **0.919** |
| | 2a | (Age\|FishID) + (1\|Year) | 8 | -311.24 | 17.8 | 0 | 163.73 | 0.932 | 0.852 |
| | **3a** | **(Age\|FishID) +(Age\|Year)** | **10** | **-329.04** | **0** | **1** | **174.68** | **0.943** | **0.898** |

**Table S3.5**. Result of intrinsic fixed effect base model selection fitted to *L. ehrenbergii* growth data. Includes optimal random effects base model 2a the Gulf and Oman. Best model is highlighted in bold.

| Region | Mod | Fixed effects structure | df | AICc | ΔAICc | AICc (Wt) | LL | $R^2$(C) | $R^2$(M) |
|---|---|---|---|---|---|---|---|---|---|
| Arabian Gulf | 2a1 | Age | 7 | -129.3 | 8.83 | 0.01 | 71.92 | 0.924 | 0.886 |
| | **2a2** | **Age + AAC** | **8** | **-138.12** | **0** | **0.99** | **77.42** | **0.935** | **0.870** |
| Oman Sea | 2a1 | Age | 7 | -186.05 | 0.59 | 0.43 | 100.19 | 0.941 | 0.884 |
| | **2a2** | **Age + AAC** | **8** | **-186.64** | **0** | **0.57** | **101.53** | **0.947** | **0.865** |

**Table S3.6**. Result of intrinsic fixed effect base model selection fitted to *P. maculosus* growth data for the Gulf. Includes optimal random effects base model 3a1. Best model is highlighted in bold.

| Region | Mod | Fixed effects structure | df | AICc | ΔAICc | AICc (Wt) | LL | $R^2$(C) | $R^2$(M) |
|---|---|---|---|---|---|---|---|---|---|
| Arabian Gulf | **3a1** | **Age** | **9** | **-345.77** | **0** | **0.56** | **182.02** | **0.942** | **0.898** |
| | 3a2 | Age + AAC | 10 | -345.3 | 0.47 | 0.44 | 182.81 | 0.942 | 0.899 |

**Table S3.7**. Results of fixed effects model selection for environmental growth predictors fitted to annual *Lutjanus ehrenbergii* growth data. The optimal base model is underlined. Grey shading indicates models removed from comparison because due to VIF values ≥ 3. Models are ranked from lowest to highest AIC score.

| Region | Mod | Fixed effects structure | *df* | AICc | ΔAICc | AICc (Wt) | LL | $R^2$(C) | $R^2$(M) |
|---|---|---|---|---|---|---|---|---|---|
| **Arabian Gulf** | 2a2 + | **max SST + Salinity** | **10** | **-145.24** | **0** | **0.29** | **83.17** | **0.9353** | **0.8703** |
| | 2a2 + | Salinity | 9 | -145.06 | 0.18 | 0.26 | 81.98 | 0.9341 | 0.8752 |
| | 2a2 + | min SST + Salinity | 10 | -143.74 | 1.5 | 0.14 | 82.42 | 0.9335 | 0.8755 |
| | 2a2 + | Salinity + Chl-a | 10 | -143.53 | 1.71 | 0.12 | 82.31 | 0.9354 | 0.8706 |
| | 2a2 + | Salinity + mean SST | 10 | -142.86 | 2.38 | 0.09 | 81.98 | 0.9322 | 0.8907 |
| | 2a2 + | Salinity * Chl-a | 11 | -141.5 | 3.74 | 0.04 | 82.41 | 0.9354 | 0.8712 |
| | 2a2 + | min SST + mean SST | 10 | -139.29 | 5.95 | 0.01 | 80.19 | 0.9332 | 0.8771 |
| | 2a2 + | min SST | 9 | -138.43 | 6.8 | 0.01 | 78.66 | 0.9342 | 0.8754 |
| | 2a2 + | Growth optimal base model | 8 | -138.12 | 7.12 | 0.01 | 77.42 | 0.9313 | 0.8932 |
| | 2a2 + | min SST + Chl-a | 10 | -137.08 | 8.16 | 0 | 79.09 | 0.9342 | 0.8758 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | 2a2 + | max SST | 9 | -136.78 | 8.46 | 0 | 77.84 | 0.9340 | 0.8766 |
| | 2a2 + | max SST + min SST | 10 | -136.36 | 8.88 | 0 | 78.73 | 0.9338 | 0.8826 |
| | 2a2 + | Chl-a | 9 | -136.04 | 9.19 | 0 | 77.47 | 0.9321 | 0.8914 |
| | 2a2 + | mean SST | 9 | -136 | 9.24 | 0 | 77.45 | 0.9336 | 0.8788 |
| | 2a2 + | min SST * Chl-a | 11 | -135.21 | 10.03 | 0 | 79.27 | 0.9333 | 0.8811 |
| | 2a2 + | max SST + Chl-a | 10 | -134.66 | 10.58 | 0 | 77.88 | 0.9322 | 0.8907 |
| | 2a2 + | max SST + mean SST | 10 | -134.63 | 10.61 | 0 | 77.86 | 0.9354 | 0.8712 |
| | 2a2 + | mean SST * Chl-a | | | | | | | |
| | 2a2 + | mean SST + Chl-a | 10 | -133.84 | 11.4 | 0 | 77.47 | 0.9325 | 0.8921 |
| | 2a2 + | max SST + Chl-a | 11 | -132.46 | 12.78 | 0 | 77.89 | 0.9325 | 0.8918 |
| **Oman Sea** | 2a2 + | **Salinity** | **9** | **-190.36** | **0** | **0.24** | **104.44** | **0.9466** | **0.8647** |
| | 2a2 + | Salinity + mean SST | | | | | | | |
| | 2a2 + | max SST + Salinity | | | | | | | |
| | 2a2 + | Salinity + Chl-a | 10 | -188.5 | 1.86 | 0.1 | 104.57 | 0.9457 | 0.8703 |
| | 2a2 + | min SST + Salinity | 10 | -188.25 | 2.11 | 0.08 | 104.45 | 0.9462 | 0.8706 |
| | 2a2 + | max SST | 9 | -186.73 | 3.63 | 0.04 | 102.63 | 0.9466 | 0.8640 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 2a2 + | Growth optimal base model | 8 | -186.64 | 3.72 | 0.04 | 101.53 | 0.9458 | 0.8704 |
| 2a2 + | Salinity * Chl-a | 11 | -186.42 | 3.94 | 0.03 | 104.59 | 0.9458 | 0.8697 |
| 2a2 + | mean SST | 9 | -186.16 | 4.2 | 0.03 | 102.34 | 0.9461 | 0.8695 |
| 2a2 + | max SST + min SST | 10 | -184.68 | 5.68 | 0.01 | 102.66 | 0.9458 | 0.8705 |
| 2a2 + | max SST + Chl-a | 10 | -184.65 | 5.71 | 0.01 | 102.65 | 0.9459 | 0.8704 |
| 2a2 + | Chl-a | 9 | -184.63 | 5.73 | 0.01 | 101.58 | 0.9456 | 0.8712 |
| 2a2 + | max SST + mean SST | | | | | | | |
| 2a2 + | min SST | 9 | -184.54 | 5.82 | 0.01 | 101.53 | 0.9466 | 0.8639 |
| 2a2 + | min SST + mean SST | 10 | -184.15 | 6.21 | 0.01 | 102.39 | 0.9455 | 0.8687 |
| 2a2 + | mean SST + Chl-a | 10 | -184.06 | 6.3 | 0.01 | 102.35 | 0.9462 | 0.8690 |
| 2a2 + | max SST + Chl-a | 11 | -182.61 | 7.75 | 0.01 | 102.69 | 0.9457 | 0.8701 |
| 2a2 + | min SST + Chl-a | 10 | -182.52 | 7.84 | 0 | 101.58 | 0.9457 | 0.8703 |
| 2a2 + | mean SST * Chl-a | 11 | -181.95 | 8.41 | 0 | 102.36 | 0.9462 | 0.8718 |
| 2a2 + | min SST * Chl-a | 11 | -181.14 | 9.22 | 0 | 101.95 | 0.9461 | 0.8722 |

**Table S3.8**. Results of fixed effects model selection for environmental growth predictors fitted to annual *Pomacanthus maculosus* growth data. The optimal base model is underlined. Grey shading indicates models removed from comparison because due to VIF values ≥ 3. Models are ranked from lowest to highest AIC score.

| Region | Mod | Fixed effects structure | df | AICc | ΔAICc | AICc (Wt) | LL | $R^2$(C) | $R^2$(M) |
|---|---|---|---|---|---|---|---|---|---|
| **Arabian Gulf** | 3a1 + | **Salinity + mean SST** | **11** | **-348.24** | **0** | **0.27** | **185.32** | **0.9416** | **0.8978** |
| | 3a1 + | Salinity | 10 | -347.47 | 0.77 | 0.19 | 183.9 | 0.9416 | 0.8977 |
| | 3a1 + | max SST + Salinity | 11 | -346.65 | 1.59 | 0.12 | 184.53 | 0.9416 | 0.8988 |
| | 3a1 + | mean SST | 10 | -346.23 | 2.01 | 0.1 | 183.28 | 0.9415 | 0.8993 |
| | 3a1 + | min SST + Salinity | 11 | -346 | 2.25 | 0.09 | 184.2 | 0.9405 | 0.8929 |
| | 3a1 + | <u>Growth optimal base model</u> | 9 | -345.77 | 2.47 | 0.08 | 182.02 | 0.9347 | 0.8817 |
| | 3a1 + | max SST + mean SST | 11 | -344.3 | 3.94 | 0.04 | 183.35 | 0.9416 | 0.8988 |
| | 3a1 + | min SST | 10 | -344.24 | 4 | 0.04 | 182.28 | 0.9415 | 0.8992 |
| | 3a1 + | min SST + mean SST | 11 | -344.17 | 4.08 | 0.04 | 183.28 | 0.9399 | 0.8912 |
| | 3a1 + | max SST | 10 | -343.72 | 4.53 | 0.03 | 182.02 | 0.9346 | 0.8817 |
| | 3a1 + | max SST + min SST | 11 | -342.17 | 6.07 | 0.01 | 182.28 | 0.9347 | 0.8818 |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| 3a1 + | min SST + Chl-a | 11 | -324.16 | 24.08 | 0 | 173.3 | 0.9415 | 0.8993 |
| 3a1 + | mean Chl-a | 10 | -323.35 | 24.9 | 0 | 171.86 | 0.9407 | 0.8938 |
| 3a1 + | min SST * Chl-a | 12 | -322.27 | 25.97 | 0 | 173.4 | 0.9351 | 0.8847 |
| 3a1 + | Salinity + Chl-a | 11 | -321.78 | 26.46 | 0 | 172.12 | 0.9350 | 0.8849 |
| 3a1 + | mean SST + Chl-a | | | | | | | |
| 3a1 + | max SST + Chl-a | 11 | -321.27 | 26.97 | 0 | 171.86 | 0.9332 | 0.8862 |
| 3a1 + | mean SST * Chl-a | | | | | | | |
| 3a1 + | Salinity * Chl-a | 12 | -319.92 | 28.32 | 0 | 172.23 | 0.9351 | 0.8807 |
| 3a1 + | max SST + Chl-a | 12 | -319.2 | 29.04 | 0 | 171.87 | 0.9354 | 0.8804 |

## (B.3) Figures

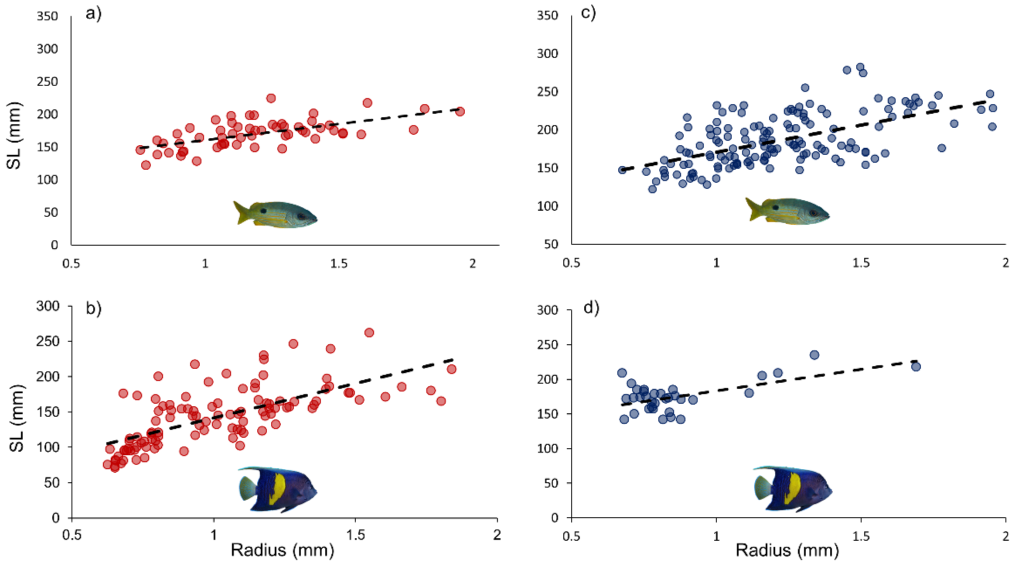


**Fig. S3.1.** Relationship between fish size (standard length) and otolith size (radius) in *L. ehrenbergii* (Linear regression: $F$ = 89.2, $df$ 1,209, p < 0.001**) (a)** and *P. maculosus* ($F$ = 387.9, $df$ 1,673, p < 0.001) **(b)** from the Arabian Gulf.

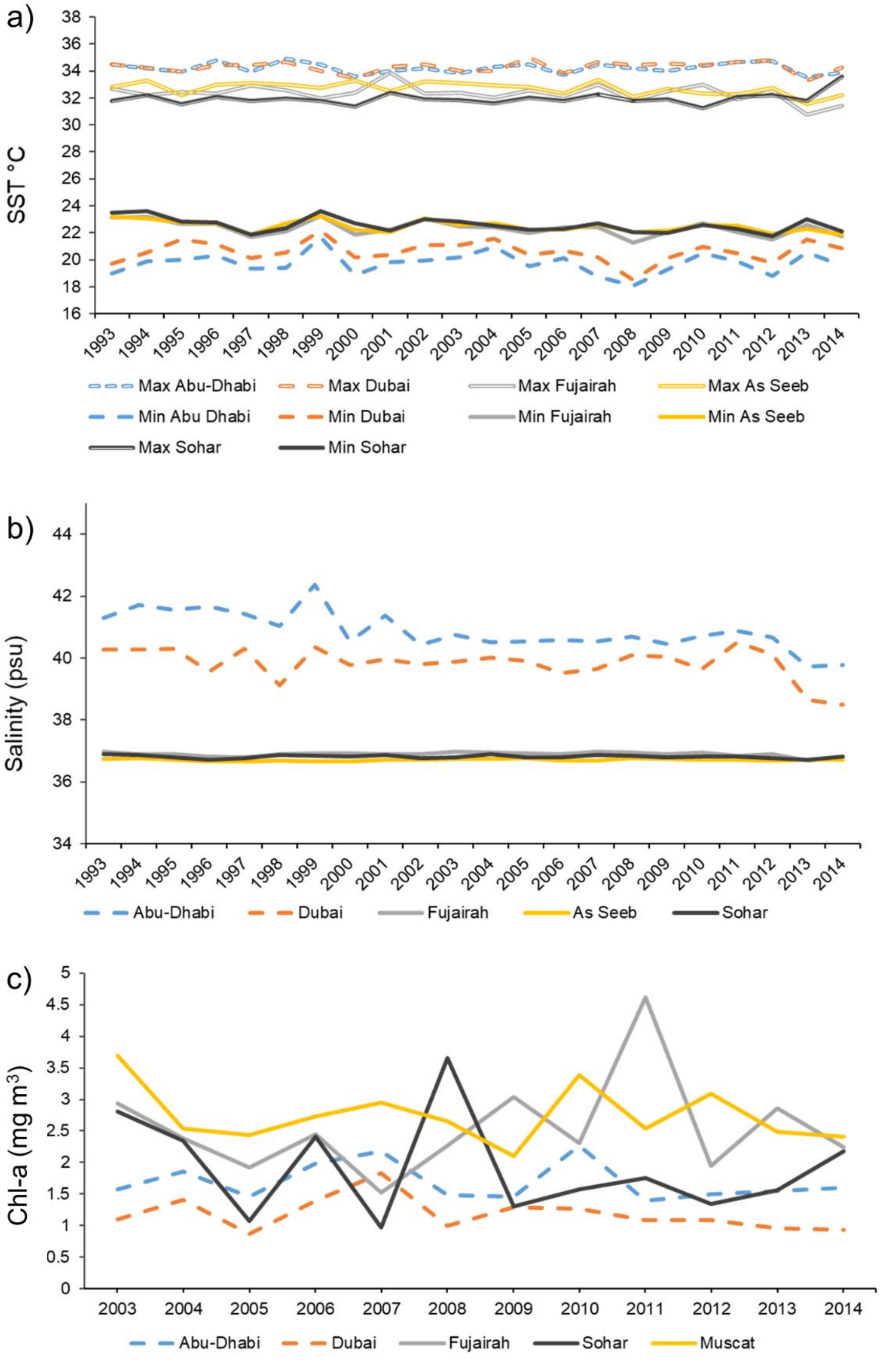


**Fig. S3.2.** Annual values in SST **(a)**, salinity **(b),** chlorophyll-a **(c)** between sites in the Arabian Gulf (dashed lines) and Oman (solid lines).

# (C) Supplementary materials Chapter 4

## (C.1) Tables

**Table S4.1** Grouping of prey species to meet chi-square test assumption.

| Targeted prey | Times targeted | Fine-scale prey abundance | Broad-scale prey abundance | Time targeted index (%) | Fine-scale prey relative abundance (%) | Broad-scale prey relative abundance (%) |
|---|---|---|---|---|---|---|
| *Chromis chromis* | 42 | 331 | 6162 | 48.28 | 64.77 | 64.00 |
| *Parupeneus forsskali* | 8 | 50 | 336 | 9.2 | 9.78 | 3.49 |
| Labridae | 28 | 80 | 530 | 32.18 | 15.65 | 5.5 |
| *Siganus rivulatus/ Sparisoma cretense* | 3 | 42 | 2585 | 3.45 | 8.22 | 26.85 |
| Rare species | 6 | 8 | 16 | 6.9 | 1.57 | 0.17 |

## (C.2) Figures

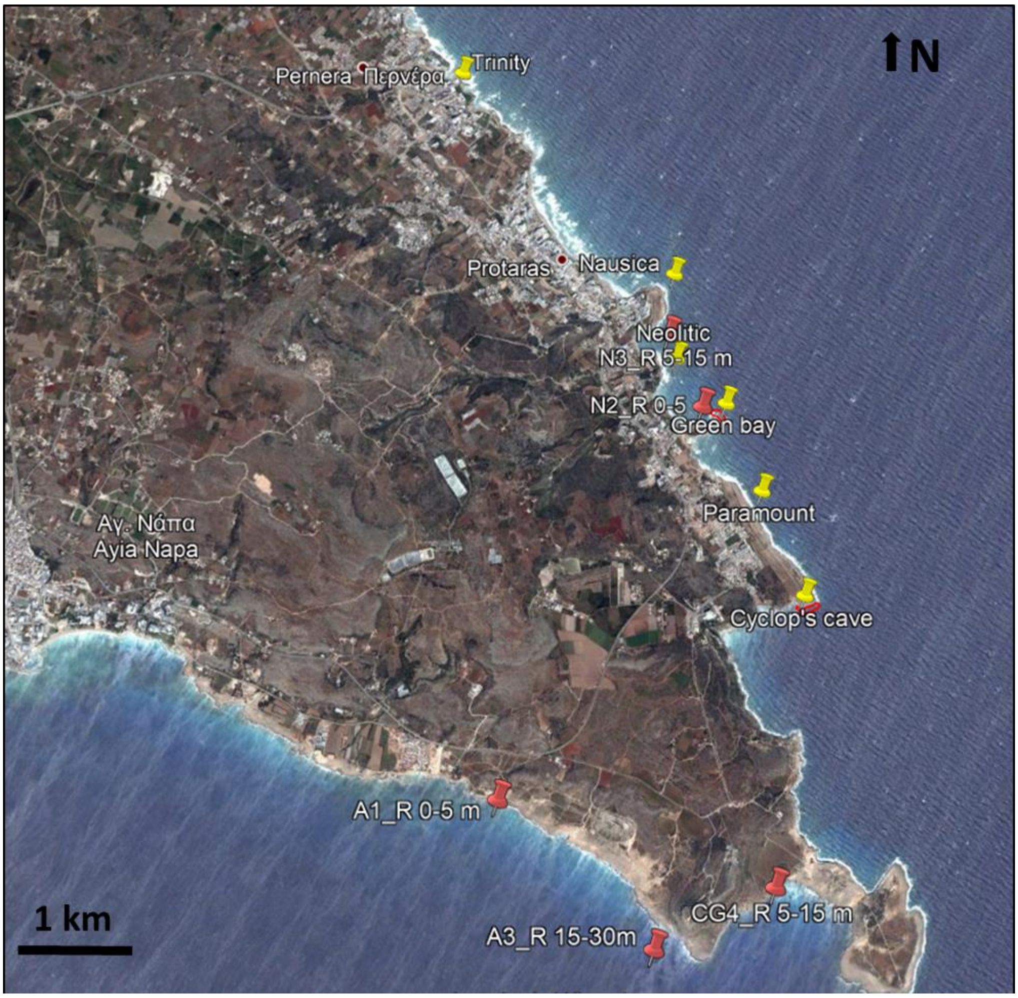


**Fig. S4.1** Study site details. Yellow pins: sites of behavioural observation and fine-scale prey abundance data; red pins: sites were fish surveys for broad–scale prey abundance data were undertaken. (Source Google earth V 7.3.2 [October 04, 2019]).

## (C.3) Videos

**Video S4.1** Example of resting behaviour of Mediterranean lionfish. The lionfish is observed resting motionless in the shade under a rock ledge, with dorsal spines held flat along the dorsal midline and pectoral fins closed. In the video is also possible to observe the presence of other Lessepsian species: *Sargocentron rubrum, Parupeneus forsskali, Siganus rivulatus* and *Torquigener flavimaculosus*.

**Video S4.2** Mediterranean lionfish hunting *C. chromis*. Min 00:20 *C. chromis* is almost cornered, lionfish has the pectoral fins flared and directed at prey, dorsal spines erected and undulating, almost ready to strike. Note how close *C. chromis* individuals approach the hunting lionfish.

**Video S4.3** Mediterranean lionfish hunting *T. pavo*. The lionfish is swimming in search of a potential prey with pectoral fins flared and dorsal fins erected. A potential prey is spotted at 00:06, the lionfish suddenly increase swimming speed and start the chase. Min 00:22 the prey seems to be almost cornered; the lionfish is blocking the escaping routes with the pectoral fins and start undulating the dorsal spines. However, the potential prey – Thalassoma pavo – escapes (00:30). The lionfish continue the chase. The same *T. pavo* individual swims towards the lionfish (00:43) before turning away again. The lionfish keep looking around in search of its prey (min 01:16), until it reappears at 01:30 and the chase resumes.

**Video S4.4** Mediterranean lionfish feeding on *Gobius vittatus*. Here is possible to see the whole sequence of a successful predation event. From the spotting of the potential prey and the beginning of the chase (min 00:14), to the successful strike (02:09). Note how the pectoral fins of the lionfish are flared to block any possible escape routes of the prey and how the lionfish dorsal spines start undulating just before the strike (01:49). Also note how *G. vittatus* seems to be naïve of the threat posed by the lionfish by moving towards the lionfish at min (00:16) and by relocating only a few cm away from the approaching hunting lionfish at min 00:48, 01:13, 01:32 and 01:40.

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# APPENDICES

## Appendix (i): conference presentation and attendance

### Conference presentations

**D'Agostino D.** (2019) "Growth impacts for two species of coral reef fish living in an extreme environment". Arabian Coral Reefs Conference, Abu Dhabi, UAE, 11 – 13 November 2019 [Talk].

**D'Agostino D.** (2019) "Behavioural traits and feeding ecology of a Lessepsian invader: the Mediterranean lionfish". 45$^{th}$ European Marine Biology Symposium (EMBS45), Dublin, August 2019 [talk].

**D'Agostino D.** (2018) "Life history impacts for coral reef fishes living in an extreme environment". Reef Conservation UK (RCUK), London, UK, December 2018 [poster].

**D'Agostino D.** (2017) "Coping with extreme environments: the influence of thermal variation on fish behavioural ecology". European Coral Reef Symposium (ECRS), 13-15 December 2017, Oxford, UK [talk].

**D'Agostino D.** (2017) "Behavioural plasticity and extreme thermal variation: a story from the world's warmest sea". 7th Congress of the Italian Society of Evolutionary Biology (SIBE), 28-31 August 2017, Rome, Italy [talk].

**D'Agostino D.** (2017) "Coping with extreme environments: the influence of thermal variation on fish behavioural ecology". Fisheries Society of British Isles 50$^{th}$ Anniversary Symposium, Exeter, UK, July 2017 [speed talk + poster].

**D'Agostino D**. (2016) "Behavioural consequences of living in the world's warmest sea". Reef Conservation UK (RCUK), London, UK, December 2016 [poster].

## Conference attendance

British Ecological Society (BES) 2018, Birmingham

# Appendix (ii): grants and awards

**2017: Conference bursary:** Fisheries Society of British Isles 50$^{th}$ Anniversary Symposium **(£240)**.

**2017: Best poster presentation award,** post-graduate symposium, University of Nottingham **(£100)**.

**2016 Fieldwork grant:** Heredity Fieldwork Grant, Genetics Society (**£1500**).

**2016 – 2019: PhD scholarship**, funded by The University of Nottingham Vice-Chancellor's Scholarship for Research Excellence (EU).

**2011: Internship grant** Norwegian National Institute of Nutrition and Seafood Research (NIFES), Bergen, Norway through the European programme “Erasmus Placement” (**€2,600**, 6 months).

# Appendix (iii): publication from the findings of Chapter 2

Coral Reefs
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REPORT

## The influence of thermal extremes on coral reef fish behaviour in the Arabian/Persian Gulf

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**Abstract** Despite increasing environmental variability within marine ecosystems, little is known about how coral reef fish species will cope with future climate scenarios. The Arabian/Persian Gulf is an extreme environment, providing an opportunity to study fish behaviour on reefs with seasonal temperature ranges which include both values above the mortality threshold of Indo-Pacific reef fish, and values below the optimum temperature for growth. Summer temperatures in the Gulf are comparable to those predicted for the tropical ocean by 2090–2099. Using field observations in winter, spring and summer, and laboratory experiments, we examined the foraging activity, distance from refugia and resting time of *Pomacentrus trichrourus* (pale-tail damselfish). Observations of fish behaviour in natural conditions showed that individuals substantially reduced distance from refugia and feeding rate and increased resting time at sub-optimal environmental temperatures in winter (average SST = 21 °C) and summer (average SST = 34 °C), while showing high movement and feeding activity in spring (average SST = 27 °C). Diet was dominated by plankton in winter and spring, while fish used both plankton and benthic trophic resources in summer. These findings were corroborated under laboratory conditions: in a replicated aquarium experiment, time away from refugia and activity were significantly higher at 28 °C (i.e. spring temperature conditions) compared to 21 °C (i.e. winter temperature conditions). Our findings suggest that *P. trichrourus* may have adapted to the Arabian/Persian Gulf environment by downregulating costly activity during winter and summer and upregulating activity and increasing energy stores in spring. Such adaptive behavioural plasticity may be an important factor in the persistence of populations within increasing environmentally variable coral reef ecosystems.

**Keywords** Behaviour · Plasticity · Climate change · Coral reef fish · Extreme environment

Topic Editor Morgan S. Pratchett

**Electronic supplementary material** The online version of this article (https://doi.org/10.1007/s00338-019-01847-z) contains supplementary material, which is available to authorized users.

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### Introduction

Over the last century, sustained climate change has resulted in average global sea surface temperature increasing by 0.6 °C, with predictions of further 4.0 °C rises by 2100 (Collins et al. 2013; IPCC 2014). As the planet warms, climate and weather variability, as well as the occurrence

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of extreme weather events, will also increase (IPCC 2012; Thornton et al. 2014). As the world's oceans absorb 93% of excess heat trapped by greenhouse gases (Laffoley and Baxter 2016), such warming is expected to have major consequences for the biodiversity, functional structure and productivity of marine ecosystems (Folguera et al. 2011; Doney et al. 2012; Bellard et al. 2012; Pecl et al. 2017). Alterations have already been documented in the diversity and assemblage structure in temperate seaweed and seagrass ecosystems (Wernberg et al. 2013; Vergés et al. 2014), coral reefs (Hughes et al. 2018) and coastal temperate rocky reefs (Lejeusne et al. 2010; Albouy et al. 2015). Despite this, our understanding of the capacity for marine ecosystems to resist or show resilience to climate change is limited (Côté and Darling 2010).

Coral reefs are particularly susceptible to a range of natural and anthropogenic disturbances that have resulted in recent degradation and loss of coral on a global scale (Wilkinson 1999; Cheal et al. 2017; Hughes et al. 2018). While these disturbances are clearly significant for the corals that serve as the biogenic engineers of these ecosystems, diverse and ecologically important reef-associated fish assemblages also often exhibit dramatic changes in composition and abundance with increasing environmental variation (Day et al. 2018; Richardson et al. 2018; Gordon et al. 2018). Indeed, in addition to susceptibility to habitat loss (Pratchett et al. 2018), coral reef fishes are also directly threatened by ocean warming, sea surface temperature anomalies and intense pulse heat stress events (such as the warm phase of El Niño Southern Oscillation—ENSO) (Claar et al. 2018; Cai et al. 2018), due to their narrow thermal tolerance range (Tewksbury et al. 2008; Sunday et al. 2011). Experimental evidence suggests that coral reef fish may already be living close to their upper thermal limits (Rummer et al. 2014) and that their population structure may be directly impacted by increased variability in water temperature (Folguera et al. 2011; Pratchett et al. 2015; Rodgers et al. 2018).

One of the primary responses to environmental temperature change is modification of behaviour, with the speed and scope of behavioural adjustment potentially determining survival (Tuomainen and Candolin 2011; Wong and Candolin 2015). Despite this, tropical reef fishes having evolved in relatively thermally stable environments are expected to show little ability to adjust behaviour adaptively with changing environmental temperatures (Candolin 2018). Furthermore, as the metabolism and neurophysiology of fishes are directly influenced by temperature (Pörtner and Farrell 2008; Pörtner et al. 2010), environmental temperatures outside an individual's optimum range may then have a substantially negative effect on ecological performance and survival via non-adaptive (dysfunctional) modification of behaviour, resulting in altered feeding rate, increased risk-taking behaviour and reduced activity levels and habitat use (Figueira et al. 2009; Nagelkerken and Munday 2016). Despite this, there is a growing body of research suggesting that coral reef fishes may show adaptive behavioural plasticity in response to temperature increases, predominantly associated with temporary reductions in aerobically costly behaviours with acute increased environmental variance (Johansen et al. 2014; Scott et al. 2017; Chase et al. 2018). For example, feeding is associated with substantial metabolic costs due to the high energy expenditure needed for digestion and nutrient uptake (McLean et al. 2018) and has been shown to be downregulated in some fish species to reduce energy costs (Nowicki et al. 2012; Fu et al. 2018). Nevertheless, how well and by what mechanisms coral reef fishes will cope with ocean warming scenarios and increased thermal variability (Thornton et al. 2014; IPCC 2014; Cai et al. 2018) is still poorly understood.

One approach to understanding how individuals may behaviourally respond to environmental variance is to study contemporary communities that exist within naturally variable environments. The fauna associated with the high-latitude reefs of the southern Arabian/Persian Gulf (hereafter the 'Gulf') provide a natural test of the impact of extreme water temperature variation on coral reef fish behaviour (Feary et al. 2010; Burt et al. 2011b). The Gulf experiences the highest annual change in water temperature for coral reefs globally (winter: < 15 °C, summer: > 35 °C), with fishes persisting for several months in conditions that would be considered lethal to reef fishes in other parts of the world (Riegl and Purkis 2012; Vaughan et al. 2019). Summer temperatures in the Gulf exceed the upper thermal limits of most tropical reef fishes (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers et al. 2018), while winter temperatures are well below the optimum temperatures reported for reef fish elsewhere in the Indo-Pacific (Eme and Bennett 2008; Figueira and Booth 2010; Nakamura et al. 2013). Indeed, contemporary summer water temperatures in the Gulf are comparable to those predicted for tropical oceans at the end of this century (Riegl and Purkis 2012; IPCC 2014), while winter conditions can be so severe as to induce cold water coral bleaching (Shinn 1976; Coles and Fadlallah 1991).

Using a combination of in situ field observations and ex situ experimental manipulations, this study examined the influence of extreme thermal variability on reef fish behaviour in the southern Gulf. Using the locally abundant *Pomacentrus trichrourus* (pale-tail damselfish; Günther, 1867), we performed field-based observations of behaviour across three thermally distinct seasons separated by a 13 °C sea surface temperature (SST) range (winter: SST = 21 °C, spring: 27 °C, and summer: 34 °C), monitoring replicate individual's distance from refugia, resting times, feeding rate and diet between three sites in the southern Gulf. We predicted that fish would respond to low and high water temperature extremes by modifying their behaviour (i.e. exhibit behavioural plasticity). Specifically, we hypothesised that fish would minimise aerobically costly behaviours (i.e. reduced distance from refugia and feeding rate, while increasing resting time) when exposed to sub-optimal temperatures for growth and locomotion in winter and summer, while compensating for energy losses and building up energetic stores by increasing activity and feeding rate in spring. We also hypothesised that *P. trichrourus* would exhibit flexibility in diet by shifting from a predominately planktonic diet during optimal conditions to one encompassing both planktonic and benthic prey, when exposed to sub-optimal temperature. Such change in diet was expected to be due to restrictions in foraging movements in sub-optimal conditions, within individuals becoming generalist in their feeding habits, exploiting more easily accessible resources. Finally, we performed an aquarium-based experiment exposing *P. trichrourus* to temperatures typical of winter (21 °C) and spring (28 °C) in order to examine the hypothesis that variation in behaviour observed in the field was directly mediated by temperature. Overall, the results of this study have important implications for understanding how coral reef fishes may use behavioural modification as a means to respond to the environmental variability that is expected to increase under future climate change.

## Materials and methods

The pale-tail damselfish is a small omnivorous damselfish common in southern Gulf coral communities, often living in association with a single 'home' coral head (Allen 1991; Shraim et al. 2017). Within the Gulf, this species shows high abundance, a benthic lifestyle with diurnal behaviour, a strong association with the reef, and high territoriality to a small area (territory size of 0.5–1.5 $m^2$). It has a small body size (max 6 cm standard length [SL]) and distinct differences in colour pattern between juvenile and adults (Randall 1995; Feary et al. 2010). All individuals within this study were adults (~ 4–6 cm SL). The optimum temperature for growth for this species is modelled to be between 24.7 and 29.3 °C (mean 27.2 °C) (Kaschner et al. 2016, based on 258 cells from the Western Indian Ocean, including the Red Sea and the Gulf).

### In situ behavioural quantification of *P. trichrourus*

To determine the effect of seasonal changes in temperature on behaviour of *P. trichrourus* in the Gulf, behavioural observations were replicated across three seasons: spring (April/May 2016, average SST = 27 °C), summer (August/September 2016, average SST = 34 °C) and winter (February/March 2017, average SST = 21 °C). Observations were undertaken at three reef sites spaced ca. 40 km apart along the Abu Dhabi coastline (United Arab Emirates—southern Gulf): Dhabiya (24°21′55.8″N, 54°06′02.9″E), Saadiyat (24°35′56.4″N, 54°25′17.4″E) and Ras Ghanada (24°50′53.4″N, 54°41′25.1″E) (Fig. 1). Sites were located at similar distances from shore (between 5.8 and 3.8 km), with available habitat dominated by hard-coral communities (ca. 40–55% live coral cover, Burt et al. 2011a) with all sites 6–7 m in depth (Grizzle et al. 2015).

#### *In situ behavioural observation*

Observations were undertaken by scuba diving on cloudless days between 10:00 and 14:00, reducing any influence of changing light levels on behaviour (Layton and Fulton 2014). In each site, across seasons, replicate coral heads holding *P. trichrourus* individuals were identified by visual searches made while swimming along haphazardly located transects of the reef. Coral heads held one (56% of coral heads examined), two (34%), three (7%) or four (2%) adult *P. trichrourus*. Individual *P. trichrourus* were haphazardly selected during each season and their territory identified and marked using numbered flags (Magalhaes et al. 2013). When several adults shared the same coral head, in order to minimise the developmental variability among individuals being sampled, the individual with the largest body size was selected. Following marking of the territory, focal fish was allowed to acclimate for 4 min, and then filmed for 2 min (using DBPOWER HD 1080P). A minimum distance of 3 m was maintained between observer and subject. Observations were aborted if fish displayed any adverse reactions to diver's presence (i.e. increased wariness, hiding after staring at diver, etc.; observed in < 5% of individuals). Across sites and seasons, a total of 226 individual behavioural observations were recorded (winter: Dhabiya $n = 26$, Saadiyat $n = 32$, Ras Ghanada $n = 25$; spring: Dhabiya $n = 26$, Saadiyat $n = 32$, Ras Ghanada $n = 25$; and summer: Dhabiya $n = 23$, Saadiyat $n = 31$, Ras Ghanada $n = 29$).

#### *Analyses of video quantifying in situ individual behaviour*

Mean distance from refugia was defined as the distance from the 'home' coral every 10 s (Beck et al. 2016) and estimated to the nearest 5 cm referenced against the territory marking flag's length (25 cm) and the individual's body size (assumed as 5 cm SL). Resting was taken as total time (seconds) spent immobile (i.e. not active swimming, foraging or chasing behaviour) across each 2-min video. Feeding rate was the total number of bites during the

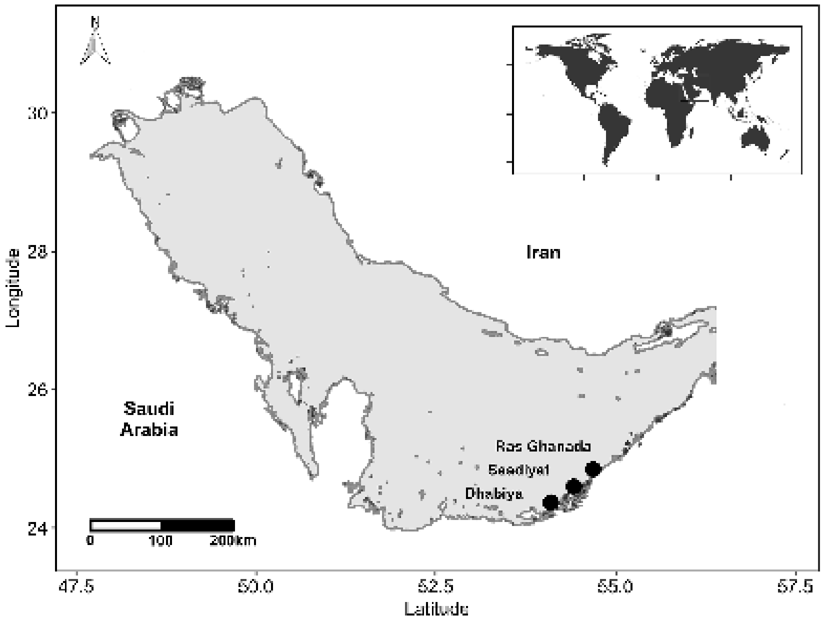


**Fig. 1** Study area and sampling locations in the southern part of the Persian Gulf

observation period, while diet was identified by classifying each food bite as either on pelagic or benthic substrates. Benthic food bites were further classified as being on live coral, coral rubble, turf or sand. Behavioural data were initially extracted from 15% of videos and independently analysed and validated by two observers. As results differed by < 5% between observers, all remaining video analyses were carried out by one observer (DD).

To estimate the relative frequency of predation or competition across seasons and sites, the abundance of predators (i.e. piscivorous fish with SL $\geq$ 15 cm observed interacting with *P. trichrourus*) and competitors (i.e. fishes with comparable ecology/body size to *P. trichrourus* observed chasing/being chased by *P. trichrourus*) entering each individual territory was quantified for each 2-min video observation.

*In situ environmental measurements*

To assess seasonal changes in abiotic variables in the Gulf, across the dates of all behavioural observations, daily in situ SST (°C) and dissolved oxygen (DO, mg $l^{-1}$) measurements were taken at 1200 h at each site using a YSI Professional Plus multi-parameter probe, while underwater visibility (in m) was visually estimated in situ by swimming over a belt transect and measuring the distance at which the diver waiting at the beginning of the transect was not visible anymore. Chlorophyll-a (chl-a, mg $l^{-1}$) measurements were downloaded as monthly composite data at 0.05 resolution from the MODIS–Aqua satellite (NASA 2014), while salinity (psu), wind (m $s^{-1}$) and currents (m $s^{-1}$) were obtained from the NCEP climate forecast system version 2 (CFSv2, Saha et al. 2011). Salinity and current data were accessible as daily means (resolution 0.25-deg × 0.25-deg), while wind data were taken at 1200 h (0.205-deg × ~ 0.204-deg) across all experimental days.

**Aquarium-based behavioural quantification**

To experimentally determine the impact of water temperature on behaviour, we examined time away from refugia and distance moved of replicate *P. trichrourus* in controlled conditions in the laboratory. Sixteen adults (mean body size 4.78 [± 0.13 SE] cm SL) were collected from Saadiyat during winter. Eight individuals were randomly allocated to separate pierced 6L bottles within either of two 900L holding tanks (control and experimental group, i.e.

one holding tank per treatment). Each bottle had a 10-cm-long plastic pipe provided for shelter. All tanks were kept at 21 °C, 40 psu, 8.15 pH, 6.5 mg $l^{-1}$ DO and 12 h dark/light cycle reflecting in situ winter condition. 25% water changes were performed weekly, with ammonia, nitrite and nitrate kept at 0 ppt. Fish were fed ad libitum twice daily with commercial pellets.

After a week for acclimation, refuge use and movement of all individuals were tested at 21 °C (Fig. 2). To do this, a randomly chosen individual had its holding container submerged in an experimental tank (80 L * 50 W *40 H [cm], filled to 20 cm H) and was left to acclimate for 10 min. The tank's base had been divided into 40 squares (10 * 10 cm grid); a 10-cm-long segment of plastic pipe was provided as shelter, and a DBPOWER HD 1080P video camera was placed one metre above the tank. Following acclimation, the individual was released and led to the shelter; a transparent bottomless bottle was used to confine the individual which was then left for a further 20 min. Subsequently, the bottle was removed and behaviour videoed for 16 min. All videoing occurred between 1000 h and 1400 h, with a 25% water change between individuals.

Water temperature within the experimental holding tank was then increased to 28 °C (~ 0.5 °C/6 h) across 4 d, while the temperature within the control remained constant (21 °C) (Fig. 2). Fish were then left for 7 d. As described above, all individuals were then retested for behaviours within either the experimental or control tank, using individual videoing.

Within all videos, the first 5 min was discarded to allow time of acclimation after activation of the video camera. Time away from refuge was quantified (in seconds) when individuals moved 10 cm from the shelter. Distance moved was quantified (in cm) by counting the number of grid lines crossed over 11 min with one cross being assumed to equal to 10 cm movement, independently of the distance from refuge.

### Statistical analysis

To determine whether abiotic and/or biotic factors significantly differed among seasons, Kruskal–Wallis test was undertaken. Abiotic factors were then combined using principal components analysis (based on the correlation matrix with centring and scaling of all variables), to identify the main axes of environmental variation among observations; axes that explained more than 15% of the total variance (PC1 to PC3, hereafter 'environmental PCs') were retained and used in further analyses (Magalhaes et al. 2016).

To determine the impact of season, site, predator/competitor abundance and environmental PCs on distance from refugia and resting time, a generalised linear mixed model (GLMM) with Gaussian errors was used, while feeding rate against all predictor variables (as above) was examined using a GLMM with Poisson error distribution and log link function. Both distance from refugia and resting were not normally distributed and were, respectively, log and log (X + 1) transformed prior to testing. In all tests, date of sampling was fitted as a random effect and backwards model selection followed, using likelihood ratio tests to examine the significance of each term removed from the model. To determine whether food preference significantly differed between seasons, individual bites on substrate were analysed using Kruskal–Wallis test.

To determine the effect of experimental change in temperature on time away from refugia and distance moved, behavioural data before and after temperature manipulation from the control and experimental groups were tested using a GLMM with binomial error distribution and logit link function. As time away from refuge and distance moved were bimodal with a high proportion of

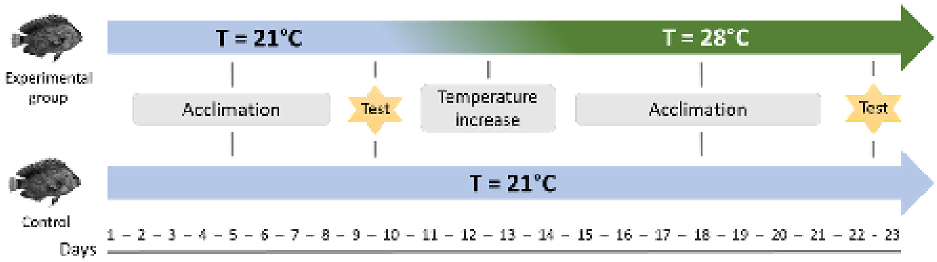


**Fig. 2** Experimental design of the laboratory behavioural experiment. Days (bottom) represent the timeline of the experiment; bottom arrow represents the control group; middle boxes represent the different activities to which the fish in the two different groups were exposed; top arrow represents the experimental group

zeros, and data transformation did not result in either normality or homoscedasticity, data were converted to binary; an individual was considered 'far from refugia' or 'moving' when time away from refugia or distance moved (respectively) was more than the median and vice versa. In all tests, 'test order' was included as a fixed factor to determine whether the order in which individual fish were tested had any influence on the result, while individual was fitted as a random effect; backwards model selection followed, using likelihood ratio tests to examine the significance of each term removed from the model. All data were analysed in R (R core development team 3.5.1, 2019).

## Results

### In situ environmental variation

Significant differences among seasons in SST, DO, chl-a, salinity and visibility were apparent (Kruskal–Wallis test: $p < 0.05$ in all cases; Table S1). SST was highest in summer and lowest in winter, while DO showed the opposite trend. Chl-a concentration was higher in summer than the other seasons. PCA showed that 82% of the variation in the raw abiotic variables was captured by the first three principal components, with a high score in PC1 (39%) being associated with low SST and chl-a, and high DO. A high score in PC2 (25%) was associated with high salinity and low visibility, and a high score in PC3 (18%) was associated with high water current (Table 1).

Across all sites and seasons, predator abundance was dominated by *Lutjanus ehrenbergii*, comprising 97% of counts (Table S2). Predator abundance significantly differed among seasons (Kruskal–Wallis test, $H = 73.790$, $df = 2$, $p < 0.001$), with predators being more abundant in summer than spring or winter, while among sites, predators were more abundant in Dhabiya than Saadiyat or Ras Ghanada (Fig. S1). The predominant competitors were

**Table 1** Loadings of each environmental variable on the first three PC axes and the per cent variance explained by each axis

| Factors | PC1 | PC2 | PC3 |
|---|---|---|---|
| Temperature | **− 0.58** | − 0.06 | − 0.04 |
| Dissolved oxygen | **0.58** | 0.11 | 0.06 |
| Chl-a | **− 0.49** | 0.25 | 0.03 |
| Salinity | − 0.10 | **0.70** | 0.14 |
| Wind speed | − 0.25 | − 0.22 | − 0.26 |
| Water current | 0.06 | − 0.14 | **− 0.83** |
| Visibility | − 0.08 | **− 0.60** | **0.47** |

The highest loadings on each of the first three PCs are showed in bold

other *P. trichrourus* and *Pomacentrus aquilis* individuals. Competitor abundance significantly differs among seasons ($H = 7.191$, $df = 2$, $p = 0.027$), with slightly higher abundance in spring than winter (Table S2).

### In situ behavioural analysis

Season, and the interaction between site and season, had a significant effect on *P. trichrourus* behaviour (Table 2), with individual from Ras Ghanada and Saadiyat showing higher distance from refuge and higher feeding rate in spring than in either winter or summer, while significantly reducing the time spent resting (Fig. 3). On the contrary, individuals from Dhabiya showed similar behavioural patterns across seasons in feeding rate only, but not in distance from refuge nor time spent resting (Fig. 3).

Significant differences in diet were apparent among seasons, with planktonic prey representing 93% and 96% of food bites in winter and spring, respectively, while only accounting for 73% in summer (Kruskal–Wallis, $H = 139.04$, $df = 2$, $p < 0.001$). Where selected, benthic food bites were predominantly taken from live corals (5 and 4% of total food bites in winter and spring, 17% in summer), with bites on coral rubble, turf and sand accounting for less than 1% of total food bites in winter and spring, and $\leq$ 4% in summer.

### Laboratory behavioural assays

While there was no difference between the control and the experimental group prior to temperature manipulation (i.e. both groups exposed to cold temperature), temperature had a significant effect on fish behaviour after manipulation, with fish spending more time far from the refuge and moving longer distances in the warm experimental treatment than the control (Fig. 4a, b; Table 3). Test order had no effect on fish behaviour.

## Discussion

Although increasing variance in global SSTs may directly impact coral reef fish community biodiversity (Pratchett et al. 2015; Day et al. 2018; Buchanan et al. 2019), coral reef fish populations might be able to mitigate the effect of rapidly changing environments through behavioural plasticity (Nagelkerken and Munday 2016; Scott et al. 2017; Chase et al. 2018). We examined the impact of seasonal changes in biotic and abiotic conditions on distance from refugia, activity and feeding ecology of the pale-tail damselfish *P. trichrourus* within the southern Gulf. We found that *P. trichrourus* substantially increased resting time and reduced distance from refugia and feeding rate at sub-

**Table 2** Results of GLMM analysis of effects of biotic/abiotic factors on *Pomacentrus trichrourus*' in situ behaviour

| Response | Predictor | Residual deviance$_{(df)}$ | Change in deviance$_{(df)}$ | *p* |
|---|---|---|---|---|
| Distance from refugia | Season | $8.298_{(5)}$ | $10.925_{(2)}$ | **0.004** |
| | Site | $-1.1050_{(5)}$ | $1.522_{(2)}$ | 0.467 |
| | Site: season | $-2.627_{(7)}$ | $30.565_{(4)}$ | **< 0.001** |
| | PC1 | $-37.767_{(14)}$ | $0.430_{(1)}$ | 0.512 |
| | PC2 | $-33.192_{(11)}$ | $3.690_{(1)}$ | 0.055 |
| | PC3 | $-37.390_{(13)}$ | $0.377_{(1)}$ | 0.539 |
| | Predators | $-36.882_{(12)}$ | $0.508_{(1)}$ | 0.476 |
| | Competitors | $-38.197_{(15)}$ | $0.176_{(1)}$ | 0.674 |
| Resting time | Season | $89.580_{(5)}$ | $4.384_{(2)}$ | 0.112 |
| | Site | $86.431_{(5)}$ | $0.539_{(6)}$ | 0.539 |
| | Site: season | $85.196_{(7)}$ | $29.556_{(4)}$ | **< 0.001** |
| | PC1 | $54.937_{(12)}$ | $1.013_{(1)}$ | 0.314 |
| | PC2 | $55.640_{(11)}$ | $0.703_{(1)}$ | 0.408 |
| | PC3 | $53.924_{(13)}$ | $1.324_{(1)}$ | 0.25 |
| | Predators | $52.042_{(15)}$ | $0.015_{(1)}$ | 0.908 |
| | Competitors | $52.601_{(14)}$ | $0.558_{(1)}$ | 0.455 |
| Feeding rate | Season | $1730.2_{(4)}$ | $31.427_{(2)}$ | **< 0.001** |
| | Site | $1700.7_{(4)}$ | $1.883_{(2)}$ | 0.39 |
| | Site: season | $1698.8_{(6)}$ | $17.959_{(4)}$ | **0.001** |
| | PC1 | $1674.6_{(12)}$ | $1.459_{(1)}$ | 0.227 |
| | PC2 | $1680.8_{(10)}$ | $3.805_{(1)}$ | 0.051 |
| | PC3 | $1677.0_{(11)}$ | $2.487_{(1)}$ | 0.115 |
| | Predators | $1672.9_{(14)}$ | $0.137_{(1)}$ | 0.137 |
| | Competitors | $1673.1_{(13)}$ | $0.165_{(1)}$ | 0.685 |

Gaussian error structure for distance from refugia and resting time; Poisson error distribution with log link function for feeding rate. Significant *p* values are highlighted in bold

optimal environmental temperatures (both high and low) when observed in situ and when tested in the laboratory. Individuals were also observed to shift from a planktonic-based diet to a mixed planktonic and benthic diet during the Gulf's extreme summer season. This reflects the finding of a recent stomach content study in this species which showed seasonal shifts in diets in the southern Gulf, with more benthic species (e.g. coral) in the diet in summer, while more planktonic species (e.g. free swimming ascidians, various protozoans) were more common in cooler months (Shraim et al. 2017). Our results show considerable scope for behavioural and trophic plasticity in *P. trichrourus*, which may allow this species to cope with seasonal variance in environmental conditions, including those that are above the mortality thresholds (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers et al. 2018) and below the optimum temperature of Indo-Pacific reef fish (Eme and Bennett 2008; Figueira and Booth 2010; Nakamura et al. 2013).

We observed substantial behavioural and trophic plasticity in *P. trichrourus*' populations among seasons. In particular, *P. trichrourus* were observed to reduce distance from refugia and feeding rate and increase resting time in winter and summer compared to spring. These seasonal changes are plausibly related to variation in water temperature, as changes in environmental temperature are known to have a direct effect on fish physiology (Angilletta 2009; Abram et al. 2017). In ectothermic animals, environmental temperatures departing from the optimum are associated with reductions in the capacity to deliver oxygen to aerobic processes and, therefore, reduction in energy for costly activities (i.e. swimming, feeding, chasing, etc.) (Pörtner and Knust 2007; Pörtner and Farrell 2008; Munday et al. 2012). The reduction in activity observed in *P. trichrourus*, is also in line with recent work suggesting that, when exposed to short-term higher than average SSTs, coral reef fish may temporarily mitigate bioenergetic inefficiency through reduction in energetically costly activities, as well as through changes in diet (Nowicki et al. 2012; Johansen et al. 2014; Scott et al. 2017; Chase et al. 2018). However, further research is now needed to confirm whether *P. trichrourus* actively reduce energetically costly behaviour to minimise energetic demand and mitigate bioenergetic inefficacy, or whether fish are being forced to change their behaviour due to being compromised at a lower level of organization (i.e. physiological constraints).

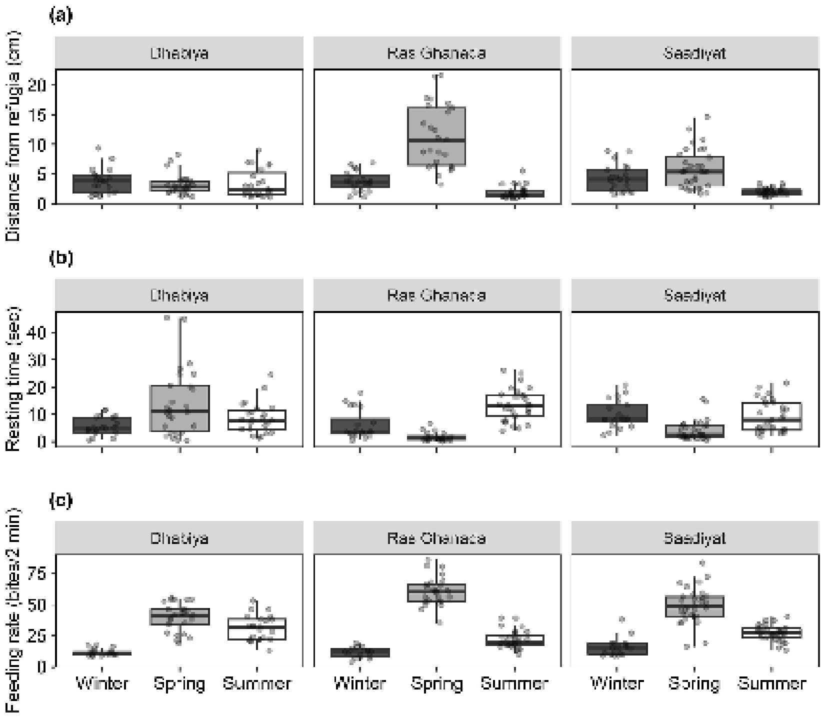


**Fig. 3** Changes in *Pomacentrus trichrourus* behaviour in situ among seasons (winter = dark grey, spring = light grey, summer = white) and locations (Dhabiya, Ras Ghanada, Saadiyat): **a** mean distance from refugia (cm); **b** time spent resting (s/120 s) and **c** number of feeding bites in 120 s. Thick horizontal lines show the median, and boxes show interquartile (IQR). Whiskers indicate the range of data, and dots show outliers that are more than 1.5 IQR above the 75th percentile, or more than 1.5 IQR below the 25th percentile

Nevertheless, even if fish are able to modulate their activity to reduce the degree of stress they are experiencing, such strategies may not be sufficient to sustain prolonged periods (i.e. months) of extreme temperature (Rummer et al. 2014; Rodgers et al. 2018). For example, reductions in food intake and quality, coupled with low aerobic scope under extreme temperatures, can disrupt an ectothermic organism's energy balance, with substantially less energy available for long-term maintenance, growth and reproduction (Gillooly et al. 2001; Pörtner et al. 2010; Neuheimer et al. 2011), impacting individual fitness and potentially survival (Chase et al. 2018).

*Pomacentrus trichrourus*' persistence within the Gulf implies that they have adapted over the long term to the extreme temperature conditions experienced there (Rummer and Munday 2017). Our results hint that the key to their survival may be their ability to undertake seasonal energy recovery in spring, compensating for energy loss during winter by building up energetic stores to endure the upcoming summer season (Armstrong and Bond 2013). Many studies on temperate fishes have highlighted the ability to compensate energetic and growth losses during periods of adverse temperatures or food scarcity through increased feeding rate and feeding activity when conditions become favourable again (Sevgili et al. 2013; Armstrong and Bond 2013; Furey et al. 2016; Peng et al. 2017). For *P. trichrourus*, such periods of recovery, where it can access highly nutritious food resources (Shraim et al. 2017) under optimal environmental temperatures (Kaschner et al. 2016), may be vital for mitigating energy loss during winter and summer and hence ultimately permit the persistence of abundant populations within the southern Gulf throughout the year.

Our laboratory experiments are consistent with the idea that the seasonal differences in behaviour observed in the field were the result of changes in temperature. However,

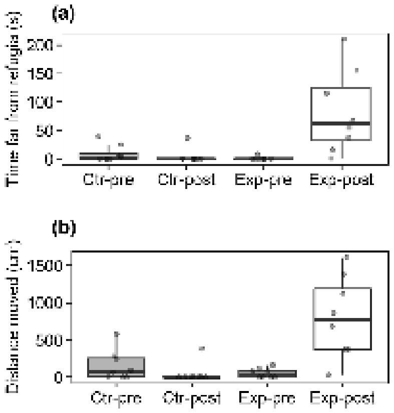


**Fig. 4** Changes in *Pomacentrus trichrourus* behaviour ex situ among temperature treatment: **a** mean time spent far from refugia (s) and **b** total distance moved (cm). Colours indicate temperature (grey = 21 °C, white = 28 °C). See Fig. 3 legend for explanation of the box plots

other potentially important environmental variables also changed with the seasons, including predators and primary productivity. These variables could plausibly be directly responsible for changes in fish behaviour. For example, predators might have had a negative effect on *P. trichrourus* movement (i.e. reduced distance from refugia) and feeding rate (Dill and Fraser 1984; Beck et al. 2016; Catano et al. 2016), potentially leading to the shift to mixed planktonic and benthic diets observed in summer, when *P. trichrourus* may have to rely more on safer benthic food resources (i.e. live corals), despite the loss of nutritional value (Shraim et al. 2017). Similarly, the higher abundance in predatory fish in Dhabiya compared to other sites (Burt and Vaughan, unpublished data) may explain why fish were seldom observed moving long distances from the refuge, even in spring. On the contrary, we did not observe any correlation between changes in primary productivity and changes in feeding activity, suggesting that shifts in diet may not be related to primary productivity (measured as chlorophyll-a concentration) (Rueda et al. 2015; Zhou et al. 2016) but the result of temperature-related differences in food preference (Shraim et al. 2017). Ultimately, manipulative experiments would be needed to confirm the potential for predators or other drivers to produce similar behavioural changes to those seen in our temperature manipulation.

The Gulf's average SST is increasing twice as fast as the global average (Al-Rashidi et al. 2009), with predictions of further increases of 0.5–1.4 °C by 2050, associated with hot salt brine discharge derived from local desalinisation plants (AGEDI 2016; Vaughan et al. 2019). As *P. trichrourus* populations live for five months of the year above their predicted thermal optimum (Jun–Oct, mean SST > 30 °C) (Kaschner et al. 2016), of which two months encompass temperatures above the mortality threshold of low-latitude Indo-Pacific damselfish (July and August, mean SST $\geq$ 33 °C) (Nilsson et al. 2009; Munday et al. 2009; Rummer et al. 2014; Rodgers et al., 2018), Gulf populations may already be living close to their upper thermal limits; further increases in temperature are expected to pose a serious threat to population persistence. In addition, *P. trichrourus* populations in the Gulf are already considered endangered, associated with a fragmented distribution and with a strong dependence on diminishing coral habitat resources (Buchanan et al. 2016, 2019). Indeed, *P. trichrourus* are highly associated with live coral colonies, utilising them for recruitment, shelter and as trophic resources (Buchanan et al. 2016; Shraim et al. 2017). Therefore, any increases in SST that pose a serious threat to local coral communities, where bleaching events and consequent coral mortality are already common (Riegl et al. 2018; Burt et al. 2019; Paparella et al. 2019), may deprive *P. trichrourus*

**Table 3** Results of GLMM analysis of effects of experimental change in temperature on *Pomacentrus trichrourus*' behaviour

| Temperature manipulation | Response | Predictor | Residual deviance$_{(df)}$ | Change in deviance$_{(df)}$ | $p$ |
|---|---|---|---|---|---|
| Pre- | Time far from refuge | Treatment | $17.119_{(3)}$ | $2.7561_{(1)}$ | 0.097 |
| | | Test order | $11.945_{(8)}$ | $5.1733_{(5)}$ | 0.395 |
| | Distance moved | Treatment | $20.088_{(3)}$ | $1.0823_{(1)}$ | 0.298 |
| | | Test order | $18.56_{(8)}$ | $1.5277_{(5)}$ | 0.910 |
| Post- | Time far from refuge | Treatment | $6.2268_{(3)}$ | $17.194_{(1)}$ | **< 0.001** |
| | | Test order | $4.1307_{(10)}$ | $2.0961_{(7)}$ | 0.954 |
| | Distance moved | Treatment | $6.2268_{(3)}$ | $17.194_{(1)}$ | **< 0.001** |
| | | Test order | $4.1307_{(10)}$ | $2.0961_{(7)}$ | 0.954 |

Significant $p$ values are highlighted in bold

'Treatment' denotes whether fish belonged to the control or experimental group populations of suitable habitat and food resources in the long-term (Keith et al. 2018; Pratchett et al. 2018).

The Gulf's marine community encompasses 241 species of coral-associated bony fish, which are considered a biogeographic subset of the Indian Ocean's fauna that recolonised the region between 6000 and 9000 yrs ago (Riegl and Purkis 2012). The coral reef fish community richness in the Gulf is thought to be lower than that in the Indian Ocean as a consequence of the Gulf's physical extremes, which fewer Indian Ocean species are able to tolerate (Coles 2003; Feary et al. 2010). However, despite a range of work examining the reef fish fauna in the region (Burt et al. 2011b; Buchanan et al. 2019), there is still little understanding of how environmental tolerance is achieved in Gulf-dwelling species. For *P. trichrourus*, this study has shown that populations may be able to behaviourally mitigate the high variance in temperature and temperature extremes which are consistent with predictions for the tropical ocean by the end of the century (IPCC 2014). It appears that by reducing movement from shelter and feeding activities within extreme seasons (summer, winter) and showing metabolic compensatory activity behaviour (including feeding) during the environmentally benign spring season, populations of *P. trichrourus* are able to thrive in one of the most thermally extreme marine environments. Such adaptive behavioural plasticity is consistent with current theory regarding how animals deal with extremes and may be an important mechanism for how increases in temperature and temperature variability may be mitigated by fishes on Indo-Pacific reefs by the end of the century.

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**Compliance with ethical standards**

**Conflict of interest** On behalf of all authors, the corresponding author states that there is no conflict of interest.

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