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Spatial and temporal variation in movement patterns and behaviour of a large, coral reef mesopredator, *Plectropomus leopardus*, on the Great Barrier Reef, Australia.

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Abstract

Rising ocean temperatures caused by anthropogenic climate change are expected to have significant negative impacts on the biodiversity and productivity of shallow tropical oceans, with concomitant effects on fisheries production. Tropical ectotherms are predicted to be particularly vulnerable to ocean warming due to the pervasive effects of temperature on their performance and physiology, combined with adaptation to relatively stable thermal environments. For many coral reef fishes, moderate increases in temperature lead to increases in individual performance and fitness. However, extreme temperatures (outside of those normally or previously experienced) often have marked adverse effects. During initial and short-term exposure to elevated temperatures, fishes may alter their foraging behaviour and increase food intake to compensate for increasing metabolic demands. Alternatively, fishes may conserve energy as temperatures increase. Or, they may move to more optimal habitats. To date, most of the studies on thermal sensitivities of coral reef fishes, have been conducted under controlled laboratory settings. As such, these studies may have overestimated the vulnerability of fishes to temperature because they do not take account of the ability of individuals to mediate the effects of increasing temperature through modification of their behaviour (i.e. moving to more optimal habitats). This is particularly true for large-bodied tropical fisheries species that are typically understudied in the wild.

To address this problem, I used *in situ* observations and high-resolution passive acoustic telemetry to explore temporal and spatial variation in behaviour and movement of coral trout, *Plectropomus leopardus* on the Great Barrier Reef, Australia. *Plectropomus leopardus* are an important coral reef mesopredator and are one of the primary species targeted by both commercial and artisanal fishers throughout the Indo-Pacific region. Previous experimental studies have shown that *P. leopardus* are sensitive to increasing temperature and ocean acidification (**Chapter 2)** though there have yet to be any field tests to establish their vulnerability to environmental change under natural conditions. To address this knowledge gap, I investigated spatial and temporal variation in foraging behaviour and activity patterns (i.e. amount of time spent resting) of *P. leopardus* from latitudinally distinct locations. From > 500 hrs of *in situ* observation, I found that *P. leopardus* exhibited increased foraging frequency in summer versus winter time, irrespective of latitude, however, foraging frequency substantially declined at water temperatures > 30 °C. In addition, the amount of time spent resting was greatest for *P. leopardus* during the summer time at both locations, however, the effect was most pronounced at the low-latitude location where individuals spent up to 62% of their time inactive, compared with 43% for the high-latitude population (**Chapter 3**). These results

provided the first indication that *P. leopardus* moderate their foraging behaviour and activity according to changes in ambient temperature.

Using fine-scale acoustic telemetry (< 0.5 km^2 arrays), I also examined the spatial and temporal variation in home range (**Chapter 4**), locomotory performance and activity patterns (**Chapter 5**), and potential use of depth refugia (**Chapter 6**) for *P. leopardus* from latitudinally distinct locations. The average home range for *P. leopardus* was 0.32 km^2 at the high-latitude location compared to 0.23 km^2 at the low-latitude location. Seasonal differences were apparent at both locations with *P. leopardus* showing contraction in home range during summer, especially when temperatures were > 27 °C (**Chapter 4)**. Further, average acceleration for *P. leopardus* was 0.69 $m.s^{-2}$ and acceleration increased with increasing temperature up to 30 °C. However, the impact of ambient water temperature strongly influenced resting patterns for *P. leopardus* from the low-latitude location, where individuals were twice as likely to be detected at low-activity (i.e. resting) than individuals from the high-latitude location. In contrast, individuals from the high-latitude location were more active and detected more often undertaking routine activity indicating higher rates of activity for *P. leopardus* from the high-latitude location (**Chapter 5)**. Finally, although *P. leopardus* altered their depth use on a daily basis, and in response to monthly temperature variation, it was notably small (< 3 m) and did not vary between locations. However, three-dimensional activity space used by *P. leopardus* differed substantially between locations with *P. leopardus* from the high-latitude location occupying much greater (> 50%) 3-D activity space than individuals from the low-latitude location (**Chapter 6**). These results indicate that *P. leopardus* are more likely to alter their horizontal rather than vertical space use in response to higher ambient temperature.

Taken together, the results of this thesis suggest that ever-increasing ocean temperatures may impose significant constraints on the capacity of *P. leopardus* to meet increasing metabolic costs associated with higher temperatures (**Chapters 2 & 3)**. Given projected increases in ocean temperature, *P. leopardus* may be increasingly constrained in their ability to obtain sufficient prey resources while forced to conserve energy (**Chapters 3 & 4)**. Reductions in movement and space use will also have ramifications for individual fitness, population viability, and ecological function (**Chapters 4, 5 & 6)**. This will likely have negative demographic consequences for *P. leopardus* potentially undermining the viability and sustainability of coral reef fisheries, particularly in low-latitude locations.

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Chapter 1 General Introduction

1.1 Introduction

Global climate change is having significant negative impacts on the structure and function of coral reef ecosystems (Graham et al. 2006; Hughes et al. 2018), significantly undermining ecosystem goods and services derived from tropical coastal waters (Bell et al. 2013; Pratchett et al. 2014). Importantly, ongoing climate change, and corresponding degradation of marine environments and habitats, is expected to result in major changes in fisheries catch potential (Cheung et al. 2010; Bell et al. 2018), with declines in productivity of up to 40% predicted in the tropics. In contrast, harvest potential is predicted to increase between 30 – 70% at high latitudes over the same period (Cheung et al. 2010). This predicted redistribution of global fisheries potential is largely attributed to poleward shifts in the distribution of fishes in accordance with geographical shifts in climate envelopes (Cheung et al. 2010), primarily driven by changes in temperature. Moreover, fishes that are unable to move poleward (e.g., Feary et al. 2014), but are nonetheless sensitive to changing environmental conditions, will exhibit changes in behaviour, fitness and survivorship (Pratchett et al. 2018) that will almost invariably lead to declines in species abundance and overall of fisheries productivity (Bell et al. 2013, 2018). In general, tropical (low-latitude) organisms are expected to be most vulnerable to increasing temperatures (Tewksbury et al. 2008) because they have narrower thermal niches and are currently living closer to their thermal maximum compared with species from higher latitudes (Deutsch et al. 2008; Sunday et al. 2014).

The effects of changing temperature on performance of fishes, and other ectotherms, varies according to the rate and magnitude of the change, as well as the absolute temperature (Portner 2001). At low to moderate temperatures, increasing temperature can have positive effects on performance and fitness of ectotherms (Angilletta 2002). However physiological performance and function are typically optimised within the range of temperatures to which populations and species are naturally exposed (Kingsolver et al. 2007; Takasuka et al. 2007) and decline rapidly with further increases in temperature. Negative effects of high temperatures result when increases in an organisms' basal metabolic rate exceed their metabolic capacity (i.e. the maximum rate of aerobic metabolic rate, (Portner 2001)). For fishes, metabolic capacity is ultimately constrained by oxygen delivery (Ficke et al. 2007) and at high temperatures, this limitation is often compounded by declines in oxygen availability and increases in oxygen demand (Portner 2010). The thermal sensitivity of metabolic performance is often described by a thermal performance curve (Janzen 1967), where performance increases from a lower critical temperature to an optimum (known as a thermal optima, Topt) and subsequently declines to an upper critical temperature. Temperatures below Topt are considered to be less energetically costly, whereas above Topt, energetic demands increase rapidly.

In controlled tank-based studies, conditions are generally very consistent within given treatments, such that study organisms have little to no opportunity to buffer exposure to sub-optimal conditions (e.g., Johansen et al. 2014). Such studies tend to reveal consistent responses, whereby fitness and performance decline rapidly among fishes exposed to temperatures above species-specific thresholds (Brett 1971; Elliott 1975a; Edmunds et al. 2010). Although individual variation in the thermal responses of fish may occur (Payne & Smith 2017). However, in natural environments, fishes may exploit fine-scale heterogeneity in environmental conditions (e.g., along depth gradients, or in relation to light intensity). This allows individuals to select thermal habitats that enhance specific physiological processes depending on their state (e.g., fed or unfed, pregnant or immature), time of day (Bertolo et al. 2011) and season (Di Santo et al. 2011) and minimise exposure to adverse environmental conditions, at least temporarily. As such, short-term experimental tests of thermal sensitivity may have overestimated the impacts of environmental change on fishes, failing to account for acclimation, adaption and / or the potential for individuals to moderate exposure (at least over short terms) to adverse environmental conditions (e.g. Sunday et al. 2014; Buckley et al. 2015)..

In the wild, fishes have multiple options to moderate effects of increasing temperatures. Firstly, fishes may withstand temperature-induced increases in metabolic rates by increasing their food consumption and energy intake (Buentello et al. 2011; Johansen et al. 2015). Empirical studies of marine fishes have demonstrated that a 10 °C increase in temperature causes a 2-3 fold increase in the rate of biochemical enzyme-catalysed reactions and whole-organism metabolism (Evans 2006). While it is generally assumed that food is limiting in natural environments (e.g., Arditi & Ginzburg 1989), recent studies have demonstrated considerable plasticity in predation rates and energetic intake for fishes (Myrick & Cech 2000; Robinson et al. 2010; Johansen et al. 2015). In these experiments, fishes responded to elevated temperatures by consuming more food with increasing temperatures indicating increased foraging efficiency as the most viable means of increasing energy intake in the short-term to compensate for increased metabolic requirements (Johansen et al. 2015). However, less common are field studies that specifically document and quantify the influence of increasing water temperatures on fish foraging behaviour, especially over long time-scales (except see Myrick & Cech 2000) or large geographic areas. There are also very few studies that have considered natural gradients in temperature (e.g., with latitude or seasons) to determine the capacity of fishes to increase food intake in the wild.

If fishes are unable to regulate their food intake to sufficiently compensate for increasing metabolic demands at higher temperatures, they may be forced to conserve energy through changes in movement and activity (Portner 2009, 2010; Johansen et al. 2014). Swimming constitutes one of the largest daily costs in the energy budget of fish and plays a pivotal role in fish survival (Brett 1964; Kerr 1982) in terms of avoiding predators (Weihs & Webb 1984), acquiring food (Rand & Lauder 1981) and partner selection (Milinsksi 1988). Even small changes in swimming behaviour and performance can have a major impact on the energy available for growth, repair and reproduction (Edmunds et al. 2010; Johansen et al. 2014). Empirical modelling, based on the respiration rates of 22 fish species over a range of swimming speeds, suggests that an increase in water temperatures of between 2 - 4 ºC predicted by the end of century (IPCC 2018) would lead to a 6 – 12% increase in the minimum amount of energy required to swim 1 m (Hein & Keirsted 2012). For example, an increase in temperature of 2.5 °C from 27.5 °C to 30 °C, causes an increase in the minimum cost of transport that is 1.5 times greater than that caused by an increase from 5 °C to 7.5 °C (Hein & Keirsted 2012). Consequently, major changes in the metabolic cost of swimming will occur in geographical regions where water temperatures are already high (Hein & Keirsted 2012). Studies of tropical reef fishes have shown that a 3 °C increase in water temperature above present-day averages significantly reduces energy efficiency and maximum swimming speeds of both small site-attached reef fishes (Johansen et al. 2011) and larger-bodied reef fishes (Johansen et al. 2014). At increased temperatures therefore, individuals may be forced to moderate energetic expenditure by adopting energy-saving strategies, potentially trading-off between food intake and energetically demanding activities such as swimming (Johansen et al. 2011).

Fishes may also moderate exposure to unfavorable conditions (specifically, supra-optimal temperatures) by exploiting thermal gradients within their environment (Baird et al. 2003; Goyer et al. 2014). Because biochemical reactions, including those characterising metabolism, increase exponentially with temperature, movements to thermally optimal habitats can improve an individual's fitness by reducing metabolic costs during periods of high activity (Furey et al. 2013), as well enhancing foraging (Thums et al. 2013) and reproductive (Hight & Lowe 2007) strategies. Nevertheless, the suitability of habitats can vary over spatial and temporal scales due to variability in biotic and abiotic factors. For example, variation in habitat use during different times of day may help fulfil requirements such as foraging, predator avoidance and resting (Currey et al. 2015). At longer temporal scales (i.e. seasonally) fish may migrate to optimal habitats to increase reproductive capacity (Jonsson & Jonsson, 2009). Refuge seeking behaviour of coral reef fishes is poorly studied and may well be very limited due to high levels of site fidelity and strong microhabitat associations (e.g., Rummer et al. 2014). Recent studies have however, demonstrated that some large-bodied coral reef fishes move to cooler, deeper waters when they experience elevated temperatures (Richards et al. 2012; Currey et al. 2015) and shelter under tabular coral structures during times of day when solar irradiance is strongest (Kerry et al. 2015). Irrespective of temporal scale, movement to more optimal habitats has the capacity to greatly moderate effects of environmental change on tropical fishes, but it is important to consider potential tradeoffs associated with using different habitats (e.g., moving to greater depths). This is particularly true for important fisheries species that have high ecological and economic value.

Coral trout (*Plectropomus* spp.) are one of the most important commercial fisheries species throughout the tropical Indo-Pacific (Randall & Hoese 1986; Ralston 1987), making them an obvious focal group to assess the potential effects of climate change on tropical fisheries. On the Great Barrier Reef (GBR) *Plectropomus* spp. are the primary fisheries target for recreational and commercial sectors of the Queensland Coral Reef Fin Fish Fishery, generating ~ $30 million p.a. to the Queensland economy (Leigh et al. 2014), and more abroad due to the lucrative live fish trade (Sadovy de Mitcheson et al. 2013). Due to their significant fisheries status, coral trout (primarily *Plectropomus leopardus*) have been a focus of scientific research for decades (Choat 1968; Goeden 1978; Zeller et al. 1997, 1998). *Plectropomus leopardus*, the common coral trout, is the main species caught within the GBR fishery due to their high abundance (Kingsford 2009; Miller et al. 2012), and wide distribution across the full width of the continental shelf (Leigh et al. 2014). As such, there is an abundance of information regarding their biology and ecology (see review by Frisch et al. 2016). Recent studies have also investigated the thermal sensitivities of various aspects of physiology and behaviour of *P. leopardus* under controlled laboratory conditions (Pratchett et al. 2013; Johansen et al. 2014).

In general, *P. leopardus* appear to be extremely sensitive to increasing temperature, exhibiting declines in survivorship (Clark et al. 2017), aerobic scope (Messmer et al. 2017), larval survival (Pratchett et al. 2013), food intake (Johansen et al. 2015) and activity (Johansen et al. 2014) with increasing temperatures above 27 °C (**Chapter 2**). Given that populations of *P. leopardus* in the northern GBR are already periodically exposed to summertime temperatures ≥ 30 °C, any further increases in ocean temperatures may significantly impact individual performance, and therefore fitness, of *P. leopardus* populations with implications for fisheries viability and sustainability (Sun et al. 2015; Pratchett et al. 2016; **Chapter 2**). However, it may be that tank-based studies overestimate the vulnerability of *P. leopardus* to increasing temperatures by failing to account for behavioural responses that can occur in the wild. A recent study by Johansen et al. (2015) demonstrated that *P. leopardus* were able to adjust food intake to maintain body condition under elevated temperatures suggesting that *P. leopardus* may be able to regulate their foraging behaviour in response to increasing temperature. *Plectropomus leopardus* is also an ecologically important mesopredator capable of influencing the structure of coral reef communities (Emslie et al. 2015; Rizzari et al. 2015; Frisch et al. 2016). Thus, any changes to their behaviour in terms of foraging, swimming and movement patterns, and habitat use has the potential to influence population dynamics by altering species interactions (Pennock et al. 2018), trophodynamics (Boaden & Kingsford 2015) and spawning or reproductively motivated movements (Zeller 1998; Bunt & Kingsford 2014).

Experimental studies (e.g., Johansen et al. 2014, 2015, Clark et al. 2017) show that coral trout are adversely affected by prolonged exposure to high temperatures. However, there is a fundamental need to assess the generality of these experimental findings in natural settings, to determine if and how *P. leopardus* may alter their behaviour in the wild as a strategy to buffer effects of increasing temperature within their environment. Improving the understanding of behavioural responses of *P. leopardus* to increasing temperature is particularly important given the predicted 3 °C increase in ocean temperature in the tropics expected for the end of century (IPCC 2014, 2018).

1.2 Thesis aims and outline

The overarching objective of this thesis is to investigate the capacity of the common coral trout, *Plectropomus leopardus* to moderate exposure to increasing temperature through behavioural modification across different spatial and temporal scales. To do this, I employed *in situ* observation and passive acoustic telemetry to examine behavioural responses of *P. leopardus* to natural variation in ambient temperature. To test for variability in responses independent of season, comparisons were made between populations from northern versus southern locations on Great Barrier Reef, Australia (**Figure 3.1 & Figure 4.1**.). The northern sites were Lizard Island (14°40’S, 145°27’E) (Chapter 3) and Opal Reef (16°14’S, 145°52’E) (Chapters 4, 5, & 6), hereafter referred to as low-latitude locations. The southern site for all studies was Heron Island (23°29’S, 151°52’E), hereafter referred to as the high-latitude site. To clarify, the low-latitude sites in this thesis are below the equator, and therefore not strictly ‘low-latitude’ however, they are separated from Heron Island by at least 7° of latitude so in this study are considered low-latitude. The average differences in water temperatures between study sites was ~ 2.5 °C (**Figure 3.2 & Figure 5.1**).

Each data chapter within this thesis represents an *in situ* study that addresses certain aspects of *P. leopardus* behaviour. Broadly, these chapters can be categorised as investigations into foraging and resting (**Chapter 3**), space use (**Chapter 4**), locomotion (**Chapter 5**) and a combination of depth use and activity (**Chapter 6**). **Chapters 4, 5 & 6** all involve acoustic telemetry and therefore contain very similar descriptions in the Materials and Methods. However, because each data chapter represents a manuscript either published or under review. I have chosen to include them as they appear in publication irrespective of the redundancy in the Material and Methods across these three chapters.

First, **Chapter 2** reviews the current literature on the thermal sensitivities of *P. leopardus* in relation to the impacts of climate change to establish the context of my thesis and provide an adaptive framework of potential management solutions. **Chapter 3** then describes an *in situ* observational study of the latitudinal and seasonal variation in two behaviours; foraging (strike rate) and resting patterns of *P. leopardus* in the wild in relation to variation in ambient temperature. **Chapter 4** incorporates passive acoustic telemetry within high-density arrays to compare latitudinal and seasonal variation in home range and space use of *P. leopardus* in relation to variation in ambient temperature. **Chapter 5** also uses acoustic telemetry in the form of accelerometry to investigate latitudinal and spatial variation in acceleration and activity patterns of the same individuals to determine whether these behaviours were influenced by fluctuations in ambient temperature. Then, **Chapter 6** uses a combination of depth, space use and accelerometry data from **Chapters 4 and 5** to compare and contrast three-dimensional habitat use and activity patterns across smaller temporal scales, (i.e. daily, monthly) to examine whether *P. leopardus* exhibit variation in habitat use and movement patterns in relation to fine-scale temperature variation and diel cycles. Finally, **Chapter 7** consists of the general discussion of the thesis, in which the main findings are synthesised and the overall implications of this research in a broader ecological and management context are summarised.

Chapter 2 Effects of climate change on coral grouper (*Plectropomus* spp.) and possible adaptation options

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2.1 Introduction

Total global fishery yields from coral reef environments are estimated to be worth at least US$5 billion per annum (Cesar et al. 2003; Sadovy 2005) and many millions of people in tropical countries are directly dependent on food harvested from coral reefs to meet their basic protein requirements (Bell et al. 2009; McClanahan et al. 2015). Global climate change is however, expected to have significant negative effects on the structure and function of coral reef ecosystems (e.g., Hoegh-Guldberg & Bruno 2010), potentially undermining tropical coastal fisheries production (Bell et al. 2013). Changes in environmental conditions will impact directly on tropical marine organisms (e.g., Munday et al. 2008), leading to changes in abundance, distribution, and/or viability of targeted stocks. A serious concern is that many of the fisheries that provide food and livelihoods for tropical nations are already fully or overexploited (Newton et al. 2007; McClanahan et al. 2015) and will, therefore, have little resilience to the sustained and ongoing impacts of global climate change. Moreover, negative effects of climate change on fisheries production are occurring against a backdrop of increasing human population growth, rising incomes, and corresponding increases in demand for fish (Dey et al. 2008; Bell et al. 2009; Foale et al. 2013), leading to further overexploitation and/or increasing shortfalls in food production.

Effects of climate change on fishes and fisheries are expected to be particularly pronounced in shallow tropical environments (Brander 2007; Cheung et al. 2010). Cheung et al. (2010) predicted that potential fisheries production will decline by 40% in the tropics by 2055, whereas harvest potential will increase 30–70% at high latitudes over the same period. This projected redistribution of global fisheries potential is largely attributed to poleward shifts in the distribution of fishes (Cheung et al. 2010), where species are assumed to move in direct accordance with geographical shifts in climate envelopes. In reality, many coral reef fishes are constrained in their latitudinal distributions by the availability of dietary and habitat resources (Feary et al. 2014), and will therefore, be increasingly exposed to changes in local environmental conditions, rather than moving to reduce such exposure. Experimental tests on the effects of changing environmental conditions on coral reef fishes tend to reveal generally negative effects of increasing temperature and changes in seawater chemistry on individual performance, condition and fitness (reviewed by Munday et al. 2012). However, understanding of the responses of fishes to changing environmental conditions comes mostly from short-term experiments exposing fishes to relatively rapid changes in environmental conditions within closed environments (e.g., Mora & Ospina 2001; Johansen et al. 2015). Such acute exposure to elevated temperatures likely underestimates the capacity for thermoregulatory behaviour or other mechanisms of acclimation and acclimatisation (Roessig et al. 2004; Harley et al. 2006), and especially adaption or heritable changes in thermal tolerance (Donelson et al. 2012; Munday et al. 2013a), which may moderate effects of environmental change in tropical marine environments (Hoey et al. 2016). Moreover, research to date on the effects of climate change on coral reef fishes has been conducted on relatively few species, with an overwhelming bias towards generally smaller-bodied and site-attached species, such as the clownfish *Amphiprion percula* (e.g., Munday et al. 2009a, b, c), which has a maximum total length of ~80 mm (Fautin & Allen 1992).

More than 5000 species of teleost fishes associate with coral reefs (Fisher et al. 2015; Victor 2015), and vulnerability to changing environmental conditions is expected to vary spatially, temporally, ontogenetically and taxonomically (e.g., Munday et al. 2012; Rummer et al. 2014). Early research on taxonomic differences in vulnerability of adult reef fishes to ocean warming suggested that larger individuals may be capable of withstanding much higher temperatures than smaller species (Mora & Ospına 2001), suggesting that the effects of ocean warming on exploited fishes and therefore, fisheries productivity, might be relatively subtle. However, more recent work is showing that thermal sensitivity is likely to be enhanced at larger body sizes (Portner & Knust 2007; Daufresne et al. 2009; Clark et al. 2013). As such, prior research on smaller-bodied fishes (e.g., *Amphiprion percula*) might have relatively limited value in understanding the climate vulnerabilities of larger-bodied, fisheries target species (Pratchett et al. 2008). Moreover, much of the work on the vulnerability of fishes to changing environmental conditions has focused on adult lifestages, whereas understanding of a species' vulnerability to environmental change requires holistic consideration of each of the key life-history stages (Portner & Peck 2010). Importantly, early life history stages of fishes (from fertilization to settlement) are generally more vulnerable to climate change than juveniles and young adults (Portner & Farrell 2008) and any effects on larval production, dispersal and/or survival, will have significant impacts on the viability of fish populations (Doherty 1991; Caley et al. 1996), especially those subject to sustained exploitation (Carr & Reed 1993).

The purpose of this review is to consider the vulnerability of coral grouper (genus *Plectropomus*) to global climate change. Coral grouper are among the most important coral reef fisheries species throughout the Indo-West Pacific (Frisch et al. 2016), and an obvious focal group to assess potential effects of climate change on tropical fisheries. Explicit experimental studies testing effects of environmental change on coral grouper (almost exclusively with just one species, *Plectropomus leopardus*) are limited and were initiated only very recently (e.g., Munday et al. 2013b; Pratchett et al. 2013; Johansen et al. 2014, 2015; Sun et al. 2015), but latest findings from this research are highlighted throughout this review.

Our approach is different from other recent reviews of effects of climate change on coral reef fishes (e.g., Munday et al. 2008) because we explicitly focus on coral grouper as an exemplar of an exploited coral reef fish, with a view to better understanding the specific impacts of climate change on fisheries production on coral reefs. A companion review on the biology, fisheries and management of coral grouper, identifed key vulnerabilities in the life-cycle of coral grouper, enabling assessment of likely responses to sustained and ongoing changes in environmental conditions on coral reefs (see Frisch et al. 2016). The present review also explores adaptation options that may be used to minimize both ecological and socioeconomic vulnerability as fisheries stocks are exposed to inevitable and accelerating changes in environmental conditions.

2.1.1 Effects of climate change on coral grouper

Projected changes in environmental conditions within shallow tropical seas are complex and varied (e.g., Harley et al. 2006; Ganachaud et al. 2011), ranging from specific localized changes in sea surface temperatures to broad-scale changes in the strength and position of major ocean currents. Each of these changes are likely to impact on the distribution, abundance, population structure and/or viability of coral reef fishes, but there is limited data on when, where and how, many of these effects will manifest (Munday et al. 2008). The formative part of this review will consider how (1) general increases in temperature (ocean warming), (2) declines in pH (ocean acidification) and (3) climate-induced habitat degradation, are expected to affect the biology, behaviour, and ultimately, availability and catchability of coral grouper. This is not to say that other environmental changes (e.g., declines in oxygen availability, changes in salinity, shifts in the position and strength of ocean currents, changes in rainfall patterns or frequency of extreme events etc.) are not important, and it is likely that there will be other emergent effects as we continue to observe the responses of tropical marine fishes and fisheries to changing environmental conditions in natural ecosystems (e.g., Harley et al. 2006; DePasquale et al.

2015). For a more comprehensive overview of the multitude of potential effects of climate change on tropical marine fishes and fish habitats see Harley et al. (2006), Munday et al. (2008), and Pratchett et al. (2011c). However, preliminary research and understanding of the likely effects of climate change on reef fishes, as is the case for coral grouper, is very much focused on effects of ocean warming, ocean acidification and climate-induced habitat degradation (Pratchett et al. 2015b).

2.1.2 Ocean warming

Increasing ambient temperature fundamentally impacts fishes (and other ectotherms) by increasing their standard metabolic rate and corresponding oxygen demands (Fry 1971). At low to moderate temperatures, fishes can often compensate for increases in metabolic demands simply by increasing food intake (e.g., Jobling 1997; Nowicki et al. 2012; Johansen et al. 2015), and unless food is limiting, such moderate temperature increases may have little impact on individual performance. Small temperature increases may even lead to improvements in individual performance of ectotherms (Tewksbury et al. 2008; Rijnsdorp et al. 2009), for which internal body temperatures are generally reflective of ambient temperatures. However, fitness and performance will inevitably decline as these organisms are exposed to even higher temperatures due to inherent limitations in meeting ever-increasing oxygen and metabolic demands (e.g., Neuheimer et al. 2011). Researchers are increasingly focused on identifying the temperature (thermal optima) where different aspects of performance (e.g., juvenile growth or swimming speeds) are maximized (Hoey et al. 2016), as a means of understanding the vulnerability of species to forecast changes in temperature.

Thermal optima for many fishes are relatively fixed across wide geographic ranges, such that there may be marked variation in response to ocean warming in different locations. For example, rapid warming of the Tasman Sea over the last 90-years has increased growth rates of the temperate marine fish, *Cheilodactylus spectabilis*, in cooler southern regions, while individuals at the warm northern edge of their distribution have decreasing growth rates (Neuheimer et al. 2011). Tropical fishes are expected to be particularly vulnerable to increasing temperatures because they experience relatively limited diurnal or seasonal fluctuations in ambient temperatures, and therefore, are predicted to have much narrower ranges of thermal tolerance than species from higher latitudes (Bush & Hooghiemstra 2005; Tewksbury et al. 2008). Tropical species may also operate much closer to their upper thermal limits (Tewksbury et al. 2008; Sunday et al. 2010), such that even fairly moderate temperature increases may lead to declines in individual performance and fitness (but see Payne & Smith 2017).

Experimental studies conducted on a handful of different coral reef fishes show, as predicted, that these species live close to their thermal optimum (Rummer et al. 2014) and are thus likely to be negatively impacted by projected increases in ocean temperatures (reviewed by Munday et al. 2012). However, the specific effects of ocean warming on tropical reef fishes will depend upon their thermal history, food availability, and energetic demands, as well as the capacity for behavioural thermoregulation, acclimation and adaptation (Munday et al. 2012, 2016). Vulnerability to ocean warming will therefore, vary greatly among species and stocks, even among fishes that co-occur in the same habitats and fulfil similar ecological roles (e.g., Nilsson et al. 2009; Johansen & Jones 2011).

Investigations into the thermal sensitivity of adult coral grouper (specifically, *P. leopardus*) were undertaken only very recently (Pratchett et al. 2013; Sun et al. 2015). Pratchett et al. (2013) exposed fishes to one of four different temperatures (24, 27, 30 and 33 ºC) to specifically test potential effects of ocean warming on wild stocks of *P. leopardus* from Australia's Great Barrier Reef (GBR). Fishes (n = 160) were sourced from two different locations (southern and northern GBR), where mean maximum summertime temperatures are currently 27 and 30 ºC, respectively, which was expected to be reflected in phenotypic differences of the spatially disparate populations. The standard (minimum or resting) oxygen consumption of *P. leopardus* increased 11.0% per 1 ºC over the temperature range from 24 to 33 ºC, while maximum oxygen consumption peaked at 30 ºC and was 16.7% lower for fishes subject to 33 ºC, regardless of the source population (**Figure 2.1**). This suggests that there is limited local adaptation or acclimation to different thermal regimes among populations of *P. leopardus* on the GBR (**Figure 2.1**). Although absolute aerobic scope (estimated based on differences between standard and maximum oxygen consumption) peaked at 30 ºC, this may exceed or at least approach the thermal optima of *P. leopardus*, as fish suffered increasing mortality at > 27 ºC (**Figure 2.1**; see also Sun et al. 2015), and also exhibited declines in spontaneous swimming speeds at 27 ºC (Johansen et al. 2014). Given that *P. leopardus* in the northern GBR (and throughout much of their geographic range) are already periodically exposed to temperatures of > 30 ºC, it appears that any further increases in ocean temperatures will significantly impact on individual performance, and therefore fitness, of *P. leopardus*.

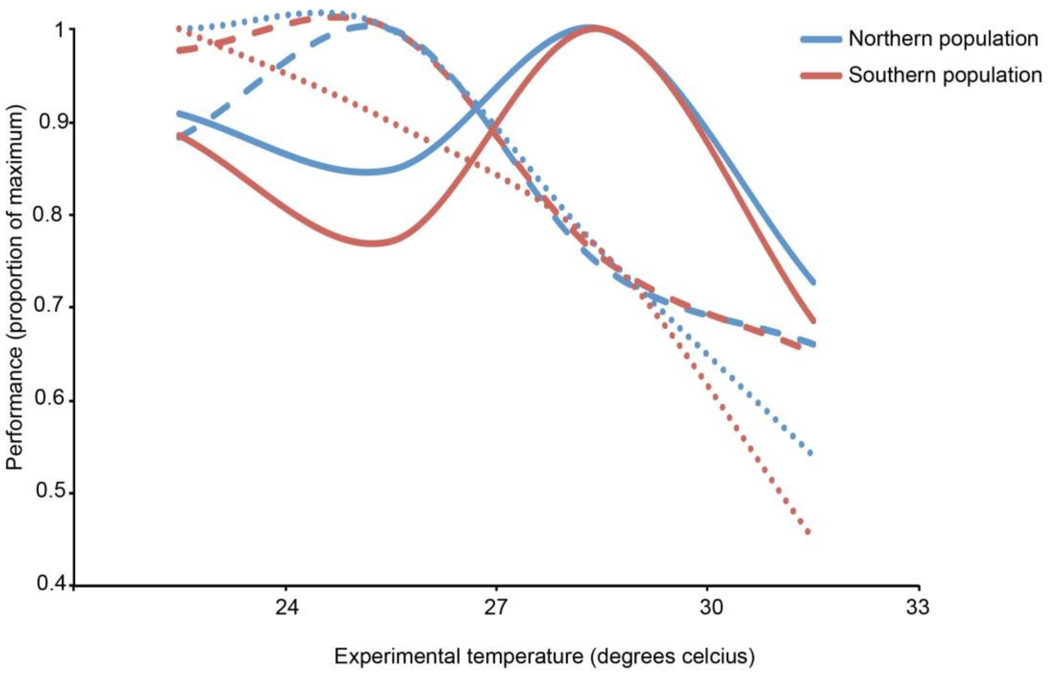

Figure 2.1: Temperature performance curves for *Plectropomus leopardus*, showing variation in absolute aerobic scope (solid lines), spontaneous swimming speeds (dashed lines) and survivorship (dotted lines) recorded for fishes collected from the northern (blue) versus southern (red) GBR, and maintained in captivity at each of four different experimental temperatures for eight weeks. All data is expressed as a proportion of maximum recorded at any given temperature, showing apparent differences in thermal optima for each measure of performance.

Long-term impacts of ocean warming on fishes may be moderated by behavioural thermoregulation, acclimation and acclimatisation (phenotypic plasticity) and/or adaptation (e.g., Donelson et al. 2012; Munday et al. 2016). Given limited differences in the thermal optima of aerobic scope for *P. leopardus* from the northern versus southern GBR, where mean maximum temperatures vary by > 3 °C, it appears that populations are not well adapted to local thermal regimes, perhaps due to very high levels of gene flow along the length of the GBR (e.g., van Herwerden et al. 2006). If so, this suggests that any further warming will have deleterious effects, especially for populations that are already exposed to temperatures > 30 °C. Alternatively, thermoregulatory behaviour (e.g., refuge seeking behaviour) by coral grouper may have minimized exposure to supra-optimal temperatures and thereby obscured the true extent of local acclimation and adaptation (*sensu* Buckley et al. 2015). For example, *Plectropomus* spp. may be able to move among habitats to exploit thermal refuges. They could also moderate activity and food intake to balance metabolic demands (e.g., Johansen et al. 2014, 2015; Sun et al. 2015) to withstand increasing temperatures.

In laboratory experiments where fish were fed *ad libitum* on dead fish, *P. leopardus* responded to elevated temperatures (>30 °C) by reducing maximum swimming speeds and spent increased time resting motionless on the bottom (Johansen et al. 2014). It remains to be tested whether similar behaviour responses occur in the wild where coral grouper need to pursue live prey, but there are several ways in which coral grouper could moderate physiological impacts of ocean warming. Buckley et al. (2015) showed that thermoregulation by lizards buffers against environmental variation, but ultimately hinders adaptation of thermal tolerance. If this is true for coral grouper, it is likely that they will appear generally resilient to short-term and to moderate changes in environmental conditions, but physiological limits may ultimately constrain their capacity to endure longer-term and more severe ocean warming (e.g., Munoz et al. 2015). Aside from impacts on adult performance, ocean warming may have further important effects on a wide range of early life history processes for coral grouper, potentially affecting fecundity, ovulation, fertilization and/or reproductive success (**Table 2.1**). For coral grouper, the most alarming findings to date arise from preliminary investigations into the survivorship of newly fertilized embryos at increasing temperatures (Pratchett et al. 2013), whereby there was negligible mortality at ≤ 29.5 °C, but mortality rates increased markedly with increasing temperatures. All embryos died within 6 h at ≥ 33.9 °C.

The next most critical period in the life cycle of coral grouper is the transition from endogenous to exogenous feeding, which occurs 3–6 days after hatching in *P. leopardus* (Frisch et al. 2016). Developmental rates and energetic demands of larval *P. leopardus* are directly proportional to temperature (Yoseda et al. 2008), such that these larvae face greatly elevated risk of starvation at higher temperatures. If however, coral grouper spawn at a fixed temperature threshold (reviewed by Frisch et al. 2016), it may be that fertilized embryos will never naturally be exposed to higher temperatures. Rather, ocean warming could cause an earlier onset of reproduction, potentially increasing variability in spawning within and among different stocks (Munday et al. 2008). Changes in the timing and predictability of spawning will have ramifications for the effectiveness of periodic fisheries closures that aim to protect spawning aggregations from fisheries exploitation (Curley et al. 2013) but may also have deleterious consequences for population replenishment if there is an emerging mismatch in the timing of spawning versus optimal conditions for larval development and survivorship (e.g., Edwards and Richardson 2004).

Table 2.1: Observed effects of ocean warming and ocean acidification on fishes that might be expected to undermine sustainability of fisheries. Effects are separated into those that have already been tested or established with coral grouper versus the broader range of potential effects apparent from studies in coral reef (CR), freshwater (FW), pelagic (P), or temperate systems (T). This table is not intended to be comprehensive, but illustrates the range of effects documented for fishes that are yet to be tested for coral grouper. Note also that for many of the reported effects, there are other studies that have recorded counter effects or no effects, depending on the specific location and environmental setting in which studies were conducted.

Effects	**Coral grouper**	**Other fishes**
Ocean Warming	Reduced maximum swimming speed (Johansen et al. 2014) Increased time resting (Johansen et al. 2014) Increased food intake (Johansen et al. 2015) Reduced aerobic scope (Pratchett et al. 2013) Reduced growth (Sun et al. 2015) Reduced survivorship (Sun et al. 2015)	Altered spawning times^{T} (Drinkwater 2005) Reduced ovulation^{T} (Jobling et al. 1995) Reduced fertilization rates ^{FW} (Pankhurst et al. 1996) Reduced reproductive capacity^{CR} (Donelson et al. 2010) Increased larval mortality^{T} (Llopiz et al. 2014) Reduced growth rate^{CR} (McLeod et al. 2015) Reduced aerobic scope^{CR} (Nilsson et al. 2009 Reduced swimming speed (Johansen and Jones 2011) Altered depth distributions (Dulvy et al. 2008) Poleward shifts in distribution^{CR} (Feary et al. 2014)
Ocean acidification	Reduced sperm motility (Pratchett et al. 2013) Reduced olfactory response (Munday et al. 2013b) Increased boldness (Munday et al. 2013b)	Increased reproductive output^{CR} (Miller et al. 2013) Reduced hatching success^{T} (Chambers et al. 2014) Reduced larval growth^{FW} (Baumann et al. 2012) Increased larval growth (Munday et al. 2009, Chambers et al. 2014) Abnormal development (Frommel et al. 2012) Increased larval mortality^{CR} (Baumann et al. 2012) Impaired social learning^{CR} (Ferrari et al 2012) Reduced lateralization^{CR} (Domenici et al 2012) Altered settlement preferences^{CR} (Devine et al. 2012) Altered prey selectivity^{CR} (Ferrari et al. 2011) Reduced condition (Hurst et al. 2012) Reduced aerobic scope^{CR} (Munday et al. 2009) Increased risk of predation (Munday et al. 2010)

2.1.3 Ocean acidification

Biological impacts of ocean acidification are well described among calcifying organisms, for which, decreased aragonite saturation will lead to declines in calcification and growth (Orr et al. 2005). However, there is increasing appreciation that changes in seawater chemistry (specifically, increases in the partial pressure of CO_2 (pCO_2) in seawater, leading to reduced aragonite saturation and lower pH) may affect larval development and growth, as well as survival across a broad range of marine organisms (Doney et al. 2009; Kroeker et al. 2013). A key concern is that higher CO_2 levels in the ocean can lead to acidosis in the blood and tissues of marine organisms (Portner et al. 2004). Fishes are highly capable acid–base regulators and are able to defend against CO_2-induced acidosis by the regulation of acid–base relevant ions (primarily bicarbonate and chloride) (Heuer & Grosell 2014). Nevertheless, higher ambient pCO_2 may impose additional physiological costs that could affect individual performance (Portner et al. 2004; Ishimatsu et al. 2008; Heuer & Grosell 2016). Sustained changes to bicarbonate and chloride concentrations during pH regulation may interfere with neuroreceptor function in marine fishes (Nilsson et al. 2012), leading to impaired sensory discrimination (Munday et al. 2009a) and abnormal behaviour (Munday et al. 2012). Although the magnitude of the response varies markedly among species (Ferrari et al. 2011a), these changes could directly lead to increased mortality of larval and early post settlement individuals. For example, Ferrari et al. (2011b) showed that predation rates on juvenile damselfishes approximately doubled when both predator and prey fish had been exposed to 700 atm pCO_2 for 4 days, compared to ambient conditions. If the responses of these damselfish are representative of reef fish generally, ocean acidification could have important ramifications for population replenishment and viability of harvested species. Elevated pCO_2 can also directly affect mortality of larval fishes, and thus impact population recruitment. For example, increased mortality of larval cod observed at 1100 data atm pCO_2 was estimated to reduce population recruitment to an average of just 8 and 24% of current recruitment levels in two different populations (Stiasny et al. 2016).

Some of the most noticeable effects of ocean acidification on marine fishes relate to changes in behaviour, which include changed olfactory and auditory preferences, altered activity levels, loss of learning ability, and changes to behavioural lateralization (reviewed by Heuer & Grosell 2014; Nagelkerken & Munday 2016). Behavioural studies have shown that juvenile *P. leopardus* appear to be equally sensitive to the effects of high CO_2 compared to other smaller-bodied reef fishes (Munday et al. 2013b). Munday et al. (2010), for example, found that juvenile damselfishes exposed to 850 atm pCO_2 for 4 days were 30% more active and ventured 60 –

80% further from shelter compared to control fishes maintained in ambient conditions. *Plectropomus leopardus*, meanwhile, reared at just 700 atm pCO$_2$ (albeit for 28 days) were 10 times more active and ventured 5 times further from shelter compared to control fishes (Munday et al. 2013b). Juvenile coral grouper are normally very cryptic, tending to stay very close to structural habitats (Wen et al. 2012) presumably to minimize the risk of predation from other larger fishes, including conspecifics (Leis and Carson-Ewart 1999). Accordingly, juvenile *P. leopardus* held in aquaria tend to spend up to 90% of their time in hides (Munday et al. 2013b). However, juvenile *P. leopardus* exposed to 700 and 960 atm pCO$_2$, spent an average of 40 and 10% in hides, respectively (Munday et al. 2013b). If such changes in behaviour occurred in natural populations, it may increase exposure to predators and increase juvenile mortality.

Ocean acidification also interferes with responses to sensory cues in *P. leopardus* (Munday et al. 2013a, b), as shown previously for smaller reef fishes (e.g., Dixson et al. 2010; Ferrari et al. 2011a). Settlement-stage coral grouper have well-developed auditory and olfactory abilities, which are used in orientating towards reefs and locating suitable settlement habitats (Wright et al. 2008). However, juvenile *P. leopardus* reared for 4 weeks at **C** 700 atm pCO$_2$ exhibited dramatically altered sensory function, orientating towards cues that they would normally avoid, such as odour cues from predators (Munday et al. 2013a, b). If CO$_2$ emissions continue on the current trajectory, atmospheric CO$_2$ will exceed 700 atm by 2100 (Meinshausen et al. 2011) and so any potential acclimation or adaptation to moderate effects of ocean acidification, would need to occur within 70–80 years. Among damselfishes there appears to be the capacity for acclimation of some behavioural effects of high CO$_2$ (Allan et al. 2014), but not others (Welch et al. 2014). Further research is required to establish sensitivities to increasing pCO$_2$ across other *Plectropomus* species, as well as establishing whether these large fisheries species can acclimate or adapt to rising CO$_2$ levels within the necessary timeframe.

Relatively little is known about the possible effects of ocean acidification on other life-history processes in fishes, such as reproduction. The few studies conducted to date suggest that negative effects of ocean acidification on reproduction by marine organisms is largely negligible (Kroeker et al. 2010; Milazzo et al. 2016). In some cases, reproduction could even be stimulated by elevated pCO$_2$ and low pH (Miller et al. 2013). Sperm motility of the flounder *Limanda yokohamae* is arrested by mild increases in pCO$_2$ (Inaba et al. 2003), but similar effects were not observed in the Baltic cod (Frommel et al. 2010), or ten other species from a range of families (Inaba et al. 2003). Sensitivity of fish eggs to elevated CO$_2$ also varies markedly between species, but eggs of most fish species seem able to tolerate levels above 10,000 µatm CO$_2$ (Ishimatsu et al. 2008). In general, it appears likely that rising ocean temperature will have a greater impact on fish reproduction than elevated CO_2 (Pankhurst & Munday 2011; Miller et al. 2015), but more research is required, especially for pelagic spawning fishes, such as coral grouper. Initial studies with coral grouper suggest that sperm motility is compromised at reduced pH, though there was no significant difference in fertilization rates across pH treatments of 8.1–7.6 (Pratchett et al. 2013).

2.1.4 Coral loss and habitat degradation

Aside from ocean warming and ocean acidification, the distribution, abundance and fitness of coral grouper may also be affected by climate-induced changes in the biological and physical structure of coral reef habitats (Graham et al. 2006; Pratchett et al. 2008; Alvarez-Filip et al. 2009). Coral reefs ecosystems are particularly susceptible to climate change (Walther et al. 2002) owing to the extreme thermal sensitivities of scleractinian corals (Jokiel & Coles 1990), which are the principle ecosystem engineers of coral reef habitats. Repeated episodes of mass coral bleaching, mostly since 1998, have already generated widespread declines in coral cover across much of the Indo-Pacific (Wilkinson 2002; Gardner et al. 2003; Hughes et al. 2003), which is being compounded by the increased incidence of extreme weather events (Webster et al. 2005; De'ath et al. 2012). Moreover, the capacity of corals to recover from successive climatic disturbances is becoming increasingly undermined as ocean warming and acidification further constrain coral growth (Pratchett et al. 2015a). The net effects of these multiple impacts are sustained declines in live coral cover, and general declines in habitat and topographic complexity (Graham et al. 2006; Alvarez- Filip et al. 2009). In the worst case, where corals are subject to thermal conditions that cause severe coral bleaching and extensive mortality on an almost annual basis, it is expected that most habitat-forming corals would essentially disappear (Sheppard 2003; Hoegh- Guldberg & Bruno 2010), thereby drastically altering the biological and physical structure of reef ecosystems.

Habitat structure is a fundamental property of coral reef systems, with structurally complex habitats moderating predation intensity and competitive interactions by increasing the number and diversity of microhabitats and refuges (e.g., Crowder & Cooper 1982; Holbrook & Schmitt 1988). Widespread degradation of coral reef habitats, caused by climate induced coral bleaching, increased incidence of extreme weather events, as well as other more direct anthropogenic disturbances, is largely manifest as marked declines in the cover of scleractinian (hard) corals (e.g., De'ath et al. 2012) and associated reductions in topographic complexity (Graham et al. 2006). These changes to reef habitats have far reaching impacts on coral reef fishes, leading to declines in abundance across many different species (Pratchett et al. 2008, 2011b).

Coral reef fishes vary in their reliance on corals and the topographic structure provided by coral rich habitats, ranging from highly specialized species that are critically dependent on a very restricted suite of specific coral species (e.g., Munday 2004; Pratchett 2005) to generalist species that display limited affinity for live corals (e.g., Wilson et al. 2008, 2010). Approximately 10% of coral reef fish species appear to be truly coral-dependent (Pratchett et al. 2008) and it is these species that are first and worst affected by declining coral cover (Kokita & Nakazono 2000; Spalding & Jarvis 2002; Munday 2004; Halford et al. 2004; Bellwood et al. 2006). However, many reef fishes prefer to settle near live corals or in coral-rich habitats even if adults are not strictly coral-dependent (Jones et al. 2004; Feary et al. 2007). As such, upwards of 60% of reef fish species (including 57% of carnivorous fish species) are negatively affected by abrupt coral loss (Pratchett et al. 2011b), especially when this is combined with declines in topographic complexity of reef habitats. Habitat degradation is expected to be one of the most pervasive impacts of climate change on fisheries production within coral reef ecosystems (Hoegh-Guldberg et al. 2007; Munday et al. 2008; Pratchett et al. 2011c; Bell et al. 2013a, b; Rogers et al. 2014), and is already very apparent in many locations (e.g., Graham et al. 2015).

Coral grouper, like many other coral reef fish, often utilise live coral habitats at settlement (Light & Jones 1997; Leis & Carson-Ewart 1999; Kingsford 2009; Wen et al. 2012), either because they provide shelter, harbour prey, and/or aid foraging (Frisch et al. 2016). At Lizard Island, in the northern GBR, Leis & Carson-Ewart (1999) found that *P. leopardus* larvae settled most frequently to structurally complex live or dead coral colonies. Given that predation is typically high during this critical life history stage (e.g., 5–17% of the larvae were eaten as they attempted to settle) it was presumed that these complex habitats provide important refugia from predators (Leis & Carson- Ewart 1999). However, Wen et al. (2013) demonstrated that juvenile *P. maculatus* preferentially utilize coral microhabitats that serve the dual purpose of offering suitable shelter while also increasing access to prey. In experiments without prey, these fishes did not distinguish between live or dead coral colonies, presumably because they are equally effective in providing refuge from potential predators. In the field, however, *P. maculatus* exhibited strong preference for live coral habitats situated over sand, which were shown to provide greatest access to potential prey (Wen et al. 2013).

If live corals increase survivorship of newly settled coral grouper (either by reducing predation or increasing access to prey), extensive coral depletion may be linked to localized declines in the abundance of coral grouper. Accordingly, inter-annual variation in the abundance of *P. maculatus* at the Keppel Islands, on the inshore GBR, was shown to closely match changes in live coral cover (Williamson et al. 2014). Moreover, Graham et al. (2006) reported a shift in the size structure of fishery target species following the 1998 coral-bleaching event in the Seychelles. Total biomass changed little in the 7-years post-bleaching, however, there was a marked decline in small fish (≤ 30 cm TL) over the same period. Graham et al. (2006) suggested that the loss of suitable settlement habitat and/or suppression of appropriate settlement cues resulted in widespread recruitment failure, which would greatly undermine the long-term sustainability of local fisheries.

The importance of live corals for adult coral grouper is unclear, but greatest densities of *P. leopardus* are often reported in areas of high coral cover (Kingsford 1992, 2009; Connell & Kingsford 1998). Moreover, adult coral grouper are often found sheltering beneath large living tabular corals (Samoilys 1997; Kerry & Bellwood 2012; Wen et al. 2013), which may facilitate hunting or reduce exposure to ultra-violet radiation. Connell and Kingsford (1998) found that live coral cover was a better predictor of *P. leopardus* abundance than topographic complexity, which they suggest might be driven by the higher abundance and diversity of potential prey fishes (e.g., pomacentrids) in coral-rich habitats. Adult coral grouper do however, feed on a wide range of fishes (Frisch et al. 2016), and might be expected to increase intake of pelagic fishes or generalist reef fishes to compensate for losses of coral-dependent prey. Certainly, adult coral grouper can persist at locations with little or no coral cover, often sheltering amongst dense stands of macroalgae (Hoey & Bellwood 2011). However, changes in the diet and condition of adult coral grouper following acute or sustained coral loss have never been explicitly studied, and it appears that the greatest vulnerability to changing habitat structure may be during settlement stages (Wen et al. 2016).

2.2 Climate change adaptation in coral reef fisheries

Climate change, for the most part, provides a renewed imperative for stronger and more effective fisheries management, capitalizing on existing management regimes, but ensuring greater compliance and increasing flexibility and responsiveness in adaptive management (Koehn et al. 2011). There are however, opportunities in most fisheries to identify, and implement, no-regrets (win–win) adaptation options that will maximise ecosystem and economic resilience to not only climate change, but a wide range of external threats (e.g., Pecl et al. 2009). There are also some effects of climate change (e.g., latitudinal variation in the vulnerability and viability of fisheries stocks) that require specific changes to existing management arrangements (Hobday et al. 2008; Madin et al. 2012). Accordingly, there have been significant and increasing efforts to explicitly consider climatic impacts in the formulation of new fisheries management and environmental protection policies (Bell et al. 2011b). Even in cases where these efforts are constrained by incomplete understanding and considerable uncertainties surrounding the effects of climate change on fishes, fish habitats, and fisheries production, it is imperative to at least consider climate risks (Pecl et al. 2014) and vulnerabilities facing fisheries and consider alternative adaptation options (e.g., Pecl et al. 2009), if only to maximise the range of possible adaptation options that can be considered. The range of possible adaptation options will erode over time as climate change impacts become manifest and more immediate (Smit & Wandel 2006). The purpose of the second part of this review is to utilise established knowledge and predicted vulnerability of coral grouper to climate change, to highlight major classes of adaption options that will help to sustain optimal long-term yields from reef-based fisheries where coral grouper are an important contributor to fisheries yields and values (**Figure 2.2**).

Vulnerability is often defined as the degree to which a system (ecological or socioeconomic) is susceptible to, or unable to cope with, negative effects of environmental change (McCarthy 2001). More contemporary treatments of vulnerability (largely informed by parallel research on resilience of social ecological systems) acknowledge that environmental change will present both risks and opportunities, and that capitalizing on new opportunities is at least as important as minimising the risks in adapting to climate change (Adger 2006). Even so, most vulnerability assessments (and associated adaption planning frameworks) are still structured around the three core elements of vulnerability; exposure, sensitivity and adaptive capacity (e.g., Bell et al. 2011). Exposure is the degree to which a system will be subjected to sustained environmental change or sudden climatic disturbances. When considering social systems, this incorporates all aspects of the vulnerability (exposure, sensitivity and adaptive capacity) of the embedded ecological system (Williams et al. 2008; Marshall et al. 2010; **Figure 2.2**). Sensitivity is the magnitude of changes (e.g., changes in potential yields) that are likely to occur as a result of climate change (IPCC 2001) and taken together with exposure determine the potential impact of climatic disturbances and environmental change. Finally, adaptive capacity is the ability of people, organisms and systems to respond or adapt to climate impacts (Gunderson & Holling 2002), thereby moderating overall vulnerability to current or emerging impacts (**Figure 2.2**).

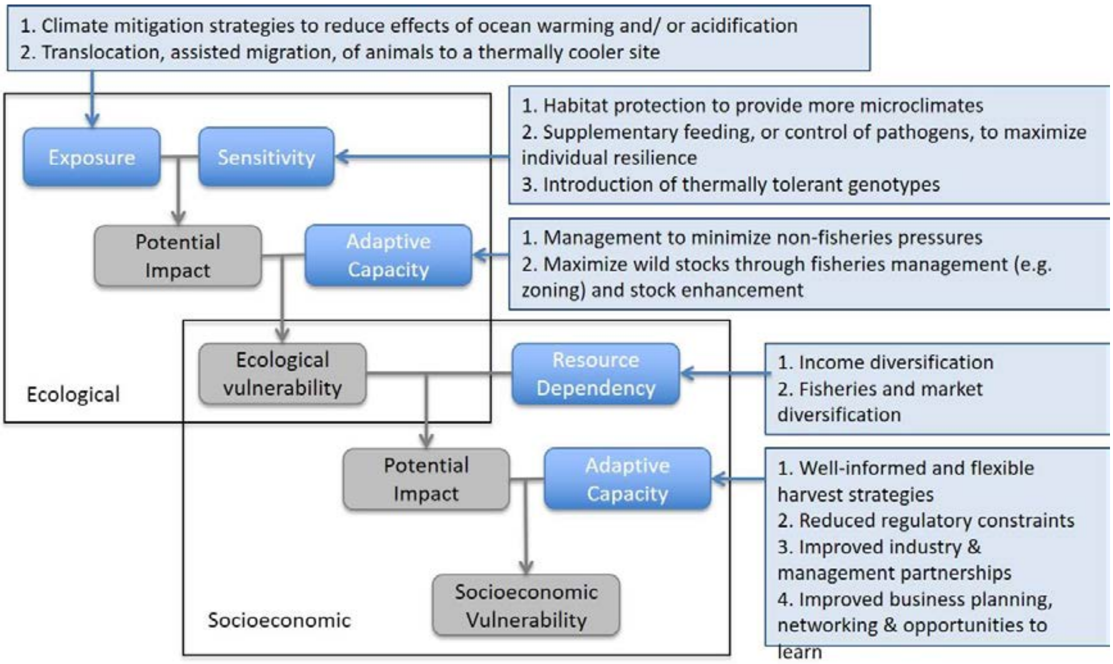

Figure 2.2: Nested socio-ecological vulnerability framework following Marshall et al. (2013), showing broad categories of adaptation options that will moderate exposure and sensitivity of fisheries stocks to climate impacts, versus maximizing adaptive capacity of stocks, reducing resource dependency and maximizing adaptive capacity within the relevant socioeconomic sectors.

Adaptation planning typically begins with identifying scenarios of change, followed by management actions, operational or organisational changes (broadly referred to as adaptation options) that will reduce exposure, reduce sensitivity, or increase adaptive capacity for the species in question or relevant stakeholders (Hobday et al. 2015). These adaptation options must ultimately be assessed for effectiveness under a range of alternative climate change scenarios (e.g Evans et al. 2013), and across different organisational scales and geographical contexts. The identification and acceptability of alternative adaptation options should also be considered by the multiple stakeholders required to adopt such changes, or potentially impacted by such changes (Hobday et al. 2015). In this review however, we simply present a range of adaptation options that are relevant to each of the five key components of the social-ecological vulnerability framework (Exposure, Sensitivity, Ecological Adaptive Capacity, Resource Dependence and Socioeconomic Adaptive Capacity) following Marshall et al. (2013). The relative benefits of proposed adaption options are not considered, nor do we consider the key sectors or sets of stakeholders that will bear the cost of implementing proposed options. These are however, the critical next steps in preparing for inevitable effects of climate change on coral grouper, recognising that adaption planning requires unequivocal consideration of overall societal priorities and preferences (Leith et al. 2013). We also note that the lead-time required to implement potential adaptation options can also vary, due to the requirement for new technology, governance arrangements, or changing of societal preferences (Hobday et al. 2015). Some options will be more feasible or realistic than others (and this may change over time), but an open discussion of a full range of potential adaptation options is needed (*sensu* Bowman 2012).

2.2.1 Reducing exposure

The exposure of the coral grouper to climate change can ultimately be reduced by action to reduce global greenhouse gas emissions and impacts to coral reefs and associated fisheries are important in raising societal awareness for the urgent need for effective global actions to reduce carbon emissions. There are also direct actions that can reduce coral grouper exposure to warmer waters, such as translocation of juvenile or adult fish to cooler environments (**Figure 2.2**). Such translocations are more common for terrestrial species but have also been proposed for marine species (Bax et al. 2013). Suitable habitats can be identified on the basis of species distribution modelling (Robinson et al. 2011) or from *in situ* monitoring of environmental conditions. Translocation of site-attached species may be more successful, and early life stages of coral grouper may be more amenable to relocation than adults, but risks associated with undesired genetic mixing and disease transmission should also be assessed. Small-scale habitat modification, such as shading, has been proposed for high value coral sites (Rau et al. 2012), and while fish may receive localised benefits from these approaches, widespread population outcomes are less likely. Pumping of cool water from deep to shallow reef environments has also been proposed (Rau et al. 2012) and may provide some local benefits for coral grouper. However, modification of the environment to reduce exposure of *Plectropomus* spp. to climate change would be very difficult on the scale of an entire reef systems (e.g., Australia's GBR).

2.2.2 Reducing sensitivity

Given that coral grouper already exist at a wide range of locations throughout the Indo-Pacific (Frisch et al. 2016), at a wide range of latitudes (> 30° north and south) with natural variation in environmental conditions, such as temperature and pH, some options to reduce sensitivity to changes in these parameters may already exist. In extreme cases, thermally tolerant genotypes may be introduced from even warmer regions (**Figure 2.2**). The ability of coral grouper to cope with warmer or more acidic waters may also be enhanced if the fish are in healthy condition, which may be achieved by supplemental feeding, control of disease and parasites, or changes to the density of competitors. Modification of the microenvironment to provide greater protection (and thus less energy expenditure on escaping from predators) may also improve coping ability. However, such interventions (e.g., culling of competitors, provision of new habitat) may prove impractical and unfeasible, as well as having potential unintended consequences, especially in an ecosystem where many species are changing their distribution, abundance and performance as a function of climate change (e.g., Feary et al. 2014). Together, the exposure and sensitivity dictate the impact on the species as a result of climate change, but this can be moderated by the adaptive capacity of the species.

2.2.3 Maximizing ecological adaptive capacity

The adaptive capacity of fish and fisheries stocks to tolerate additional impacts is exacerbated by local levels of exploitation (e.g., Hsieh et al. 2008) and other anthropogenic threats to fisheries species and habitats (Pratchett et al. 2011a). Accordingly, one of the most effective ways to mitigate effects of environmental change is to minimize anthropogenic disturbances to natural ecosystems and reverse widespread habitat degradation (Creighton et al. 2015). Coral reef ecosystems have been subject to a long history of anthropogenic degradation and exploitation in many countries (Jackson et al. 2001), which both increases susceptibility to, and exacerbates the effects of, global climate change (e.g., Wooldridge & Done 2009). Similarly, many of the predominant species targeted by contemporary reef fisheries (including coral grouper) might be resilient to environmental change and habitat degradation, were it not for ongoing exploitation that suppresses local abundance and replenishment (e.g., Hsieh et al.

2008). Fisheries and environmental managers will need to balance increasing demand for fishes against the need to maximize resilience of species and maintain ecosystem processes (Bell et al. 2013a, b), which will become increasingly difficult within degraded environments.

The foremost strategy to enhance adaptive capacity of fisheries stocks is to maximize stock size, and thereby potentially restrict exploitation to levels below those that are otherwise considered sustainable. Further constraints on fisheries exploitation may however, lead to increasing shortfalls in food supply, especially among Pacific Island nations where there is considerable reliance on coral reef fisheries and food demand is ever increasing with rapid population growth (Bell et al. 2013a, b), as well as undermining the viability of commercial fisheries. Spatially explicit adaptations are also necessary where impacts and outcomes differ among locations. On the GBR, for example, it is expected that risks, opportunities and adaptation responses will be different in the northern GBR (north of Cairns, ~17° S) compared to the south (south of Mackay, > 21° S), which needs to be considered in the formulation of any revised fisheries management arrangements.

2.2.4 Reducing resource dependence

The extent to which fisheries sectors or stakeholders are exposed to climate change is largely dictated by the climate vulnerability of specific targeted species or stocks, as described for the previous three elements (**Figure 2.2**; Marshall et al. 2013). Sensitivity of fisheries, fishery sectors or specific stakeholders to climate change is largely influenced by their specific reliance on certain fisheries stocks. The fisheries targeting coral grouper are typically multi-species, whereby there are several similar and often closely related species that are caught and retained using essentially the same gear types. Under current fishery management arrangements on the GBR, commercial fishers predominantly target *P. leopardus* as they offer the greatest economic return, but fishers will also retain *P. maculatus* and *P. laevis*. The predominance of *P. leopardus* in harvests also largely reflects their numerical dominance in much of the area (offshore reefs) where commercial fishers are operating (Newman et al. 1997). If however, other *Plectropomus* or Serranidae species are more resilient to changing environmental conditions (noting again that virtually all the experimental studies conducted to date have focused on *P. leopardus*), then increased take of these alternative species may reduce sensitivity of reef-based fisheries to climate change. Reducing resource dependence is not simply a matter of supplementing declining harvests of species that are highly sensitive to climate change with increased harvests of more resilient species (Metcalf et al. 2015). On the GBR for example, many commercial fishers explicitly target fishes for the live food fish trade (Welch et al. 2008), where market demand and logistical constraints impose significant constraints on both the species and size range of fishes considered acceptable. On top of issues of specialized markets, fishers will often develop a sense of identity around the harvesting of particular species. Faced with the prospect that they are no longer able to continue fishing as they normally do, fishers not only lose a means of earning an income, they may lose an important part of their self-identity (Marshall et al. 2007). Commercial fishers within the GBR region are also reluctant to change where they live and work, are inflexible with alternate employment, have a lifestyle approach to their occupation, and have invested a significant time and effort in developing their ecological and biological knowledge relevant to particular fisheries and unwilling to lose it (Tobin et al. 2014). Reducing sensitivity in these cases is difficult, and efforts to enhance adaptive capacity would likely be better investments.

Resource dependency might be reduced in other ways, such as through decreasing the level of specialization upon single species or fishery type. Specialization often occurs as the result of capital being secured in vessels and equipment (Nord 1994). This increases the efficiency of the operation, decreases the price of the product and maintains social status (Poggie & Gersuny 1974). However, fishers that target only a few species, or are reliant on a single resource, are severely constrained in their ability to be flexible and adapt to changes in resource availability (Bailey & Pomeroy 1996). Specialist behaviour is typical of regions in which resources are predictable, and the system is regarded as ‘‘stable’’. However, a ‘‘stable’’ system is not necessarily resilient in the face of changes such as climate change. In the short term, financial assistance packages may help to reduce resource dependency, but educational opportunities and income diversification to achieve the same outcome are more likely to be sustainable.

2.2.5 Maximizing socio-economic adaptive capacity

Adaptive capacity in the socio-economic part of the vulnerability model is the ability that people have to mobilise natural, physical, financial, human, social resources for useful adaptation responses (Marshall et al. 2013). It describes the ability to respond to challenges through learning, managing risk and impacts, developing new knowledge and devising effective approaches. A key ingredient is the flexibility to experiment and adopt novel solutions (Berkes & Seixas 2005). It is enhanced by the existence of institutions and networks that learn and store knowledge and experience and create flexibility in problem solving without compromising the ability to cope and adapt to future change (Olsson et al. 2006). Adaptive capacity can significantly offset the impacts of climate change and minimize vulnerability, but there are limits (Barnett et al. 2015). Developing the appropriate skills at the scale of both commercial fishers and fisheries managers to anticipate and meet the challenges of the future are key to increasing adaptive capacity. Decision makers, including politicians need to be appropriately informed of the negative consequences of poor adaptive capacity and empowered to make difficult decisions. In addition to the factors that can help reduce resource dependency (e.g., access to credit or financial assistance), commercial fishers will benefit from increased awareness of risk, prior experiences of change, engagement in governance, and trust (Cinner et al. 2015). At a broader level, factors such as political stability, regulatory quality, rules of law, and voice and accountability become important (Allison et al. 2009). Deploying such assets effectively will involve fostering creativity and innovation for identifying solutions and adaptation options; testing and experimenting with options; recognising and responding to effective feedback mechanisms; employing adaptive management approaches; possessing flexibility; being able to reorganize given novel information; managing risk and, having necessary resources at hand (Cinner et al. 2015; Marshall & Stokes 2014). Strategies will need to be developed that pertain to the local situation, and are tested, refined and shared (Leith et al. 2013). A constructive approach would be to plan for a range of plausible climate scenarios and take the path of ''least regrets'' (Webb et al. 2013), although that may only result in incremental adaptation and could over the longer-term even prevent transformative adaptation.

2.3 Conclusions

Preliminary research into the sensitivities of coral grouper (predominantly, *P. leopardus*) to projected changes in ocean temperatures, seawater chemistry and degradation of coral reef habitats suggest that sustained and ongoing climate change will likely have negative demographic consequences for coral grouper, and thereby undermine the viability and sustainability of coral reef fisheries, in at least some locations. Most notably, recent experimental studies suggest that coral grouper cannot withstand temperatures > 30 °C (Pratchett et al. 2013; Sun et al. 2015) even for fishes sourced from locations where they are already exposed to > 30 °C during summer months. If so, sustained and ongoing increases in ocean temperatures are likely to impose increasing constraints on performance and fitness of coral grouper in equatorial and low latitude regions, especially during warmer months. Even if it is possible that fishes can buffer effects of temporary (seasonal) exposure to supra-optimal temperatures (e.g., by moving to greater depths, and/or reducing activity) resulting changes in distribution and behaviour will directly impact upon catchability of coral grouper. Ongoing climate change (especially projected warming) is, therefore, likely to cause sustained declines in harvests of coral grouper across many equatorial locations (which currently sustain the world's largest *Plectropomus* fisheries), due to declines in catchability, if not availability.

Given the apparent sensitivities of coral grouper to sustained and ongoing environmental change, it is prudent to consider potential adaptation options that will reduce vulnerability of reef-based fisheries to declining availability or catchability of these species. In reality, adaptation to environmental change is often autonomous and/or responsive to unanticipated shocks (e.g., Adger et al. 2005), but this does not negate the need for concerted efforts to manage and plan for adaptation to environmental change (Creighton et al. 2015). Several previous adaptation planning exercises have revealed ''no regrets'' or ''win–win'' adaptation options, that will have short-term benefits for relevant stakeholders regardless of the longer-term or eventual impacts of climate change (Bell et al. 2013a, b). In these instances, there is no impediment to immediate implementation of these adaptation options. In the case of reef-based fisheries, however, it is anticipated that at least some of the potential adaption options will have disproportionate benefits for one or more fisheries sectors, and/or represent a significant impost on certain stakeholders. If for example, fishers in the northern GBR move southwards to more favourable fishing environments, even if only during the summer months, this will directly impact on fishers already established in southern waters.

A critical issue facing fisheries management worldwide is the need to balance diverse and often conflicting biological, economic, social and/or political objectives (Hilborn 2007; Jennings et al. 2016). Similarly, adaptive planning needs to consider the wide range of objectives held by different stakeholder groups, including commercial, recreational and charter fishing sectors, indigenous fishers, fisheries managers and scientists, non-government organisations, as well as other reef users (e.g., tourism operators). Potential adaption options that might reduce species exposure, reduce sensitivity, or increase adaptive capacity, and reduce fisher resource dependency and increase adaptive capacity in reef fisheries, do exist. The next step is to engage the stakeholders through a participatory approach, and evaluate the potential implementation pathways, and the associated costs, benefits, risks and impacts of adaptations on specific sectors or stakeholders.

Chapter 3 A large predatory reef fish moderates feeding and activity patterns in response to temperature variation

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3.1 Introduction

Sustained and ongoing ocean warming (IPCC 2014), is exposing marine organisms to unprecedented and ever-increasing temperatures. For ectothermic animals, such as most fishes, temperature fundamentally affects individual metabolic rates, which influence growth, reproduction, movement, behaviour, and consequently fitness and survival (Brown et al. 2004; Donelson et al. 2010; Payne et al. 2016). Whole animal performance in fishes is often measured in terms of the scope for aerobic metabolism (i.e. metabolic scope), which is the difference between resting and maximum aerobic metabolic rate. Metabolic scope is underpinned by the uptake, transport, and delivery of oxygen throughout an organism's tissue (Portner 2001; Portner 2009). For fishes, metabolic capacity (i.e. the maximum rate of aerobic metabolic rate) is ultimately constrained by oxygen delivery (Ficke et al. 2007) and at high temperatures, this limitation is often compounded by declines in oxygen availability and increases in oxygen demand (Portner 2010). Temperature-driven changes in oxygen budgets can compromise the respiratory energy available for fitness and performance (Neuheimer et al. 2011) and at higher temperatures individuals may be forced to adopt energy-saving strategies, which may lead to reductions in energetically demanding activities, such as swimming and foraging (Johansen et al. 2014; Johansen et al. 2015).

The vulnerability of populations and species to changing environmental regimes will be determined by their ability to adapt (Edmunds et al. 2010), acclimate or acclimatize (Donelson et al. 2014). Adaptation is genetic change that occurs across generations or among populations in relation to environmental change (Angilletta et al. 2002). Acclimation refers to short-term changes in behaviour, physiology, or both, that arise in an individual in response to a single environmental variable (Guderley 1990). Acclimatisation is a behavioural or physiological response to multiple environmental variables, typically recorded under field conditions (Guderley 1990). Short-term temperature fluctuations can directly influence an organism's capacity for acclimation or acclimatisation through the impact on physiological reaction rates.

Individuals may alter behavioural patterns and fitness if they cannot compensate physiologically for temperature variability (Angilletta et al. 2002). For example, it has been shown that fishes change their foraging behaviour and increase food intake and time spent feeding to compensate for increases in metabolic demands at higher temperatures (Nowicki et al. 2012; Como et al. 2014; Johansen et al. 2015). Fishes may also increase their time spent resting to regulate increasing metabolic costs at higher temperatures (Hein & Keirsted 2012; Johansen et al. 2014). Crucially, any modifications to behaviour may come at a cost to the individual and consequently, the ecosystem. For example, movement and activity are directly related to prey encounter and predator evasion (Dell et al. 2014), and alterations may therefore limit food intake and increase susceptibility to predation (Ohlund et al. 2015). Alternatively, an increase in food intake may cause potential distortion to food webs, as intake may not be met by greater production at lower trophic levels (Johansen et al. 2015). Changes in behavioural patterns, therefore, may not only affect individual fitness, but also species interactions, population dynamics, community structure and ultimately biodiversity and ecosystem function (Gilman et al. 2010; Candolin & Wong 2012).

Tropical species are considered to be more vulnerable to increasing temperatures than temperate counterparts because they generally experience limited diurnal and seasonal variation in temperature (Janzen 1967). In shallow coral reef ecosystems, for example, seasonal ocean temperatures may only differ by up to 5-6 °C annually (AIMS 2015), although localised variations may be greater, particularly for shallow, lagoonal waters. In contrast, temperate waters regularly vary up to 10 °C annually (AIMS 2015). This means that for coral reef species, small increases in ambient water temperature may subject individuals and populations to unprecedented temperatures, leading to a greater energetic cost of maintaining standard metabolic activity (Portner 2008; Feary et al. 2014). Experimental studies conducted on a variety of coral reef fishes demonstrate that some species are already living close to their thermal optima (Gardiner et al. 2010; Rummer et al. 2014) and are likely to be negatively impacted by projected increases in ocean temperatures (Munday et al. 2012). Ultimately, however, species response to ocean warming depends on how populations are affected by increasing temperature throughout their geographic range.

Studies of latitudinally distinct populations of fishes have revealed differences in thermal tolerances suggestive of local acclimation (Edmunds et al. 2010; Rummer et al. 2014). Notably, low-latitude populations subjected to higher summertime temperatures can tolerate higher temperatures and often perform best at higher temperatures, compared to conspecifics from higher latitudes (Edmunds et al. 2010; Rummer et al. 2014). For common coral trout (*Plectropomus leopardus*), however, there does not appear to be any difference in thermal sensitivity (i.e. sensitivity of metabolic scope to variations in water temperatures), between fish sampled from latitudinally distinct locations where average maximum summer temperatures differ by up to3 °C (Pratchett et al. 2013). Individuals from both populations exhibited declines in physiological (i.e. aerobic scope) and behavioural (i.e. movement patterns) measures of performance when subjected to water temperatures > 30 °C (Van Herwerden et al. 2009; Johansen et al. 2014). These findings suggest that populations of *P. leopardus* on the Great Barrier Reef (GBR) are poorly acclimated to local temperature regimes, possibly due to high levels of genetic exchange at the scale of the entire GBR (Van Herwerden et al. 2009). As such, sustained increases in ocean temperatures may already compromise body condition and physiological performance of *P. leopardus* at low latitudes (where summertime temperatures already exceed 30 °C) (Pratchett et al. 2016). Conversely, larger, more mobile fishes, such as *P. leopardus* may have greater capacity to moderate exposure to high summertime temperatures by exploiting natural gradients (e.g., with depth) in environmental conditions, thereby concealing any capacity for local acclimation. *P. leopardus* may also compensate for temperature-induced increases in metabolism by increasing their food intake (Johansen et al. 2015), provided food is not limited by prey availability or abundance (Arditi & Ginzburg 1989), and through a reduction in swimming activity (Johansen et al. 2014).

Experimental studies may overestimate the impacts of elevated temperatures on wild populations of fishes because they generally expose individuals to rapid and pronounced changes in temperature. Exposure to acute temperature variations has the potential to undermine an individual's capacity for acclimation (Donelson et al. 2010; Johansen et al. 2014; Rummer et al. 2014) and may also fail to account for the ability of fishes to behaviourally moderate exposure to increasing temperatures (Biro et al. 2007; Goyer et al. 2014). *In situ* behavioural plasticity may also be limited by the abiotic environment, such as water quality and topography. Consequently, there is a need to understand whether large-bodied, coral reef predators can buffer exposure to environmental changes through modification of their behaviour. Coral trout, *Plectropomus* spp., are commercially and economically important fisheries species on the GBR. They are relatively mobile with predicted home ranges of 0.5 km^2 (Matley et al. 2015), and are an ecologically important mesopredator, with a primarily generalist, piscivorous diet (Frisch et al. 2016).

This study explores seasonal variation in the *in-situ* foraging behaviour and activity of *P. leopardus* at two latitudinally distinct locations on Australia's GBR separated by approximately 1,200 km. Specifically, this study quantifies spatial and temporal differences in strike rates (and predation success) as well as resting patterns for *P. leopardus.* We expected that *P. leopardus* would exhibit seasonal and latitudinal differences in foraging behaviour and resting patterns corresponding to differences in water temperature. Specifically, fish were expected to respond to moderate increases in temperature by increasing foraging activity and food intake. Increases in foraging activity would, however, require greater energy investment and movement, further increasing metabolic demands. Therefore, it is likely that there will be a tradeoff between food intake and conservation of energy that will constrain the extent to which individuals can increase foraging activity at high temperatures. It is also expected that responses of *P. leopardus* to increasing temperature will be strongly size-dependent, whereby larger-bodied individuals are more thermally sensitive than smaller individuals (Messmer et al. 2017). We predict, therefore, that larger-bodied individuals will exhibit more pronounced seasonal and latitudinal differences in foraging behaviour and activity, though it is also likely that larger fishes feed less often (Johansen et al. 2015).

3.2 Materials and Methods

In situ observations of foraging behaviour and activity were undertaken for *P. leopardus* in summer (February – March 2016) and winter (July – August 2016) at Lizard Island (14°40'S, 145°27'E) in the northern GBR (low-latitude population) and Heron Island (23°29'S, 151°52E) in the southern GBR (high-latitude population). Observations were carried out between 0700 – 1730 hrs to test for diurnal variation in foraging and activity. Ambient temperatures varied both seasonally and latitudinally, ranging from 20 °C (during winter at Heron Island) up to 32 °C (during summer at Lizard Island) (**Figure 3.2**).

3.2.1 Study locations

This study was conducted across two latitudinally distinct locations on Australia's Great Barrier Reef (GBR); Lizard Island (14°40'S, 145°27'E) in the northern GBR (low-latitude population) and Heron Island (23°29'S, 151°52E) in the southern GBR (high-latitude population) (see **Figure 3.1**). The locations are separated by approximately 1200 km and 10 degrees of latitude. Sampling was conducted in summer (February - March 2016) and winter (July – August 2016) to encompass maximum and minimum annual temperatures experienced by each population of *P. leopardus* (**Figure 3.2**). Each location was situated within a 'Marine Park' zone on the GBR implying a negligible impact of fishing pressure at both locations. Specific sampling was conducted within comparable coral reef habitat at each location, and all surveys were conducted along the shallow reef crest and adjacent slope areas < 10 m. Temperature was recorded from dive computers which are accurate to 0.01 degrees.

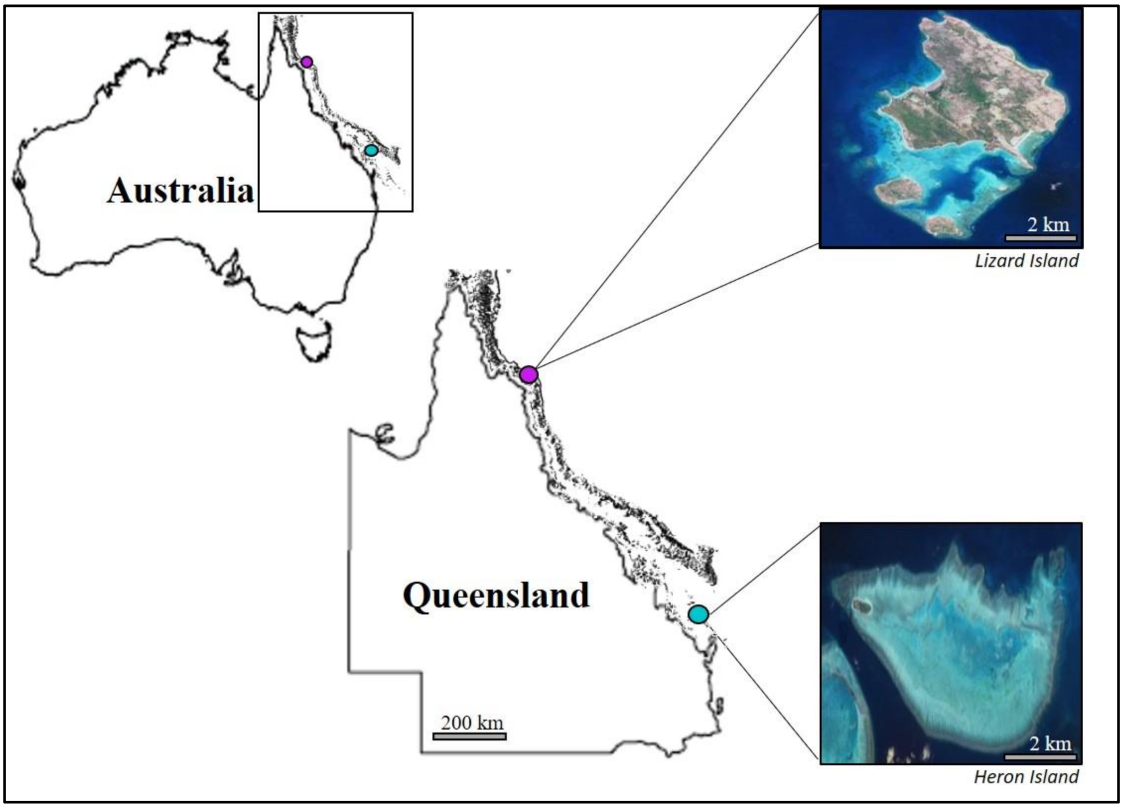

Figure 3.1: Map of each study location in relation to Australia, Queensland, and the Great Barrier Reef. The northern (low-latitude) site was Lizard Island (purple circle) and the southern site was Heron Island (blue circle).

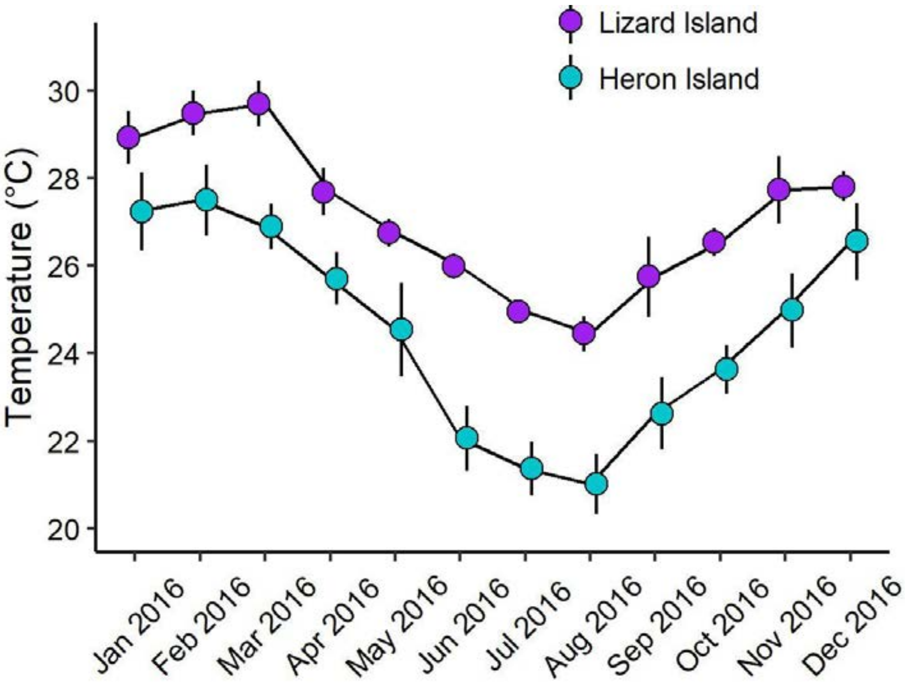

Figure 3.2: Average monthly temperature (± SD) for Lizard Island (purple circles) and Heron Island (blue circles) throughout the study period between January 2016 – December 2016.

3.2.2 Foraging behaviour

A strike was determined if a *P. leopardus* was observed making an uncharacteristically fast, i.e. > 1 body length per second, purposeful burst towards a prey item (Allan et al. 2015). To test for diurnal variation in feeding behaviour of *P. leopardus*, field observations were undertaken within three distinct time periods: morning (0700-1100 hrs, n= 290), midday (1101 – 1400 hrs, n=187) and afternoon (1401 – 1730 hrs, n=118). These time periods were chosen based on similar studies investigating diurnal variation of strike rates in coral reef fish (Feeney et al. 2014). Sites at each location were chosen haphazardly and 2-3 sites were sampled each day. At each site, 3-5 trout observations were made by 2 observers giving an average of 10-12 trout observations per day. For each sampling period between 125 and 164 individual fish observations were made, giving a total of 595 observations. To reduce observer bias, each observer was given a 60-minute guided observation by the chief investigator to ensure all observers were observing and recording *P. leopardus* behaviour accurately. Upon entering the water, the first *P. leopardus* found was chosen and observed for up to 60 minutes at a distance > 5 m. These parameters were chosen based on previous observational studies of coral trout (pers. comm. A. Vail). This distance caused no apparent distress to the fish, and fish appeared to behave normally (as per Sweatman 1984). An individual trout was followed on snorkel or SCUBA at a random depth between 1 - 10 m and the number of strikes were recorded. Where possible, observations were conducted for 60 minutes, but even where fish were lost or observations aborted, data was retained as long as the observation period was > 15 minutes. This allowed for strike rate (number of strikes per unit of time observed) to be measured as a proxy for foraging behaviour. Other variables measured were: water temperature (°C), total length of the individual (nearest 5cm), type of habitat over which the individual was hunting, the distance over which the individual moved to hunt prey (m), depth of the hunt (m), visibility (m), the outcome of the predation event. Predation success was recorded by all observers. However, to reduce observer bias, only the primary observer's data were used in statistical analysis. In addition to foraging behaviour, the amount of time an individual spent stationary or inactive throughout the observation was recorded, enabling a measurement of the proportion of time spent resting.

3.2.3 Statistical Analysis

Spatial and temporal variation in strike rates of *P. leopardus* were examined using a negative binomial generalized linear model from the package '*MASS*' in R Statistical Software™. Variance inflation factors (VIF) were calculated to determine the multicollinearity of the variables location, temperature and season. Season and temperature had VIF > 5 so season was included in all models, and the data were centered around temperature to reduce collinearity. Other predictors tested were; body size, location, method of observation (i.e. snorkel or scuba), and time of day on strike rates. Negative binomial regression is useful for modelling count variables, with a moderate proportion of zeros, particularly if they are overdispersed (Logan 2010). Coefficients from the negative binomial correlation of coefficients table (z-values) were converted to p-values. A generalized additive model (GAM) was then used to separately analyse the relationship between temperature and body size as continuous predictors against strike rate, which was expected to be non-linear. GAM's allow for non-linear relationships between the response variable and explanatory variables and for the combination of both linear and complex additive responses by adding a smoothing curve through the data. The *'mgcv'* package was used because it allows for cross-validation, a process that automatically determines the optimal amount of smoothing. To determine the differences in success rates between seasons, locations and size class a generalized linear model with quasibinomial distribution (chosen when the response variable is a proportion) and a logit link function was used and the best fit model was selected according to Akaike Information Criteria (AIC). Differences in strike rate with habitat were analysed by a one-way ANOVA comparing strike rates between 3 habitat groups; reef matrix, water column, and other. To analyse *P. leopardus* resting behaviour, a GAM tested the proportion of time spent resting in relation to temperature and body size which were treated as continuous variables. All analyses were performed in the R-Environment (R Core Team, 2011).

3.3 Results

3.3.1 Foraging behaviour

A total of 486 feeding strikes were recorded across the 595 individuals observed during this study, with an average of 0.96 strikes per hour. The majority of strikes took place over coral reef habitat, compared with the water column ($p = 0.003$) or ‘other’ habitat (i.e. sand or algal covered rocks) ($p < 0.001$). Strike rates varied considerably with season, but not location (**Table 3.1**), averaging 1.14 (± 0.002 SE) per hour in summer versus 0.78 (± 0.001 SE) per hour in winter. Seasonal differences in strike rates were most pronounced at the high-latitude location, because of the very low winter average strike rate, 0.6 (± 0.001 SE) per hour, compared with 1.2 (± 0.002 SE) per hour for the low-latitude population (**Figure 3.3a, Table 3.2**). Strike rates were highest at 30 °C and every 3 °C increase in temperature between 21 °C and 30 °C led to a 1.4 – fold increase in strike rate. Beyond 30 °C, strike rates declined, indicating the potential for a negative response of foraging activity to increases in temperature, and this effect was consistent across all body sizes (**Figure 3.3b**, **Table 3.2**).

Table 3.1: Coefficient table of the negative binomial generalised linear model showing the influence of season, trout length, location, and time on strike rate for *P. leopardus* once the data have been centred for temperature. *P*-values (in bold) have been converted from z-scores such that significance is measured as $p < 0.05$.

Strike rate	**Estimate**	**St. Error**	**p-value**
Intercept	-2.805	0.269	**< 0.001**
Season	-0.836	0.392	**0.033**
Body Size (TL)	-0.027	0.006	**< 0.001**
Location	0.070	0.120	0.563
Time of day	-0.008	0.0315	0.796
Season x Body Size (TL)	0.011	0.016	0.284

Table 3.2: Generalised additive modelling; Intercept, effective degrees of freedom (*edf*) and significance (*p*-value) of temperature and body size (TL) on strike rates for *P. leopardus*. Coefficient of determination (R^2), the explained deviance, and the AIC values are given for each model. Significant terms are in bold.

	Strike Rate				**Activity**			
	Model 1: TEMP + BODY SIZE		**Model 2: TEMP * BODY SIZE**		**Model 1: TEMP + BODY SIZE**		**Model 2: TEMP * BODY SIZE**	
	Estimate	p-value	Estimate	p-value	Estimate	p-value	Estimate	p-value
Intercept	-4.18	<0.001	-4.17	<0.001	0.47	<0.001	0.47	<0.001
SE	0.06		0.06		0.01		0.01	
	edf	p-value	*edf*	p-value	*edf*	p-value	*edf*	p-value
Temperature	2.68	0.0065	2.44	0.01	6.89	<0.001	7.08	<0.001
Body Size	1.69	<0.001	1.80	< 0.001	3.32	<0.001	1.00	<0.001
Temp x Body Size	-	-	1.00	0.176	-	-	4.73	0.005
R^2	0.07		0.07		0.14		0.15	
Deviance explained	8.69%		8.85%		15.5%		17.2%	
n	595		595		595		595	
AIC	1451.4		1452.2		20.54		14.64	

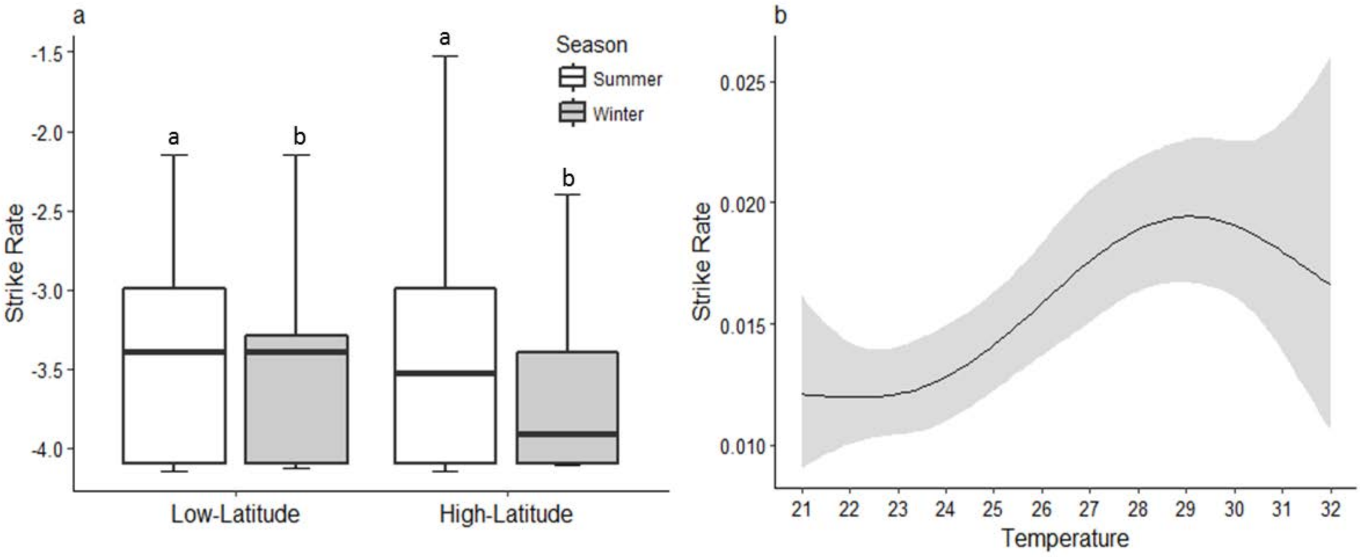

Figure 3.3: a) Box plots showing log transformed average strike rates of *P. leopardus* from low-latitude and high-latitude locations during summer (white) and winter (grey). Data (n=595) are for each individual observation. The whiskers are extended to extreme values. Boxplots with the same letter are not significantly different. b) The modelled values of the relationship between strike rate and increasing temperature from a Generalised Additive Model with a smoothing function. The shaded region around the curve represents a 95% confidence interval.

Although smaller individuals displayed substantially higher strike rates than larger individuals (**Figure 3.4**), it appears that the foraging frequency of *P. leopardus* is equally compromised by higher temperature regardless of body size (**Table 3.2**).

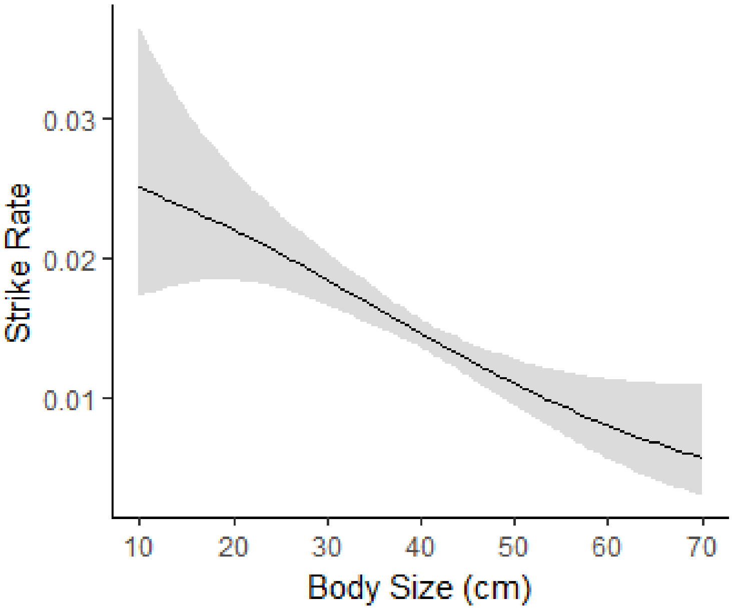

Figure 3.4: The modelled values of a Generalised Additive Model with a smoothing function demonstrating the negative relationship between strike rate and body size of *P. leopardus* (measured in total length to the nearest 5cm). The shaded region around the curve represents a 95% confidence interval.

Similarly, the proportion of successful strikes of *P. leopardus* (recorded by one observer to reduce observer bias), did not vary with body size, suggesting all size classes were equally likely to make a successful strike. Further, success rates did not differ between seasons ($p = 0.87$), but were significantly different between locations ($p = 0.02$), a pattern driven by consistently higher success rates in summer and winter of the low-latitude population (**Figure 3.5**). Overall, of the 278 strikes made by individual *P. leopardus*, 47 were considered successful, giving an overall strike success rate of 17%. In general, the low-latitude population had a higher proportion of successful strikes than the high-latitude population. For the low-latitude population in the summer 26% of strikes were successful, compared with 16% success in the winter. For the high-latitude population strike success was 21% in summer and 10% in winter.

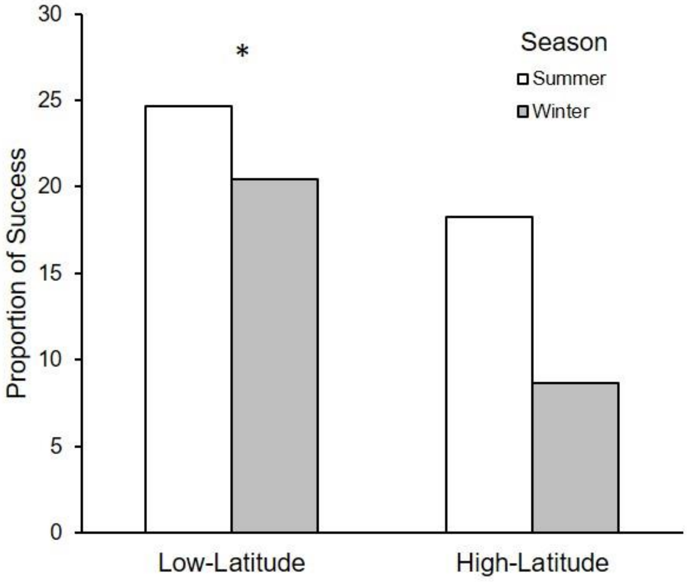

Figure 3.5: Proportion of successful strikes made by individual *P. leopardus* between low-latitude and high-latitude locations in summer (white) and winter (grey). Of the 278 strikes recorded, 47 strikes were considered successful, giving an overall strike success rate of 17%. Significant differences are marked with an *, based on a chi-squared test of proportional data.

There was no significant diurnal variation in feeding behaviour of *P. leopardus* (**Figure 3.6**), however, the majority of strikes were observed in the morning (0700 – 1100) and fewest strikes at midday at both locations (1100 – 1400) (**Table 3.1**).

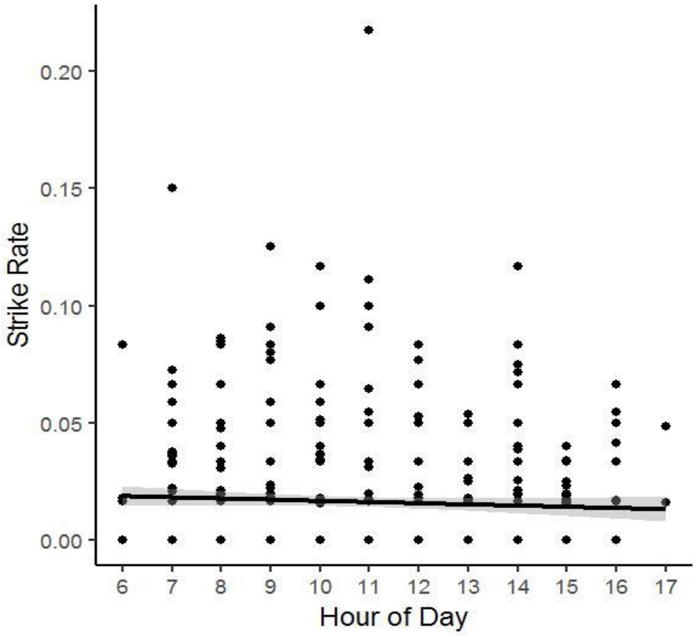

Figure 3.6: The modelled trend (bold line) with residuals from a generalised linear model illustrating the non-significant relationship between strike rates (± 95% CI, grey ribbon) with hour of day.

3.3.2 Resting patterns

The proportion of time an individual spent stationary increased with increasing temperature (**Figure 3.7a**, **Table 3.2**). On average, the time spent resting increased from 25.3 ± 0.03 % at 21 °C to 90.6 ±0.05 % at 32 °C. This behaviour was most pronounced for the low-latitude population in the summer, who spent approximately 62% of their time inactive, compared with 47% in the winter. Whilst the high-latitude population in summer spent 43% of their time inactive compared with 37% in winter (**Figure 3.7b**).

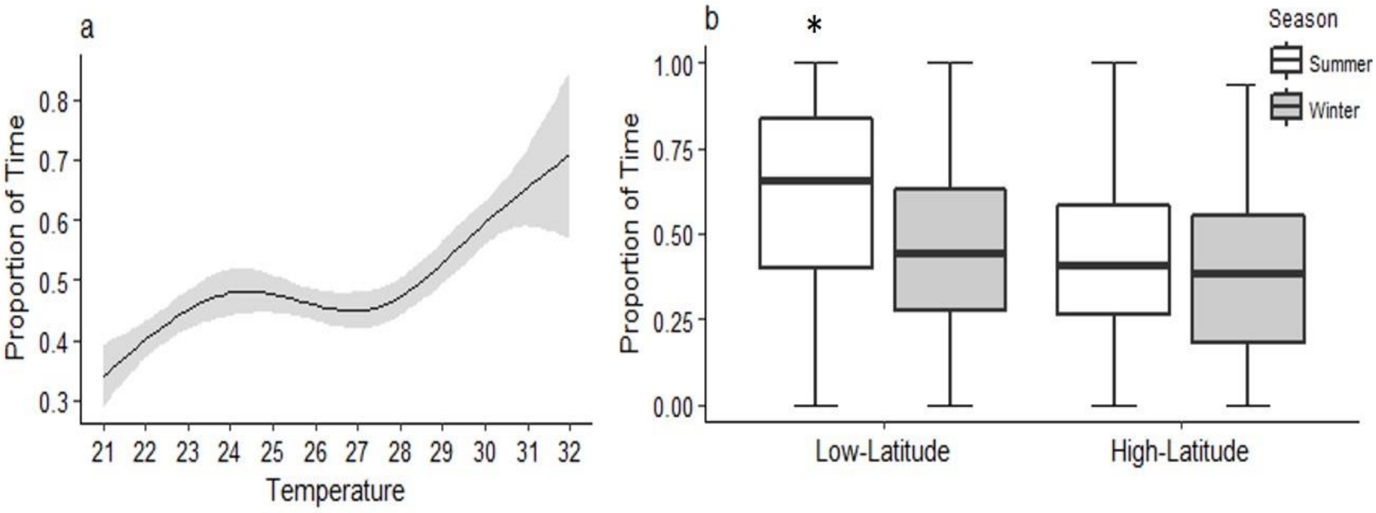

Figure 3.7: a) Modelled values of a generalised additive model with a smoothing function displaying the relationship between the proportion of time *P. leopardus* spent stationary with increasing temperature. The shaded region around the curve represents a 95% confidence interval. b) Box plots demonstrating the median proportion of time low-latitude and high-latitude populations of *P. leopardus* spent stationary during summer (white) and winter (grey). Data (n=595) are for each individual observation. The whiskers are extended to extreme values. Linear models were used to test for differences in time spent stationary between location and season. Significant differences are marked with an *.

The proportion of time spent inactive was further influenced by body size (**Table 3.2**), with medium (35 – 45 cm, TL) and larger (> 50 cm, TL) individuals spending a greater proportion of time inactive than smaller individuals (< 35 cm, TL). The impact of water temperature on activity patterns was greatest for larger individuals (**Figure 3.8**).

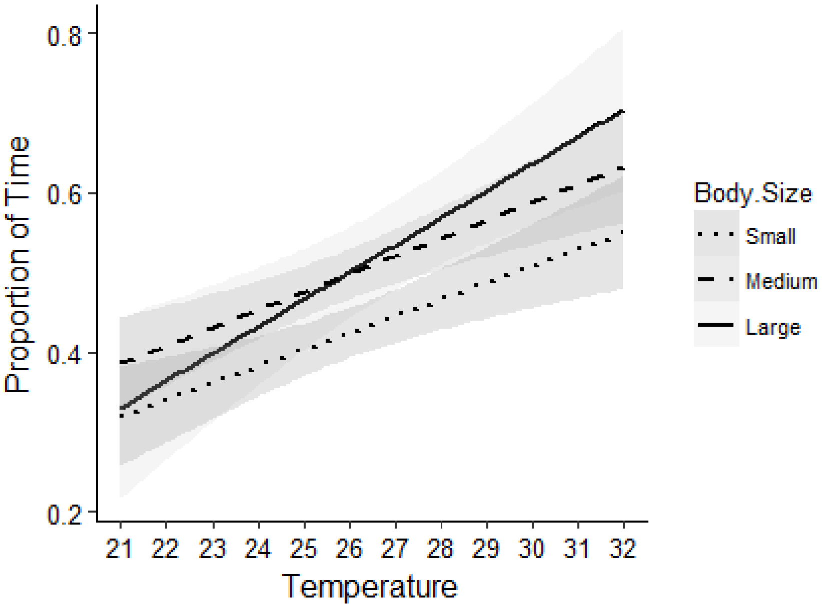

Figure 3.8: Modelled values (bold lines) depicting the interaction between the proportion of time spent resting at increasing temperatures with body size (measured as total length to the nearest 5cm) of *P. leopardus* with small (10 – 30 cm, TL, dotted line), medium sized (35 – 45 cm, TL, dashed line) large body size (> 50 cm, TL, bold line). The shaded region around each line curve represents the 95% confidence interval.

3.4 Discussion

The effects of global warming on large predatory and commercially important coral reef fishes is critically important given the potential of increasing ocean temperatures to compromise fitness and performance of coral reef fisheries species (Pratchett et al. 2013). Given that fishes are ectotherms, increases in ocean temperature will lead to inevitable increases in baseline metabolic rates (Portner 2009) which may be partially compensated for through increased food intake. In this study, we show that strike rates by *P. leopardus* increased from 0.015 strikes per hour at 21 °C up to 0.023 strikes per hour at 30 °C equating to a 1.4 – fold increase in strike rate for every 3 °C temperature rise. This increase is consistent with the expected 1.2 – 1.4 fold increase in energy need associated with a 3 °C temperature rise identified in previous studies (Evans & Claiborne 2006; Johansen et al. 2015). However, strike rates did not increase beyond 30 °C, suggesting that *P. leopardus* may not be able to compensate for temperature induced increases in metabolic rate beyond this threshold, which closely corresponds with the mean maximum temperature to which fishes are already exposed from low-latitude regions on the GBR (AIMS 2015). Constraints on food intake with projected increases in ambient temperatures from low-latitude regions (IPCC 2013) may be further compounded by limited food availability (Pratchett et al. 2008) as well as constraints on energetic expenditure and movement.

Increased food intake by *P. leopardus* will almost certainly require increased foraging activity and energy expenditure. Conversely, temperature-induced increases in basic metabolic demands will reduce energy available for movement and feeding. Our data show that the proportion of time that *P. leopardus* are inactive increases with increasing temperature from 21 to 32 °C. Already, fish from low-latitude regions of the GBR spend a significant proportion of their time completely inactive when exposed to high temperatures during summer. These behavioural changes may have implications for the fitness of individuals and populations under warming oceans (Cheung et al. 2010). For example, any reductions in swimming and activity patterns are likely to not only influence foraging efficiency and the ability to capture prey (Blake 2004; Johansen & Jones 2011), but may also increase the risk of predation, and potentially influence species demography through changes to longer term activity patterns and space use (Andrew & Mapstone 1987; Jetz et al. 2004). Importantly, *P. leopardus* are known to undertake periodic spawning related movements (Samoilys 1997). Decreased mobility and a greater need to conserve energy may reduce overall space use (Scott et al. 2019; Chapter 5) and consequently reproductive capacity (Bunt & Kingsford 2014). This may influence population replenishment and the viability of fisheries stocks at lower latitudes, especially given larger-bodied individuals are likely to be disproportionately impacted (Messmer et al. 2016) if they are unable to seek thermal refuge.

In this study, larger individuals (> 50 cm, TL) exhibited a more pronounced response to increasing temperatures and spent proportionally more time inactive than their smaller conspecifics. Larger individuals are considered to be more thermally sensitive than smaller individuals due to size-dependent oxygen limitation to tissues and organs meaning that temperature-dependent aerobic limits are experienced earlier by larger individuals (Portner & Knust 2007; Daufresne et al. 2009). This pattern has been demonstrated for *P. leopardus* under laboratory conditions (Messmer et al. 2016) and is consistent with slower swimming speeds and longer resting times found in large *P. leopardus* at elevated temperature (Johansen et al. 2014). I found that smaller individuals had consistently higher strike rates than larger individuals, this pattern was not consistent for increasing body size with temperature, meaning the responses of individuals to increasing temperature were consistent across all size classes for strike rates. Johansen et al. (2015) demonstrated a similar response, that relative to body size, small and medium sized *P. leopardus* consumed more food than larger individuals. Smaller individuals typically have higher mass-specific metabolic rates than larger individuals, which may be associated with higher growth rates and elevated activity levels (Baudron et al. 2014; Hou et al. 2008). However, increased foraging efficiency of smaller individuals may come at a cost, as energy expenditure and risk of predation may increase with foraging frequency (Lönnstedt et al. 2012).

The differential effects of temperature on body size may modify predator-prey interactions by impacting predation success or prey escape response (Allan et al. 2015; Ohlund et al. 2015). If increasing temperatures have a disproportionate impact on larger bodied individuals or species (Baudron et al. 2014; Messmer et al. 2016), the capacity of predators to exert the necessary energy may be increasingly constrained while prey may be better able to escape predators (Ohlund et al. 2015). Alternatively, prey may exhibit a decreased escape response at elevated temperature, increasing capture success by predators (Allan et al. 2015). Differences in the temperature dependence of predator-prey interactions may lead to changes in trophodynamics, community structure and function.

Whilst individual plasticity in foraging behaviour is likely to compensate for increased metabolic demands in *P. leopardus* exposed to moderate increases in temperature, it appears that individuals may be adversely affected by temperatures > 30 °C (Clark et al. 2017). Notably, *P. leopardus* from low-latitude regions of the GBR are already exposed to summer temperatures > 30 °C (AIMS 2015). Slight declines in strike rates and foraging efficiency at higher temperatures, along with reduced movement and activity patterns, tends to suggest thermal constraints on these behaviours for *P. leopardus* with projected increases in ocean temperatures due to climate change. Low-latitude populations of *P. leopardus* may be particularly vulnerable to increases in ocean temperature. Unless fish are able to seek thermally favourable habitats by moving to cooler, deeper waters, or shift their distribution to higher latitudes, physiological limits (Pratchett et al. 2013; Messmer et al. 2016) and food availability (Johansen et al. 2015) may constrain their capacity to endure longer-term and more severe ocean warming (Munoz et al. 2015).

This study has shown that a predatory coral reef fish species modifies its foraging behaviour and activity *in situ* in response to seasonal and latitudinal differences in temperature. The combination of our data and previous laboratory studies of *P. leopardus* (Pratchett et al. 2013; Johansen et al. 2014; Johansen et al. 2015; Messmer et al. 2016) provide a holistic overview of the temperature dependence of behavioural and physiological performance of a coral reef predator. *P. leopardus* play a significant role in structuring fish communities and maintaining ecosystem health (Frisch et al. 2014; Rizzari et al. 2015). Any alterations to their feeding patterns and activity may therefore have significant implications for trophic food webs and community dynamics . If *P. leopardus* are unable to adapt, acclimate, or acclimatize to increasing temperatures (behaviourally or physiologically) it is likely that the fitness of *P. leopardus* populations on the GBR, especially in the low-latitude region, may be undermined by continued increases in ocean temperature. Further research is needed to investigate how these individual level effects scale up to affect whole communities and over spatial and temporal time scales relevant to the pace of climate change.

Chapter 4 Latitudinal and seasonal variation in space use by a large, predatory reef fish, *Plectropomus leopardus*

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4.1 Introduction

Space use and movement patterns are a fundamental component of an animals' ecology (Börger et al. 2008). For the most part (except during migrations), animals tend to move within a relatively confined area, often referred to as their home range (Welsh & Bellwood 2014). The size and extent of an animals' home range has significant consequences for individual distributions and densities (McNab 1963; Makarieva et al. 2005), intra- and interspecific interactions (Harestad & Bunnel 1979), as well as community structure and ecosystem function (Buchmann et al. 2011; Nash et al. 2015). The size (and location) of an animal's home range is largely influenced by biotic determinants, including resource availability (Owen-Smith et al. 2010), predation risk (Ohlund et al. 2015), and reproductive opportunities (Samoilys 1997b). However, space use and movement patterns are also influenced by abiotic drivers or environmental conditions (Nakamura et al. 2013). Notably, temperature has a fundamental influence on the metabolism and physiology of all animals, leading to changes in both the capacity and need for movement (Niehaus et al. 2012). In the extreme, temperature is the primary driver of large-scale redistributions of species, reflected in seasonal migrations (Hasler et al. 2012) and climate-induced range shifts (Nagelkerken & Munday 2016). For animals that do not relocate in response to changing environmental conditions, temperature may lead to changes in space use, as well as the rate and extent of localised movement.

For most ectothermic animals, including fishes, metabolic rates and processes are strongly influenced by temperature, which in turn, influences movement (Johansen et al. 2014), food intake (Scott et al. 2017), reproduction (Donelson et al. 2014), growth (Zarco-Perello et al. 2012), and survival (Payne et al. 2016). The relationship between temperature and performance (i.e. the ability for an individual to undertake basic activities) is however, non-linear, whereby exposure to unusually high temperatures may have significant adverse effects on fitness and survival (e.g., Peck et al. 2012; Messmer et al. 2016). Tropical species are particularly sensitive to positive thermal anomalies compared with temperate species (Tewksbury et al. 2008; Sunday et al. 2011) because they are normally subject to much more stable thermal regimes. However, animals from low-latitudes can generally tolerate higher absolute temperatures compared with conspecifics from higher-latitudes (Edmunds et al. 2010; Rummer et al. 2014), reflecting local adaptation to specific thermal regimes.

Ocean warming, caused by anthropogenic climate change, is projected to cause major declines in the biodiversity and productivity of shallow tropical ocean systems (Cheung et al. 2010), with concomitant effects on fisheries production (Bell et al. 2013). Cheung et al. (2010) predicted large-scale redistribution of global catch potential with a decline of 40% in the tropics by 2055, and an increase of 30-70% at high latitudes over the same period. These projected shifts of global fisheries potential are largely attributed to poleward shifts in the distribution of fisheries target species (Cheung et al. 2010), where species are presumed to move in direct accordance with geographical shifts in preferred climate envelopes (Habary et al.2017). In reality however, some coral reef fishes will be constrained in their latitudinal distributions by the availability of dietary and habitat resources (e.g., Feary et al. 2014), and will therefore, become increasingly exposed to potentially adverse environmental conditions.

Plectropomus leopardus, is one of the most important tropical fisheries species, supporting recreational and commercial fisheries throughout the Indo-West Pacific (Frisch et al. 2016). Experimental studies, revealing constraints on feeding, movement and survival of *P. leopardus* when exposed to end of century environmental conditions (Johansen et al. 2014; Messmer et al. 2016) have led to justifiable concerns that ongoing climate change may undermine the viability and sustainability of fisheries targeting this species (Pratchett et al. 2016). *Plectropomus leopardus* is also an ecologically important mesopredator capable of influencing the structure of coral reef communities (Emslie et al. 2015; Rizzari et al. 2015; Frisch et al. 2016). The ecological function of mesopredators has been linked to their home-ranging behaviour (Nash et al. 2015) such that any changes in space use may influence population dynamics by altering species interactions (Pennock et al. 2018), trophodynamics (Boaden & Kingsford 2015) and spawning or reproductively motivated movements (Zeller 1998; Bunt & Kingsford 2014).

This study explores seasonal and latitudinal variation in home range extent and movement patterns for *P. leopardus* on Australia's Great Barrier Reef. Space use was measured using acoustic telemetry within small, high-density arrays, which necessarily constrains the number of sampling locations. Because of this, this study provides detailed information on patterns of movement and space use for individual fishes throughout the course of an entire year. Previous telemetry studies (e.g., Matley et al. 2015) confirm that these fishes exhibit high site fidelity and have relatively small (< 0.5 km^2) home ranges. Conversely, active tracking has shown that *P. leopardus* can move up to 5 – 15 km d^{-1} within localised areas (Zeller 1998; Bunt & Kingsford 2014) especially during spawning. However, there is not currently any information on the changes in localised patterns of movement or space use with respect to seasonal or latitudinal differences in temperature. Experimental studies have suggested that *P. leopardus* are less mobile when exposed to elevated temperatures (Johansen et al. 2014). We expect therefore, that *P. leopardus* would exhibit latitudinal differences in home range corresponding to differences in water temperature. Specifically, the low-latitude population would have smaller home ranges compared with the high-latitude population as a behavioural response to conserving energy at higher temperatures. To test these questions, we used passive acoustic telemetry from two small-scale arrays of approximately 0.5 km^2 in area to determine the fine scale home ranges of *P. leopardus* over an annual period.

4.2 Materials and Methods

4.2.1 Study sites

This study was conducted on Australia's Great Barrier Reef (GBR) at Opal Reef (16°14'20.77"S, 145°52'12.59"E) in the northern GBR (low-latitude location) and Heron Island Reef (23°25'57.86"S, 151°55'57.65"E) in the southern GBR (high-latitude location). The two study locations are separated by approximately 1,000 km and seven degrees of latitude. At each location, the specific study sites were situated within no-take marine park zones and were chosen because they comprised similar fringing and patch reefs along depth gradients extending to ~25 m along the reef slope. Daily temperatures were recorded on four temperatures loggers (Vemco Minilog-II-T) attached to the receivers at approximately 7 m depth (**Figure 4.1**).

To investigate fine-scale habitat use and activity patterns of *P. leopardus*, acoustic tracking was undertaken at both sites using Vemco VR2W acoustic receivers (Vemco Ltd., Halifax, Canada). Similar arrays were established by deploying 18 VR2W receivers at Opal Reef (low-latitude location) and 14 VR2W receivers at Heron Island (high-latitude location) (**Figure 4.1**). Receivers were deployed in an identical arrangement, ~ 2 m above the substrate (reef or sand) using a chain and float mooring and set approximately 100 m apart in three lines. Inner receivers were positioned close to the reef crest (5 - 12 m depth) and outer receivers were positioned in sandy habitats (18 - 21 m depth). The middle row was also positioned in sand (10 - 18 m depth) at both locations. Both arrays occupied an area of approximately 0.5 km^2, encompassing the reef crest and out c. 100 m from the reef slope to deeper sandy habitat (**Figure 4.1**). Data from receivers were downloaded every six months in May and September 2016.

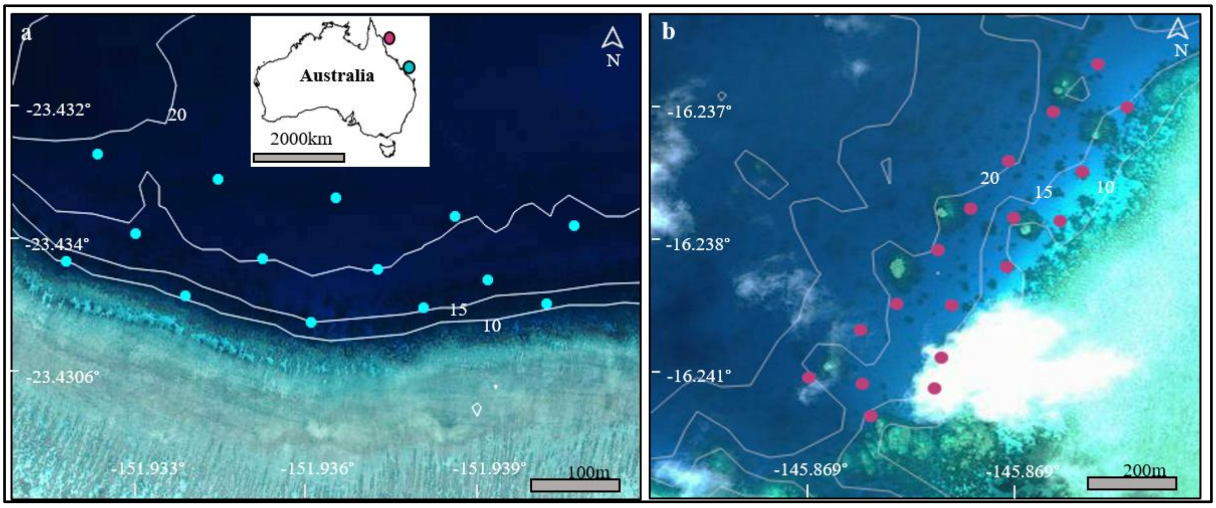

Figure 4.1: Map of each location in relation to Australia and the Great Barrier Reef. The blue circles indicate the array at Heron Island Reef (a), Australia (high-latitude location) and the red circles indicate the array at Opal Reef (b) (low-latitude location). Each circle represents an acoustic receiver which were deployed in three lines parallel to the reef crest across a depth gradient from those closest to the reef (inner) to middle and outer receivers on the deeper reef slope. Contour lines indicate underwater bathymetry with depth (m).

4.2.2 Range testing

Tracking at both sites was done within the context of a high-resolution positioning array (Vemco Positioning System; VPS). The maximum distance between adjacent receivers was ~ 120m based on receiver detection range estimates of 50 – 120 m, resulting in ~90% acoustic coverage of the area. Detailed verification of acoustic receiver detection ranges was undertaken at Heron Island by Currey et al. (2014). Range testing was conducted via six permanent sentinel tags deployed at varying distances from receivers (70 to 270 m) in representative substrates and monitored during the course of the study (Currey et al. 2014). Receivers detected transmitters within 270 m and to 25 m in depth (depth of the substrate away from the reef crest). As part of establishing a VPS tracking array the capacity of sync and sentinel tags to be detected on a minimum of 3 adjacent receivers is conducted. All receiver position is predicated on this continuous detection and as such the detection range at each site was factored into the study design and testing prior to the release of any transmitters. Therefore, the functionality of the two networks was as identical as possible with receiver deployments configured to optimise continuous detection within the arrays.

4.2.3 Fish collection and tagging

Within each array, 19 adult (> 35 cm) *P. leopardus* were caught using barbless hooks. Once caught, individual fish were immediately placed in an anesthetic bath of Aqui-S® (~ 30 L) diluted with seawater (1:10000). Prior to removing the hook, the swim bladder was vented to avoid barotrauma, if necessary. Once individuals lost equilibrium, they were measured (fork length to the nearest millimeter), fitted with an external dart tag (PDS; Hallprint®) in the dorsal musculature for identification and moved to a fresh seawater bath. A V13A-P transmitter (13 mm x 42 mm) was surgically implanted into the abdominal cavity via a small incision (20 – 30 mm) in the ventral body wall. Each transmitter had a pressure (depth) and accelerometer (acceleration) sensor and was programmed to randomly emit a unique coded signal (69 kHz) every 60-120 seconds, with an expected battery life of 349 days. The incision was closed by simple, uninterrupted stitches using absorbable sutures. Fish were released after fork length and dart tag number were recorded. Generally, the entire procedure took < 10 minutes and a total of 38 *P. leopardus* were caught, processed and tagged. At Opal Reef, the detection period ranged from October 1st 2015 – September 16th 2016, totalling 351 days. At any time within that period 12 – 18 fish were detected within the array at all times (**Table 4.1**). At Heron Island, the detection period ranged from September 9th 2015 – August 31st 2016, a total of 357 days. At any time within that period 14 – 18 individuals were detected within the array at all times. The average number of detections of an individual fish throughout the detection period was approximately 17,000.

4.2.4 Statistical Analysis

All data were analysed in the R environment version '3.3.0' (R Core Team, 2013). Detections during the first 48 hours of the study were removed to exclude any effect of handling on fish behaviour. Data were also examined to eliminate any spurious detections e.g., data that represented erratic movements (i.e. consistent with fish consumed by a predator) or lacked vertical movement aside from a consistent tidal signature (i.e., perished individual, Matley et al. 2015). Because home range values are constrained by the design of each array, a weighting factor was added to each model to incorporate differences in receiver arrangement, coverage and array specific error variance when comparing responses across the two study sites.

4.2.4.1 Presence

Trends relating to the presence of *P. leopardus* within the arrays were investigated using mean monthly residency indices (Matley et al. 2015). Monthly residency indices were calculated by dividing the number of days an individual was detected at any receiver by the number of days in each month. This measure estimated an individual's tendency to remain within the array or close to receivers.

4.2.4.2 Horizontal space use

The position of individual fish was estimated at 15-minute intervals using a mean position algorithm to provide centers of activity (COA) (Heupel et al. 2002). Time intervals were based on previous studies for other larger-bodied reef fishes (Currey et al. 2015). Horizontal space use patterns (i.e., two-dimensional bird's eye view perspective) of *P. leopardus* within and between locations were evaluated based on COAs using 50% (core use area) and 95% (home range extent) kernel utilization distributions (KUDs) and calculated using the *adehabitat* package (Calenge 2006). A smoothing parameter (h) of 100 was used to estimate KUDs based on visual trials testing different values (e.g., values that were too high overlapped too much with reef flat areas; values that were too low underestimated receiver detection ranges). KUDs were calculated at weekly, monthly and all data (pooled detections for each individual) levels to obtain space use estimates across different temporal resolutions. To normalise the data, the response variable (50% KUD or 95% KUD) was log-transformed prior to analysis. Differences in 50% and 95%KUDs between location and time period (weekly, monthly, all) were tested using a repeated measures ANOVA (RM-ANOVA) from the package *lme4* (Pinheiro et al. 2013), with temperature and fish size as predictor variables and individual fish as a random factor. Repeated measures models are used to account for the autocorrelation inherent in observations of individuals through time (Logan 2010). Irrespective of fish size (**Table 4.1**), there were large differences in 95% KUD and different temperature ranges at each location, so locations were analysed separately. To determine whether space use differed seasonally or between months a planned comparison compared 50% and 95% KUDs from austral summer (i.e., December, January, February) with the rest of the months of the year and compared austral summer to austral winter (i.e., June, July, August); both locations were analysed separately. In addition, cumulative activity spaces demonstrating periods of expansion of activity space into previously unused areas within the arrays were calculated by iteratively adding each new week's position data then recalculating a KUD for both weekly 50% and 95% KUDs.

To determine whether the location of weekly activity spaces changed through time, the proportion of overlap between 50% and 95% KUDs from week to week was calculated using the *ks* package (Duong 2007). Overlap was represented as the proportion of the previous week's value. The proportion of overlap between weeks determined how site attached an individual was to areas within the arrays (Heupel & Simpfendorfer 2015). For example, an overlap value of 1 signifies complete overlap in weekly activity space compared with the previous week, i.e. the individual used the same amount and location of space compared with the previous week. Whereas an overlap value of 0 signifies complete difference in weekly activity space compared with the previous week, i.e. the individual moved into a new space compared with the previous week. KUD overlap and cumulative models included the factors week, fork length, and temperature and the interaction between week and temperature. KUD overlap was measured as a proportion, so data were tested for normality and arcsine-transformed prior to analysis, and cumulative area data were tested for normality and log-transformed prior to analysis. RM-ANOVA with individual treated as a random factor were once again used to analyse metrics of space use. Results from monthly and weekly KUDs were similar, so results from weekly KUDs only were used for most analyses because of higher resolution of the data and to reduce repetition. Additional R packages used for analysis include *chron* (James & Hornik 2013), *maptools* (Bivand & Lewin-Koh 2013), and *PBSmapping* (Schnute et al. 2013).

4.3 Results

Tagged *P. leopardus* ranged in size from 336 mm – 565 mm (mean fork length ± SE = 431± 13, n= 18) at Opal Reef, and from 401 mm – 634 mm (mean fork length ± SE = 543± 13.20, n= 18) at Heron Island (**Table 4.1**). Although size structure differed between locations, the size of fish had no significant effect on core space use (50%KUD) or home range extent (95%KUD) (**Table 4.1**, **Figure 4.2**).

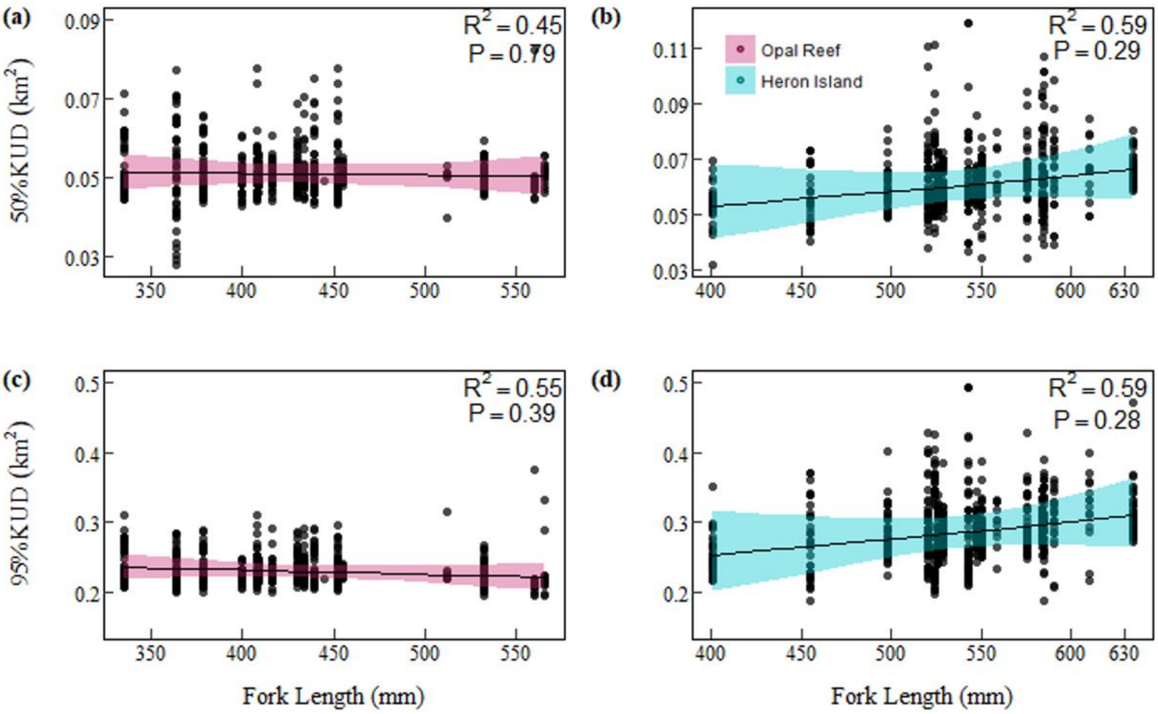

Figure 4.2: Modelled trends (bold line) of the relationship between fork length and 50% (top-row, a & b) and 95% (bottom row- c & d) KUDs for *P. leopardus* at Opal Reef (red) and Heron Island (blue). Coloured ribbons around each trend represent 95% confidence intervals for the response value at each location.

Mean monthly residency indices varied between 0.7 – 1 (mean ± SE = 0.87 ± 0.01, n= 36) indicating that *P. leopardus* were within range of the receivers approximately 87% of the detection period (**Table 4.1**). Nonetheless, we excluded two individuals (one from each site) that were detected < 25 times and/or < 15 days throughout the study from subsequent analyses.

Table 4.1 Sampling summary of *P. leopardus* from Opal Reef (low-latitude location) and Heron Island (high-latitude location) including; exact dates and number of days for each detection period, the number (n) of fish detected within each array at any one time, mean (±SE) size range (mm), average number of days detected for individual fish (numbers in brackets is the range of days), and monthly residence index (±SE).

Location	Detection Period (days)	n	Size Range (±SE) (mm)	Days detected (±SD)	Monthly Residency Indice (±SE)
Opal Reef	Oct 1st 2015 – Sep 16th 2016 351 days	12-18	431.12 ± 13.06 (336 – 565)	288.18 ± 25.34 (32 – 354)	0.91 ± 0.004
Heron Island	Sep 9th 2015 – Aug 31st 2016 357 days	14-18	543.35 ± 13.20 (401 – 634)	287.39 ± 22.31 (102 – 354)	0.89 ± 0.004

4.3.1 Home range extent (95% KUD) and core space use (50% KUD)

Plectropomus leopardus exhibited marked differences in home range extent (95% KUD) between locations; at Heron Island the average overall 95% KUD was 0.32 km^2, compared to 0.23 km^2 at Opal Reef (**Table 4.2**, **Figure 4.3**). By comparison, there were very limited differences in core space use (50% KUD) between locations, which suggests that *P. leopardus* exhibit strong site fidelity (**Figure 4.3** & **Figure 4.4**, **Table 4.4**).

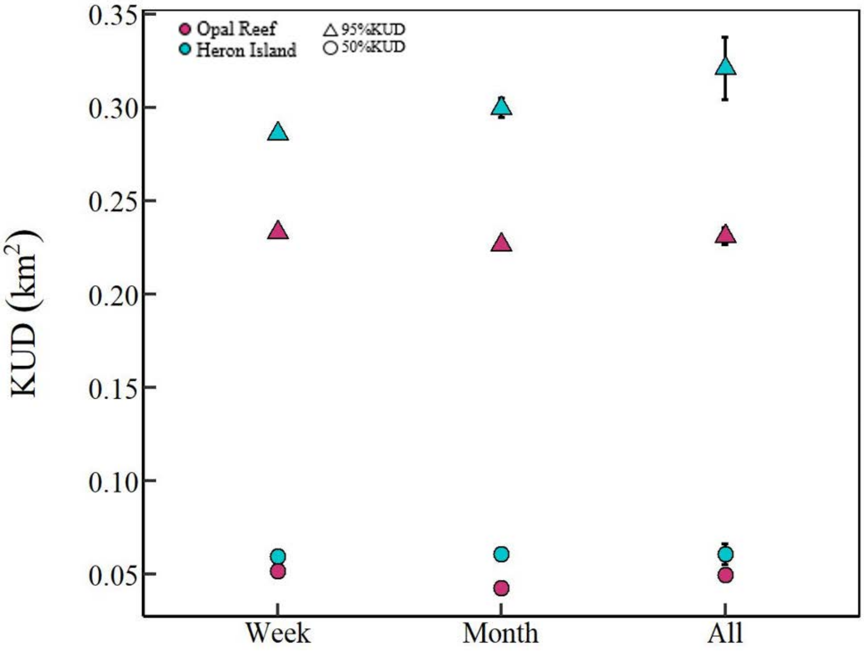

Figure 4.3: Mean (±SE) 50% (circles) and 95% (triangles) KUDs for weekly, monthly, and all detections pooled for each individual at Opal Reef (red) and Heron Island (blue) throughout the detection period.

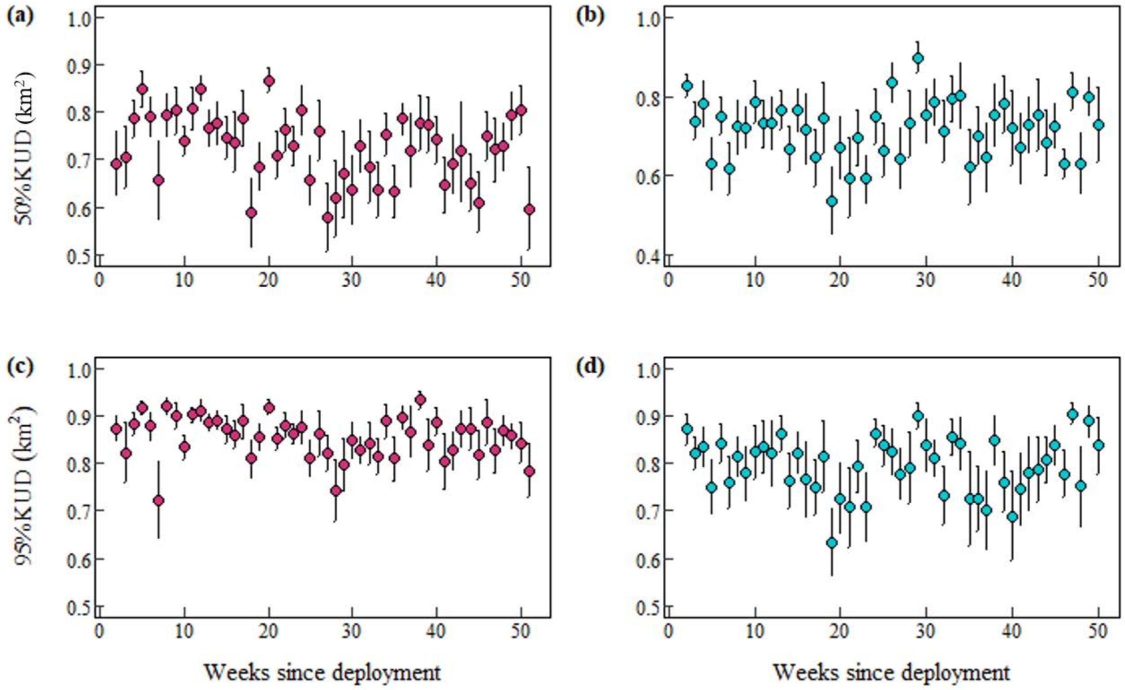

Figure 4.4: Mean (±SE) of the proportional differences in weekly overlap for 50% (top-row – a & b) and 95% KUDs (bottom-row – c & d) of *P.leopardus* from both locations; Opal Reef (red circles) Heron Island (blue circles). Weeks since deployment along the x-axis begin in October at Opal Reef and September at Heron Island.

Table 4.2: Mean ± SE core use (50%KUD) and home range extent (95%KUD) over temporal period (week, month, all) from each location

	Opal Reef (km^2)		Heron Island (km^2)	
	50%KUD ± (SE)	**95%KUD ± (SE)**	**50%KUD ± (SE)**	**95%KUD ± (SE)**
Weekly	0.05 ± 0.0002	0.37 ± 0.0009	0.06 ± 0.0005	0.28 ± 0.002
Monthly	0.04 ± 0.0008	0.23 ± 0.002	0.06 ± 0.0001	0.30 ± 0.005
All	0.05 ± 0.001	0.23 ± 0.004	0.06 ± 0.0005	0.32 ± 0.02

4.3.2 Seasonal differences in home range extent (95%KUD) and core space use (50%KUD)

To test for seasonal differences in core use (50% KUD) and home range extent (95% KUD) within locations, we compared 50% and 95% KUDs between austral summer and austral winter (**Table 4.3**) and then between austral summer and the rest of the months of the year. At Opal Reef, monthly home range extent (95% KUD) was significantly lower in summer compared with winter , and between summer and the rest of the months of the year, however core use areas (50% KUD) did not differ between summer and winter, or summer and the rest of the year (**Table 4.3**). In contrast, at Heron Island, there were no differences in home range extent (95% KUD) or core use areas (50% KUD) between summer and winter (**Table 4.3**) or between summer and the rest of the months of the year (**Table 4.3**). **Figure 4.5** shows the relationship of home range extent (95% KUD) corresponding to temporal variation in ambient temperature at both locations, highlighting that 95% KUD increased and decreased inversely with temperature. This relationship was particularly pronounced at Opal Reef, where 95%KUD ranges contracted considerably between October 2015 – April 2016, and increased from May 2016, corresponding with decreasing temporal variation in temperature (**Figure 4.5**). Although the smallest 95%KUD was recorded at Heron Island during the summer,individuals from Heron Island exhibited much higher variability in monthly space use compared with individuals from Opal Reef potentially masking any temperature-dependent patterns related to space use at this location.

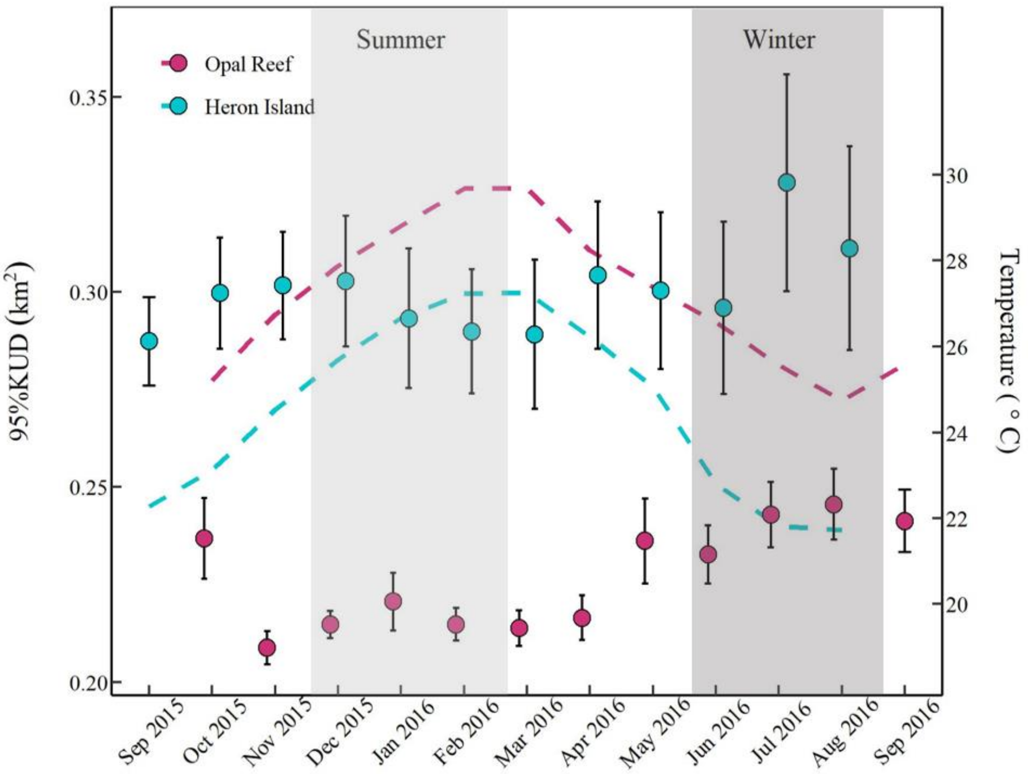

Figure 4.5: Mean (±SE) monthly 95% KUDs for Opal Reef (red) and Heron Island (blue) populations. Shaded regions represent summer (light-grey) and winter (dark-grey); dashed line colours represent the average monthly temperatures at each location. Annual maximum water temperatures over the course of the study differed by approximately 2.5 °C, ranging from 19.9 °C – 27.4 °C at Heron Island (mean ± SE = 24.5 °C ± 0.005), and 23.1 °C – 30.1 °C at Opal Reef (mean ± SE = 27.4 °C ± 0.003).

Table 4.3: Planned comparisons of monthly and seasonal variation in activity space for core use (50% KUD) and home range extent (95% KUD) between locations

Location	Response	Contrast	Test stat	SE	*P*-value
Opal Reef	**50% KUD**	Summer v Winter	-0.002	0.04	0.96
		Summer v Rest of year	-0.05	0.05	0.33
	95% KUD	Summer v Winter	-0.02	0.009	0.02
		Summer v Rest of year	-0.03	0.01	0.001
Heron Island	**50% KUD**	Summer v Winter	-0.04	0.04	0.29
		Summer v Rest of year	-0.04	0.05	0.38
	95% KUD	Summer v Winter	< -0.001	0.05	0.98
		Summer v Rest of year	0.009	0.05	0.85

Table 4.4: Results of generalised linear mixed effects models for the relationship between temporal space use (e.g., weekly, monthly, and all activity space use) between locations and overall 50% KUD and 95% KUD activity space in relation to temperature and fork length.

	Response	Model	Estimate	SE	*t*-value	*P*-value
Temporal space use	**50% KUD**	Full model (R^2= 0.61, $F_{1,1784}$=315.74, AIC = -1321.53)				
		Intercept	-2.87	0.05	4.71	<0.0001
		Location (All)	-0.13	0.07	-1.74	0.09
		Month	0.05	0.039	1.33	0.18
		Week	0.07	0.38	1.97	0.05
	95% KUD	Full model (R^2= 0.72, $F_{1,1786}$=28.21, AIC = -2498.51)				
		Intercept	-1.19	0.038	-31.42	<0.0001
		Location (All)	-0.25	0.06	-5.35	<0.0001
		Month	-0.05	0.02	-2.29	0.02
		Week	-0.05	0.02	-2.46	0.01
Overall space use	**50% KUD**	Full model (R^2= 0.61, $F_{1,1394}$=11.11, AIC = -1530.80)				
		Intercept	-2.87	0.22	-13.43	<0.0001
		Location	0.12	0.067	1.78	0.08
		Temperature	-0.007	0.003	-2.75	0.006
		Fork Length	0.0003	0.0004	0.73	0.47
	95% KUD	Full model (R^2= 0.69, F_{11394}=27.95, AIC = -2445.99)				
		Intercept	-1.19	0.20	-6.03	<0.0001
		Location	0.17	0.06	2.78	0.009
		Temperature	-0.01	0.002	-4.57	<0.0001
		Fork Length	0.0002	0.0003	0.48	0.64

Cumulative activity space analysis was used to define periods of expansion of activity space into previously unused areas within the arrays. Differences in the change in weekly cumulative 50% KUD and 95% KUD activity spaces were evident at both locations (**Table 4.5**, **Figure 4.6**). At Opal Reef, there were no substantial changes in 50% and 95% KUD cumulative activity spaces between weeks 1 to 26, indicating individuals remained within the same area throughout these weeks. This period is represented by austral spring to the end of summer (i.e., between November and March) when temperatures were increasing towards and reaching the annual maxima. After week 26, cumulative activity space expanded until week 41, signifying movement to new areas within the array. This period of increased space use coincided with decreasing ambient temperatures around the beginning of austral autumn in March. Between weeks 41 - 52 cumulative activity space reached an asymptote but remained larger relative to previous weeks indicating there was a greater extent of movement by individuals in winter whilst still maintaining high overlap at Opal Reef (**Figure 4.4a & c**). At Heron Island, there were no substantial differences in 50% or 95% KUD cumulative activity space throughout the year, suggesting that *P. leopardus* at Heron Island utilise similar areas of activity space year-round irrespective of season or temperature (**Table 4.5**, **Figure 4.4b & d**).

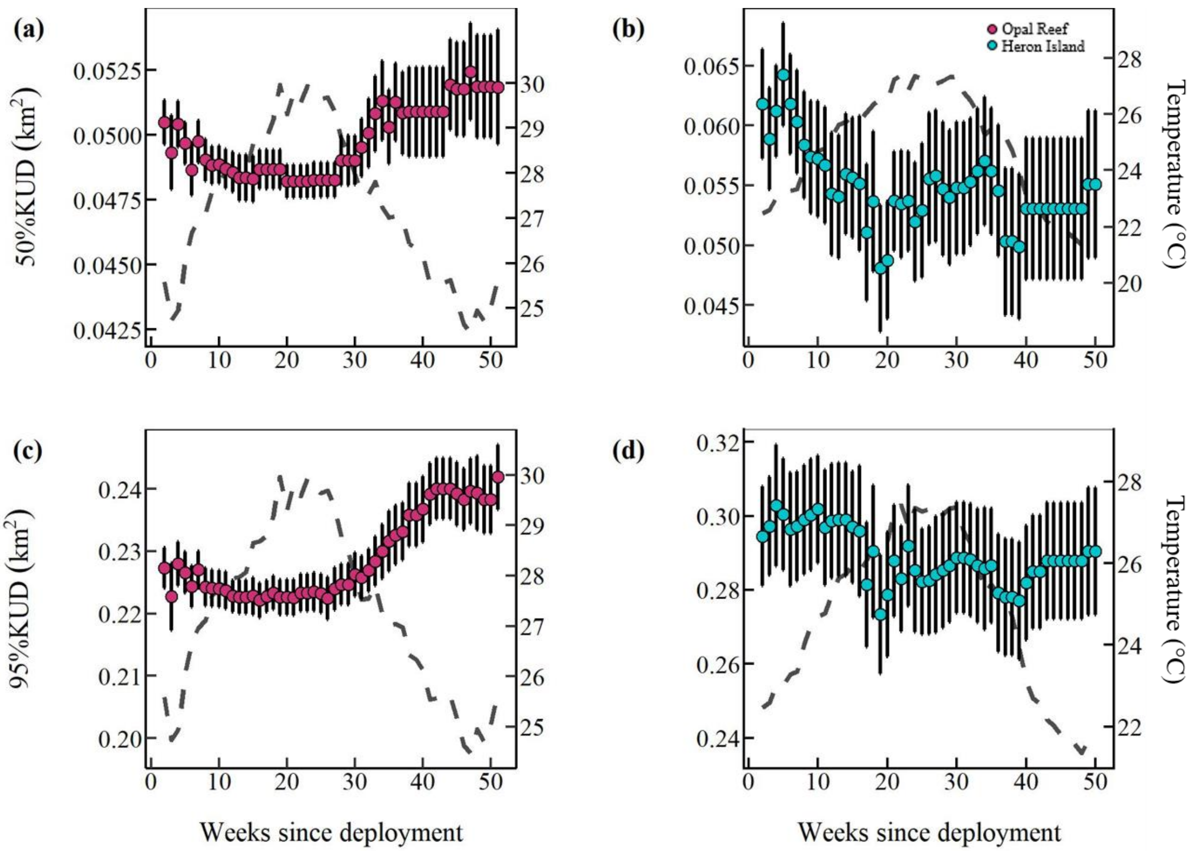

Figure 4.6: Mean (±SE) weekly cumulative activity space for 50% (top row – a & b) and 95% (bottom row – c & d) KUDs for *P. leopardus* from Opal Reef (red circles) and Heron Island (blue circles) with weeks since deployment along the x-axis. Weeks since deployment begin in October at Opal Reef and September at Heron Island. Dashed lines indicate average weekly temperatures at each location.

Table 4.5: Results of generalised linear mixed effects models for the relationship between activity space, cumulative area, and percentage overlap for core use (50% KUD) and home range extent (95% KUD) within and between locations. Only the best models are shown.

Opal Reef	**Response**	**Model**	**Estimate**	**SE**	***t*-value**	***P*-value**
Activity Space	**50% KUD**	Full model (R^2= 0.46, $F_{1,696}$=46.58, AIC = -1180.30)				
		Intercept	-2.29	0.18	-12.44	<0.0001
		Temperature	-0.02	0.003	-6.82	<0.0001
		Fork Length	<0.0001	<0.0001	-0.27	0.79
	95% KUD	Full model (R^2= 0.55, $F_{1,696}$=50.0, AIC = -1811.91)				
		Intercept	-0.77	0.16	-4.75	<0.0001
		Temperature	-0.02	0.003	-7.07	<0.0001
		Fork Length	-0.0002	<0.001	-0.88	0.39
Cumulative Area	**50% KUD**	Full model (R^2= 0.84, $F_{1,598}$=77.69, AIC = -1180.30)				
		Intercept	-2.82	0.21	-13.60	<0.0001
		Temperature	-0.01	0.001	-8.81	<0.0001
		Fork Length	<0.0001	<0.0001	0.53	0.60
	95% KUD	Full model (R^2= 0.95, $F_{1,598}$=315.74, AIC = -2706.15)				
		Intercept	-1.23	0.19	-6.65	<0.0001
		Temperature	-0.01	0.0006	-17.77	<0.0001
		Fork Length	<0.0001	<0.0001	0.16	0.87
Percentage Overlap	**50% KUD**	Full model (R^2= 0.36, $F_{1,598}$=368.13, AIC = 224.52)				
		Intercept	0.68	0.41	1.67	0.1
		Weeks	-0.004	0.007	-0.54	0.003
		Fork Length	0.0009	0.0008	1.15	0.27
	95% KUD	Full model (R^2= 0.59, $F_{1,598}$=353.23, P<0.001, AIC = -135.09)				
		Intercept	0.90	0.45	2.01	0.04
		Temperature	-0.006	0.005	-1.23	0.22
		Fork Length	0.0009	0.0009	0.93	0.37
Heron Island	**Response**	**Model**	**Estimate**	**SE**	***t*-value**	***P*-value**
Activity Space	**50% KUD**	Full model (R^2= 0.59, $F_{1,697}$=0.71, AIC = -504.27)				
		Intercept	-3.40	0.48	-7.09	<0.0001
		Temperature	0.004	0.004	0.86	0.39
		Fork Length	0.0009	0.0008	1.09	0.29
	95% KUD	Full model (R^2= 0.59, $F_{1,697}$=, AIC = -892.48)				
		Intercept	-1.53	0.43	-3.55	0.0004
		Temperature	-0.007	0.004	-1.54	0.12
		Fork Length	0.0008	0.0007	1.13	0.28
Cumulative Area	**50% KUD**	Full model (R^2= 0.80, $F_{1,635}$=2.42, AIC = -373.56)				
		Intercept	-3.16	0.78	-4.02	0.001
		Temperature	-0.01	0.003	-3.21	0.001
		Fork Length	0.001	0.001	0.72	0.48
	95% KUD	Full model (R^2= 0.88, $F_{1,635}$=3.53, AIC = -1548.15)				
		Intercept	-1.42	0.45	-3.12	0.002
		Temperature	-0.0003	0.001	-1.88	0.06
		Fork Length	0.0005	0.0008	0.64	0.53
Percentage Overlap	**50% KUD**	Full model (R^2= 0.40, $F_{1,635}$=315.74, AIC = 524.33)				
		Intercept	1.25	0.29	4.36	<0.0001
		Temperature	-0.001	0.007	-0.16	0.90
		Fork Length	-0.0002	0.0004	-0.74	0.47
	95% KUD	Full model (R^2= 0.02, $F_{1,635}$=315.74, AIC = 321.88)				
		Intercept	0.99	0.21	4.71	<0.0001
		Temperature	-0.004	0.006	-0.66	0.51
		Fork Length	0.0005	0.0002	2.01	0.06

4.3.3 Activity space in relation to spatial and temporal variation in temperature

Overall (i.e., with locations combined), our data suggest that increasing - temporal variation in ambient temperature across latitudes may be a potential driver for a decline in both 50% and 95% KUDs. Core space use (50% KUD) decreased from 0.13 km^2 at 21 °C to 0.02 km^2 at 29.9 °C, whilst home range extent (95% KUD) decreased from 0.49 km^2 at 21 °C to 0.19 km^2 at 29.9 °C (**Table 4.5**, **Figure 4.7**).

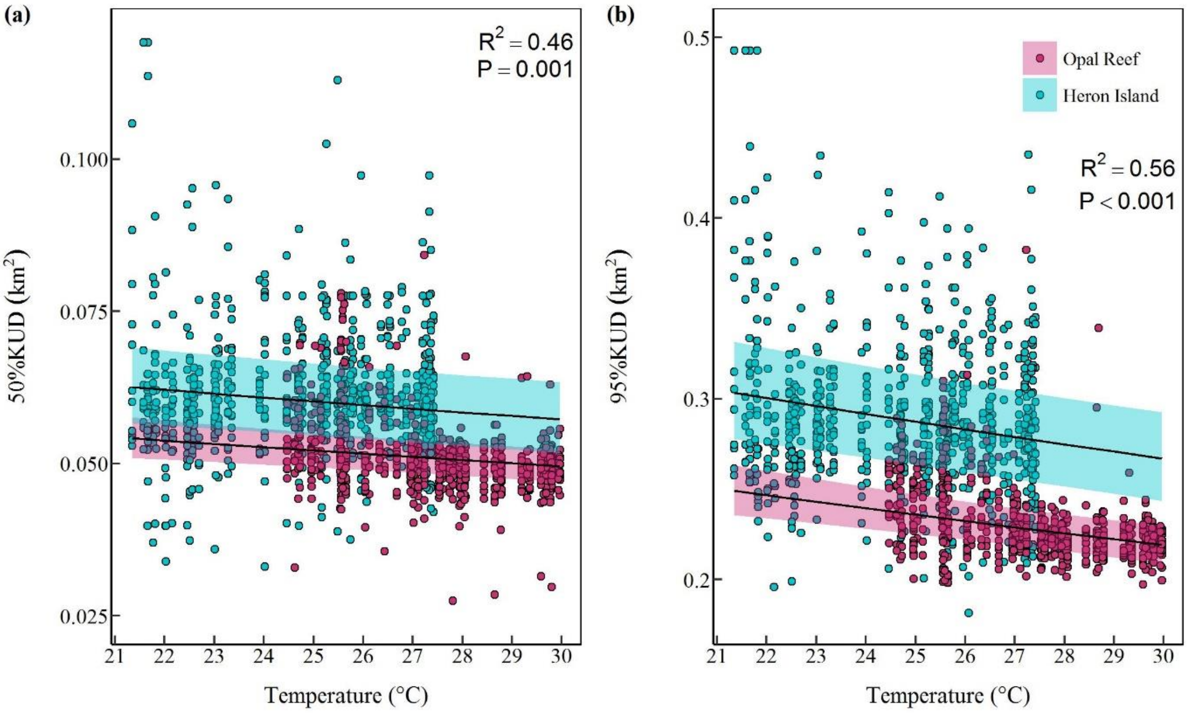

Figure 4.7: Modelled data depicting the influence of spatial and temporal variation in ambient temperature (bold lines) on a) core use (50% KUD) and b) home range extent (95% KUD) for Opal Reef (red) and Heron Island (blue). The coloured ribbons show 95% CI of the response variable at each location.

4.4 Discussion

This study showed that the home range extent (95% KUD) of *P. leopardus* on the Great Barrier Reef (GBR) varied spatially and temporally. Most notably, home ranges were > 25% larger at Heron Island in the southern GBR compared to Opal Reef in the northern GBR, irrespective of fish size. Home range extent of fish at Opal Reef was also significantly reduced during summer, when temperatures exceeded 27 °C. Observed differences in activity space and home range are consistent with seasonal and latitudinal differences in ocean temperature, reinforcing that elevated temperatures may constrain movement and activity for *P. leopardus*. Notably, experimental studies (e.g., Johansen et al. 2014; Johansen et al. 2015) have revealed that optimal temperatures for *P. leopardus* are ~ 27 °C, regardless of whether individuals were sampled from the northern or southern GBR. Aside from temperature, differences in home ranges (especially among locations) may be attributable to differences in habitat structure and prey availability, as well as other abiotic influences such as topography, currents and wave exposure. Without accounting for all these potentially confounding variables we cannot unequivocally attribute observed differences in space use patterns to temperature, though changes in temperature do have important, inexorable effects on the physiology and behaviour of fishes (Portner & Knust 2007; Pauly 2010). Metabolic performance and function of fishes is underpinned by the delivery of oxygen throughout an organism's gills and tissue (Portner & Knust 2007; Pauly 2010). Metabolic capacity is therefore ultimately constrained by oxygen delivery and at high temperatures, this limitation is often compounded by declines in oxygen availability and increases in oxygen demand (Portner & Knust 2007). For marine fishes therefore, increases in ocean temperature will lead to inevitable increases in baseline metabolic rates, which may be partially compensated for by increasing food intake or reducing movement and activity (Johansen et al. 2014; Johansen et al. 2015; Scott et al. 2017; **Chapter 3**).

Importantly, *P. leopardus* on the GBR have been shown to reduce movement and activity patterns in response to increasing temperatures (Johansen et al. 2014; Scott et al. 2017; **Chapter 3**) and this may account for apparent declines in home range extent with increasing spatial and temporal variation in ambient temperature recorded in this study. Reductions in space use and mobility will have major implications for individual fitness as well as population dynamics and ecosystem function (Cheung et al. 2010). Any decrease in activity patterns is likely to influence foraging efficiency and the ability to capture prey (Blake 2004; Johansen et al. 2014) and may influence species demography through changes to longer term activity patterns and space use (Andrew & Mapstone 1987; Jetz et al. 2004). Reduced space use and mobility may also modify predator-prey interactions (Ohlund et al. 2015). For example, if increasing temperatures disproportionately impact larger bodied individuals or species (Baudron et al. 2014; Messmer et al. 2016), prey species may be increasingly able to evade piscivores (Ohlund et al. 2015). Alternatively, prey may exhibit a decreased escape response at elevated temperatures, increasing capture success by predators (Allan et al. 2015). Alterations to these interactions may lead to changes in trophodynamics (Rizzari et al. 2015), dependent upon the regulation of prey populations (Hempson et al. 2017) and this has implications for community structure and function.

Variability in monthly space use for *P. leopardus* showed strong correspondence with location-specific temperature regimes. However, seasonal variation in space use for *P. leopardus* may also relate to gametogenesis and spawning (Samoilys 1997b; Zeller 1998). On the GBR, the onset of the spawning season corresponds with a rise in water temperatures after the austral winter, generally between September – December (Samoilys 1997a), but primarily between November – December (Bunt & Kingsford 2014; Matley et al. 2015). The reproductive dynamics of *P. leopardus* are complex and relatively flexible; it has been shown that some individuals increase their movement patterns during spawning season and undertake spawning migrations up 5 – 15 km d^{-1} from their regular territory (Zeller 1998). However, other studies have found that *P. leopardus* greatly constrain their movement during the reproductive period (Samoilys 1997a), most likely due to a re-direction of resources towards reproduction (Zeller & Russ 1998; Bunt & Kingsford 2014). At Heron Island, *P. leopardus* increased space use during this time which may be indicative of spawning related movements, a finding that was reflected by Matley et al. (2015). Whereas, at Opal Reef, space use was highest in October, and then declined substantially from November indicating either, an early spawning season in 2015 or that individuals at Opal Reef make fewer reproductively motivated movements throughout the spawning period compared to individuals at Heron Island. It is unlikely that individuals in this study undertook large spawning related movements because individuals were detected within each array upwards of 85% throughout the detection period. However, each receiver is only able to detect individuals that are within 200 m of a receiver, so if individuals did make long distance movements away from the array > 200 m, they would not have been detected. Bunt & Kingsford (2014) found that *P. leopardus* demonstrated increased movement and space use during the post-reproductive period (between January - February) and suggested that some individuals may become more engaged in foraging activities to replace resources lost during reproduction. However, we found a negative correlation between space use and increasing temperature for *P. leopardus* at both locations, particularly between January – March. Although the effect was more pronounced at Opal Reef, this suggests reductions in home range extent may be driven more strongly by thermoregulatory constraints on movement and space use rather than post-reproductive movements.

Cumulative activity space analyses, defined as periods of expansion of activity space into previously unused areas within the array (Heupel et al. 2004) provides further indication that temperature may constrain movement and space use, particularly for *P. leopardus* in the northern GBR. At Opal Reef, the lack of expansion in activity space from October until temperatures began to decrease around austral autumn (end of March), may indicate a thermal threshold around 27 °C which initiates a contraction of space use and movement for individuals at the northern location. Experimental studies conducted for *P. leopardus* from northern and southern sites on the GBR suggest that the optimal temperature for physiological function and performance is approximately 27 °C, with individuals suffering increased mortality, declines in spontaneous swimming speeds as well as an increase in time spent resting at temperatures ≥ 27 °C (**Chapter 2**; Pratchett et al. 2013; Johansen et al. 2014; Johansen et al. 2015). Although temperatures for *P. leopardus* at Opal reef regularly exceed 27 °C, a contraction in home range extent at this temperature, may indicate thermally motivated behavioural modification by individuals to avoid maximising their physiological capacity. In the wild the biological limits imposed by physical constraints are generally well below the maximum physiological capacity identified in laboratory experiments (Pauly & Cheung 2018). Alternatively, the large variability in both 95% KUD and cumulative activity space for *P. leopardus* at Heron Island may be indicative of differing activity patterns between locations. For example, individuals at Heron Island may generally be more active than individuals at Opal Reef, possibly due to cooler ambient temperatures or because temperatures at Heron Island are generally close to the thermal optima for *P. leopardus.* In their study, Scott et al. (2017) (**Chapter 3**) showed that *P. leopardus* from Heron Island (high-latitude) spend substantially less time resting than *P. leopardus* from a low-latitude location on the GBR, as a potential response to increasing ambient temperature. Furthermore, a recent study (Scott et al. *unpublished data*; **Chapter 5**) investigating activity patterns of *P. leopardus* from these same locations show that individuals from Heron Island spend more time in routine activity states than individuals from Opal Reef. This lends further evidence to the suggestion that higher activity rates of *P. leopardus* from Heron could potentially reflect different thermoregulatory demands due to temperature constraints on metabolic processes.

Plectropomus leopardus are known to range as mobile, opportunistic predators, but also maintain core use for access to shelter and cleaning stations (Samoilys 1997a). Using fine-scale telemetry we estimate the average home range extent (95% KUD) for *P. leopardus* to be

~ 0.26 km^2 and average core use area to be ~ 0.05 km^2. The high density arrays used in this study show that home ranges are much smaller than previous estimations (e.g., Matley et al. 2015) suggesting that sufficient resources, such as food and habitat, are likely to be available within a very small area for *P. leopardus* (Matley et al. 2015). This also indicates that *P. leopardus* exhibit patterns of high residency and site fidelity which has also been observed in previous studies (Zeller 1997; Matley et al. 2015), and other *Epinephelid* spp, (Hutchinson & Rhodes 2010). High site fidelity has benefits such as increased foraging efficiency, particularly if resources are distributed unpredictably (Wakefield et al. 2015), but may be maladaptive in environments undergoing acute or long-term change (Faille et al. 2010). Importantly, fishes that do not or cannot move among habitats will be much more susceptible to habitat perturbations. On the GBR, large-scale disturbances (e.g., coral bleaching, cyclone, crown-of-thorns-starfish outbreaks) have caused substantial coral loss and habitat modification in recent years (Cheal et al. 2017; Hughes et al. 2017). Although the direct importance of live corals for adult *P. leopardus* remains unclear, *Plectropomus* spp. often utilize live coral habitat during their settlement phase (Leis & Carson-Ewart 1999; Wen et al. 2013), and are often found sheltering beneath live tabular corals (Kerry & Bellwood 2012) or feeding on prey that are directly dependent on live coral (St John et al. 2001). Given the size and mobility of *P. leopardus* we'd expect that they may respond to environmental disturbances by moving to more favourable habitats (Pratchett et al. 2013; **Chapter 2**). Future studies would therefore benefit from incorporating a vertical aspect of animal movement to enable the detection of finer scale depth use and potential habitat preferences of individuals, particularly in relation environmental change (Simpfendorfer et al. 2012).

The spatial extent of an organism's movements and activities has important implications for population structure and abundance (Adams et al. 2000), predator-prey interactions and the relationship between individual fitness and habitat quality. If observed differences in activity space and home ranges are related to temperature, ocean warming would be expected to cause marked changes in behaviour and biology of ecologically and economically important reef fishes (Currey et al. 2015; Pratchett et al. 2018). Any alterations to movement patterns or home range size may impact trophic food webs and consequently community dynamics (Rizzari et al. 2015; Frisch et al. 2016). As ecosystems continue to experience unprecedented environmental change, understanding the mechanisms that may provoke trade-offs of alternative behavioural strategies is an important component of anticipating species responses to future change (Nagelkerken & Munday 2016; Abrahms et al. 2018).

Chapter 5 Latitudinal and seasonal variation in activity patterns of a large, coral reef mesopredator, *Plectropomus leopardus*

Manuscript under review at *Journal of Fish Biology*

5.1 Introduction

The thermal environment influences the fitness and survival of all organisms (Angilletta et al. 2002; Portner & Peck 2010; Lelièvre et al. 2013). Temperature fundamentally impacts most biological processes, from enzyme activities to animal behaviour (Tuomainen & Candolin 2011; Nagelkerken & Munday 2016). For ectothermic animals such as fishes, metabolic processes are directly related to temperature, which in turn influences movement (Johansen et al. 2014), food intake (Johansen et al. 2015), reproduction (Donelson et al. 2014), growth (Zarco-Perello et al. 2012), and survival (Payne et al. 2016). In general, the influence of temperature on the physiological performance of ectothermic organisms is non-linear, whereby performance peaks at an optimal temperature, and declines or plateaus above this optimum (Cossins & Bowler 1987; Angilletta et al. 2002). Consequently, higher temperatures such as those caused by anthropogenic global warming may have significant adverse effects on fitness and survival of ectothermic organisms (e.g., Crossin et al. 2008; Peck et al. 2013; Messmer et al. 2016).

Tropical organisms are particularly sensitive to positive thermal anomalies compared with temperate species (Tewksbury et al. 2008; Sunday et al. 2011), because they are normally subjected to more stable thermal regimes and have adapted by minimising the thermal buffer between thermal optima and normal maximum temperatures that they experience. Tropical populations can therefore tolerate higher absolute temperatures compared with conspecifics from higher-latitudes (Edmunds et al. 2010; Rummer et al. 2014). For widespread species, vulnerability to ongoing anomalous temperatures may vary depending on the rate and extent of warming relative to historical thermal regimes. More specifically, to assess variation in susceptibility among populations explicit information is required on specific responses of ectothermic organisms to seasonal temperature extremes.

For most ectothermic fishes, temperature affects a range of behaviours including movement (Hurst 2004), foraging activity (Scott et al. 2017; **Chapter 3**), predator avoidance (Allan et al. 2015), dispersal (Sadovy de Mitcheson 2012) and migration (Walther et al. 2002). Although behaviour in fishes can take many forms (e.g. Martin et al.1993), it can be documented through assessment of locomotion, or lack of it. Locomotion is a vital component in the survival of fishes. It facilitates the critical tasks of acquiring food, avoiding predators, and finding mates (Batty & Domenici 2000; Blake 2004). Locomotion also represents one of the major daily costs in the energy budget of fishes (Boisclair & Sirois 1993) and even small changes in activity levels can have a major impact on the energy available for growth, repair and reproduction (Edmunds et al. 2010; Pratchett et al. 2013; **Chapter 2**). Consequently, examining the activity patterns of fishes, particularly in relation to environmental variation, can provide insight into the factors that affect the fitness of individuals and viability of populations (Huey & Stevenson 1979). Although the effects of temperature on fish physiology are well documented (Hurst 2004; Clark et al. 2013; Messmer et al. 2016), critical gaps remain in our understanding of the behavioural responses of fishes to temperature variation, particularly the influence of temperature on activity and foraging in free-ranging fishes.

The common coral trout (*Plectropomus leopardus*), is one of the most important tropical fisheries species, supporting recreational and commercial fisheries throughout the Indo-West Pacific (Frisch et al. 2016). Experimental studies reveal constraints on feeding, movement and survival of *P. leopardus* when exposed to end-of-century environmental conditions (**Chapter 2**; Pratchett et al. 2013; Johansen et al. 2014; Messmer et al. 2016; Clark et al. 2017), leading to concerns that ongoing climate change may undermine the viability and sustainability of fisheries that target this species (Pratchett et al. 2016). *Plectropomus leopardus* is also an ecologically important mesopredator capable of influencing the structure of coral reef communities (Emslie et al. 2015; Rizzari et al. 2015; Frisch et al. 2016). Any changes to the activity patterns of mesopredators may influence population dynamics by altering species interactions (Pennock et al. 2018), trophodynamics (Boaden & Kingsford 2015), and spawning-related movements (Zeller & Russ 1998; Bunt & Kingsford 2014). An improved understanding of behavioural responses to temperature is therefore critical to predict the response of fish populations to climatic variation, and the ecological or social consequences of these responses (Ovadia & Schmitz 2002).

This study used tri-axial accelerometer transmitters to assess spatial and temporal variation in activity patterns in free-ranging *Plectropomus leopardus*. Tri-axial accelerometer loggers are a powerful tool used to address a diversity of objectives pertaining to animal behaviour and energy use in a wide range of species (see Review by Payne et al. 2014). Accelerometers provide real-time data on the occurrence of a range of behaviours in free-living organisms (Wilson et al. 2006; Watanabe & Takahashi 2013) offering a unique opportunity to reliably assess variation in the interplay of animal movement, behaviour and physiology over relatively long time periods. Three modes of activity were classified to determine how fishes partition time and energy to regulate foraging and fitness: burst activity (maximum acceleration sustained for less than 10 seconds), routine activity (motivationally regulated measures of activity), and low activity (resting or inactive). To test the thermal sensitivity of acceleration and activity patterns, 36 *P. leopardus* were tagged within two small-scale (0.5 km^2) acoustic telemetry arrays separated by 1,000km over the course of a year. It was expected that *P. leopardus* would exhibit latitudinal differences in modes of activity corresponding to differences in water temperature. Specifically, the low-latitude population was expected to have higher average burst and routine activity levels at higher temperatures (up to a point) compared to the high-latitude population reflecting temperature induced increases in metabolic demands and consequently physiological performance at higher temperatures. Moreover, fish from low-latitudes are expected to spend more time resting compared to those from higher-latitudes given that basal metabolic rates are likely to be much higher and reduce metabolic scope for activity (Gleiss et al. 2013; Clark et al. 2017).

5.2 Materials and methods

5.2.1 Study Area

This study was conducted on Australia's Great Barrier Reef (GBR) at Opal Reef (16°14'20.77"S, 145°52'12.59"E) in the northern GBR and Heron Island Reef (23°25'57.86"S, 151°55'57.65"E) in the southern GBR. The two study locations are separated by approximately 1,000 km and seven degrees of latitude. The specific study sites used at each location were comparable, comprising fringing and patch reefs along depth gradients extending to ~25 m along the reef slope. Daily temperatures were recorded on four temperatures loggers (Vemco Minilog-II-T) attached to the receivers at approximately ~ 7 m depth (**Figure 5.1**).

5.2.2 Field Methods

To monitor activity patterns of *P. leopardus*, acoustic tracking was undertaken at both sites using Vemco VR2W acoustic receivers (Vemco Ltd., Halifax, Canada). Similar Vemco Positioning System (VPS) arrays were established by deploying 18 VR2W receivers at the low-latitude location and 14 VR2W receivers at the high-latitude location. Receivers were deployed in an identical arrangement, ~ 2 m above the substrate (reef or sand) using chain and set approximately 100 m apart (to increase accurate range of detection) in three lines. Inner receivers were positioned close to the reef crest (5 - 12 m depth) and outer receivers were positioned in sandy habitats (18 - 21 m depth). The middle row was also positioned in sand (10 - 18 m depth) at both locations. Both arrays occupied an area of approximately 0.5 km^2, encompassing 500 m along the reef crest and out 100 m from the reef slope to deeper sandy habitat (see **Figure 4.1**).

Within each array, 19 adult (> 35 cm) *P. leopardus* were caught using barbless hooks. Once caught, individual fish were immediately placed in an anesthetic bath of Aqui-S® (~ 30 L) diluted with seawater (1:10000). Prior to removing the hook, the swim bladder was vented to avoid barotrauma, if necessary. Once individuals lost equilibrium, they were measured (fork length to the nearest millimeter), fitted with an external dart tag (PDS; Hallprint®) in the dorsal musculature for identification and moved to a fresh seawater bath. A V13A-P transmitter (13 mm x 42 mm) was surgically implanted into the abdominal cavity via a small incision (20 – 30 mm) in the ventral body wall running parallel to the length of the animal. The transmitters were always oriented the same way for each fish (i.e. accelerometer sensors facing anteriorly). The incision was closed by simple, uninterrupted stitches using absorbable sutures. Fish were released after fork length and dart tag number were recorded. Generally, the entire procedure took < 10 minutes and a total of 38 *P. leopardus* were caught, processed and tagged. Each transmitter had a pressure (depth) and accelerometer (acceleration) sensor and was programmed to randomly emit a unique coded signal every 60-120 seconds, with an expected battery life of 349 days. The transmitters alternated in the transmission of acceleration and depth, however the depth data were not used for this study. Activity ($m.sec^{-2}$) was determined by calculating the root mean square (RMS) of tri-axial acceleration. Acceleration due to gravity is filtered prior to signal transmission, so acceleration data can be considered dynamic body acceleration (Wilson et al. 2006). Dynamic body acceleration was then used to define differing levels of activity in tracked *P. leopardus* throughout the sampling period and ranged between 0.001 – $4.9ms^{-2}$ (resolution to $0.014\ ms^{-2}$).

Sampling summary

At Opal Reef, the detection period ranged from October 1st 2015 – September 16th 2016, totalling 351 days. At any time within that period 12 – 18 fish were detected within the array at all times (see **Table 4.1**). At Heron Island, the detection period ranged from September 9th 2015 – August 31st 2016, a total of 357 days. At any time within that period 14 – 18 individuals were detected within the array at all times. Tagged *P. leopardus* ranged in size from 336 mm – 565 mm (mean fork length ± SE = 431± 13, n= 18) at Opal Reef, and from 401 mm – 634 mm (mean fork length ± SE = 543 ± 13.20, n= 18) at Heron Island (see **Table 4.1**). Annual maximum water temperatures differed by approximately 2.5 °C, ranging from 19.9 °C – 27.4 °C at Heron Island and 23.1 °C – 30.0 °C at Opal Reef (**Figure 5.1**).

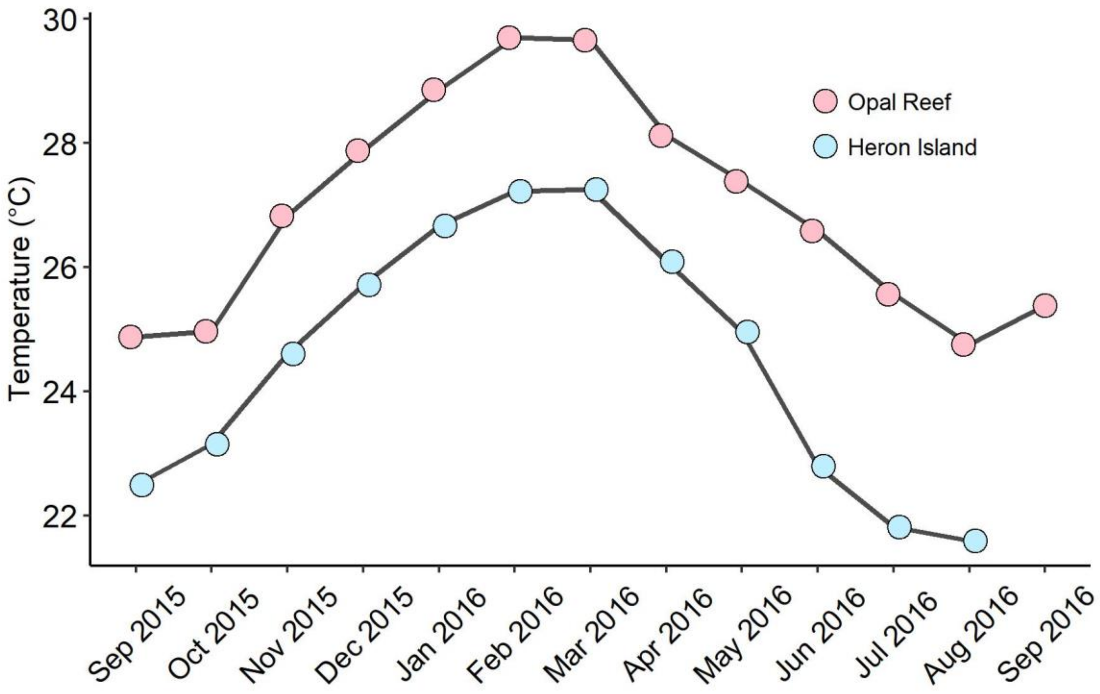

Figure 5.1: Average monthly temperature (± SD) for Opal Reef (pink circles) and Heron Island (blue circles) throughout the study period September 2015 – September 2016.

5.2.3 Calculating levels of activity

Acceleration values were classified into: i) burst activity (BA), ii) routine activity (RA), and iii) low activity (LA) based on the distribution of measurements for each individual (see **Figure 5.2a**). Burst activity (BA m.s^{-2}) was calculated as the average of the 90th percentile of acceleration values across each tagged individual (n=36) throughout the entire sampling period. Burst activity is generally defined as maximum acceleration sustained for less than 20 seconds (Beamish 1978). *Plectropomus leopardus* are a relatively sedentary, ambush mesopredator and *in situ* observations and previous studies (Samoilys 1997; Zeller & Russ 1998; Scott et al. 2017) have shown that burst events of *P. leopardus* take place within several seconds. . From *in situ* observation, these BA events are generally linked to foraging events rather than predator evasion (Scott et al. 2017; **Chapter 3)**. Burst activity values ranged between 1.04 – 4.9 m.s^{-2}. Low activity (LA m.s^{-2}), classified as resting or stationary behaviour was calculated as the average of the bottom 20% of acceleration values for each individual. Low activity values ranged between 0.01 – 0.35 m.s^{-2}. Finally, routine (or voluntary) activity (RA m.s^{-2}) was defined as the middle 70% of acceleration values and RA values ranged between 0.36 – 0.99 m.s^{-2}. Because *P. leopardus* are not a high activity species, I expected individuals to be detected more often at low or routine activity.

5.2.4 Statistical analysis

All data from receivers were analysed in the R environment version '3.3.0' (R Core Team, 2013). Detections during the first 48 hours of the study were removed for all individuals to exclude any effect of handling on fish behaviour. Data were examined to identify any spurious detections e.g. data that represented fast, erratic movements (i.e. consistent with fish consumed by a predator), or data that lacked vertical movement aside from a consistent tidal signature (i.e. perished individual, Matley et al. 2015). Fish that exhibited these characteristics were assumed to have died and were removed from analyses. There were two individuals who exhibited these characteristics, i.e. detected < 25 times and/or < 15 days throughout the study, which meant 36 individuals, 18 (out of 19) from each location were included in the analyses. To reduce autocorrelation within the data, acceleration values were averaged over 15-minute time steps for each individual. These time steps are based on previous studies which used between 10 – 15 minute intervals for detecting other larger bodied reef fishes (Currey et al. 2015). To ensure the full spectrum of acceleration values were being captured, data were also analysed at 5 and 10-minute time steps. There was no difference in acceleration values in either time step so 15 minutes was chosen to align with previous studies. To standardise for differences in the number of detections between locations, acceleration values were averaged for each individual in each hour each day over the course of the study period.

To first test the influence of spatial and temporal variation in ambient temperature on all acceleration values a repeated measures ANOVA (RM-ANOVA) from the *lme4* package (Bates et al. 2013) was used. Acceleration (response variable) was log-transformed to fulfil model assumptions of normality and homogeneity of variance and tested against temperature and fish size. Repeated measures models are used to account for autocorrelation inherent in observations of individuals through time (Logan 2010). First-order correlation structure (corAR1) was also incorporated into the models to account for serial autocorrelation (a violation of the assumption of independence in model-fitting). There was no residual serial correlation (evaluated using the 'acf' autocorrelation function in R). In all analyses, to account for the non-independent nature of sampling individuals through time, individual fish was included as a random effect. To estimate the variance components of the random effects (i.e. individual fish) residual maximum likelihood estimation (REML) was used. REML is useful for maximising the likelihood of the residuals and is less bias when dealing with different correlation structures (Logan 2010). Variance inflation factors (vif < 3) were also checked to evaluate multicollinearity of predictor variables within the models.

The categorisation of acceleration values (i.e. BA, RA, LA) reflected different energetic behaviours. A two-way analysis of variance (ANOVA) determined whether temperature influenced acceleration values within each category. Because it did, acceleration values within each activity category were analysed separately. Latitudinal differences in activity patterns were also tested using RM-ANOVA. All data were screened for normality and homogeneity of variance and burst and routine activity values were log-transformed to fulfil model assumptions. To compare seasonal differences in activity patterns between locations planned contrasts were used from the *lsmeans* package (Lenth 2018). Finally, to determine the latitudinal and seasonal variation in activity patterns in relation to variation in ambient temperature, the proportion of detections of each activity mode was calculated. To do this, the average number of detections per individual per day at each site were calculated. Then the total number of daily detections were divided by the number of detections within each activity mode to provide a daily proportion. There was no indication of overdispersion in the residuals, however because the response variable was a proportion, data were logit transformed to fulfil model assumptions and analysed using a generalized linear mixed effects model with a binomial distribution and fish treated as a random effect within the *lme4* package.

5.3 Results

Acceleration values for free-swimming *P. leopardus* ranged from 0.01 up to 4.9 $m.s^{-2}$ (**Figure 5.2a**). Average activity for *P. leopardus* was 0.69 $m.s^{-2}$ and values did not differ substantially between locations ($F = 0.02$, $p = 0.52$). Overall, average activity increased with temporal variation in ambient temperature from 0.62 $m.s^{-2}$ at 21 °C to 0.76 $m.s^{-2}$ at 30 °C (**Figure 5.2b**).

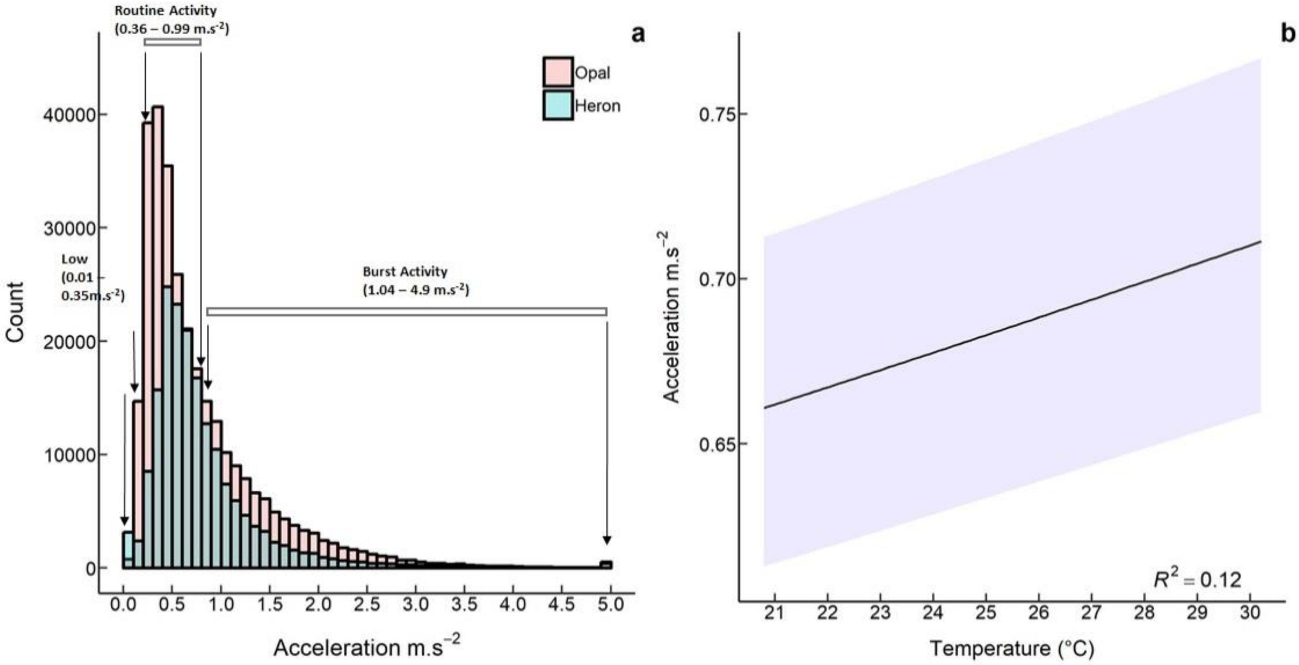

Figure 5.2: a) Histogram of acceleration values of *P. leopardus* in the wild. Values for low activity, routine activity, and burst activity have been overlaid for reference and b) The modelled values of the positive relationship between increasing temperature on the combined overall activity of *P. leopardus.*

The majority (~ 64%) of acceleration values fell within the routine activity category (**Figure 5.2**, **Table 5.1**). However, the most pronounced differences in activity patterns between locations were within the low activity category (*F* = 98.6, *p* < 0.001) which accounted for only 14% of all detections.

Table 5.1: Mean ± SE of low activity , routine activity and burst activity and the proportion of these acceleration values throughout the entire monitoring period.

	Opal Reef (low-latitude)		**Heron Island (high-latitude)**	
	Accel (ms^{-2}) (±SE)	**Proportion detected (±SE)**	**Accel (ms^{-2}) (±SE)**	**Proportion detected (±SE)**
Low	0.23 ± 0.0002	0.18 ± 0.002	0.20 ± 0.0007	0.09 ± 0.001
Routine	0.57 ± 0.0005	0.56 ± 0.002	0.61 ± 0.0005	0.70 ± 0.002
Burst	2.27 ± 0.004	0.26 ± 0.002	2.11 ± 0.006	0.21 ± 0.002

Notably, *P. leopardus* at Opal Reef were twice as likely to exhibit low activity (18%) than individuals at Heron Island (9%) (**Table 5.1**, **Figure 5.3**) irrespective of body size ($F = 0.71$, $p = 0.47$). At Opal Reef, the proportion of LA detections were consistently higher across all seasons compared with Heron Island (**Figure 5.3a**), a pattern that corresponded with variation in ambient temperature between locations (**Figure 5.3b**). Conversely, the proportion of LA detections at Heron Island decreased with increasing ambient temperature, suggesting *P. leopardus* at the high latitude location spend more time resting at lower temperatures and become more active as temperatures increase (**Figure 5.3c**). Taken together, the overall proportion of LA detections for *P. leopardus* increased 2-fold with ambient temperature between 21 °C and 30 °C.

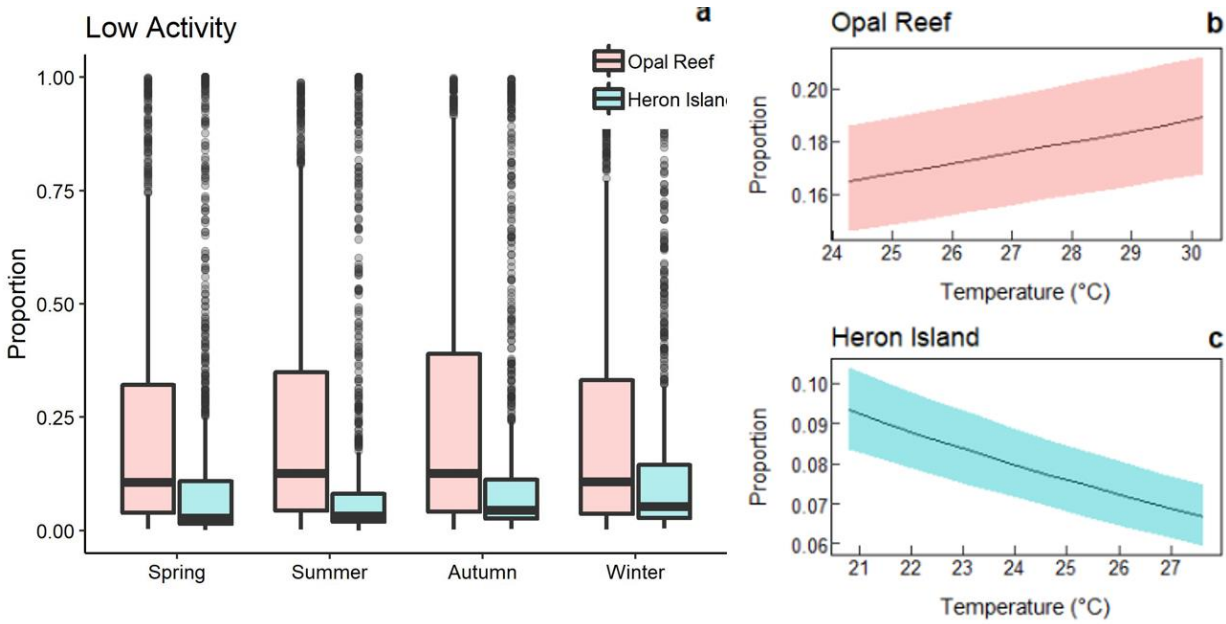

Figure 5.3: a) Boxplots demonstrating the latitudinal and seasonal variation in the proportion of low-activity detections between Opal Reef (pink) and Heron Island (blue). And modelled values showing the influence of temporal variation in ambient temperature on the proportion of low-activity detections (± 95% C.I, coloured ribbons) at b) Opal Reef and c) Heron Island.

Plectropomus leopardus also exhibited spatio-temporal differences in the proportion of routine activity within and between locations. At Heron Island, approximately 70% of detections were RA compared with 56% of detections at Opal Reef (**Figure 5.4a**, **Table 5.1**). The proportion of RA was consistently higher at Heron Island across all seasons compared with Opal Reef ($F = 42.2$, $p < 0.001$) (**Table 5.2**). At Heron Island, RA detections were lowest in the summer and highest in winter (**Figure 5.4a**, **Table 5.2**), whereas at Opal Reef RA detections were highest in summer and lowest in autumn (**Table 5.2**). Irrespective of latitude, the proportion of RA detections decreased with increasing water temperature ($F = 937.07$, $p < 0.001$, **Figure 5.4 b & c**) from 74% of detections at 21 °C to 54% of detections at 30 °C. This equates to a 1.1- fold decrease in the proportion of RA with every 3 °C increase in ambient temperature.

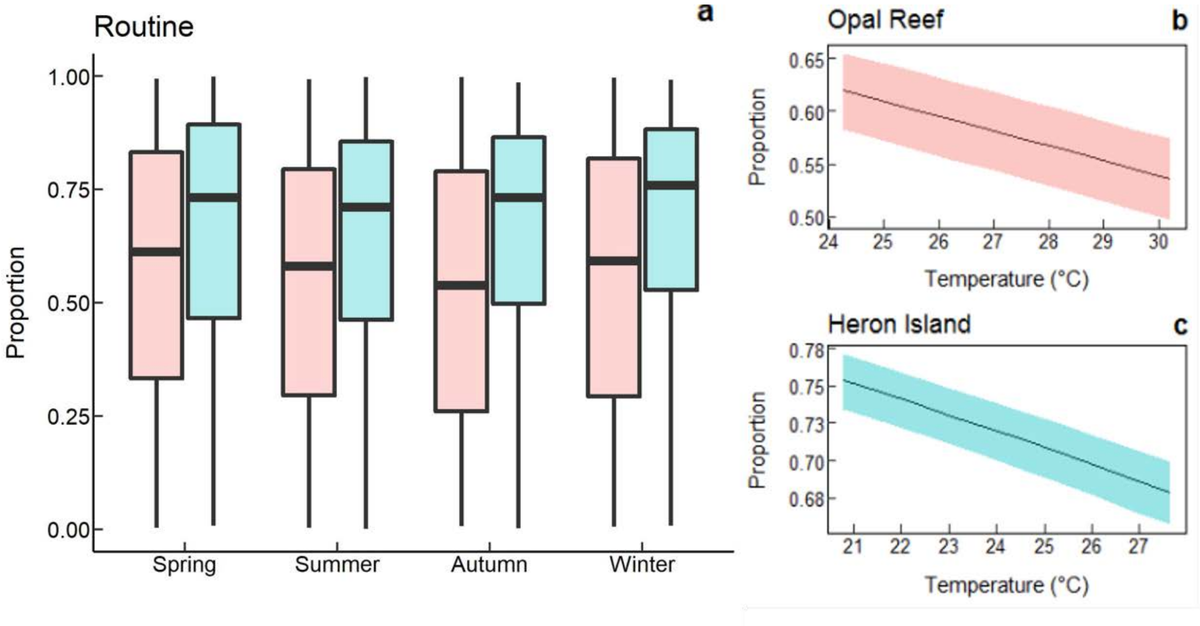

Figure 5.4: a) Boxplots demonstrating the latitudinal and seasonal variation in the proportion of routine activity detections between Opal Reef (pink) and Heron Island (blue). And modelled values showing the influence of temporal variation in ambient temperature on the proportion of routine activity detections (± 95% C.I, coloured ribbons) at b) Opal Reef and c) Heron Island.

There were no substantial differences in the overall proportion of burst activity between locations ($F = 0.12$, $p = 0.73$), however the proportion of BA was higher at Opal Reef (26%) compared with Heron Island (21%) (**Table 5.1**). *Plectropomus leopardus* exhibited seasonal differences in BA within locations (**Figure 5.5a**). At Opal Reef, BA detections were consistently high in summer, autumn and winter, but declined during spring (**Figure 5.5b**, **Table 5.2**). Whereas, at Heron Island *P. leopardus* exhibited the highest proportion of BA during summer compared with other seasons (**Figure 5.5c**, **Table 5.2**). BA is a particularly important metric because it can be considered a proxy for foraging behaviour. These results may therefore indicate differences in foraging behaviour between locations, where foraging activity for *P. leopardus* from Opal Reef was relatively consistent throughout the year (except lower during spring), whereas at Heron Island foraging activity was highest during the summertime compared with rest of the year. Taken together, spatio-temporal differences in burst events corresponding to seasonal and latitudinal differences in ambient temperature indicate a potential increase in the proportion of BA with increasing temperature. This reveals the proportion of BA increased with increasing temperature from 17% at 21 °C to 28% at 30 °C, which equates to 1.2-fold increase in the proportion of BA with every 3 °C increase in temperature.

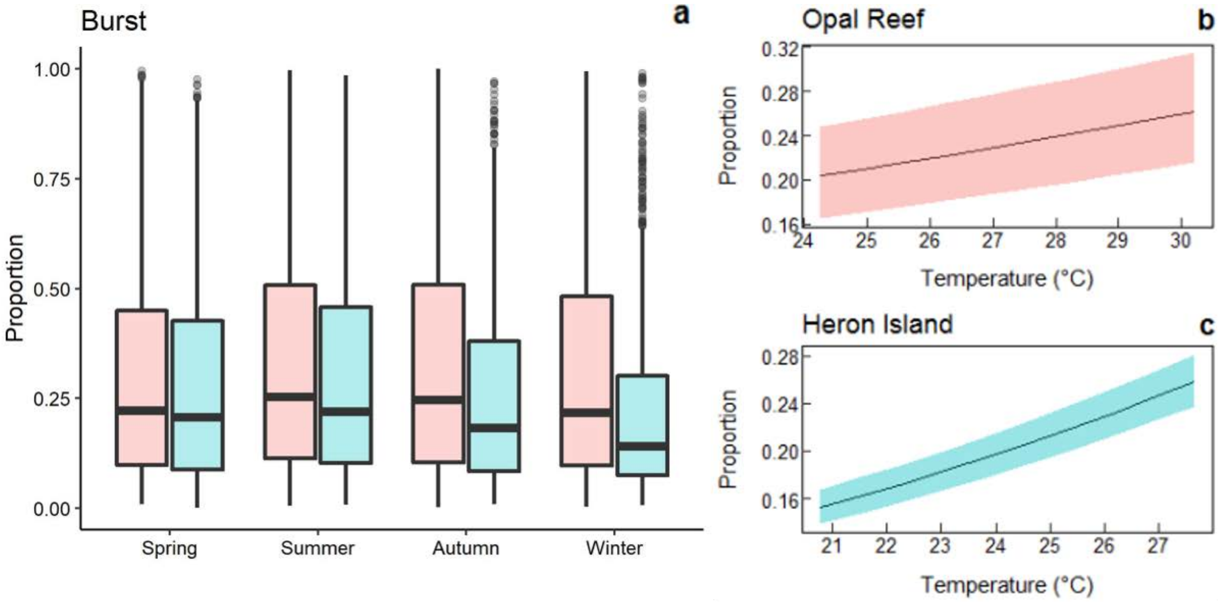

Figure 5.5: a) Boxplots demonstrating the latitudinal and seasonal variation in the proportion of burst activity detections between Opal Reef (pink) and Heron Island (blue). And modelled values showing the influence of temporal variation in ambient temperature on the proportion of burst activity detections (± 95% C.I, coloured ribbons) at b) Opal Reef and c) Heron Island.

Spatial and temporal differences in the proportion of detections at each activity level, may indicate a potential energetic tradeoff for *P. leopardus* from the low-latitude location in which they decrease the amount of time spent undertaking routine activity and increase the amount of time spent resting in relation to increasing ambient temperature. In contrast, at Heron Island, *P. leopardus* may reduce the amount of time spent in routine activity, to facilitate increased burst events during warmer seasons.

Table 5.2: Statistical output from planned contrasts showing seasonal differences in the proportion of detections at each activity level (low, routine, burst) within and between locations.

Seasonal contrasts for proportion of detections within and between locations

Response	Contrast	Season	Estimate	SE	z-ratio	*p*-value
Low Activity	**Opal vs Opal**	Summer vs Autumn leopardus	-0.09	0.01	-7.25	<0.0001
		Autumn vs Winter	0.08	0.013	6.18	<0.0001
		Autumn vs Spring	0.06	0.14	4.08	0.0012
	Opal vs Heron	O-Summer vs H-Summer	1.10	0.10	11.3	<0.0001
		O-Summer vs H-Autumn	0.82	0.09	8.48	<0.0001
		O-Summer vs H-Winter	0.78	0.10	8.20	<0.0001
		O-Summer vs H-Spring	0.91	0.09	9.52	<0.0001
		O-Autumn vs H-Summer	1.18	0.10	12.26	<0.0001
		O-Autumn vs H-Autumn	0.91	0.10	9.42	<0.0001
		O-Autumn vs H-Winter	0.88	0.10	9.14	<0.0001
		O-Autumn vs H-Spring	0.99	0.10	10.47	<0.0001
		O-Winter vs H-Summer	1.10	0.10	11.37	<0.0001
		O-Winter vs H-Autumn	0.82	0.10	8.54	<0.0001
		O-Winter vs H-Winter	0.79	0.09	8.25	<0.0001
		O-Winter vs H-Spring	0.91	0.10	9.57	<0.0001
		O-Spring vs H-Summer	1.12	0.10	11.64	<0.0001
		O-Spring vs H-Autumn	0.85	0.10	8.80	<0.0001
		O-Spring vs H-Winter	0.81	0.09	8.53	<0.0001
		O-Spring vs H-Spring	0.94	0.10	9.84	<0.0001
	Heron vs Heron	Summer vs Autumn	-0.27	0.03	-8.65	<0.0001
		Summer vs Winter	-0.30	0.03	-9.94	<0.0001
		Summer vs Spring	-0.18	0.03	-6.40	<0.0001
		Autumn vs Spring	0.09	0.03	3.0	0.06
		Winter vs Spring	0.12	0.03	4.21	0.0007
Routine Activity	**Opal vs Opal**	Summer vs Autumn	-0.13	0.01	-12.42	<0.0001
		Summer vs Winter	-0.11	0.01	-9.99	<0.0001
		Summer vs Spring	-0.11	0.01	-10.15	<0.0001
		Autumn vs Winter	0.1332	0.010	-12.42	<0.0001
		Autumn vs Spring	-0.14	0.01	-12.35	<0.0001
	Opal vs Heron	O-Summer vs H-Summer	-0.49	0.09	-5.5	<0.0001
		O-Summer vs H-Autumn	-0.65	0.09	-7.27	<0.0001
		O-Summer vs H-Winter	-0.81	0.09	-9.08	<0.0001
		O-Summer vs H-Spring	-0.67	0.09	-7.52	<0.0001
		O-Autumn vs H-Summer	-0.52	0.09	-5.77	<0.0001
		O-Autumn vs H-Autumn	-0.67	0.09	-7.54	<0.0001
		O-Autumn vs H-Winter	-0.84	0.08	-9.35	<0.0001
		O-Autumn vs H-Spring	-0.70	0.09	-7.81	<0.0001
		O-Winter vs H-Summer	-0.38	0.09	-4.28	0.0005
		O-Winter vs H-Autumn	-0.54	0.09	-6.05	<0.0001
		O-Winter vs H-Winter	-0.71	0.08	-7.86	<0.0001
		O-Winter vs H-Spring	-0.56	0.09	-6.31	<0.0001
		O-Spring vs H-Summer	-0.37	0.09	-4.23	0.0006
		O-Spring vs H-Autumn	-0.54	0.09	-6.0	<0.0001
		O-Spring vs H-Winter	-0.70	0.09	-7.71	<0.0001
		O-Spring vs H-Spring	-0.56	0.09	-6.25	<0.0001
	Heron vs Heron	Summer vs Autumn	-0.16	0.02	-8.39	<0.0001
		Summer vs Winter	-0.32	0.02	-17	<0.0001

		Summer vs Spring	-0.18	0.02	-10.61	<0.0001
		Autumn vs Winter	-0.16	0.02	-8.27	<0.0001
		Autumn vs Spring	-0.02	0.02	-1.02	0.97
		Winter vs Spring	0.14	0.12	7.676	<0.0001
Burst Activity	**Opal vs Opal**	Summer vs Winter	0.45	0.14	3.13	0.03
		Summer vs Spring	0.59	0.13	4.24	0.0006
		Autumn vs Spring	0.63	0.37	1.68	0.003
	Heron vs Heron	Summer vs Winter	0.51	0.13	3.48	0.01
		Winter vs Spring	-0.52	0.15	-3.46	0.013

Overall, *P. leopardus* exhibited similar responses in activity in relation to latitudinal and seasonal differences in ambient temperatures. Irrespective of latitude ($F = 0.60$, $p = 0.44$), LA acceleration values decreased with seasonal increases in water temperature ($F = 305.32$, $p < 0.001$, **Figure 5.6a & d**). In contrast, RA for *P. leopardus* increased with seasonal differences in ambient temperature at both locations ($F = 249.76$, $p < 0.001$, **Figure 5.6b & e**), although RA of *P. leopardus* was higher at Heron Island at 0.61 m.s^{-2} ± 0.001 (SE) compared with Opal Reef at 0.55 m.s^{-2} ± 0.001 (SE) ($F = 28.69$, $p < 0.001$, **Figure 5.6b & e**). Interestingly, individuals at Opal Reef exhibited higher burst acceleration than individuals at Heron Island, and whilst this was not significantly different between locations ($F = 2.97$, $p = 0.09$), only burst activity events of *P. leopardus* at Heron Island were influenced by increasing ambient temperature ($F = 31.3$, $p < 0.001$, **Figure 5.6c & f**).

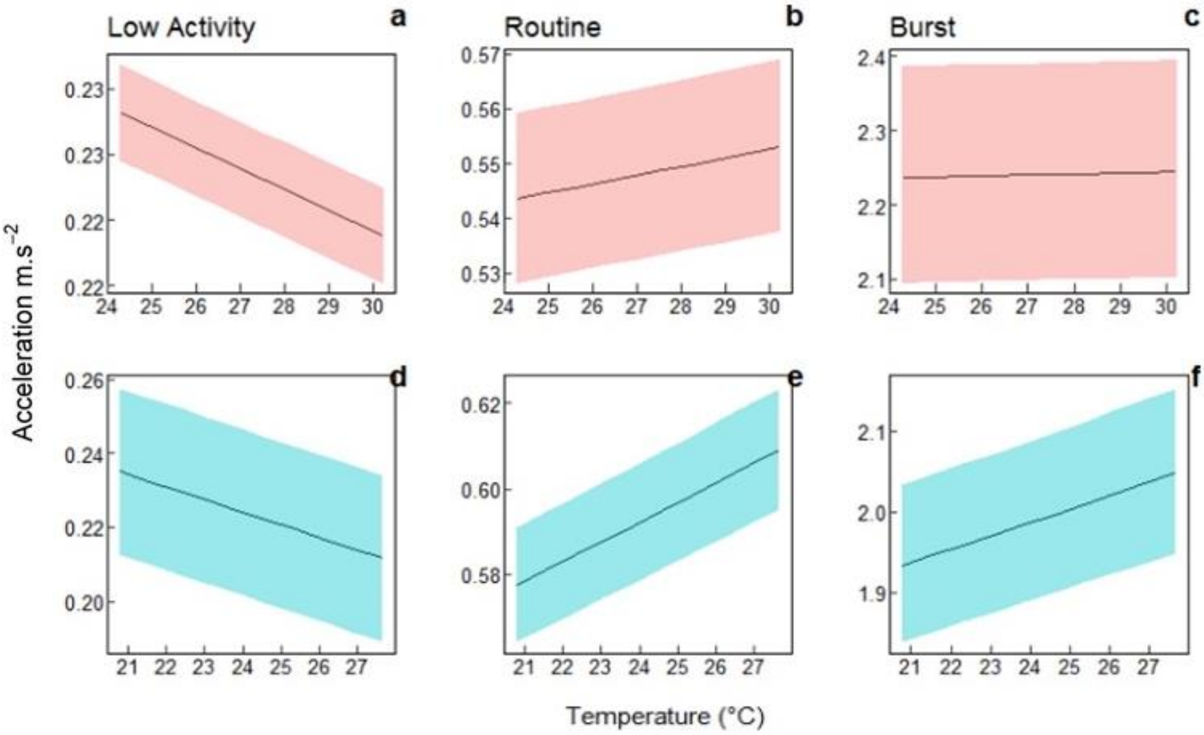

Figure 5.6: The modelled effects of increasing temperature on low activity (a & d), routine activity (b & e) and burst activity (c & f) of *P. leopardus* from Opal Reef (pink – top row) and Heron Island (blue - bottom row). The coloured ribbons represent the 95% confidence interval for average activity at each location.

Finally, RA of *P. leopardus* was consistent across all body sizes ($F = 0.17$, $p = 0.68$, **Figure 5.7a & c**) although larger individuals were detected more often at RA than smaller individuals ($F = 29.7$, $p < 0.001$, **Figure 5.7a & c**). In contrast, smaller individuals exhibited higher BA ($F = 19.9$, $p < 0.001$, **Figure 5.7b**) at both locations ($F = 2.97$, $p = 0.13$) and were detected more often at BA than larger individuals ($F = 26.25$, $p < 0.001$, **Figure 5.7d**). This effect was most pronounced at Heron Island ($F = 4.61$, $p = 0.03$) suggesting that smaller bodied *P. leopardus* from the high-latitude location undertake more burst activity compared with than larger individuals.

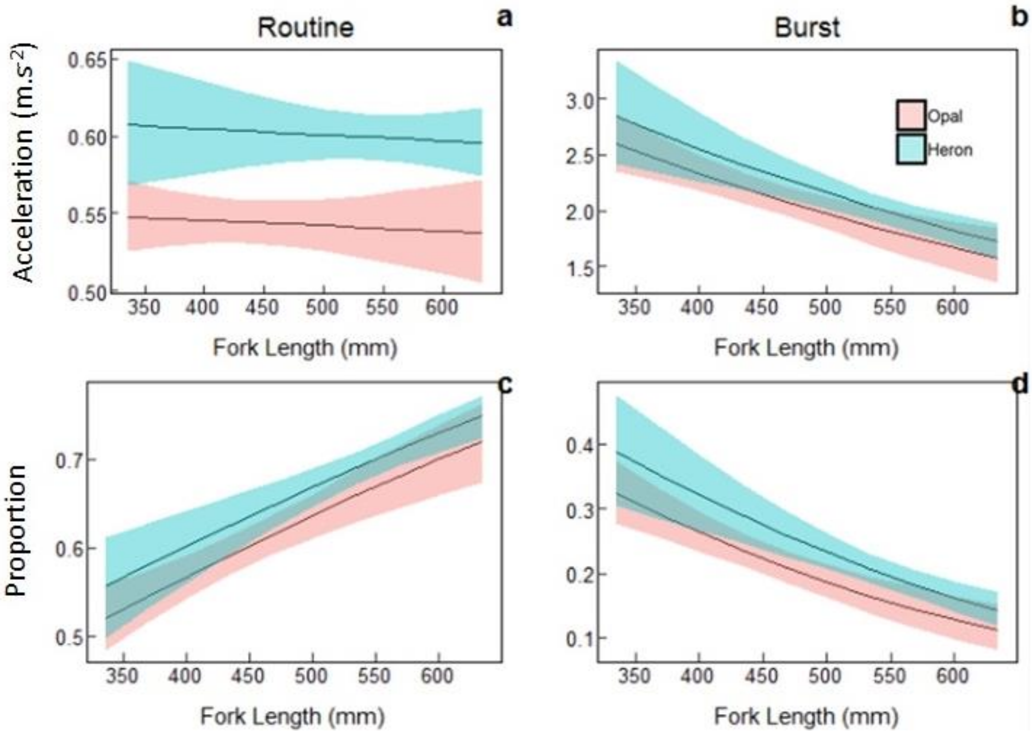

Figure 5.7: Influence of fork length (to the nearest millimetre) on routine activity (a) and proportion of routine activity detections (c) and burst activity (b) and proportion of burst activity detections (d) at Opal Reef (pink) and Heron Island (blue).

5.4 Discussion

This study shows that activity patterns for *P. leopardus* on the Great Barrier Reef (GBR) vary significantly with season and location. Most notably, fishes were much less active at Opal Reef in the northern GBR (low-latitude) compared to Heron Island in the southern GBR (high-latitude) irrespective of fish size. Moreover, activity levels varied with both seasonal and latitudinal variation in water temperature such that for every 3 °C increase in ambient temperature (between 21 °C and 30 °C) there was a 1.3-fold increase in the proportion of low activity detections. These results may indicate that higher water temperatures could place energetic constraints on *P. leopardus*, particularly at low-latitude locations on the GBR which are currently exposed to summertime temperatures > 30 °C (**Chapter 2;** Pratchett et al. 2013).

For many fishes, rising ocean temperatures will lead to inevitable increases in standard metabolic rates, which may be partially compensated for by increasing food intake or reducing movement and activity (Johansen et al. 2014; Johansen et al. 2015; Scott et al. 2017; **Chapter 3**). Previous studies from the GBR have shown that *P. leopardus* reduce movement and activity (Johansen et al. 2014) and can spend > 60% of their time resting (Scott et al. 2017; **Chapter 3**) when exposed to high summertime temperatures. These behavioural changes may have implications for individual fitness and community dynamics under warming oceans. Any reductions in activity patterns may have implications for the reproductive capacity of this species. *Plectropomus leopardus* are known to undertake spawning related movements and any reduction in activity patterns could directly influence population replenishment and the viability of fisheries stocks through reduced visits to spawning sites. This may cause a decline in larval export, dispersal, and affect the replenishment of stocks, not only for *P. leopardus* but also for other commercially important fish species that respond similarly to increases in water temperature and migrate to spawn (Colin 2012). This is especially pertinent because larger-bodied fishes are disproportionately susceptible to higher temperatures (Messmer et al. 2016), though larger fishes may have greater capacity to move and exploit thermal gradients and refuges. Alternatively, resting when temperatures are higher (> 30 °C) and maximum capacities are reduced may save energy that can be used for escape responses or predation events (Ottmar & Hurst 2012).

In this study, activity levels revealed different responses to spatial and temporal variation in water temperature. Fish locomotion relies on overlapping but distinct physiological systems, and these discrete physiological bases could contribute to differential responses to temperature (O'Steen & Bennett 2003). For example, burst activity of *P. leopardus* at Opal Reef (low-latitude), did not appear to be influenced by seasonal variation in water temperature, presumably due to reduced thermal dependence of anaerobic versus aerobically based locomotor performance (Bennett 1990). During burst-type exercise in fish, the muscles derive energy almost exclusively from the anaerobic metabolism of glycogen. This process is not dependent on oxygen from the environment making it considerably less thermally dependent than aerobic energy which requires oxygen to restore glycogen once anaerobic metabolism has ceased (Bennett 1978). Because burst swimming events can generally be used as a proxy for foraging behaviour, these patterns suggest that foraging capacity of *P. leopardus* may not necessarily be impacted by temperatures up to 30 °C. Instead, there was an increase in the proportion of burst activity detections with increasing ambient temperature, suggesting that *P. leopardus* make more foraging attempts at higher temperatures. This pattern was also reflected in a study by Scott et al. (2017) **(Chapter 3**) that showed increases in strike rates of *P. leopardus* at higher temperatures, most likely due to increases in baseline metabolic rates with increasing temperature (Messmer et al. 2016). However, whilst plasticity in foraging behaviour is likely to compensate for increased metabolic demands in *P. leopardus* exposed to moderate increases in temperature, Scott et al. (2017) showed that foraging capacity for *P. leopardus* may be adversely affected by temperatures > 30 °C (**Chapter 3**). In this study, temperatures did not exceed 30 °C, so it is not possible to infer any impacts of temperatures > 30 °C on activity. Nevertheless, given the universal influence of temperature on metabolic rates of ectothermic fishes (Brown et al. 2004), *P. leopardus* may exhibit behavioural strategies favouring foraging opportunities at higher temperatures whilst reducing predation vulnerability at lower temperatures (Johansson & Leonardsson 1998). It is important to note that in this study, burst activity events are being used as a relative proxy for foraging behaviour. This does not imply definite feeding attempts nor can it validate the success of foraging attempts. However, *in situ* observation (> 400 hours) of approximately 500 *P. leopardus* can verify the majority (> 95%) of burst events undertaken by *P. leopardus* are related to foraging attempts rather than evasion of predators (*pers.obs*. M.Scott, February 2016).

The thermal environment often acts as a determining factor in swimming performance of fishes due to the effect of temperature on physiological requirements of ectotherms (Beamish 1978; O'Steen & Bennett 2003). In this study, average and routine activity of *P. leopardus* increased with increasing temperature up to 30 °C. In general, routine activity is a behaviourally mediated response, limited by the capacity for aerobic metabolism. This means that routine activity mostly increases with increasing water temperature (Precht 1958; Bennett 1990). At higher temperatures, studies have shown that fish can increase swimming performance (Dickson et al. 2002; Koumoundouros et al. 2002; Ottmar & Hurst 2012) and depending on the context, the positive relationship between temperature and activity could reflect the changing metabolic demands with temperature as increased activity rates likely increase encounter rates with prey in natural habitats (Linlokken et al. 2010). Increases in locomotory performance in warmer waters, although often physiologically induced, can promote behavioural thermoregulation and enable fish to exploit more optimal thermal niches (Magnuson et al. 1979). For *P. leopardus* this may mean exploiting thermally favourable habitats by moving to cooler, deeper waters or shifting their distributions to higher-latitudes if food availability or physiological limits become constrained (**Chapter 6**). However, these results show that the proportion of time spent at routine activity levels for *P. leopardus* from both locations declines with increasing temperature suggesting a potential energetic trade-off between activity and conservation of energy. Although thermal impacts on activity level may vary with body size of fish (Baudron et al. 2014; Messmer et al. 2016).

In general, swimming performance increases with increasing body size of fishes (Peck et al. 2006; Ottmar & Hurst 2012). In this study, body size did not influence average or routine activity for *P. leopardus,* however smaller individuals had substantially higher burst activity and were detected more often at burst activity compared to larger individuals. This may indicate size-specific differences in foraging behaviour. For example, it is possible that larger individuals are more experienced at foraging and require fewer and less energetically costly foraging attempts to successfully capture prey. In their study, Scott et al. (2017) showed that smaller *P. leopardus* exhibited consistently higher strike rates than larger individuals (**Chapter 3**). Smaller individuals typically have higher mass-specific metabolic rates than larger individuals, which may be associated with higher growth rates and elevated activity levels (Hou et al. 2008; Baudron et al. 2014). However, increased foraging efficiency of smaller individuals may come at a cost, as energy expenditure and risk of predation may increase with foraging frequency. In contrast, larger individuals were detected more often undertaking routine activity compared with smaller individuals which may be a tactic employed by larger *P. leopardus* in order to defend their territories by chasing away or displacing smaller individuals (Johnsson et al. 1999).

Results from this study in combination with other recent research on the thermal sensitivities of *P. leopardus* demonstrate the complexity of the influence of temperature on physiology, movement, activity and behaviour of this important fisheries species (**Chapter 2**; Pratchett et al. 2013; Johansen et *al.* 2015; Messmer et al. 2016; Scott et al. 2017; **Chapter 3**). Experimental studies have revealed that optimal temperatures for *P. leopardus* are ~ 27 °C, regardless of whether individuals were sampled from the northern or southern GBR (Johansen et al. 2014, 2015). In the wild, free-swimming *P. leopardus* exhibit contraction in their home range

(**Chapter 4;** Scott et al. 2018) most likely due to an increase in time spent resting at temperatures > 27 °C (Scott et al. 2017; **Chapter 3**). Whereas, routine activity and foraging frequency increase with temperatures up to 30 °C while foraging capacity declines sharply at temperatures > 30 °C (Scott et al. 2017; **Chapter 3**). In reality, there is likely a range of optimal temperatures for different functions of performance for *P. leopardus* (Angilletta 2002; Clark et al. 2013), which may assist them in mediating unfavourable temperatures in the wild. Latitudinal variation in activity patterns suggest that *P. leopardus* exhibit considerable behavioural plasticity in relation to spatial and temporal variation in ambient temperature, but individuals may be faced with an energetic trade-off. For example, individuals from Opal Reef (low-latitude) exhibited a preference for low activity at higher temperatures rather than more energetically expensive routine activity. Whereas, *P. leopardus* at Heron Island (high-latitude) reduced their time spent resting in preference of increasing burst activity at higher temperatures. Reduced motility (i.e. more time resting) at higher temperatures may have implications not only for the reproductive capacity of populations, i.e. individuals may choose to forgo spawning related movements in order to conserve energy, but also for fisheries viability of this valuable species. For example, increased periods of inactivity may make fish easier to catch and more likely to take bait at higher temperatures rather than using energy for foraging. Alternatively, if they choose to move to cooler, deeper waters or remain in sheltered habitats away from strong currents, this may alter fishing effort or practices (e.g. fishing at greater depths).

This study is the first to use biologging to demonstrate spatial and temporal differences in activity patterns of a free-ranging, predatory coral reef fish in response to seasonal and latitudinal differences in temperature. Given the fundamental importance of locomotor performance to the survival and function of fishes, this study adds to the range of changes in behaviour and activity patterns of reef fishes in response to ongoing environmental change (Currey et al. 2015; Pratchett et al. 2018). Any alterations to movement patterns may impact trophic food webs and the function of fish communities (Rizzari et al. 2015; Frisch et al. 2016), potentially increasing vulnerability to exploitation. It appears likely that low-latitude populations of *P. leopardus* on the Great Barrier Reef may be living close to their thermal optima and although individuals have the capacity to regulate their behaviour, further increases in ocean temperature may have negative consequences for fitness and performance of this important species. Future studies would therefore benefit from investigating individuals from even lower latitudes (i.e. in the Western Pacific) to determine whether populations closer to the equator exhibit physiological adaptations to higher temperatures.

The ability of biologging to increase our understanding of activity and movement patterns (as well as foraging patterns) may help to inform bioenergetic models and provide insight into population dynamics of important fisheries species under changing environmental regimes (Essington 2003; Hasler et al. 2012; Cooke et al. 2016). Future research should seek to estimate the relationship between acceleration, swim speeds, metabolic rates, and temperature to evaluate daily and seasonal energetic requirements for wild *P. leopardus* to help determine how energetic budgets may be altered by environmental change (Gleiss et al. 2011; Brodie et al. 2016). Incorporating temperature-induced behavioural changes into predictions of how species will be affected by future climate warming is an important component for anticipating species responses to future change (Nagelkerken & Munday 2016; Abrahms et al. 2018).

Chapter 6 Fine-scale space use and activity patterns of latitudinally distinct predatory reef fish, *Plectropomus leopardus*

Manuscript in preparation

6.1 Introduction

Patterns of movement and space use by mobile animals have important influences on access to resources (Hussey et al. 2015), risk of predation (Furey et al. 2013), sociality (Alanara et al. 2001) and reproductive success (Samoilys & Squire 1994), as well as potentially moderating exposure to extreme and changing environmental conditions (Kahler et al. 2001). Importantly, the suitability of habitats can vary spatially and temporally, such that organisms may need to move between habitats to maximise fitness (Furey et al. 2013), though there are likely to be inherent trade-offs among the various biotic and abiotic factors that determine which habitats are most optimal. Diurnal cycles are among the most predictable environmental cues to which organisms are exposed, and a significant driver of biological and ecological activity patterns (Kronfel-Schor & Dayan 2003).

In the marine environment, diurnal rhythms allow animals to adapt to and anticipate environmental changes and choose the right time for a given response or activity (Aronson et al. 1993). Fishes generally exhibit regular fluctuations in their locomotor and feeding activity over diel and seasonal cycles (Sánchez-Vázquez et al. 1996). While seasonal fluctuations allow fish to cope with predictable changes in the environment (Daan 1981), diel patterns result from the need to concentrate vital activities to the time of day when the balance between food availability and predation risk is best (Helfman 1986). Fishes vary in the extent to which they are diurnally or nocturnally active depending on their physiological and mechanical adaptations to specific light conditions (Fox & Bellwood 2011). However, fish may modify their diel rhythms in relation to a range of environmental conditions, such as social interactions (Alanara et al. 2001), nutritional status (Metcalfe & Steele 2001), rainfall (Travers et al. 2006), tides (Taylor et al. 2013), wave exposure (Fulton & Bellwood 2004) and temperature (Freitas et al. 2015).

Many fishes move between habitats (on hourly, daily or seasonal scales), thereby experiencing different environmental conditions (e.g., varying ambient temperature), which will in turn affect their metabolic rates (Brown et al. 2004), foraging (Cartamil & Lowe 2004), mobility (Azumaya

& Ishida 2005; Thums et al. 2013), and digestion (Neverman & Wurtsbaugh 1994). One of the best opportunities that fishes have to exploit heterogeneity within their environment is with depth (Goyer et al. 2014) as there are marked changes in light and temperature over relatively short distances (Bertolo et al. 2011). Quantifying if and how fishes respond to temporal and spatial variation in environmental conditions can generate a better understanding of population fitness and potential for adaptation. Until recently, most research on space use by fishes was concerned with measuring species-specific home ranges, based on the maximal extent of the area used (Nash et al. 2014; Scott et al. 2018), often assuming that home ranges were static and rarely considering differential use of areas within their home range. Moreover, space-use by fishes is generally measured in only the horizontal plane (but see Simpfendorfer et al. 2012; Roberts et al. 2017), largely due to technological limitations in measuring depth use. Recent technological advances have allowed for fine-scale spatial and temporal measurements of depth use, providing much higher resolution analysis of movement and space use in three dimensions (Cooke et al. 2005; Udyawer et al. 2013).

Common coral trout, *Plectropomus leopardus*, are an important fisheries species throughout the tropical Indo-West Pacific (Frisch et al. 2016). *Plectropomus leopardus* are also an ecologically important mesopredator capable of influencing the structure and function of coral reef communities (Emslie et al. 2015; Rizzari et al. 2015; Frisch et al. 2016). It is critical therefore, to establish vulnerabilities of these species to changing environmental conditions. To date, studies have shown that *P. leopardus* exhibit spatial and temporal variation in habitat and space use as well as activity patterns in relation to seasonal and annual fluctuations in environmental characteristics (Zeller 1998; Matley et al. 2015, 2016; Scott et al. 2018; **Chapter 6**). However relatively few studies have looked at diurnal variation in habitat use (but see Matley et al. 2016) and activity patterns of *P. leopardus* at a high-resolution. Diel movement patterns and habitat use of large-bodied coral reef fishes may be limited due to high levels of site fidelity and strong microhabitat associations (e.g., Rummer et al. 2014). However, recent studies have demonstrated that some large-bodied coral reef fishes move to cooler, deeper waters when they experience elevated temperatures (Richards et al. 2012; Currey et al. 2015) and shelter under tabular coral structures during times of day when solar irradiance is strongest (Kerry & Bellwood 2015).

The purpose of this study was to investigate spatial variation in activity patterns (i.e., burst, routine, resting) and three-dimensional (3-D) activity space of *P. leopardus* from two latitudinally distinct locations on Australia's Great Barrier Reef. Building upon my previous chapters, this study uses a combination of accelerometry and depth data to examine fine-scale movement patterns of *P. leopardus* within high-density acoustic telemetry arrays over the course of a year. My previous chapters have identified increases in foraging frequency (**Chapter 3**), but reductions in home range (**Chapter 4**) and activity patterns (**Chapter 5**) for *P. leopardus* from a low-latitude location in response to increases in ambient temperature. However, there is not currently any information regarding changes in localised patterns of depth and habitat use, as well as activity patterns at smaller temporal scales (i.e., daily, monthly). Taking this into account, I expected that *P. leopardus* would exhibit latitudinal differences in daily depth use, 3-D activity space and activity patterns based on diurnal cycles (depending on time of year) and diel fine-scale temperature variation. More specifically, individuals from the low-latitude location exposed to higher temperatures are expected to use deeper depths throughout the hottest times of year to exploit depth as a thermal refuge, and this may be reflected in activity space metrics. Further, latitudinal variation in activity patterns of *P. leopardus* would exhibit diurnal variation to reflect differences in foraging, sheltering and locomotory behaviour between locations.

6.2 Materials and Methods

6.2.1 Study sites

This study took place at two latitudinally distinct locations on Australia's Great Barrier Reef (GBR). The northern (low-latitude) location was Opal Reef (16°14'20.77"S, 145°52'12.59"E), and the southern (high-latitude) location was Heron Island Reef (23°25'57.86"S, 151°55'57.65"E) (Figure 2.4). Daily temperatures were recorded on four temperatures loggers (Vemco Minilog-II-T) attached to receivers at approximately 7 m depth (see **Figure 5.1** for monthly temperatures).

6.2.2 Field Methods

Acoustic tracking was undertaken to monitor movement and activity patterns of *P. leopardus*. Between 14-18 Vemco VR2W acoustic receivers (Vemco Ltd., Halifax, Canada) were established on the leeward side of each reef (**Figure 4.1**). Receivers were deployed ~ 2 m above the substrate (reef or sand) using a chain and float mooring and set approximately 100 m apart in three lines (**Figure 4.1**, see **section 4.2** for more detail). Between adjacent receivers, the maximum distance was ~ 120m. Estimates of detection ranges between receivers were 50 – 120 m, resulting in ~90% acoustic coverage of the area (see **section 4.2.2** for more detail). Detection range at each site was factored into the sampling design and verified before any tagged fish were released into the array. Data were downloaded in May and September 2016.

From each location, 19 adult (> 35 cm) *P. leopardus* were caught using barbless hooks, anesthetized in Aqui-S® (~ 30 L) diluted with seawater (1:10000), and a V13A-P transmitter (13 mm x 42 mm) was surgically implanted into the abdominal cavity. Each transmitter had a pressure (depth) and accelerometer (acceleration) sensor and was programmed to randomly emit a unique coded signal every 60-120 seconds, with an expected battery life of 349 days. For this study, we were interested in both depth and acceleration data. In total, fish were detected for 351 days at Opal Reef and 357 days at Heron Island (see **Table 4.1**).

6.2.3 Calculating levels of activity

Latitudinal differences in daily activity patterns for *P. leopardus* were investigated by classifying acceleration values into three groups: i) burst activity (BA), ii) routine activity (RA), and iii) low activity (LA) based on the distribution of values for each individual (see **section 5.2.3** for more detail). Burst activity (m.s^{-2}) was calculated as the mean of the top 10% of acceleration values for each individual throughout the sampling period. Burst activity in this study was generally defined as maximum acceleration sustained for less than 10 seconds (*pers.obs.* M.Scott, 2016, **Chapter 5**). From *in situ* observation, burst events for *P. leopardus* are generally linked to foraging events rather than predator evasion (Scott et al., 2017, **Chapter 3**). Burst activity values ranged between 1.04 – 4.9 m.s^{-2}. Low activity (LA m.s^{-2}), classified as resting or stationary behaviour was calculated as average of the bottom 20% of acceleration values for each individual. Low activity values ranged between 0.01 – 0.35 m.s^{-2}. Finally, routine (or voluntary) activity (RA m.s^{-2}) was defined as the middle 70% of acceleration values and values ranged between 0.35 – 0.99 m.s^{-2} (see **Figure 5.2**).

6.2.4 Data analysis

All data from receivers were analysed in the R environment, version 3.4.4. Detection data were examined to identify any spurious detections (e.g., data that represented fast, erratic movements consistent with fish consumed by a predator) or lacked vertical movement aside from a consistent tidal signature (i.e. individual had perished). Fish with these detection characteristics were assumed to have perished and were removed from analyses. For individuals detected on > 15 days by two or more receivers, average positions were calculated at 15 min intervals (see Scott et al. 2018, **section 4.2** for more detail). To estimate diel individual space use, four discrete periods were selected from the data to represent dawn, day, dusk and night. The hours selected for dawn (0400-0659), day (0700 – 1659), dusk (1700-1959) and night (2000 – 0359) were based on timing of local sunrise and sunset and astro-twilight calculated across the 12 months of monitoring. Since dawn and dusk behaviours typically occur over 1 hour of changing light (Howard et al. 2013), a portion of these periods would likely encompass day and night behaviours.

Depth use

Fish depth utilisation patterns were derived from the transmitter pressure sensor. Mean depth (m) was calculated for each individual, for each month (1-12), in each hour (0-23). To assess the influence of various predictor variables on depth use, we used repeated measures analysis of variance (RM-ANOVA). Mean depth was treated as the response variable and hour, time period (dawn, day, dusk, night), location, temperature and fork length (to the nearest mm) were modelled as fixed factors. Temperature was averaged every 10 minutes for each day to detect any fine-scale temperature differences. For all models, individual fish was treated as a random effects term to account for the lack of temporal and spatial independence among individuals and reduce the effect of individuals with more detections. First-order correlation structure (corAR1) was also incorporated into the models to account for serial autocorrelation (a violation of the assumption of independence in model-fitting). There was no residual serial correlation (evaluated using the 'acf' autocorrelation function in R).

Three-dimensional (3-D) activity space use

The development of 3-D kernel utilisation distributions (3-D-KUD) models has enabled the integration of both horizontal and vertical movement together to reveal new insights (in three dimensions) into fish volumetric space utilisation (Simpfendorfer et al. 2012). Core (50% 3-D-KUD) and extent (95% 3D-KUD) of 3-D activity space use by *P. leopardus* were calculated using code adapted from Simpfendorfer et al. (2012) and Cooper et al. (2014) in the '*ks*' package (Duong 2007) in the R environment and rendered using the '*rgl'* and '*misc3d*' packages (Feng & Tierney 2008; Adler & Murdoch 2016). To determine latitudinal variation in daily core and extent of 3-D activity space use of *P. leopardus* we used RM-ANOVA. Measures of 3-D space use were log transformed to normalise the data before analysis. Here, 3-D activity space (50 or 95% 3-D-KUD) was the dependent variable and various combinations of; hour, time period (dawn, day, dusk, night), and month, location, temperature and fork length (to the nearest mm) were the independent variables. Models were constructed using with the '*lme'* function with restricted maximum likelihood from the '*lme4'* package (Bates et al. 2013) with the R statistical environment.

Activity patterns

To determine any latitudinal variation in daily activity patterns of *P. leopardus* the proportion of detections of each activity level; burst, routine, low were analysed. To do this, I calculated the average number of hourly detections for each individual per day and divided the total number of detections per hour by the number of detections of each activity level in each hour. This provided a proportion of detections of each activity level per hour. There was no indication of overdispersion in the residuals, so these data were logit transformed to satisfy model assumptions and analysed using a generalized linear mixed effects model with a binomial distribution and fish treated as a random effect within the '*lme4'* package (Bates et al. 2013).

6.3 Results

6.3.1 Depth use

Plectropomus leopardus made extensive use of vertical space within their habitats, ranging in depth from 1-22m. However, the average depth recorded (by hour and month) was between 10 – 13 m (**Figure 6.1**) and there was no overall difference in patterns of depth use among individual fish ($F = 0.14$, $p = 0.71$). The inter-quartile range (i.e. middle 50% of depths used) was 8.4 – 14.0 m and the middle 95% of depths used was between 4.5 – 17.2 m. Despite remarkable consistency in patterns of depth use across all tagged fish both within and among locations (Opal; $F= 0.03$, $p =0.86$, Heron; $F= 0.44$, $p = 0.51$), depth use did vary temporally both diurnally and seasonally. In general, *P. leopardus* used shallower depths during the day and deeper depths at night ($F= 843.09$, $p < 0.001$; **Figure 6.1a**). Among seasons, individuals utilised deeper depths during the austral summer months (December 2015 – February 2016) and shallower depths in winter (June– August 2016) (Fig 2b). It was apparent however, that in winter, *P. leopardus* from Opal Reef used shallower depths compared to conspecifics at Heron Island (**Figure 6.1b**).

Whilst monthly depth use corresponded to monthly variation in ambient temperature (**Figure 6.1b**), *P. leopardus* exhibited location specific responses to temperature. At Opal Reef as temperature increased, *P. leopardus* utilised deeper depths ($F= 661.69$, $p < 0.001$), however at Heron Island *P. leopardus* used shallower depths with increasing ambient temperature ($F= 100.69$, $p < 0.001$). At all temporal scales (hour and month) however, average depth range occupied were notably small (< 3) and consistently between 10 – 13 m (**Figure 6.1**).

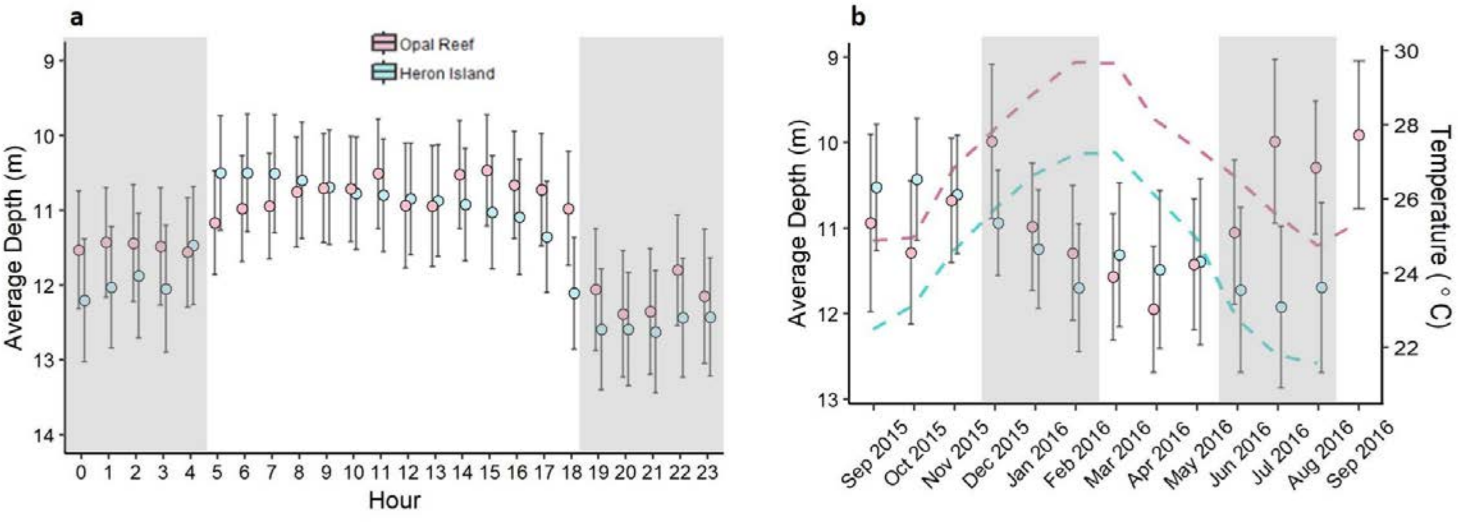

Figure 6.1: Depth use (mean ± SE) for *P. leopardus* grouped by (a) hour of day (grey shaded areas indicate night time) and (b) month of year (grey shaded bars indicate summer and winter) at Opal Reef (pink circles) and Heron Island (blue circles).

6.3.2 Volumetric activity space use

There were marked differences between locations in both core (50% 3-D-KUD) and extent (95% 3-D-KUD) of 3-D activity space. Most notably, the 50% 3-D-KUD for *P. leopardus* at Heron Island (29511 m^3) was nearly three times higher than at Opal Reef (11371 m^3), with the most pronounced differences occurring during the day (**Table 6.1**). Similarly, 95% 3-D-KUD was > 2 times greater at Heron Island (218218 m^3) compared with Opal Reef (94525 m^3) (Fig. 3). Fish size did not influence core (F= 0.99, p =0.42) or extent (F= 0.04, p =0.33) of 3-D activity space for *P. leopardus* at Opal Reef, whereas at Heron Island, larger fish occupied greater 50% 3-D-KUDs (F= 4.82, p =0.04), but not 95% 3-D-KUDs (F= 0.44, p = 0.51), compared with smaller individuals. The activity space of *P. leopardus* also varied on diurnal cycles (**Figure 6.2**), peaking during the day whereas fish were largely inactive throughout the night.

Table 6.1: Mean ± SE core 3-D space use (50%3-D-KUD) and extent (95%3-D-KUD) for both locations in total, and during dawn, day, dusk and night.

	Opal Reef (m^3)		**Heron Island (m^3)**	
	50%3-D-KUD ± (SE)	**95%3-D-KUD ± (SE)**	**50%3-D-KUD ± (SE)**	**95%3-D-KUD ± (SE)**
Dawn	8461.13 ± 522.72	74757.9 ± 3761.50	34592.0 ± 3474.02	235769.4 ± 18938.44
Day	19634.15 ± 834.42	160626.56 ± 5278.02	50132 ± 3085.59	374634.2 ± 17368.96
Dusk	13409.93 ± 727.68	106526.73 ± 4712.96	20836.86 ± 2309.89	154005.8 ± 13859.43
Night	4178.27 ± 351.30	37458.74 ± 2455.54	3918.0 ± 661.43	49223.1 ± 6571.064
Total	11370.69 ± 388.63	94525.39 ± 388.62	29510.72 ± 1617	218218.3 ± 9755.64

At a daily scale, location-specific differences in 3-D activity space varied with time period (**Figure 6.2)**. At Heron Island *P. leopardus* occupied larger 50% (**Figure 6.2a**) and 95% (**Figure 6.2b)**. 3-D activity spaces during dawn and day time, whereas at Opal Reef individuals occupied larger volumes of activity space during the day and dusk (although far less than their high-latitude counterparts) (**Figure 6.2a&b, Figure 6.3a&b**). Variation in diurnal patterns of 3-D activity space suggests *P. leopardus* exhibit location-specific preferences in habitat use and activity patterns with time of day. Unsurprisingly, there was no difference in 3-D activity space at night when *P. leopardus* are assumed to be resting or inactive.

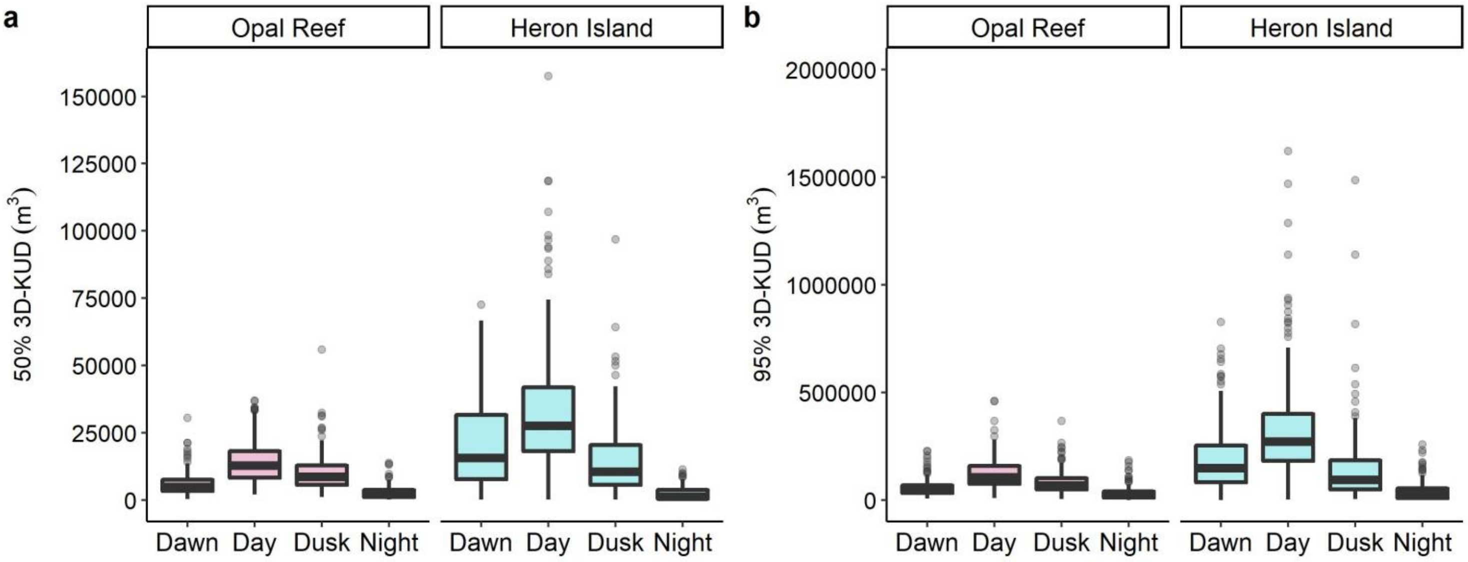

Figure 6.2: Comparison of the daily a) core (50% 3-D-KUD) and b) extent (95% 3-D-KUD) of volumetric activity space patterns for all tagged *P.leopardus* separated into time periods; dawn, day, dusk and night from Opal Reef (pink) and Heron Island (blue).

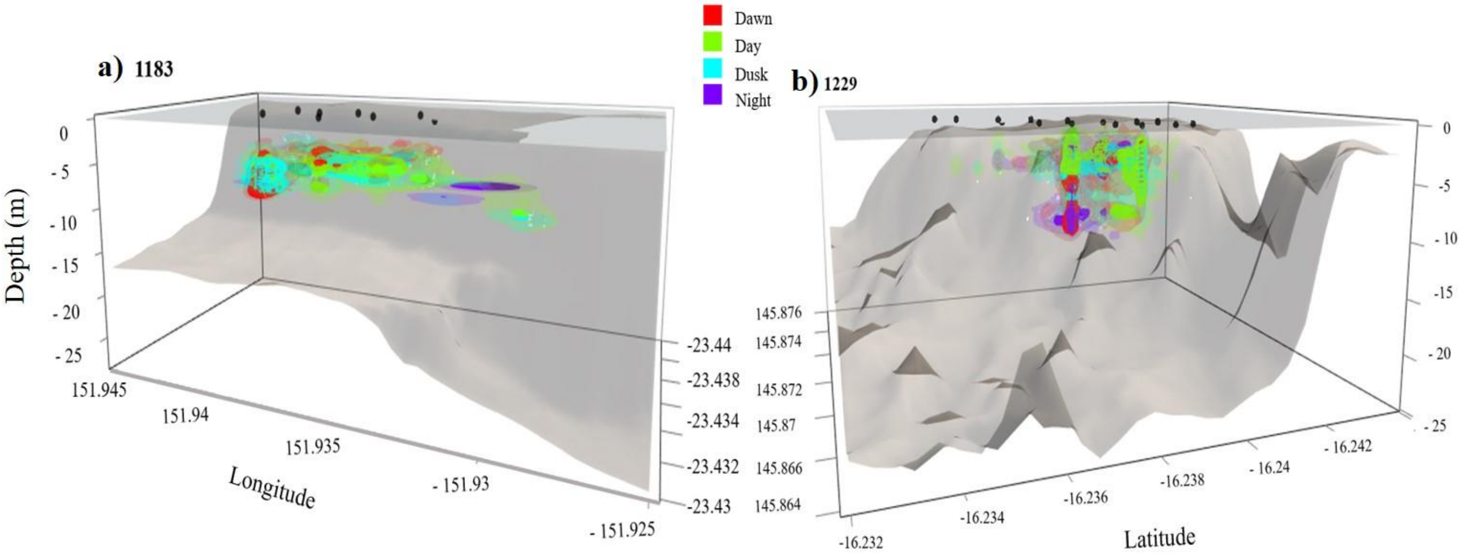

Figure 6.3: 3-D activity space utilisation across; dawn (red), day (green), dusk (blue), and night (purple) for two *P. leopardus* from a) Heron Island and b) Opal Reef. In each plot, the extent (95% 3-D-KUD) of habitat utilisation space is represented as the lighter, more transparent shade, and core (50% 3-D-KUD) habitat utilisation space is represented as the darker shade. The black dots represent the location of receivers within each array.

6.3.3 Diel activity patterns

Activity modes (i.e., the proportion of detections of activity; burst, routine, low activity) were investigated across the same four time periods (dawn, day, dusk, and night) to see whether diel activity patterns may explain any differences in daily 3-D activity space between locations (**Figure 6.4**). Burst activity (which can be used as a proxy for foraging) showed diel variation between locations (**Figure 6.4a**). In general, *P. leopardus* from Opal Reef were detected more frequently in burst activity compared with individuals from Heron Island. The proportion of burst activity detections at Opal Reef were greatest during the day (39%) followed by dusk (25%) (**Figure 6.4a**), a pattern that corresponded closely with diel 3-D activity space at Opal Reef. Whereas, at Heron Island the proportion of burst activity detections were relatively consistent between dawn (26%), day (23%) and dusk (23%) (**Figure 6.4a**). This pattern did not appear to correspond with daily 3-D activity space at Heron Island, suggesting larger space use at Heron Island may not necessarily be related to foraging attempts. There were very few burst activity detections at night at either location.

The proportion of daily routine activity detections indicate that *P. leopardus* from Heron Island tend to be more active (i.e. more routine activity detections at all time periods) compared with individuals from Opal Reef (**Figure 6.4b**). At Heron Island ~70% of detections were routine activity compared with ~60% at Opal Reef. In general, routine activity detections at both locations were fairly consistent throughout all time periods, including night time, suggesting that *P. leopardus* do not necessarily seek shelter in holes for long periods during the night. Unsurprisingly, the proportion of low activity detections were highest at night time at both locations presumably because *P. leopardus* are less active during this time (**Figure 6.4c**). However, individuals at Opal Reef were detected consistently more often at low activity at all time periods compared with individuals from Heron Island suggesting that individuals from Opal Reef spend a larger proportion of their day resting or inactive than their high-latitude counterparts. Latitudinal variation in daily activity patterns indicate that *P. leopardus* may exhibit location-specific preferences for resting, foraging, and moving throughout their habitat in relation to diel cycles.

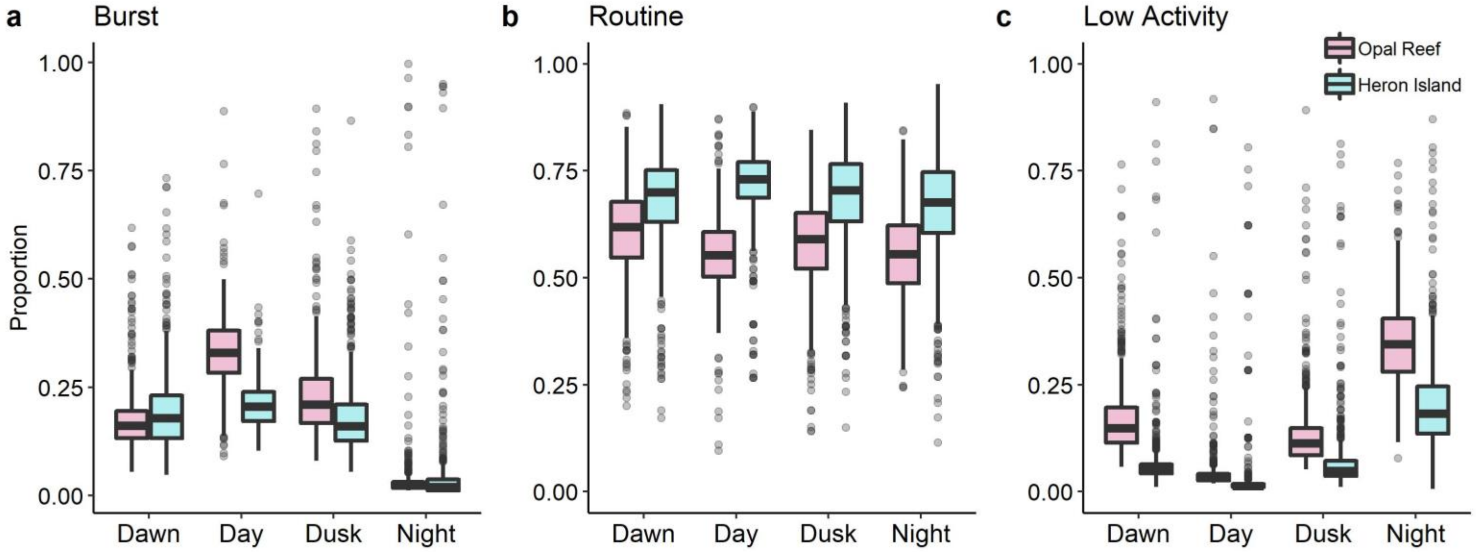

Figure 6.4: Comparison of daily activity patterns of *P. leopardus* determined by the proportion of detections at within each activity category; burst (a) routine (b) and low activity (c) at Opal Reef (pink) and Heron Island (blue).

6.4 Discussion

Fine-scale movements and corresponding use of different areas within the home range of fishes is fundamental in understanding how individuals access resources (Roessig et al. 2004), evade predation (Ohlund et al. 2015), and moderate exposure to sub-optimal environmental conditions (Goyer et al. 2014). This study shows that *P. leopardus* utilise slightly different depth strata throughout the day and trends were consistent between locations. Previous studies have demonstrated similar patterns of diel depth use, in which *P. leopardus* tend to occupy shallower depths during the day compared with night time (Matley et al. 2016) potentially due to diurnal foraging (Scott et al. 2017; **Chapter 3**) and taking shelter during the night (Zeller 1998). However, in this study, I show that average depth range of *P. leopardus* was relatively small (10 – 13 m). Despite this, *P. leopardus* did exhibit seasonal variation in depth use (± 3m), corresponding with variation in ambient temperature. At both locations, *P. leopardus* tended to utilise deeper depths during the summer months confirming similar patterns in previous studies (Matley et al. 2015; 2016). During the winter however, *P. leopardus* from Opal Reef (low-latitude) used shallower depths, whilst individuals at Heron Island (high-latitude) remained slightly deeper. These results may therefore represent an important mechanism by which these large and relatively mobile fish can moderate exposure to sub-optimal (especially supra-optimal) temperatures, particularly at low-latitude regions.

Irrespective of small differences in depth use, *P. leopardus* displayed substantial variation in 3-D activity space between locations across different times of day, peaking during daylight hours. The overall core (50% 3-D-KUD) and extent (95% 3-D-KUD) of maximum daytime 3-D activity space for *P. leopardus* was > 50% larger at Heron Island (high-latitude) compared with Opal Reef (low-latitude). Taken together, these results suggest that rather than exploiting their vertical environment, *P. leopardus* from the high-latitude location utilise a much broader horizontal environment compared to their low-latitude counterparts. These findings correspond with results from **Chapter 4** (Scott et al. 2018) in which horizontal home range estimates of *P. leopardus* from Heron Island were approximately > 25% larger than individuals from Opal Reef. Variation in space use for *P. leopardus* has been shown to correspond with seasonal fluctuations in ambient temperature (Matley et al. 2016; Scott et al. 2018; **Chapter 4**). Thus, broader horizontal space use may indicate location-specific physiological, energetic, and /or behavioural requirements under different thermal regimes. In this study, *P. leopardus* from Heron Island were more active than individuals from Opal Reef. Ambient temperatures at Heron Island are closer to the thermal optima (~27 °C) for *P. leopardus* (Pratchett et al. 2013; **Chapter 2**). Optimal temperatures enhance metabolic processes (Portner & Farrell 2008), and may therefore increase activity levels, for *P. leopardus* from the high-latitude location compared with individuals from Opal Reef where ambient temperatures regularly exceed 27 °C (**Chapter 5**), and may therefore, already moderate activity levels. Furthermore, broader horizontal space use may also be influenced by body size (Nash et al. 2015). In this study, *P. leopardus* from Heron Island were on average ~96 mm larger than individuals from Opal Reef and as such broader horizontal movements may indicate that individuals from Heron Island are more energetically driven to find prey, resulting in broader movements (Matley et al. 2016; **Chapter 5**).

Although 3-D space use was constrained at the low latitude location, analyses of activity patterns revealed that *P. leopardus* from Opal Reef had a greater frequency of burst activity (a proxy for foraging) at different times throughout the day compared with individuals from Heron Island, irrespective of body size. This increase in potential foraging activity by *P. leopardus* from the low-latitude location may be necessitated by increased metabolic requirements at higher ambient temperatures (Johansen et al. 2015; Scott et al. 2017; **Chapter 3**). Given the universal influence of temperature on metabolic rates of ectothermic fishes (Portner & Peck, 2010), *P. leopardus* may exhibit behavioural strategies favouring foraging opportunities at higher temperatures. Foraging is energetically expensive, and individuals may forage in areas and at times of day to minimise energy expenditure and maximise energy gain (Wilson et al. 2012; Brownscombe et al. 2014). Foraging activity of *P. leopardus* can vary among habitats and between reefs according to the availability of prey (Kingsford 1992; St John et al. 2001), and previous studies suggest that *P. leopardus* tend to forage primarily at dawn and dusk (Zeller, 1997). Crepuscular periods can be advantageous for foraging since low light levels can provide predators with an advantage (Pitcher & Turner 1986). However, this study reveals that potential foraging activity of *P. leopardus* (indicated by the frequency of burst detections) is also common during daylight hours, consistent with Scott et al. (2017) (**Chapter 3**). Overall, despite their low occupancy of 3-D space, burst activity detections were highest for *P. leopardus* from Opal Reef (low-latitude) during the day. This potential mismatch between 3-D activity space and foraging suggests, that *P. leopardus* from Opal Reef may not move far to forage (Scott et al. 2018; **Chapter 4**) and may be able to sustain themselves within small areas < 0.25 km^2 (Scott et al. 2018; **Chapter 4**).

Patterns in daily activity influence how species persist in their environment, adapt to different niches, and reduce the impact of competition by partitioning resources (Schoener 1974; Aronson et al. 1993). Increased 3-D activity space during the daylight hours (i.e., dawn, day, and dusk), suggests that *P. leopardus* are generally diurnal, a pattern reflected in previous studies (Zeller 1998; Matley et al. 2015, 2016). Other coral reef mesopredators show strikingly different daily activity patterns to that of *P. leopardus.* For example, *Lethrinus miniatus* (red throat emperor) exhibit primarily nocturnal mobility and foraging behaviour (Currey et al. 2015), whilst *Carcharhinus melanopturus* (blacktip reef shark) are primarily crepuscular and tend to be most active during the early evening and expand their foraging areas during the night (Papastamatiou et al. 2018). Differences in diel temporal partitioning between mesopredators may facilitate coexistence between potential competitors (Alanara et al. 2001). However, while *P. leopardus* were generally diurnal, these results reveal differences in crepuscular activity space use across locations, with individuals at Heron Island utilising more space at dawn, and individuals at Opal Reef utilising more space at dusk. This variation in diurnal activity space may relate to site-specific differences in temperature (**Figure 5.1**), competitor behaviour (Brannas & Alanara 1997), inter and intra-specific interactions (Harestad & Bunnel 1979), prey abundance and behaviour (Kingsford 1992) or habitat complexity (Wilson et al. 2012).

Incorporating depth into habitat-use analyses is critically important for understanding the space requirements of fishes (Simpfendorfer et al. 2012; Udyawer et al. 2015). However, our analyses of 3-D space use revealed that variations in depth on daily and seasonal temporal scales are minor compared to that of horizontal space use. Although *P. leopardus* were detected at a range of depths between 1 – 22 m throughout the study, and exhibit changes in depth use in relation to seasonal temperature fluctuations, individuals were mostly found between 10 – 13 m, and any differences in temperature over this limited depth range are likely to be negligible. Despite the known sensitivities of *P. leopardus* to their thermal environment (**Chapter 2**; Pratchett et al. 2013; Johansen et al. 2014; Messmer et al. 2016), these data do not really demonstrate that *P. leopardus* are using depth to moderate temperature exposure. Rather, as ocean temperatures continue to rise (IPCC 2018), individuals may be more likely to contract their horizontal movement and space use patterns (Scott et al 2018; **Chapter 4**) to regulate for supra-optimal temperatures in their environment (Pecl et al. 2017). The restricted range of depth use exhibited by *P. leopardus* in this study may also have implications for its fisheries. Approximately 85 % of the fishing pressure for *Plectropomus* spp. on the GBR is concentrated on sections of reef < 20 m (Little et al. 2008) such that the risk of capture decreases when deeper waters are selected. However, if the small variation in depth use exhibit by *P. leopardus* in this study is true for other individuals inhabiting environments < 20 m, this may increase their susceptibility to capture. Though, it remains to be tested whether broader horizontal movements of individuals at Heron Island may increase or decrease fisheries encounters, or if their removal will have larger reef-scale implications.

As an ecologically important mesopredator, the fine-scale habitat use and activity patterns of *P. leopardus* has important implications for population structure and abundance (Adams et al. 2000), predator-prey interactions (Rizzari et al. 2015), and trophic food webs (Boaden & Kingsford 2015). Using high-resolution biotelemetry, this study has provided new information on the fine-scale 3-D space use and activity patterns of this commercially important tropical fisheries species. Notably, alterations to habitat use and activity patterns due to changing environments may have consequences for ecosystem function exacerbating the need to understand how these strategies are implemented within a highly variable environment. Future studies would benefit from identifying very fine-scale temperature variations (~1 m resolution) to see whether *P. leopardus* are likely to exploit subtle temperature changes within their environment. Similarly, future studies may also benefit from identifying the depth distribution (and subsequent temperature profile) of *P. leopardus* at across a larger range of depths between 25 - 100 m to determine whether individuals may use depth as a thermal refuge, especially during the warmer months. This information could be used to evaluate the daily energetic requirements of *P. leopardus* by understanding how much energy is expended and how often animals use different habitats. Providing a gauge of the importance of particular habitats, can help to identify patterns in habitat-mediated energy partitioning that are otherwise difficult to observe (Udyawer et al. 2015, 2017). Ultimately, a greater understanding of habitat use and energy requirements of commercially important fisheries species will be vital for their management and conservation as their environment and habitat continue to change.

Chapter 7 General discussion

Global climate change is one of the major threats to coral reefs and reef organisms (Hughes et al. 2018), potentially undermining important revenue and food security provided by coral reef fisheries (Bell et al. 2013). While further work is required to assess differential vulnerabilities of major fisheries species and potential alternative species, thereby establishing which species should be targeted under altered environmental conditions (Graham et al. 2014), it is clear that some fisheries species are extremely vulnerable to changing environmental and habitat conditions.

Coral trout (and mainly *Plectropomus leopardus*) are among the most important coral reef fisheries species on the Great Barrier Reef and throughout the Indo-Pacific (Randall & Hoese 1986; Ralston 1987) and appear to be extremely sensitive to increasing ocean temperature (**Chapter 2**). More specifically, in experimental studies, *P. leopardus* subjected to elevated temperatures (> 30 ºC) exhibit declines in aerobic scope (Messmer et al. 2016), movement (Johansen et al. 2014) and survivorship (Clark et al. 2017). Moreover, experimental tests on effects of ocean acidification show that *P. leopardus* exhibit disrupted sensory discrimination when exposed to elevated partial pressures of CO_2 (Munday et al. 2013), which is consistent with effects of ocean acidification reported for other coral reef fishes (Dixson et al. 2010; Ferrari et al. 2011). These findings lead to justifiable concerns regarding the viability and sustainability of reef fisheries, particularly at low-latitudes where maximum summer temperatures already exceed temperatures (> 30 ºC) that adversely affect coral trout. However, controlled experiments and the necessary short duration of these studies fails to account for potential thermoregulatory behaviour or other mechanisms of acclimation and acclimatisation that may moderate effects of environmental change.

In the wild, fishes may respond to environmental change in several ways. Firstly, fishes may increase consumption rates to buffer temperature induced increases in metabolic rates (Buentello et al. 2011; Johansen et al. 2015). In **Chapter 3**, I show that coral trout increase food intake in accordance with natural variation (seasonal and latitudinal) in ambient temperature (**Chapter 3**). If food is limited however, fish may be forced to conserve energy through a reduction in movement and activity. Similarly, this thesis demonstrates that *P. leopardus* contract their home range and increase resting patterns corresponding with increasing ambient temperature (**Chapters 4 & 5**). Finally, fish may seek out thermally favourable habitats by exploiting fine-scale heterogeneity within their environment. In **Chapter 6**, I demonstrate that *P. leopardus* exhibit notably small (< 3 m) changes in depth use in response to ambient temperature. Rather, it appears *P. leopardus* are more likely to alter their horizontal space use as a response to supra-optimal temperatures (**Chapter 6)**. If *P. leopardus* are able to modify their behaviour it is likely that this species may be generally resilient to short-term and moderate changes in environmental conditions, but physiological limits may ultimately constrain their capacity to endure longer-term and more severe ocean warming (e.g., Munoz et al. 2015).

7.1 Summary and synthesis of findings

This thesis represents a novel and timely investigation of behavioural changes in *P. leopardus* that correspond with natural variation in environmental conditions, and mainly temperature. A combination of *in situ* observation and passive acoustic telemetry was used to investigate latitudinal and seasonal variability in specific aspects of behaviour. Behaviours were selected based on their capacity to regulate temperature-induced increases in metabolic processes in the wild. These were; foraging activity and resting behaviour (**Chapter 3**), space use and home range (**Chapter 4**), activity patterns (**Chapter 5**) and depth use and 3-D activity space (**Chapter 6)**. Overall, I found substantial latitudinal variation in several aspects of behaviour for *P. leopardus* that generally corresponded to seasonal fluctuations in temperature. First, I showed foraging activity for *P. leopardus* was highest during the summertime at a low and high-latitude location, with strike rates increasing in accordance with increasing temperature up to 30 °C. However, above 30 °C, strike rates declined, indicating a potential thermal threshold above which *P. leopardus* may switch to conserving energy and forsaking increased foraging activity (**Chapter 3**). This potential energetic trade-off may have long-term ramifications for *P. leopardus*, particularly from low-latitude locations, that are already exposed to summertime temperatures > 30 ºC. Reductions in movement and activity may decrease foraging efficiency and the ability to capture prey (Ohlund et al. 2015) potentially reducing food intake and resulting in a decline in body condition for *P. leopardus* (Grayton 1977). This may have consequences for the fitness, performance and survival of individuals. Further, *P. leopardus* are known to make spawning related movements during austral spring (Samoilys 1997). Any reduction in activity patterns could directly influence population replenishment and the viability of fisheries stocks through reduced visits to spawning sites, and subsequent decline in larval export and dispersal. This in turn may affect species demography through changes to longer term activity patterns and space use (Andrew & Mapstone 1987).

Using acoustic telemetry, this thesis quantified spatial and temporal variation in movement and space use patterns of *P. leopardus*, relating this to seasonal and latitudinal variation in ambient temperature. Notably, *P. leopardus* reduced their home range during the summertime at both a low and high-latitude location, however this effect was more pronounced at the low-latitude location where individuals initiated a contraction in home range at temperatures > 27 °C (**Chapter 4**). Accelerometry tags (measuring acceleration) placed in the same individuals to investigate latitudinal and seasonal variation in activity patterns, revealed that whilst activity increased with increasing temperature up to 30 °C, *P. leopardus* from the low-latitude location were twice as likely to be detected resting than their high-latitude counterparts. These results indicate that *P. leopardus* may reduce activity in order to conserve energy at higher ambient temperatures (**Chapter 5**).

Chapter 6 combines telemetry and depth data to examine the fine-scale activity patterns and corresponding use of different areas within the home range of *P. leopardus* to determine the variation relation to fine-scale temperature variation and daily cycles. These results show that irrespective of location, *P. leopardus* occupied a limited range of depths throughout the year, between 10 – 13 m. However, individuals from the high-latitude location occupied far larger 3-D activity space than *P. leopardus* from the low-latitude location. This suggests that *P. leopardus* are more likely to contract their horizontal space use with increasing ambient temperature, rather than exploit a greater range of depths within their environment. Taken together, results from this thesis illustrate that although *P. leopardus* are able to modify their behaviour in response to variation ambient temperature, it appears likely that low-latitude populations of *P. leopardus* will be negatively impacted by continued increases in ocean temperature. As such, the natural activity patterns of *P. leopardus* may be altered as individuals are forced to make energetic tradeoffs between conserving energy versus increasing food intake.

Finally, the observed differences in behavior of *P. leopardus* found in this thesis strongly correspond with variation in ambient temperature. However, aside from temperature, there may be other biotic and abiotic factors that influence latitudinal differences in *P. leopardus* behavior. These include site-specific differences in; habitat structure topography, wave exposure, and currents as well as prey availability. Without accounting for all these potentially confounding variables we cannot explicitly attribute spatial differences in behaviour to temperature alone. However, the influence of temperature on the physiology and behaviour of ectothermic fishes is indisputable (Portner & Knust 2007; Pauly 2010).

7.2 Ecological and management implications

7.2.1 Ecological implications

The ecological, social and economic importance of *P. leopardus* (**Chapter 2**) means that results from this thesis have critical ecological and management implications. Most importantly, field based observations from this study support previous findings from experimental studies highlighting that *P. leopardus* are sensitive to increasing temperature. These results suggest that future increases in temperature are likely to impact the behaviour of *P. leopardus* which may have important implications for ecological function, population viability and fisheries potential of coral trout, especially at low latitudes.

Mesopredators, such as *P. leopardus*, play an important ecological role on coral reefs in structuring assemblages of smaller bodied fishes (Rizzari et al. 2015; Boaden & Kingsford 2014). Alterations to their foraging capacity, activity patterns, home ranges, and habitat use may therefore have important and far reaching ecological ramifications. Firstly, temperature induced increases in metabolic rates will almost certainly necessitate increased foraging for *P. leopardus* (**Chapter 3**). Alterations to foraging behaviour is likely to directly impact multiple trophic layers of food web (Rizzari et al. 2015), the health of the ecosystem (Boaden & Kingsford 2014), and even the potential viability of reef-based fisheries (Tobin et al. 2013). Changes in foraging behaviour of *P. leopardus* will likely have implications at lower trophic levels (Rogers et al. 2014), and these changes will be further compounded by bottom-up processes (Graham et al. 2006) and climate induced changes in habitat structure (Hoegh-Guldberg et al. 2010; Hughes et al. 2017). However, I have shown the foraging capacity of *P. leopardus* decreased at temperatures > 30 °C suggesting that higher temperatures may impose significant constrains on the capacity of *P. leopardus* to obtain sufficient prey resources whilst simultaneously conserving energy (**Chapter 3**). Any reduction in movement and activity patterns (**Chapters 3, 4, 5 & 6**) are likely to not only influence foraging capacity by directly influencing prey encounter rates and an ability to avoid predators (Blake 2004), but may also elicit contraction in home ranges and space use (**Chapter 4**).

A decrease in space use and home range patterns for *P. leopardus* at higher temperatures may have implications for population dynamics and viability of fishery stocks under changing environmental conditions. In **Chapter 4** I showed that the home range of *P. leopardus* is relatively small (< 0.35 km^2) and further contracts with increasing ambient temperature. Such high site fidelity comes with associated costs and benefits. For instance, high-site fidelity confers advantages through site familiarity in terms of optimising habitat, seeking shelter, and finding prey (Wakefield et al. 2015). However, individuals that exhibit high site fidelity will be more susceptible to habitat disturbance (Faille et al. 2010). This is particularly relevant for *P. leopardus* on the GBR, and throughout much of their range, where habitats have undergone substantial coral loss and modification in recent years (Cheal et al. 2017; Hughes et al. 2017). Whilst the direct importance of live coral cover for *P. leopardus* remains unclear, *Plectropomus* spp. often use live coral habitats during settlement phase (Leis & Carson-Ewart 1999; Wen et al. 2013), and are known to shelter under tabular corals (Kerry & Bellwood 2012) and forage on prey directly reliant on live coral (St John et al. 2001). Increasing environmental disturbances, particularly on reefs with high abundances of *P. leopardus* may place increasing strain on limited prey resources altering food webs and trophic interactions (Feary et al. 2014).

7.2.2 Management implications

This thesis has highlighted latitudinal variation in the susceptibility of *P. leopardus* to ocean warming (see also; Johansen et al. 2014, 2015; Messmer et al. 2016), necessitating regional variation in fisheries management. On the GBR, for example, spatially explicit restrictions on catch and stock size may be necessary for low-latitude populations. Fishing effort and catches of *P. leopardus* are already much higher in the southern GBR, compared to the northern GBR (Leigh et al. 2014), largely reflecting differences in the condition and abundance of fishes from the different regions (Leigh et al. 2014). Such differences are likely to be further magnified with ocean warming and global climate change but need to be explicitly managed both to ensure that fish stocks in the northern GBR are sufficient to maintain the ecological integrity of these systems, as well as preventing further concentration of effort and potential overfishing in areas with highest abundance of these species. Adaptation options exist for the sustainable management of this important fishery that capitalise on existing management regimes (already implemented on the GBR) but should also ensure better compliance (QDAF 2017) and quicker responsiveness in adaptive management (Koehn et al. 2011). The capacity of wild stocks to withstand environmental change is undermined by excessive exploitation (e.g., Hsieh et al. 2008) and other anthropogenic threats to fisheries species and habitats (Pratchett et al. 2011). The best adaptation options will therefore maximise ecosystem and economic resilience to a wide range of threats (e.g., Pecl et al. 2009; **Chapter 2**). Ultimately, it is imperative to consider climate risks and vulnerabilities in new management regimes and measures to reduce global greenhouse gas emissions and the ensuing impacts to coral reefs and associated fisheries is vital (see **Section 2.2**).

While ongoing ocean warming will almost certainly have adverse effects on *P. leopardus*, moderate and short-term increases in ocean temperature may benefit reef fisheries. Increased foraging frequency (**Chapter 3**) combined with potentially decreased feeding opportunities under warming oceans (Tobin et al. 2013) may compel *P. leopardus* to take bait and therefore increase fishing opportunities. Similarly, although *P. leopardus* occur across a wide range of depths in the environment (up to 100m, Sih et al. 2017), the limited depth range (10 – 13 m) exhibited by tagged *P. leopardus* in **Chapter 6**, indicates that individuals inhabiting shallower environments (< 20 m) may be consistently vulnerable to capture given the majority of fishing effort for coral trout occurs < 20 m (Little et al. 2008). As such, ocean warming may bring short-term gains in catches, which will need to be carefully managed to avoid over-exploitation and collapse of already threatened stocks.

7.2.3 Future directions

Results from this thesis, in combination with other recent research on the thermal sensitivities of *P. leopardus*, have significantly improved our understanding of the influence of temperature on physiology, movement, activity and behaviour of this important fisheries species (Pratchett et al. 2013; Johansen et *al.* 2015; 2015, Messmer et al. 2016; Scott et al. 2017; **Chapter 3**; Scott et al. 2018; **Chapter 4**). This thesis provides the first investigation of *in situ* behaviour of wild stocks of an important fisheries species in relation to variation in ambient temperature. As such, there are numerous gaps for future research to build and expand upon. Firstly, future studies would benefit from investigating the amount of variability in marine environments and whether, given the opportunity, fishes may exploit this variation to moderate exposure to extreme temperatures. To do this, increased sampling at additional sites within each latitude, as well as expanding sampling to encompass a broader latitudinal gradient, i.e. at central (mid-latitude) locations on the GBR and at lower-latitudes towards the equator, is recommended. An increase in the latitudinal range of sampling locations would help to establish specific thresholds in behavioural responses of *P. leopardus* from low – high latitude regions across the GBR. This information could then be used to ascertain whether *P. leopardus* exhibit any capacity for thermal acclimation at local scales, which is currently thought to be limited (Pratchett et al. 2016; **Chapter 2**). In addition to sampling larger geographic areas, future studies would also benefit from identifying very fine scale temperature variations (~ 1 m resolution) either with depth or between habitats (i.e. lagoonal versus reef slope) at an individual reef scale. To further this, future studies would benefit from sampling at deeper depths (i.e. up to 100m), and across a larger thermal gradient, that are known to encompass *P. leopardus* depth range (e.g. Heemstra & Randall 1993). This could help to determine whether *P. leopardus* are likely to exploit subtle temperature changes with small changes in depth and distance within their environment. Recent technological advances have already superseded the equipment used in the current study, enabling fine-scale measurements of depth use, while simultaneously measuring associated temperature and metabolic rates (based on heart rate) of tagged fishes (Norling et al. 2017).

The logical step after this, would be to use this information to evaluate the specific energetic costs of feeding and movement in coral trout, and determine whether these energetic costs can help explain behavioural strategies to increase food intake versus conserve energy at higher temperatures. Swimming respirometry is a common technique used to evaluate the energetic requirements of fishes. This method allows for the relationship between accelerometry, swimming speed, metabolic rate and temperature to be estimated under controlled conditions and compared with field measurements across temporal scales to determine if and how energetic budgets may be altered by environmental change (Payne et al. 2011; Gleiss et al. 2011; Brodie et al. 2016). Incorporating temperature-induced behavioural changes, as well as the selection of particular habitats for individuals can help to anticipate how species will respond to future environmental change (Nagelkerken & Munday 2016; Abrahms et al. 2018). Ultimately, increased knowledge of the energy requirements and habitat utilisation of commercially important fisheries species will be fundamental for their management and conservation as their environment and habitat continue to transform.

Chapter 8 References

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