Towards understanding how exploitation influences the wild energetic response of marine fish to temperature variability

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By

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Preface

This thesis consists of a general introduction (Chapter 1); a study site and species profile (Chapter 2); two research chapters (Chapter 3 and 4) and a general discussion (Chapter 5).

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Declaration

I, Michael Richard Skeeles, hereby declare that the work described in this thesis was carried out in the Department of Ichthyology and Fisheries Science, Rhodes University, under the supervision of Professor Warren Potts, Dr Amber Childs, Dr Alex Winkler and Dr Murray Duncan. The components of this thesis comprise original work by the author and have not been submitted to any other university.

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Abstract

Exploitation of fish populations can exacerbate the effects of climate change, yet our understanding of their synergistic effects remains limited. As fish are increasingly exposed to temperatures on the edges of their optimal thermal performance window, their physiological response is expected to shape their future performance. It is therefore concerning that exploitation can select for specific physiological phenotypes, as this may affect fished populations' physiological response to temperature change. A recent laboratory study revealed fewer high-performance metabolic-scope phenotypes in an exploited population of the marine Sparid *Chrysoblepus laticeps* across a range of experimental temperatures in comparison to an unexploited population. This suggested that individuals in exploited populations may have less available energy for aerobic performance at thermal extremes, which may reduce the resilience of the population to changes in temperature. However, since laboratory experiments exclude numerous other variables that fish encounter in the wild, it was necessary to test this finding in a natural setting.

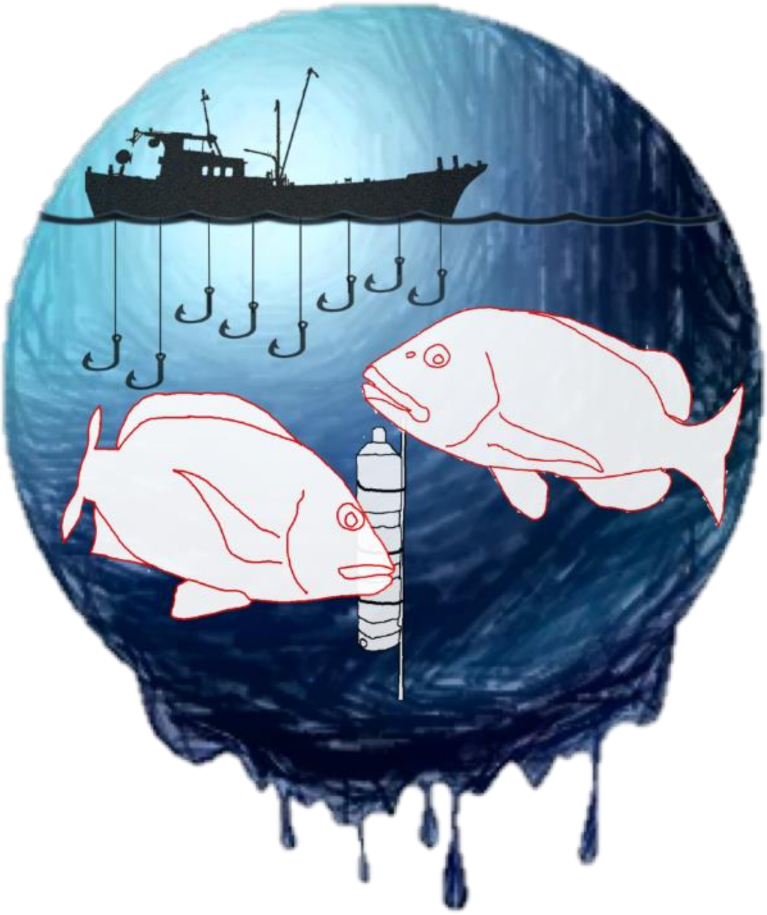
This thesis aimed to further develop the laboratory study by assessing whether exploitation effects the wild energetic response of *C. laticeps* to thermal variability. To achieve this, the field metabolic rate of *C. laticeps*, a resident and endemic South African fish, from a near-pristine population (Tsitsikamma National Park) and a heavily exploited population (Port Elizabeth) was compared using acoustic accelerometry.

A laboratory-based study using a swim-tunnel respirometer and accelerometer transmitters was conducted to develop a model to predict metabolic rate from acceleration data at temperatures from 10 to 22ºC. Acceleration, temperature, mass and population (exploited/unexploited) were found to be the best predictors of the metabolic rate of *C. laticeps* and were incorporated into the model to estimate the field metabolic rate of fish tagged with acoustic accelerometers in the wild.

To examine the combined effects of temperature and exploitation on the field metabolic rate of *C. laticeps* in their natural state, two fine-scale telemetry arrays with temperature loggers were used to assess the acceleration of the fish across different temperatures in the wild for three months during a period of high thermal variability. Ten fish from the exploited and unexploited populations were caught, surgically implanted with accelerometer transmitters and released back into the wild. Close to 500 000 and 400 000 acceleration estimates were recorded from wild exploited and unexploited fish, respectively. The field metabolic rate of both populations was estimated by combining the field acceleration and temperature data with the laboratory calibration model.

The field metabolic rate of *C. laticeps* from the exploited population was constrained near cold and warm extremes compared to no constraints observed in the unexploited population. This was attributed to reduced inter-individual variability in the field metabolic rate-temperature relationship within the exploited population. There appeared to be a greater proportion of individuals that maintained a high field metabolic rate at extreme temperatures in the unexploited population. In contrast, all but one fish from the exploited population did not maintain a high field metabolic rate at extreme temperatures. These findings aligned with the laboratory-based metabolic-scope study on both populations of *C. laticeps* and demonstrate that passive-fishing may be removing thermally tolerant individuals and rendering exploited populations less resilient to thermal change. These findings are discussed in the context of fisheries management and particularly on the role that marine protected areas could play in maintaining physiological diversity, and therefore the resilience of fish in the Anthropocene. This study highlights the importance of applied conservation physiology in understanding the consequences of fisheries-induced evolution in an increasingly variable climate.

Chapter 1: General introduction



Graphical depiction of the overarching themes in this thesis (image credit: Mike Skeeles).

1.1 Rationale behind this study

Anthropogenic climate change is causing changes to the physical and chemical properties of the marine environment inhabited by coastal fish populations (Pörtner and Farrell, 2008, Rhein *et al.,* 2013, Potts *et al.,* 2015). Of these changes, temperature variation is regarded as the leading physical stressor because of its direct influence on the physiological processes of fishes (Fry, 1947) and other ectotherms (Holt and Jørgensen, 2015). Thermal dependency drives fish to function within a limited window of environmental temperatures where their metabolic processes are optimized (Portner and Knust, 2010). As global average temperatures increase, and some areas are subject to a rise in thermal variability (Bates *et al.,* 2018), fish populations are increasingly exposed to temperatures towards the edges of their optimal windows (Horodysky *et al.,* 2015). Thus, the metabolic tolerance of populations to these changes is considered a key determining factor of their distribution and performance sensitivity (Pörtner and Farrell, 2008, Deutsch *et al.,* 2015).

The impacts of climate change are exacerbated in overexploited fish populations (Perry *et al.,* 2010, Planque *et al.,* 2010) and it is no surprise that exploitation, together with climate change, are considered the two primary threats to the sustainability of fish populations into the future (Brander, 2010). Despite this, the importance of understanding their synergistic effects has been highlighted only recently (Perry *et al.,* 2010, Planque *et al.,* 2010). Exploitation is selective and can remove fish with certain life-history, behavioural and physiological traits that are associated with vulnerability to capture (Klefoth *et al.,* 2017, Lennox *et al.,* 2017b, Hollins *et al.,* 2018). The selective removal of these traits not only reduces the genetic diversity but also alters the patterns of natural selection, a process referred to as fisheries-induced evolution (FIE) (Jørgensen *et al.,* 2007, Heino *et al.,* 2015). When faced with shifting selection pressures from a changing climate, the reduction in genetic diversity and truncation of specific phenotypes could reduce the resilience of exploited populations to temperature change (Ward *et al.,* 2016). While this is theoretical, there is already some evidence for the intensified impacts of climate change on exploited populations (Planque *et al.,* 2010). For example, the link between the abundance of fish within exploited North-east Arctic Cod (*Gadus* morhua) populations and climate conditions has increasingly strengthened over time (Otterson *et al.,* 2006).

The impacts of exploitation on the demographic and life-history traits of fish populations is well-recognized (Kuparinen and Merilä, 2007, Jørgensen *et al.,* 2009). A wealth of evidence demonstrates a general selection by passive fishing for large, mature individuals, resulting in FIE for smaller, earlier maturing populations (Law, 2000, Heino, and Godø, 2002). By removing highly fecund, large and older individuals, exploitation can reduce recruitment levels as well as the buffering capacity recruitment provides when faced with environmental variability (Bates *et al.,* 2014). However, accurately predicting future responses of exploited populations to climate change is difficult to rely solely on such recruitment-based assumptions (Horodysky *et al.,* 2015). Exploring cause-and-effect relationships is required to provide mechanistic insights into how exploitation can modify responses to temperature change (Helmuth, 2009, Pörtner, 2012, Somero, 2012).

As the physiological processes of an individual are the mechanistic link to their environment, physiological trait diversity is likely to govern the response of a population to changing temperatures (Ward *et al.,* 2016). However, our knowledge of how fisheries-induced evolution effects the physiological traits of fish populations remains limited (Hollins *et al.,* 2018). There is some evidence suggesting that passive-fishing selects for traits other than size, as studies have highlighted a connection between vulnerability to fishing gear and behavioural phenotypes such as boldness and exploration (e.g., Biro and Post 2008, Wilson *et al.,* 2015, Klefoth *et al.,* 2017). These vulnerable behavioural traits have been shown to be associated with underlying physiological phenotypes (Killen *et al.,* 2011, Binder *et al.,* 2016, Rupia *et al.,* 2016) which suggests that exploitation may remove individuals with specific physiological qualities (e.g., Hessenauer *et al.,* 2015). Because physiological attributes (such as metabolic rate) can evolve rapidly (Auer *et al.,* 2018), physiological trait diversity within exploited populations may decrease under FIE. Therefore, the potential decrease in the range of physiological responses within exploited populations to temperature change may lead to reduced resilience (Mckenzie *et al.,* 2016).

Very little research has been attempted to assess fisheries-induced effects on physiological characteristics and how this may influence future population performance in response to climate change. However, a recent study by Duncan *et al.,* (2019a) assessed whether passive fisheries can alter the distribution of metabolic phenotypes in a heavily-fished South African Sparid, *Chrysoblephus laticeps,* to understand exploitation effects on population climate resilience. The metabolic traits of an exploited (Port Elizabeth (PE)) and protected (Tsitsikamma National Park (TNP)) population of *C. laticeps* were determined using intermittent respirometry in a laboratory and compared (Duncan *et al.,* 2019a). They found that there were fewer high-performance metabolic-scope phenotypes in the exploited population across all experimental temperatures. It is assumed that metabolic-scope indicates the amount of energy available for activities beyond maintenance (Fry, 1947) and high-performance metabolic-scope phenotypes have more energy for fitness-related activities. Therefore, a fisheries-induced reduction of high-performance metabolic-scope phenotypes may reduce the population's resilience to increasing thermal variability by decreasing the physiological capacity of individuals, and thereby reduce the energy available for feeding, reproduction and predator avoidance, particularly at the thermal extremes of a population (Hessenauer *et al.,* 2015).

Quantifying the isolated effects of temperature on a population's aerobic capacity provides a framework for understanding their potential response to future change (Gannon *et al.,* 2014) but possibly lacks real-world applicability (Horodysky *et al.*, 2015). In their natural environment, fish are exposed to multiple simultaneously interacting variables which can have an additive, or synergistic effect on different physiological processes (Todgham and Stillman, 2013). Interactive effects on fish performance from temperature and other variables associated with climate change, including hypoxia (McBryan *et al.,* 2013) and CO_2 (Munday *et al.,* 2009, Ferrari *et al.,* 2015), have been documented. Assessing energy states of fish populations in the wild should therefore encapsulate all variables to provide more of a pragmatic understanding of temperature effects on performance (Todgham and Stillman, 2013). In addition, field-based research holds more integrity amongst the public and management (Cooke and O'Connor, 2010), which is particularly useful when communicating results such as those of Duncan *et al.,* (2019a), to relevant conservation authorities.

Advances in acoustic telemetry have revolutionized the ability to assess energy states of fish in the field (Metcalfe *et al.,* 2016). A variety of implantable acoustic accelerometers are now available which function by measuring acceleration in two or three axes (x = lateral, y = forward, z = vertical) and processing this data with an on-board algorithm before transmission. Accelerometers which exclusively record lateral and vertical acceleration capture the undulating movements associated with tail beats (Cruz-font *et al.,* 2016). Recorded acceleration is a valid proxy of fish energy expenditure because it can be correlated with metabolic rate (Wilson *et al.,* 2013, Wright *et al.,* 2014, Cruz-font *et al.,* 2016, Brownscombe *et al.*, 2017). By calibrating the relationship between acceleration and metabolic rate, energy expenditure (termed field metabolic rate (FMR)) can be estimated from acceleration data in the field (Brownscombe *et al.*, 2017). Simultaneous records of environmental parameters (e.g., temperature, habitat and tide state) during the deployment of these transmitters can then provide insight into the natural physiological response and tolerances of fish to environmental or anthropogenic changes over space and time (Horodysky *et al.*, 2015).

The field of conservation physiology, which the aforementioned research forms part of, is a relatively new discipline of marine science and is of increasing importance in a rapidly changing world (Wikelski and Cooke, 2006). Understanding physiological tolerance to environmental and anthropogenic stressors can significantly improve the predictive accuracy of species responses to future change (Cooke *et al.*, 2013, Mckenzie *et al.*, 2016). In turn, fisheries management and conservation authorities can make informed decisions for forthcoming strategies. Authorities may adjust catch rates for fisheries sensitive to thermal and anthropogenic change (e.g., Patterson *et al.*, 2016) whilst marine protected areas (MPA's), regions where extractive activities are limited or prohibited (Roberts *et al.*, 2017), may be implemented where populations are highly vulnerable to such change. Accurate information for the development of MPA's is of particular importance as a global resolution (WCC-2016-Res-050) aims to protect 30 % of earths marine environment by the year 2030 (IUCN, 2016), of which only 5.7 % is protected to date (http://www.mpatlas.org).

Although knowledge on the energy states of wild fish can significantly contribute to improving management decisions, little is known about the interactive effects of climate change and exploitation on the energetic response of wild fish. Thus, the overarching aim of this thesis is to further develop the findings of Duncan *et al.*, (2019a) by assessing whether exploitation effects the wild energetic response of a commercially important coastal fishery species to thermal variability. To achieve this, the specific objectives of the thesis are to:

(i) calibrate accelerometer transmitters with metabolic rate and temperature for an exploited and protected population of *C. laticeps* in the laboratory, and

(ii) use accelerometer transmitters in the field to assess the wild energetic performance of an exploited and protected population of *C. laticeps* in response to temperature variability.

The thesis is divided into five chapters, with the current chapter providing a general introduction to the topic.

Chapter 2 provides a concise description of the study site and species, which is based on the study of Duncan *et al.*, (2019a), and explores the site/species' underlying characteristics with respect to exploitation, climate change and our study aims. This is followed by two primary research data chapters (Chapters 3 and 4).

Chapter 3 details how swim-tunnel respirometry was used to determine the relationship between acceleration, site, mass and metabolic rate of the study species. The combined effect of temperature and acceleration on metabolic rate is briefly discussed, however the aim of this chapter was to develop a model to estimate the FMR of fish, as detailed in Chapter 4.

Chapter 4 details how two fine-scale acoustic receiver arrays, accelerometer transmitters, temperature loggers and the model developed in Chapter 3 were used to compare the wild energetic response to temperature variability of *C. laticeps* from an exploited and protected population, to enable identification of the presence and diversity of thermal performance phenotypes.

Chapter 5 briefly addresses key findings, focusing on the physiological phenotypes presented in Chapter 4 and the role of spatial management in conserving phenotypic diversity.

Chapter 2: Study site and species

Mike Skeeles with a red roman seabream in front of the characteristic sheer cliffs of Tsitsikamma National Park (image credit: Alex Winkler)

2.1 Study site

To assess whether exploitation has affected the physiology of *C. laticeps*, Duncan *et al.*, (2019a) used fish from South Africa's largest and oldest marine protected area (MPA), Tsitsikamma National Park (TNP), as a baseline reference (unexploited control site) for comparison with an exploited environment. Tsitsikamma National Park is a 60 km protected stretch of the south-east coastline of South Africa, with a 5 km seaward boundary (Figure 2.1a, b) (Buxton 1987). All extractive activities were prohibited in 1964 when the area was declared a no-take reserve, and therefore the status of resident fish is considered pre-exploited (Buxton 1993). Despite small areas of the park having recently been opened for shore-based fishing, the offshore habitat has remained protected and well monitored by South African National Parks (SANparks).

Given the impact of historical exposure to thermal regimes on fish physiology (Norin *et al.*, 2014, Mckenzie *et al.*, 2016), it was critical to select an environmentally similar site to ensure comparability. Duncan *et al.*, (2019a) selected an exploited area adjacent to the Port Elizabeth (PE) metropole, offshore from the Noordhoek ski-boat club, due to its almost identical long- and short-term temperature trends to TNP. This area is also characterized by high levels of commercial (Figure 2.1b) and recreational boat-based hook and line fishing. The PE site is approximately 140 km from TNP and has previously been used for comparative life-history studies between exploited and unexploited reef fishes (Buxton, 1987).

To augment the findings of Duncan *et al.*, (2019a), TNP and PE were selected as the unexploited control site and exploited site, respectively, for this study. However, given the effect of habitat type on wild fish energy expenditure (Brownscombe *et al.*, 2017), selecting comparable habitats between sites was deemed important. Consequently, analogous 10–25 m high profile sandstone originated reefs, that were confirmed to have identical benthos (Buxton 1987), were chosen within each site. These reefs are high energy environments (Buxton 1987), but deep enough to be unaffected by energy-altering tidal influences (Brownscombe *et al.,* 2017). In addition, the study species favour these depths (Buxton 1987).

2.2 Thermal and climate change characteristics of the study site

The thermal regime of South Africa's Southern Cape coastal region is considered to be highly variable. This is due to the complex interactions between coastal and deep-ocean processes which causes local temperature fluctuations (Rouault *et al.,* 2010, Goschen and Schumann, 2011). The Agulhas Current, which transports tropical waters southward (Figure 2.1a), drives warm water over the shelf and into the shore through episodic meanders in the form of shear-edge eddies and plumes (Goschen and Schumann, 1995, Goschen and Schumann, 2011). Conversely, strong easterly winds generate offshore surface Ekman transport (Schumann, 1999), resulting in high levels of coastal upwelling from on-shore transport of cold bottom waters, as seen in Figure 2.1a (Goschen and Schumann, 1995). These contrasts are largely a summer occurrence which can cause an intense thermocline, changing temperatures of the entire water column by more than 10°C within a few hours (Schumann *et al.,* 1995). Resident fish in these waters face sharp variations in their environmental temperature (Figure 2.1c) which lends itself to the analysis of natural energy expenditure across both thermal means and extremes.

Impending effects of climate change at these study sites (Duncan *et al.,* 2019b) supports the applicability of these sites in understanding how exploitation may influence the wild energetic resilience of fish to temperature variability. Besides rapid thermal fluctuations, Schelegel *et* *al.*, (2017) demonstrated an increase in the occurrence of local marine heat-waves (MHW) in the southern Cape region which appears to be consistent with global trends (Frölicher *et al.*, 2018). This is most likely driven by the warming of the Agulhas Current, which is expected to continue to drive warmer waters into the coastline (Rouault *et al.*, 2010). In addition, Duncan *et al.*, (2019b) established a link between an increase in extreme intermittent upwelling events along this coast and an intensifying and more variable *El Niño*-Southern Oscillation (ENSO) phase state. Together, these processes are expected to drive increased levels of thermal variability along the Southern Cape coast. Increasing temperature variability is predicted to have a greater effect on marine ecosystems than long-term mean changes and thus is emerging as an important component of climate change (Vasseur *et al.*, 2014, Dillon *et al.*, 2016, Bates *et al.*, 2018), illustrating the applicability of the chosen study sites.

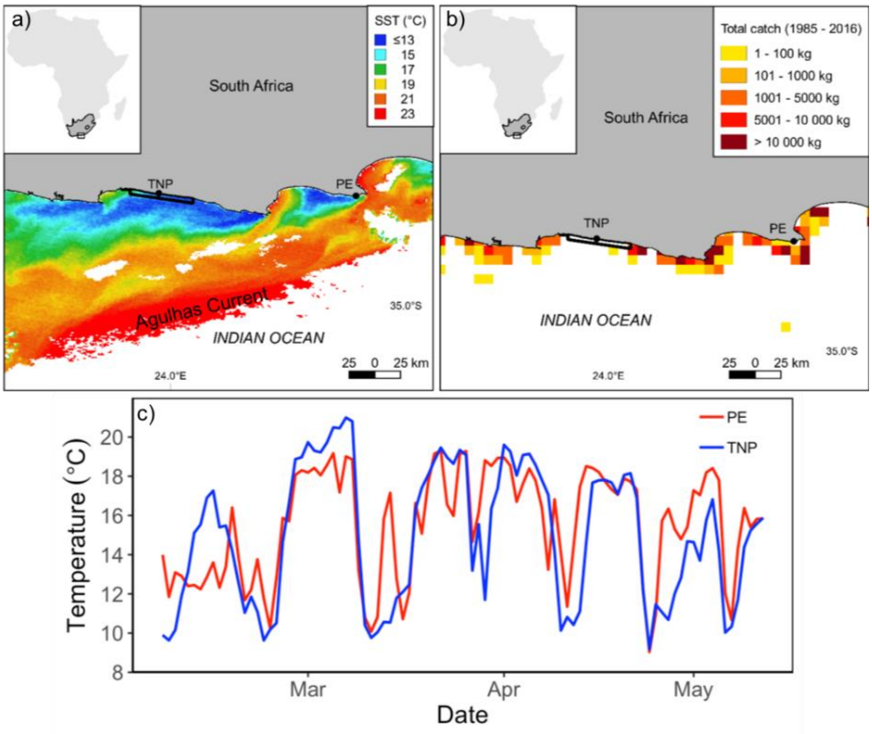


Figure 2.1: Study site visual review. a) Location of exploited Port Elizabeth (PE) and protected Tsitsikamma National Park (TNP) (black box) sites and evidence for synchronized upwelling events (modified from Duncan *et al.*, 2019a). b) Total reported catch of *C. laticeps* between 1985–2016 (5 x 5 nautical mile grids) in PE and TNP demonstrating their exploited and protected properties respectively (taken from Duncan *et al.*, 2019a). c) Average daily temperature data for PE (14 m middle mooring (see Fig 4.4)) and TNP (18 m middle mooring

(see Fig 4.4)) recorded during the study period (February–June 2019), indicating corresponding fine-scale thermal regimes and the presence of intense variability.

2.3 Study Species

Duncan *et al.,* (2019a) conducted a rigorous assessment to find a suitable model species based on the characteristics of core distribution, commercial exploitation, site fidelity, hardiness and panmixia, which lead to the selection of the red roman seabream, *Chrysoblephus laticeps* (Valenciennes, 1830), shown in Figure 2.2. *Chrysoblephus laticeps* is a Sparid that is endemic to South Africa's warm-temperate coast, with a core distribution extending from the Western Cape through to the Eastern Cape (Götz and Kerwath, 2013), which adequately overlaps the study sites. It is a highly exploited species, targeted by both South African commercial and recreational boat-based hook and line fisheries, with reports of significant catches west of PE between 1985 and 2000 (Figure 2.1b) (Brouwer and Buxton 2002; Duncan *et al.,* 2019a). The effects of exploitation on *C. laticeps* populations has been demonstrated, with evidence for fishing-induced changes to their demographic traits (Buxton 1993; Götz and Kerwath, 2013). The life history traits of *C. laticeps* make these fish particularly vulnerable to exploitation. They are protogynous hermaphrodites with females reaching 50% maturity at 2.5–4.27 years (167–190 mm fork length (FL)) (Buxton 1987, 1990, Götz *et al.,* 2008) meaning the TNP population has been unexploited for an estimated 14 generations. The sex change to male is 50% complete by the age of 8–10.25 years (275–350 mm FL) (Buxton 1993, Götz *et al.,* 2008), before attaining a maximum age of 19 years (Götz *et al.,* 2008).

Chrysoblephus laticeps spawn in the summer months between October and January (Buxton 1990) and have shown to display complex courtship behaviours that noticeably occur in the late afternoon (Buxton 1987). This diurnal behaviour is further seen in their feeding patterns as they appear to feed intensively at first light (Buxton 1987). *Chrysoblephus laticeps* are benthic carnivores that constantly swim close to the reef when foraging (Buxton 1984). They adopt a head-down searching mode and rapidly consume prey when found (Buxton 1984). Their opportunistic feeding behaviour contributes towards their vulnerability to exploitation by line-fishers (Buxton 1984).

Several key characteristics make *C. laticeps* an ideal species to use in achieving the aims of this thesis, beginning with their predicted sensitivity to climate change (Ortega-Cisneros *et al.*, 2018). Evidence of *C. laticeps* being extremely hardy (Davis, 1996) illustrates their competency for laboratory experiments (Duncan *et al.*, 2019a). High levels of site fidelity have been demonstrated by Kerwath *et al.*, (2007b), who used acoustic telemetry to estimate their small home range to be 1000–3000 m^2 (see Kerwath *et al.*, 2007a). High levels of residency make *C. laticeps* an ideal candidate for acoustic accelerometry as the receiver array can be placed over a small area, increasing the likelihood of transmitter detections. Additionally, Kerwath *et al.*, (2007b) demonstrated their ability to recover from capture-induced barotraumatic effects and this characteristic provided some assurance that fish released after surgical implantation of transmitters would survive. Finally, South African *C. laticeps* are a single, well-mixed population with displays of genetic connectivity throughout its distribution, suiting the goals of protective-management (Tseke *et al.*, 2010) (discussed further in Chapter 5). Overall, this species proves to be highly appropriate for the experimental protocol and aims of this study.

Figure 2.2: The study species, the red roman seabream *Chrysoblephus laticeps* (image credit: Mike Skeeles).

Chapter 3: Calibrating accelerometer transmitters for estimating wild energy used by *Chrysoblephus laticeps*

A *Chrysoblephus laticeps* swimming in a custom-built swim-tunnel respirometer (image credit: Mike Skeeles)

3.1 Introduction

Understanding the energy use of fish is essential in the study of their physiology and behaviour (McNamara and Houston, 1996), and is especially important in a time of accelerated anthropogenic impacts and climate change (Pörtner and Farrell, 2008, Deutsch *et al.,* 2015). Because fish energetics are influenced by numerous interacting environmental factors (Shepard *et al.*, 2013, Todgham and Stillman, 2013), assessing the wild energy use by fish (the field metabolic rate (FMR)) which encapsulates these factors is of increasing importance. Initial approaches in determining FMR, including the doubly-labelled water and heart rate method have been constrained by high levels of uncertainty (Metcalfe *et al.,* 2016). Research into alternative methods for determining FMR have thus been explored (Wilson *et al.,* 2006).

Above all basic bodily functions, the energetic cost of acceleration comprises a large component of a fish's energetic budget as body movement is a fundamental precursor of common ecological activities such as predator avoidance, foraging and social interactions (Baker, 1978, Blake, 2004, Johansen and Jones, 2011). The correlation between acceleration and oxygen consumption (MO_2) (Clark *et al.,* 2010, Gleiss *et al.,* 2010, Yasuda *et al.,* 2012, Wilson *et al.,* 2013, Wright *et al.,* 2014, Mori *et al.,* 2015, Cruz-font *et al.,* 2016, Laer *et al.,* 2017) makes acceleration a valid proxy of energy expenditure and for this reason has become a preferred metric for estimating the energetic responses of fish to their environment (Metcalfe *et al.,* 2016). Acoustic accelerometer transmitters now allow the measurement of the acceleration of fish in the wild (Cooke *et al.,* 2016) and provided that the correlation between acceleration and MO_2 is calibrated, the field metabolic rate can be estimated (Halsey *et al.,* 2011, Brown *et al.,* 2013, Metcalfe *et al.,* 2016).

To date, these calibrations of the relationship between acceleration and MO_2 have been conducted on red sea bream (*Pagrus major*; Yasuda *et al.,* 2012), Japanese sea bass (*Lateolabrax japonicas*; Mori *et al.,* 2015), European sea bass (*Dicentrarchus labrax*; Wright *et al.,* 2014), Pacific salmon (*Oncorhynchus nerka*; Clark *et al.,* 2010, Wilson *et al.,* 2013), bonefish (*Albula vulpes*; Brownscombe *et al.,* 2017), lake trout (*Salvelinus namaycush*; Cruz-font *et al.,* 2016), whitetip reef sharks (*Triaenodon* obesus; Barnett *et al.,* 2016), nurse sharks (*Ginglymostoma cirratum*; Laer *et al.,* 2017), lemon sharks (*Negaprion brevirostris*; Bouyoucos *et al.,* 2017; Laer *et al.,* 2017) and blacktip sharks (*Carcharhinus limbatus*; Laer *et al.,* 2017). All studies used triaxial loggers which recorded overall body dynamic acceleration (OBDA) apart from that of Cruz-font *et al.,* (2016) who used tailbeat frequency transmitters that exclusively recorded movement on the x and z axis.

Despite the apparent effects of temperature on fish metabolism, only a few studies have incorporated this factor into their acceleration-MO2 calibration (Wilson *et al.,* 2013, Wright *et al.,* 2014, Brownscombe *et al.,* 2017, Laer *et al.,* 2017). Wilson *et al.,* (2013) investigated the acceleration-MO_2 relationship of *O. nerka* at temperatures from 12 –22°C, whilst Wright *et al.,* (2014) assessed this in *D. labrax* from 5.5–17.5°C. Brownscombe *et al.,* (2017) used a two-step experimental approach on *A. vulpes* by first calibrating acceleration with swimming speed and then swimming speed with MO_2 across different temperatures. Two temperatures were used in the calibration of acceleration and MO_2 by Laer *et al.,* (2017) for several shark species. All aforementioned studies found a significant temperature effect on metabolic rate, illustrating the importance of including temperature in the calibration procedure for accurate estimates of FMR.

Acceleration represents the rate in change of movement, and thus accelerometer transmitter calibrations with MO_2 across a temperature gradient can provide a useful insight into the energy requirements for movement at different temperatures (Robson *et al.,* 2016). This contributes towards understanding the ability of fish to alternate between resting and active states (engage in fitness-related activities) under different environmental conditions. Despite limited understanding of the interactive effects between temperature and acceleration on fish MO_2, Robson *et al.,* (2016) found an elevated metabolic cost during increased acceleration of swimming and spinning at colder temperatures in King scallops (*Pecten maximus*). In addition, although this does not pertain to acceleration, the swimming capabilities of fish have been known to decrease with cooling (Claireaux *et al.,* 2006). With an observed relationship between metabolic cost and temperature, it is evident that the acceleration-MO_2 calibration for estimating FMR must be validated across a biologically relevant thermal regime.

The aim of this section of the study was to calibrate acoustic accelerometer transmitters in *C. laticeps* from PE and TNP. This was done by implanting accelerometer transmitters into individual *C. laticeps* and submitting these fish to a swimming respirometry protocol at different temperatures. The relationship between acceleration and temperature on MO_2 was measured and the metabolic costs of *C. laticeps* accelerating at different temperatures was then explored.

3.2 Methods and materials

3.2.1 Animal capture and care

A total of 75 *C. laticeps*, 35 (0.624–1.405 kg) from PE and 40 (0.598–1.800 kg) from TNP, were caught with rod and line at depths between 15 and 25 m from reef habitats. All animals were transported to the Aquatic Ecophysiology Research Laboratory at the South African Institute for Aquatic Biodiversity (SAIAB) and Department of Ichthyology and Fisheries Science (DIFS), Rhodes University (Makhanda, Eastern Cape, South Africa) where they were held in two separate 5900 L indoor cylindrical tanks connected to a saltwater recirculating aquaculture system. Fish were housed for an acclimation period of one month at their mean environmental temperature (16°C) and photoperiod (11 L: 13 D). Fish were fed a mixed diet of fish, shellfish and cephalopods every other day.

3.2.2 Surgery and swim temperature acclimation

Fish were captured with a net from the holding tanks and anesthetized in a solution of 2-Phenoxyethanol ($C_8H_{10}O_2$; 0.2 mL L^{-1}) until loss of equilibrium. Fish were then transferred to a surgery trough that was partly submerged in saltwater. An incision of approximately 2–3 cm was made on the mid-ventral portion of the abdomen, just anterior to the anal pore, and an acoustic accelerometer pressure transmitter (V13AP, 12.2 g in air, 50–70 s transmission delay, ±4.9 m/s^2 acceleration range, 69 kHz sampling frequency: Vemco, Bedford, Nova Scotia) was implanted. These transmitters included a tail-beat activity algorithm whereby movement on the X and Z axes are averaged every 50 to 70 s. In order to facilitate an accurate detection of tail movement, the transmitter was tethered to the incision using a single suture wrap (Clinisut® silk suture; 3-0) to ensure that the transmitter remained in a posterior and parallel position within the fish (Cruz-font *et al.*, 2016). The incision was closed with one to two intermittent stitches and this was followed by the application of an antiseptic wound-gel powder. Fish were then placed into individual 200 L tanks connected to a temperature-controlled aerated recirculating system at their holding tank temperature. An ecologically relevant temperature change of 1°C / hour was implemented until experimental temperatures of either 10, 14, 18 or 22°C were reached and maintained. These temperatures represent the general temperature range that *C. laticeps* usually experience in the wild. Fish were kept here for 48 hours to acclimate to the transmitter and experimental temperature prior to swimming respirometry trials (Brownscombe *et al.,* 2017).

3.2.3 Swim tunnel respirometry

Thirty-five red roman (17 from PE and 18 from TNP) were tested in a custom-built Blazka swim tunnel respirometer to calibrate their relationship between MO_2 and acceleration values at a variety of temperatures (Figure 3.1). The 180 L rectangular respirometer, with mounted inlet and outlet pipes, was designed to house a clear tube with a 20 cm diameter. Within the tube, fish swam against a current generated by a Minn Kota Endura C2 12 V motor, connected to a custom-built controller box and 12 V battery that powered a propeller of 24 cm. Motor controller switches were calibrated against known water velocities with a flowmeter (Marsh-McBirney Flo-mate 2000). Inlet and outlet pipes were connected to a 500 L recirculating aerated system where water temperature could be manipulated by a heat pump (AquaHeat 9.2 kw). A FireStingO2 fibre optic oxygen meter (FSO2-4, Pyro Science GmbH) coupled with a robust probe (OXROB10, Pyro Science GmbH), calibrated in 100% saturated water, was used to record MO_2 within the tunnel. An acoustic receiver (VR2W, Vemco, Bedford, Nova Scotia) was used to detect acceleration transmissions and was fixed to the floor below the tube (Figure 3.1a), while a GoPro Hero 6 (Gopro, San Mateo, California) was mounted above the swim tunnel for the validation of swimming performance through video analysis.

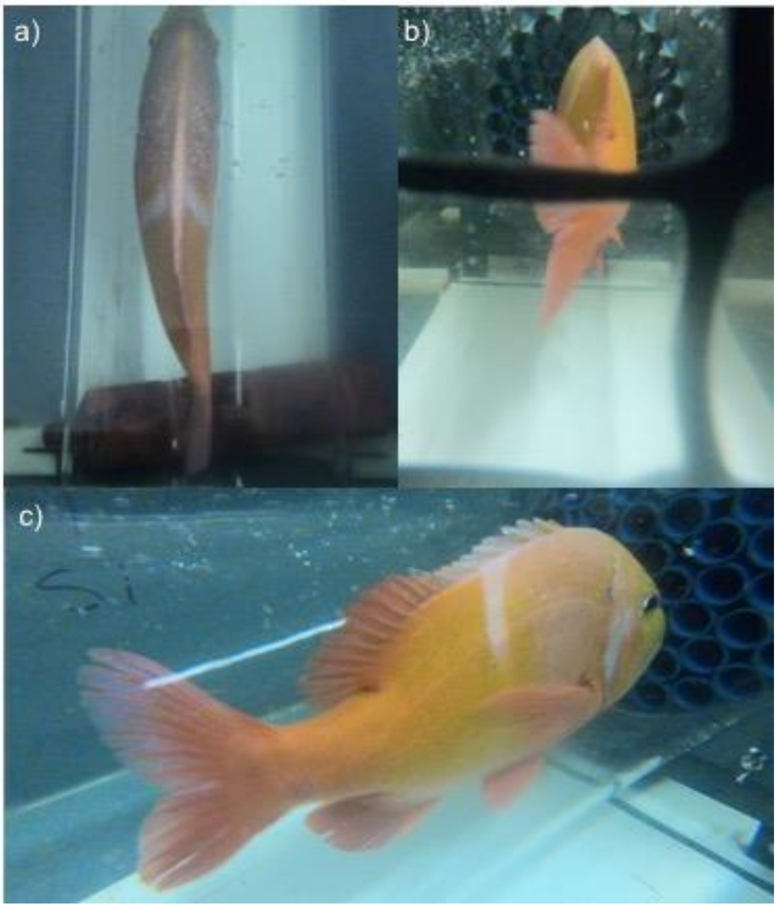


Figure 3.1: Photographs of fish during swimming respirometry to illustrate a) the presence of an acoustic receiver to detect transmissions, b) undulating motion of the tail producing acceleration values and c) straight-line swimming of a *Chrysoblephus laticeps* with tucked pectoral fins. Video examples of swim trials can be found at https://twitter.com/FishSciSkeeles.

Following the two-day acclimation to the transmitter and experimental temperature, fish were placed in the swim tunnel for an hour to acclimatize to finer confinement with a constant current speed of 2 cm/s before testing (Cruz-font *et al.*, 2016). Exploration of data from Duncan et al. (2019a) revealed that metabolic rate of *C. laticeps* stabilises within an hour when placed in a respirometer which supports this acclimation period. The speed was subsequently increased to 20 cm/s for a swim event of 20 minutes. The inlet/outlet taps were kept open to replenish dissolved oxygen (DO) during the first five minutes, after which they were shut to measure the decline in DO in a closed system over the last 15 minutes. This 20-minute procedure was repeated at a speed of 30, 40, 50 and 60 cm/s for each fish. Dissolved oxygen was measured every five seconds throughout the trial (mg/L). Times at which each swim event occurred were recorded to match oxygen, accelerometer, swim speed and video data. Following the swim trial, the receiver was removed to download acceleration data. The fish were euthanised with an overdose of 2-Phenoxyethanol ($C_8H_{10}O_2$; 0.5 mL L^{-1}), the transmitter was retrieved and the sex, length, height, width, tail length and mass of the individual were recorded. A blank run was performed without a subject after each event to assess background respiration. Two fish, one from each site, were tested per day, during daylight hours and the procedure was repeated on at least four fish per temperature treatment (10, 14, 18, 22°C) for each site.

3.2.4 Data processing

Before the data were included, the video footage was examined to confirm that individuals swam consistently in a straight line for the majority of the swim event (i.e., steady-state swimmers) which was considered to be a prerequisite for inclusion. Accelerometer data, returned as single values in m/s^2, was averaged for the duration of the consistent swimming period at the respective swim tunnel velocity. The mass-specific oxygen consumption rate (MO_2, mg O_2/ kg/ min) for the last 10 minutes of each 20-minute swimming interval was calculated using equation 3.1 (Svendsen, 2016):

$$MO_2=\left(\left(\frac{V_R\text{- }M}{W}\right)\left(\frac{\Delta[O_{2\text{trial}}]}{\Delta t}\times 60\right)\right)\left(\left(\frac{V_R\text{- }M}{W}\right)\left(\frac{\Delta[O_{2\text{blank}}]}{\Delta t}\times 60\right)\left(\frac{V_R}{(V_R\text{-}M)}\right)\right)\text{Equation 3.1}$$

where V_R is the total volume of the respirometer in litres, M is the volume of the specimen in litres, W is mass of the specimen in kg, $\frac{\Delta[O_{2trial}]}{\Delta t}$ is the linear rate at which oxygen concentration decreased during the measurement period and $\frac{\Delta[O_{2blank}]}{\Delta t}$ is the slope of the linear decrease in oxygen concentration in the absence of a specimen in the chamber (i.e., background respiration). MO_2 values were subsequently linked to the average acceleration value belonging to the corresponding swimming interval.

3.2.5 Statistical analysis

Linear mixed models were developed to quantify the relationship between acceleration, temperature, site, mass and metabolic rate for each population using the nlme (Pinheiro *et al.*, 2016) R package (http://CRAN.R-project.org/). Keeping individual fish as the random intercept and including all combinations of acceleration, temperature, site and mass as predictor variables of MO_2, a restricted maximum likelihood (REML) approach, with model comparisons based on the small-sample Akaike's information criterion (AICc), log-likelihood and R^2 scores, was used to first identify the best fit random effects structure. Once identified, the optimum fixed effects on the response variable (MO_2) were explored using maximum likelihood (ML) and a backwards selection process. Again, models were compared using AICc and the optimum model taken as the model that minimised AICc. Normality of final model residuals was assessed visually by constructing quantile-quantile and residuals versus fitted value plots. Using this best fit model, MO_2 predictions for an average sized fish were plotted to assess the variation in metabolic requirements to increase acceleration at different temperatures.

3.3 Results

Of the 35 swim trials, 23 were classified as steady-state swimmers, which covered all four experimental temperatures and thus were included in the analysis (Figure 3.2). Those excluded used side-to-side pectoral-dominated swimming motions that potentially exaggerated the x-axis logger recording, resulting in elevated acceleration values, especially at lower swim tunnel speeds. In addition, two cases of burst swimming occurred where fish accelerated frantically towards the front and drifted with the current effortlessly to the back.

Of the steady-state swimmers, swim speeds ranged from 0.29 body lengths per second (BL/s) to 2.19 BL/s, and acceleration values ranged from 0.25 to 1.39 m/s^2. The highest recorded MO_2 of 6.73 mg O_2/kg/min was observed for an individual in the upper acceleration range (1.39 m/s^2) at 14°C. The lowest MO_2 of 0.91 mg O_2/kg/min was observed for an individual with an acceleration of 0.26 m/s^2 at 10°C. All fish maintained an upright position during the trials and none exhibited signs of exhaustion.

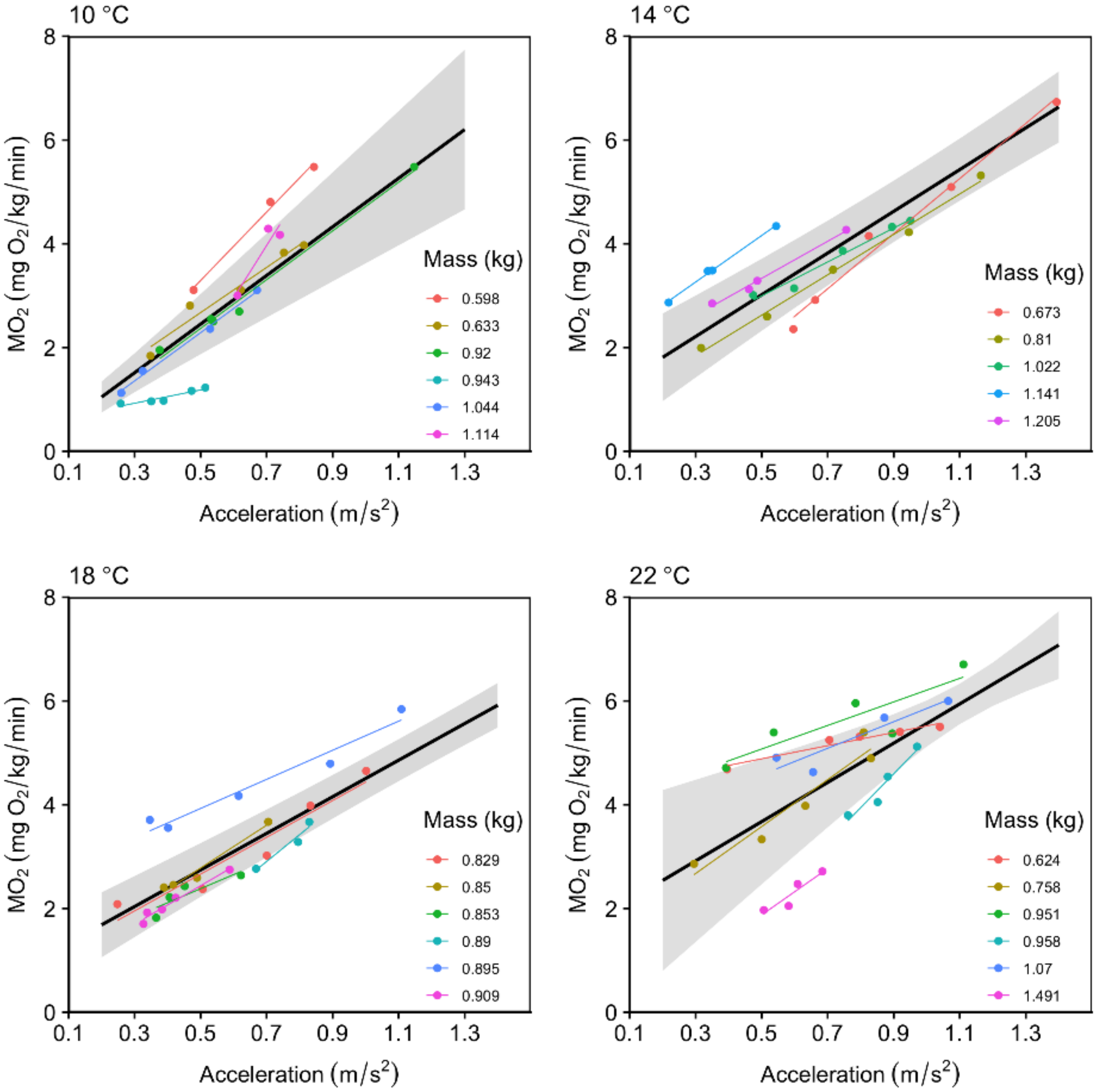


Figure 3.2: Relationship between acceleration (m/s^2) and metabolic rate (MO$_2$; mg O$_2$/kg/min) of *Chrysoblephus laticeps* that were exercised in a swim tunnel at 10, 14, 18 and 22°C. Individual linear regression lines for each swim trial are in colour. Black lines indicate linear mixed effects model predictions of MO$_2$ with individual as the random intercept and acceleration as the random slope (± 95% CI is shaded grey) for each test temperature separately.

3.3.1 Model selection

Acceleration had a positive linear relationship with MO$_2$ at all temperatures, and the slope of individual responses varied the most at thermal extremes (Figure 3.2). The combination of acceleration as a random slope and the individual as a random intercept was the best random effect structure for the predictive model (Table 3.1). Based on these random effects, the overall model with the best fit criterion included acceleration, temperature, site, mass and the interaction between acceleration and temperature as fixed effects (Table 3.1). The unification of these random and fixed effects produced an optimal model to estimate FMR (Equation 3.2) with an R^2 of 0.98 (Table 3.1). There was no deviation of model residuals from normality.

$$\mathrm{FMR} = -0.705 + 0.413(\mathrm{site\ TNP}) + 5.972(\mathrm{acceleration}) + 0.164(\mathrm{temperature}) - 1.114(\mathrm{mass}) - 0.133(\mathrm{acceleration} : \mathrm{temperature}) \qquad \text{Equation 3.2}$$

Table 3.1: Model selection process for the metabolic rate (MO_2; mg O_2/kg/min) of *Chrysoblephus laticeps* as a response to various fixed effect (site = Port Elizabeth (PE) and Tsitsikamma National Park (TNP), acc = acceleration, temp = temperature) and random (ID = individual fish identification) effect structures with respective criteria scores of log-likelihood (LL), small-sample size Akaike's information criterion (AICc), change in AICc and the coefficient of determination (R^2). Models in bold were selected as the best effect structures and when combined formed the optimal model for field estimation.

Effects	**Model**	**LL**	**AICc**	**ΔAICc**	**R^2**
Random	MO_2 ~ fixed + (~1 | ID)	69.32	163.60	36.00	0.96
	MO_2 ~ fixed + (~1 + temp | ID)	68.77	167.72	40.12	0.96
	MO_2 ~ fixed + (~1 + mass | ID)	68.41	167.01	39.41	0.97
	MO_2 ~ fixed + (~1 + acc | ID)	**48.71**	**127.60**	**-**	**0.98**
Fixed	MO_2 ~ site*acc*temp + mass + random				
	MO_2 ~ site*acc+ acc*temp + site:temp + mass + random	49.12	125.80	4.65	0.97
	MO_2 ~ site*acc + acc*temp + mass + random	49.13	123.23	2.08	0.97
	MO_2 ~ site + acc*temp + mass + random	**49.35**	**121.15**	**-**	**0.98**
	MO_2 ~ site + acc + temp + mass + random	52.10	124.18	3.03	0.97

Mass and site were not statistically significant predictors of MO_2 (Table 3.2). Mass had a negative relationship with MO_2 whilst the TNP population appeared to have an increased MO_2 (Table 3.2). Acceleration and temperature both had a significant positive effect on MO_2 ($p < 0.05$, Table 3.2), as shown in Figure 3.3. In addition, there was a significant negative interaction effect between acceleration and temperature on MO_2 ($p < 0.05$, Table 3.2) with an outcome of a steeper rise in MO2 when factoring in increasing acceleration at colder temperatures (Figure 3.3).

Table 3.2: Parameter estimates of the optimal linear mixed effects model for the estimation of MO_2 of *Chrysoblephus laticeps* in the field. DF refers to degrees of freedom and CI represents confidence intervals. Bold p-values indicate significance.

	Co-efficient	**Standard Error**	**DF**	**t-value**	**p-value**	**95% CI lower**	**95% CI upper**
Intercept	-0.705	1.081	76	-0.652	0.516	-2.793	1.383
Site (TNP)	0.413	0.316	19	1.307	0.207	-0.228	1.054
Acceleration	5.972	0.819	76	7.290	**0.000**	4.390	7.555
Temperature	0.164	0.053	19	3.113	**0.006**	0.057	0.271
Mass	-1.114	0.797	19	-1.398	0.178	-0.003	0.001
Acceleration: temperature	-0.133	0.049	76	2.725	**0.008**	-0.228	-0.039

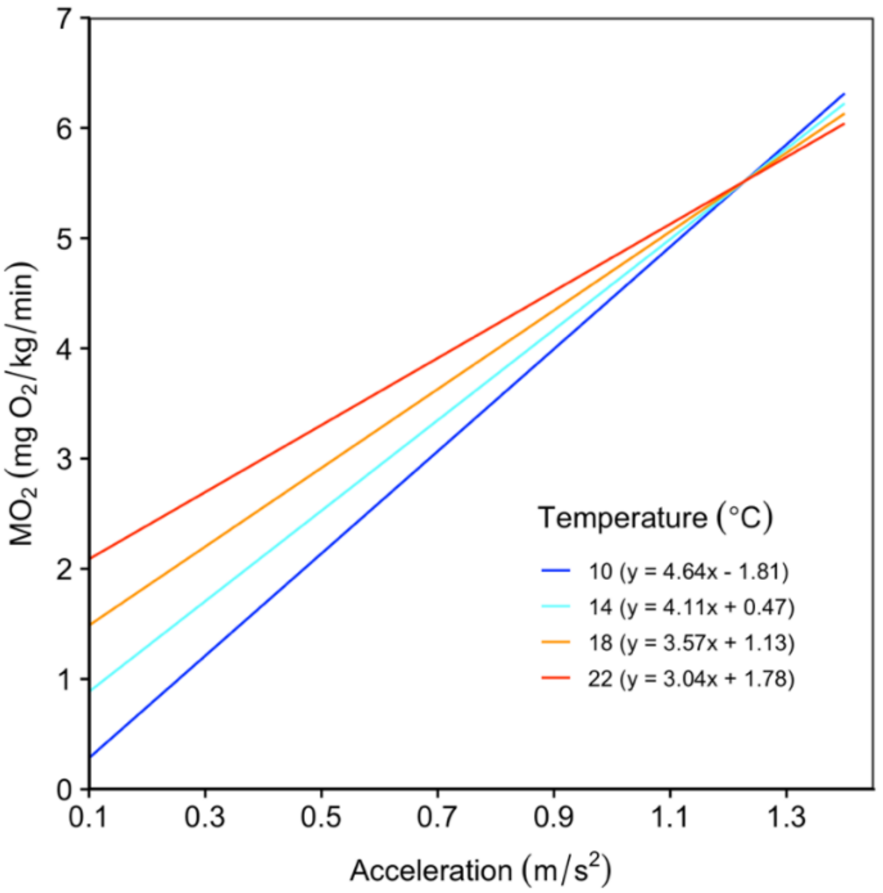


Figure 3.3: Best fit linear mixed effect model predictions of metabolic rate (MO_2, mg O_2/kg/min) for a 1 kg Port Elizabeth *C. laticeps* at different temperatures (°C) and rates of acceleration (m/s^2). Linear equations of relationships corresponding to temperatures are represented in brackets in the legend and are in the form of MO_2 = acceleration*slope + intercept.

3.4 Discussion

This chapter discussed how the effects of acceleration, temperature and mass on the metabolic rate of *C. laticeps* from PE and TNP was examined using acoustic accelerometer transmitters and swim tunnel respirometry. The optimal model for predicting metabolic rate included site, mass, acceleration, temperature and the interaction between acceleration and temperature as predictor variables. This model can be used to estimate the FMR of both *C. laticeps* populations (discussed in Chapter 4). It was also found that *C. laticeps* incurs a greater metabolic cost when accelerating at colder temperatures (Figure 3.3) and this could have implications for the energetic performance of *C. laticeps* in the future as the frequency of upwellings along South Africa's south east coast increase (Duncan *et al.,* 2019b).

Acceleration and temperature have been determined to be significant predictor variables of MO_2 in several previous studies. For example, an increase in MO_2 with the acceleration output of the same tailbeat transmitters used in this study was also found in *S. namaycush* by Cruz-font *et al.,* (2016). Several studies have used similar accelerometers in sharks and other fish (Clark *et al.,* 2010, Gleiss *et al.,* 2010, Yasuda *et al.,* 2012, Wilson *et al.,* 2013, Wright *et al.,* 2014, Mori *et al.,* 2015, Brownscombe *et al.,* 2017, Laer *et al.,* 2017), and a significant positive relationship between acceleration and MO_2 was found. A rise in temperature causing intercepts of acceleration-MO_2 curves to significantly increase within *C. laticeps* (Figure 3.3) was also found for *D. labrax* (Wright *et al.,* 2014), *O. nerka* (Wilson *et al.,* 2013), *A vulpes* (Brownscombe *et al.,* 2017) and several shark species (Laer *et al.,* 2017). By extrapolating the acceleration-MO_2 curves to zero acceleration (i.e., the intercept) an estimate of standard metabolic rate (SMR) could potentially be made (Claireaux *et al.,* 2006). In this context, the intercept increasing with temperature is no different to the increase of SMR with temperature, which is a standard relationship in ectotherms (Fry, 1947).

Although site and mass were not significant predictors of MO_2, the optimum model included both of these parameters, suggesting that they play a role in determining oxygen consumption rates of *C. laticeps*. While a negative relationship between mass and metabolic rate is well documented (Brown *et al.,* 2004) and therefore expected, the inclusion of site in the optimal model is interesting and is attributed to the higher (on average) metabolic rate in fish from TNP. Because swimming respirometry is another method in determining maximum metabolic rate (MMR) (Clark *et al.,* 2013), our findings could reflect the underlying MMR characteristics of these fish. This would make sense as the TNP fish were found to have a higher MMR in the static respirometry experiments by Duncan *et al.,* (2019a). The findings of this study therefore support those of Duncan *et al.,* (2019a).

The significant interaction effect between acceleration and temperature, which suggests that fish incur a greater metabolic cost to accelerate at colder temperatures, is to our knowledge, a novel finding among fish studies. In this case, the oxygen consumption required to accelerate above basal rates was almost double at 10°C, compared with 22°C for *C. laticeps* (Figure 3.3). Although less significant, Wright *et al.,* (2014) also produced similar results in that slopes of acceleration-MO_2 curves for *D. labrax* doubled from 17 to 6°C, while Robson *et al.,* (2016) found a steeper increase in the metabolic rate when *P. maximus,* a scallop, increased acceleration at colder temperatures.

The mechanisms driving the increased energetic cost of acceleration in cold temperatures are not clear. However, it is possible that the increase cost of white muscle activity at cold temperatures may contribute to this. Temperature affects the onset of white muscle (fast glycolytic fibres) when red muscle (slow oxidative fibres) cannot sustain enough power for steady swimming (Rome, 1990). The onset of white muscle to sustain swimming in fish occurs at a lower work rate in colder temperatures (Rome, 1990, Rome, 1995). The majority of aerobic capacity and blood flow of a fish occurs in the white muscle due to its large share of body mass (Goolish, 1991). Therefore, the use of such a metabolically demanding muscle at a lower work rate (i.e., acceleration) in colder temperatures, would ultimately increase metabolic rate. This may explain why, to proportionally increase acceleration at colder temperatures compared to warmer temperatures, *C. laticeps* was found to incur a greater metabolic cost. This finding is supported by Seebacher *et al.,* (2014) who demonstrated that the oxygen requirement by muscles to achieve a given work output increased with decreasing temperatures in African clawed frogs, *Xenopus laevis*.

Regardless of the mechanism driving it, the implications of higher relative rates of energy expenditure for acceleration at cold temperatures may have negative implications for *C. laticeps* due to the predictions of an increase in the frequency of upwelling events (Duncan *et al.,* 2019b). For example, the greater movement costs at colder temperatures could impede behaviours that may directly impact fitness. *Chrysoblephus laticeps* display rigorous courtship behaviours during their spawning period over the summer months (Buxton, 1990), the peak time for upwelling-favourable winds (Goschen and Schumann, 2015). As upwelling intensity is increasing, particularly in the study area of the target species (Duncan *et al.,* 2019b), and if acceleration-based energy requirements are too demanding for courtship during prolonged cold periods, a reduction in reproductive success may occur. Acceleration is also critical for feeding and avoiding predators and cooling temperatures may therefore reduce energy intake whilst increasing vulnerability to predation.

This type of research also emphasizes the importance of understanding local ocean variability on organisms (Bates *et al.,* 2018). Indeed, if the pattern of increased energy expenditure for acceleration at lower temperatures holds true for other fishes, energy constraints may be a concern for fishes in all areas that are subjected to increasing thermal variability. However, although the cost of acceleration at cooler temperatures may have an impact on the fitness of fishes in areas with increasing thermal variability, it is likely that this will be mediated by phenotypic plasticity and the adaptive capacity of individuals will determine the resilience of fish species to this variability in the future (Bernhardt and Leslie, 2013, Norin *et al.,* 2016). In this study, the individual variation in the metabolic response to acceleration was the largest at temperature extremes (Figure 3.2) indicating that there is some level of physiological phenotypic plasticity. Thus, if temperatures do continue to cool, individuals with the most efficient metabolic response to accelerating may excel, and if these traits are heritable, adaptive resilience may occur (Munday, 2014).

Although it is likely that the calibration model predicting MO_2 in response to temperature and acceleration is accurate, as with most studies, there may be some concerns with the methods employed. The intercept of acceleration-MO_2 curves in red seabream at 20°C (Yasuda *et al.*, 2010) and Japanese seabass at 20.7°C (Mori *et al.*, 2015), both relatable eurythermal species, were 2.30 ± 0.3 and 1.79 mg O_2/kg/min, respectively. At 22°C, the model for *C. laticeps* predicted an intercept of 1.78 mg O_2/kg/min (for a 1 kg PE fish). The alignment in the results between these studies does suggest some form of repeatability, and supports the experimental procedure used in this study. However, a drawback of this study was the limitations in the capabilities of the swim tunnel, which only allowed the calibration of straight-line swimming fish up to a maximum acceleration of 1.5 m/s^2. As the acceleration of *C. laticeps* can exceed 1.5 m/s^2 (this was observed when fish were swimming in a side to side motion in the swim tunnel) it is likely that FMR cannot be reliably calculated at high rates of acceleration using current modes of testing. Therefore, some of the greater field acceleration estimates in the second part of this study had to be excluded during the analysis of FMR. The challenges in assessing the metabolic cost of rotational locomotion elucidates the path for future research.

In conclusion, the technological enhancement of acoustic transmitters provides an exciting future for eco-physiologists (Lennox *et al.*, 2017a). As acceleration forms the basis of most fitness-related behaviours, the development of accelerometer transmitters has been fundamental in a deeper understanding of fish bioenergetics and behaviour (Boisclair and Leggett, 1989; Cooke *et al.*, 2016). This chapter demonstrates the usefulness of these accelerometers in calibrating MO_2 with acceleration in a marine Sparid and highlights the importance of integrating temperature into this procedure. The optimum model was subsequently used to estimate the FMR of *C. laticeps*, where behaviour during cold extremes was closely assessed due to the elevated energetic cost to accelerate at these temperatures, which is documented in Chapter 4.

Chapter 4: The effects of exploitation and temperature on the field metabolic rate of *Chrysoblephus laticeps*

A big underwater thumps-up after locating the first acoustic receiver following a suspenseful four-month wait (image credit: Matt Parkinson)

4.1 Introduction

In a world with changing thermal conditions, individuals are continuously faced with energy trade-offs and must balance the need to optimize their physiological performance with the need to conduct activities that ensure their survival (such as feeding and breeding) (Papastamatiou *et al.,* 2015). For aquatic ectotherms, the balance of these trade-offs may determine the abundance and distribution of populations as ocean temperatures change (Tomlinson *et al.,* 2014). Thus, understanding the wild energetic outputs of fish across their environmental temperature gradient provides insight into these trade-offs and, in turn, their sensitivity to change (Horodysky *et al.,* 2015, Metcalfe *et al.,* 2016).

Given that localized temperature variability is predicted potentially to have a greater impact on aquatic organisms than long-term mean change (Bates *et al.,* 2018), understanding the energetic requirements of fish in environments characterized by thermal variability is essential to fully understand the impacts of climate change. As thermal variability is increasing along South Africa's south coast (Duncan *et al.*, 2019b), non-migrating, resident fishes may experience greater physiological stress during prolonged periods of extreme temperatures. As a result, the persistence of these populations will ultimately depend on the distribution and diversity of physiological phenotypes (Bernhardt and Leslie, 2013, Norin *et al.,* 2016). Those species that are more sensitive to thermal extremes are expected to suffer greater stress and potentially reduced fitness as a consequence of increasing thermal fluctuation (Neubauer and Andersen 2019). Understanding the thermal physiological phenotypes of fish in areas of thermal variability is key to predicting local population responses to rising temperature variability (Norin *et al.,* 2014).

Passive exploitation can selectively remove fish with physiological characteristics linked to thermal tolerance (Duncan *et al.,* 2019a), which may interfere with a population's balance of energetic trade-offs. Duncan *et al.,* (2019a) provide evidence for this by demonstrating a reduction in the presence of high-performance aerobic-scope phenotypes in *C. laticeps* from PE compared to those from TNP. However, it is difficult to extrapolate these laboratory-based measurements of aerobic scope to dynamic ecological scenarios (Tomlinson *et al.,* 2014) and there is a contentious debate over the ecological applicability and accuracy of the aerobic scope metric (Jutfelt *et al.,* 2018). Therefore, by examining the energy expenditure of fish from both populations in their natural state during periods of extreme thermal variability, the presence and performance of different physiological phenotypes can be validated in a meaningful ecological context.

Understanding the wild energetics of fish in relation to environmental factors has become easier with the technical advances in biotelemetry and the miniaturization of environmental parameter measuring sensors (Metcalfe *et al.,* 2016). Implantable acoustic accelerometer transmitters (VEMCO series transmitters) can transmit the average acceleration of a fish for extended periods to receivers within range. Using laboratory calibrated mathematical energy expenditure models describing the relationship between acceleration and metabolic rates, and including factors such as temperature, fish size and location (as presented in Chapter 3), field acceleration data can quantify wild energy expenditure, otherwise known as field metabolic rate (FMR) (Brown *et al.,* 2013). In addition, simultaneous records of environmental parameters such as temperature captured during the deployment of transmitters can provide insight into individual energetic responses over space and time (Horodysky *et al.,* 2015).

A significant benefit in determining FMR is the ability to capture an individual's energetic response across the entirety of their thermal range. Laboratory studies of fish energetics involving respirometry are often restricted to using one temperature per individual, and population trends are subsequently inferred from several individual responses at different temperatures (Clark *et al.,* 2013). This method only provides a snapshot of an individual's thermal tolerance, whereas the use of field accelerometry has the capacity to assess an individual's thermal response across a temperature continuum (Gannon *et al.,* 2014). Accelerometry allows for a comprehensive analysis of thermal physiological phenotypes, and individual responses to temperature change can be used to scale-up and predict population responses (Ward *et al.,* 2016).

Previous studies using transmitters to capture activity have been successful in laboratory and mesocosm environments (Bouyoucous *et al.,* 2017, Hori *et al.,* 2019). This technology has allowed the investigation of such disparate factors as effects from anthropogenic events such as ecotourism on shark activity (Barnett *et al.,* 2016), seismic surveys on fish behaviour (Bruce *et al.,* 2018) and stress hormone effects on the activity of parenting fish (Algera *et al.,* 2017). Habitat, diurnal, seasonal and other environmental drivers of energy expenditure have been quantified in a range of marine species (O'Toole *et al.,* 2011, Murchie *et al.,* 2011, Gannon *et al.,* 2014, Papastamatiou *et al.,* 2015, Stehfast *et al.,* 2015, Struthers *et al.,* 2017, Shipley *et al.,* 2018, Baker *et al.,* 2019). Through calibrations similar to that detailed in Chapter 3, the FMR of a cephalopod (Payne *et al.,* 2011), freshwater fish (Cruz-Font *et al.,* 2016) and several marine species of fish (Wilson *et al.,* 2013, Brodie *et al.,* 2016, Brownscombe *et al.,* 2017) have been estimated in relation to ecological effects. Only two studies have comprehensively explored the effects of temperature on wild fish energetics. Gannon *et al.,* (2014) used acceleration and temperature values from the field to approximate a thermal performance curve for a population of estuarine fish (*Platycephalus fuscus*), whilst Brownscombe *et al.,* (2017) assessed the spatiotemporal energy expenditure of a tropical population of bonefish (*Albula* *vulpes*). Both of these studies identified a strong relationship between temperature and fish performance.

Despite the importance of temperature variability modulating energy expenditure in fishes and the development of technologies to quantify this, no study (to my knowledge) has investigated this intrinsic relationship across dynamic thermal contexts or attempted to assess the effects of exploitation on wild energy states. This chapter details how acoustic accelerometer transmitters and temperature loggers were used to examine the fine-scale activity of *C. laticeps* from the exploited (PE) and protected (TNP) populations during three months of extreme temperature variability (Chapter 2). The FMR of each individual was then estimated using the model developed in Chapter 3 and this information was used to examine the combined effects of temperature and exploitation on the energy expenditure of this species in its natural state. The relevance of these findings is discussed in this chapter in the context of the resilience of fishes in the Anthropocene.

4.2 Methods and materials

To quantify the relationship between temperature and FMR for both populations, two fine-scale acoustic telemetry arrays were deployed from February to June 2019, when temperature variability is most prominent in these areas (Duncan *et al.*, 2019b).

4.2.1 Array details

4.2.1.1 Range test

Due to the propensity for noise interfering with the transmission of acoustic signals, it has been recommended that attempts should be made to understand the effects of noise interference within the site when collecting acoustic telemetry data (Gjelland *et al.*, 2013). A week-long range test was conducted at each site to determine detection range efficiency. Five acoustic receivers (VR2W, VEMCO, Bedford, Nova Scotia) were attached to moorings and deployed (see Appendix 1 for design and layout) between 4 to 14 December 2018, in the proposed array sites at PE and TNP. Two sentinel transmitters (VEMCO V13-1x, 12.2 g in air, 30 s transmission delay, 69 kHz sampling frequency, VEMCO, Bedford, Nova Scotia), programmed to emulate the V13AP transmitters used in the studied fish (see section 4.2.2), were attached to the outer moorings (Appendix 1). After retrieval, data were downloaded using the VEMCO software program (VUE), and the detection data was analysed using the VEMCO Range Test software (version 1.10.29.0). Detection range was similar in both sites, with a 90% probability of detection obtained at a distance of 70 m (Figure 4.1).

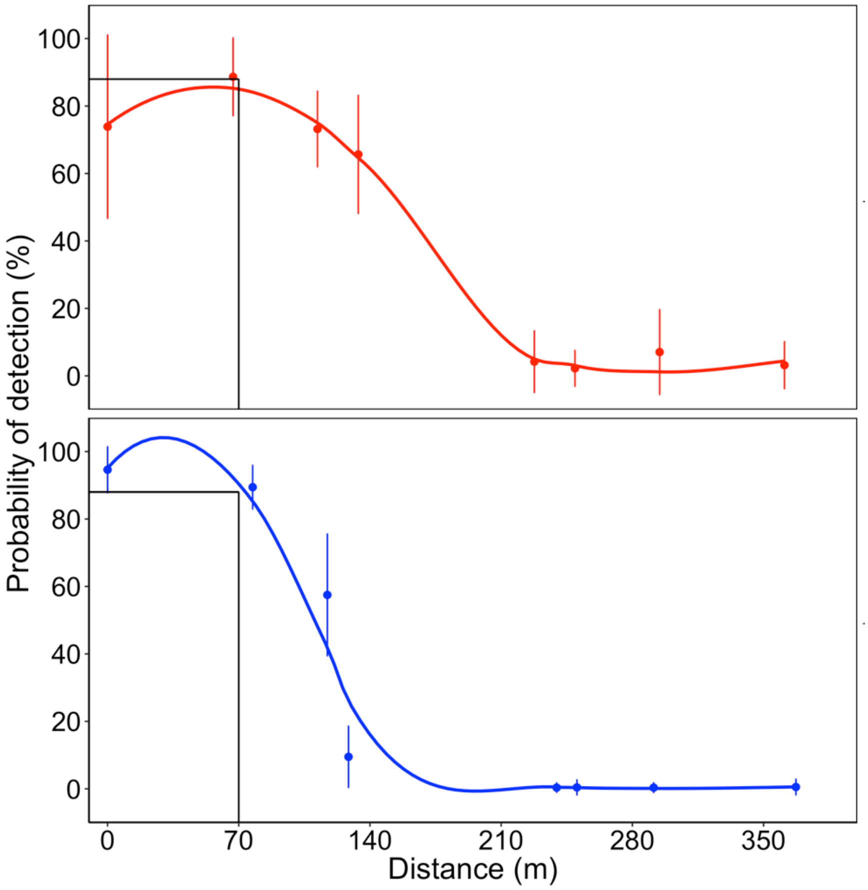


Figure 4.1: The probability of a V13AP transmitter being detected by a VR2W receiver in Port Elizabeth (PE) (red) and Tsitsikamma (TNP) (blue). Raw points represent the average probability of detection (± SD) from the week-long range test. Vertical black lines indicate our chosen optimum distance of 70 m producing an approximate 90 % likelihood of detection.

4.2.1.2 Array design

Thirteen receivers were available for each site and a square-shaped array with triangulated receivers no further than 140 m apart was deployed (Figure 4.2). This array provided a total detection coverage of 176 400 m^2 (420 x 420 m), which is much larger than the estimated home range size found for *C. laticeps* by Kerwath *et al.*, (2007b). Two sentinel transmitters were placed between receivers in the array and used to assess the potential effects of environmental noise during the experimental period. A temperature logger (Hobo Water Temperature Pro v2, Onset Computer Corporation, Bourne, Massachusetts) was placed on the mooring at the centre of each array and was programmed to capture environmental water temperature every 30 minutes.

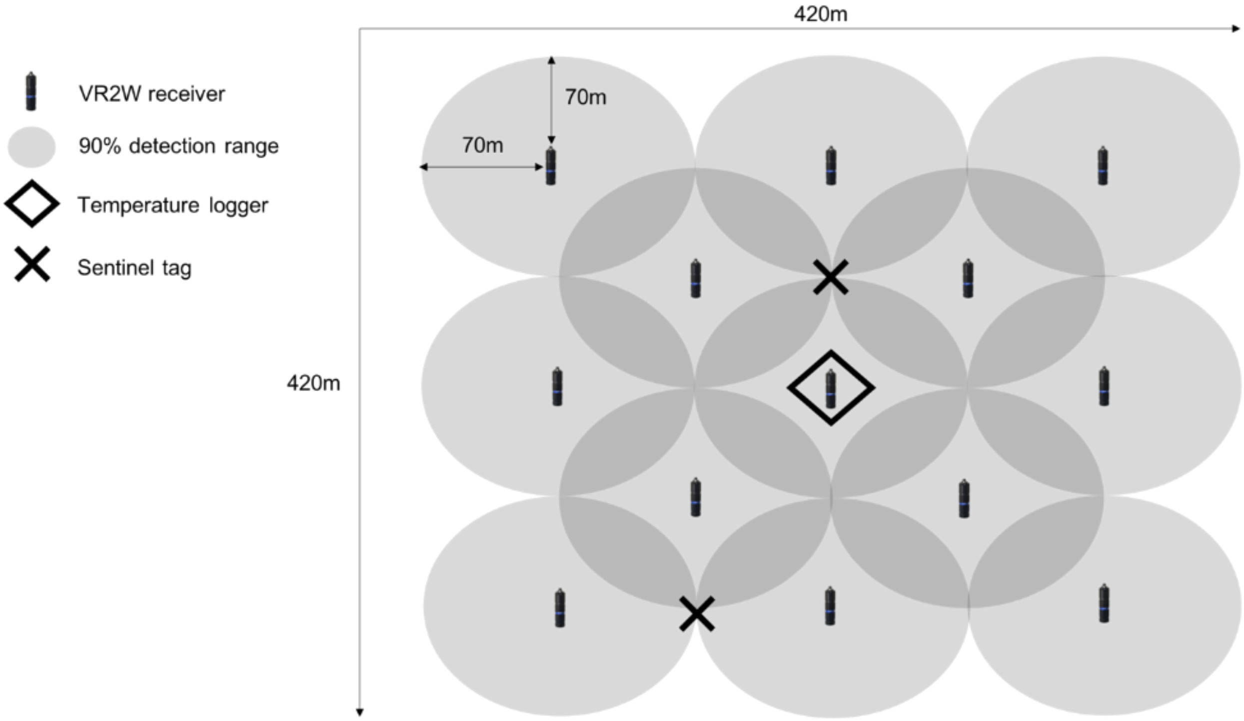


Figure 4.2: The acoustic telemetry array design for measuring the relationship between water temperature and acceleration of *Chrysoblephus laticeps* in sites adjacent to Port Elizabeth and the Tsitsikamma National Park.

4.2.1.3 Array site selection and receiver deployment

To minimise the effects of pseudo replication it was important to control for as many confounding factors between sites as possible. Study sites were chosen based on similar bathymetry profiles (Figure 4.3) and comparable habitat types were confirmed from underwater videos obtained by SCUBA divers whilst retrieving receivers during the range tests. Each receiver/ sentinel transmitter was attached to a mooring and deployed over a boat at allocated coordinates (Appendix 2). Soak times following the PE (5 February 2019) and TNP (6 February 2019) deployment were four and five months, respectively, after which receivers were retrieved by divers using SCUBA gear.

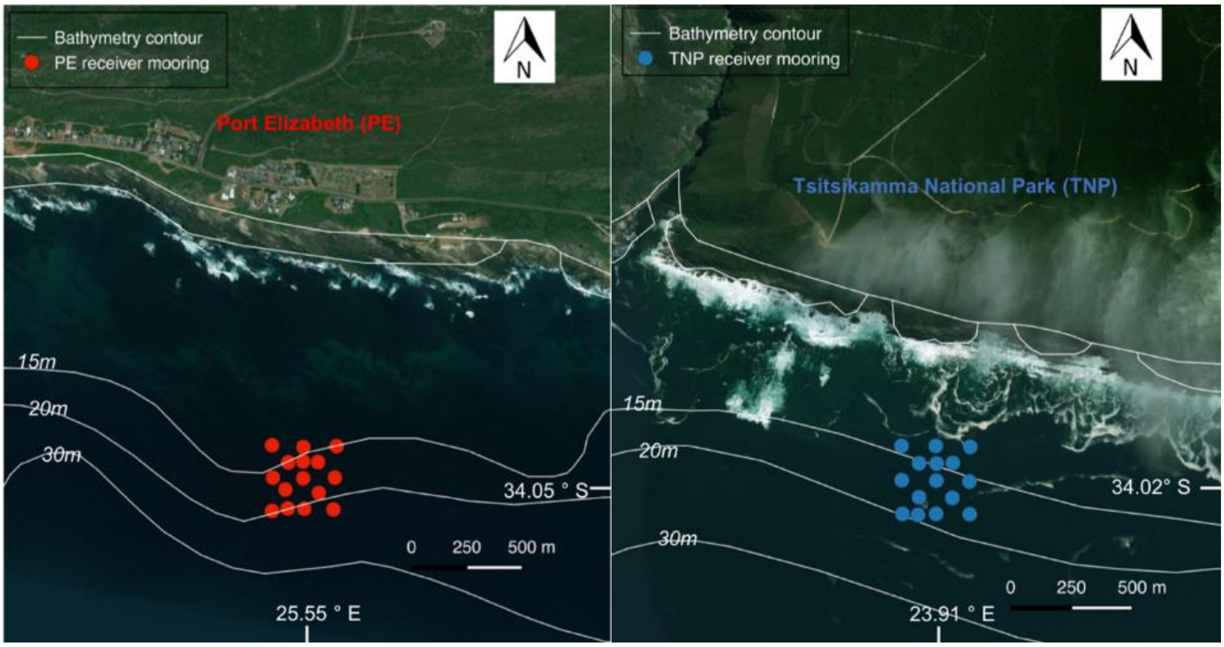
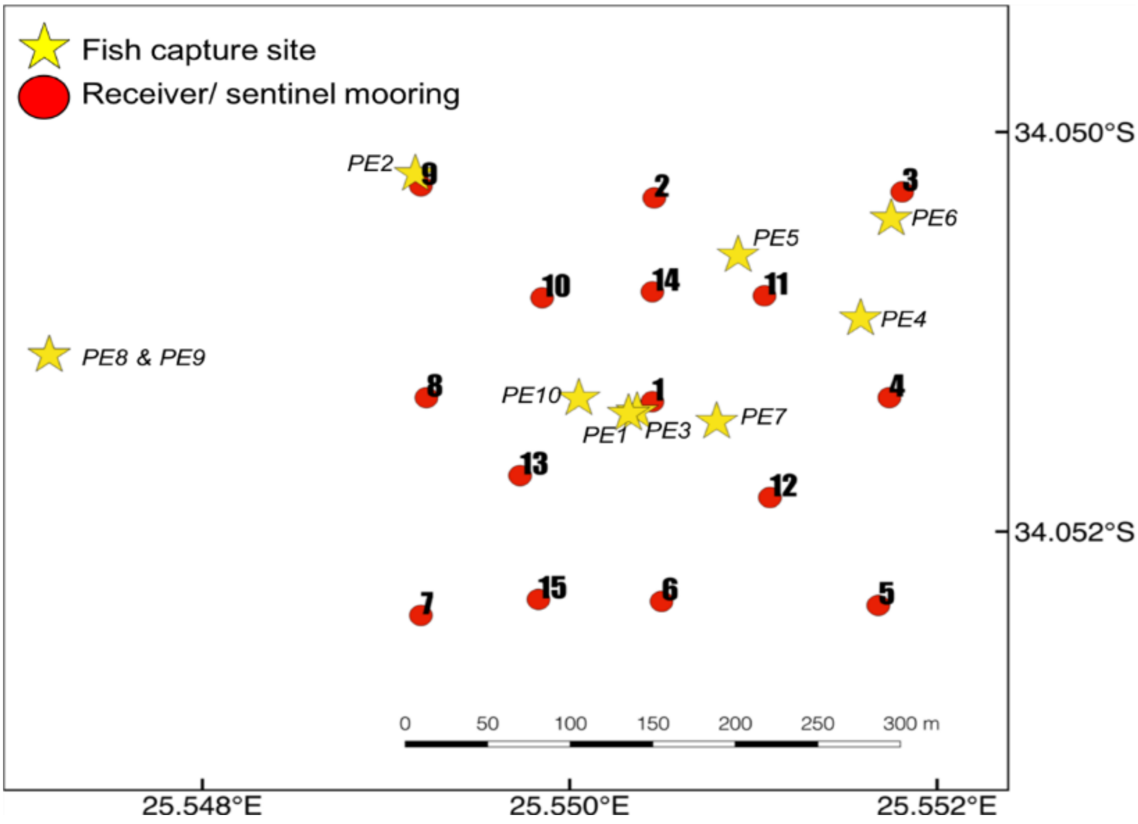


Figure 4.3: An aerial view of the location and layout of the Port Elizabeth (PE, exploited) and Tsitsikamma National Park (TNP, protected) fine-scale acoustic receiver arrays to detect fine-scale acceleration of *Chrysoblephus laticeps*. Each dot represents an acoustic/ sentinel transmitter mooring and bathymetric contours (sourced from MARIP) to illustrate analogous depth profiles between sites. (Maps made with Quantam GIS, version 2.18.)

4.2.2 Fish tagging

Fishing took place over similar temperature regimes (13–16°C) between sites on 28 January and 5 February 2019 in PE and on 9 February 2019 in TNP. Standardised fishing equipment, tackle (barbless 4/0 circle hook) and bait (squid *Loligo reynaudii*) was used either inside or just (not more than 250 m) outside each acoustic receiver array. Upon capture, fish were first measured to ensure that they fell within a preselected size range (260–400 mm FL). Each appropriately-sized fish was anesthetized (2-Phenoxyethanol, $C_8H_{10}O_2$, 0.2 mL L^{-1}), their gas-bladders were deflated using a sterilized hypodermic needle and an acoustic accelerometer pressure transmitter (VEMCO V13AP, 12.2 g in air, 50–70 s transmission delay, ± 4.9 m/s^2 acceleration range, 69 kHz sampling frequency, high power output, 87 days estimated battery life, VEMCO, Bedford, Nova Scotia) was surgically implanted into the coelomic cavity (description of surgical procedure in Chapter 3). Fish were then allowed to recover in an aerated

200 L tank on board the boat for 30 minutes before being released at the centre of the array (receiver 1, Figure 4.4). The capture location of each fish was recorded (Figure 4.4, Table 4.2) and fishers in the exploited area were made aware of the project (Appendix 3). A total of 10 fish from PE (mean ± SD: 319 ± 43 mm fork length (FL), range: 260–390 mm FL) and 10 from TNP (mean ± SD: 327 ± 43 mm FL, range: 270–390 mm FL) were acoustically-tagged and released in the study sites (Table 4.2). As fish from both sites were of similar sizes it was assumed that there was also a similar sex-ratio of tagged fish between sites.



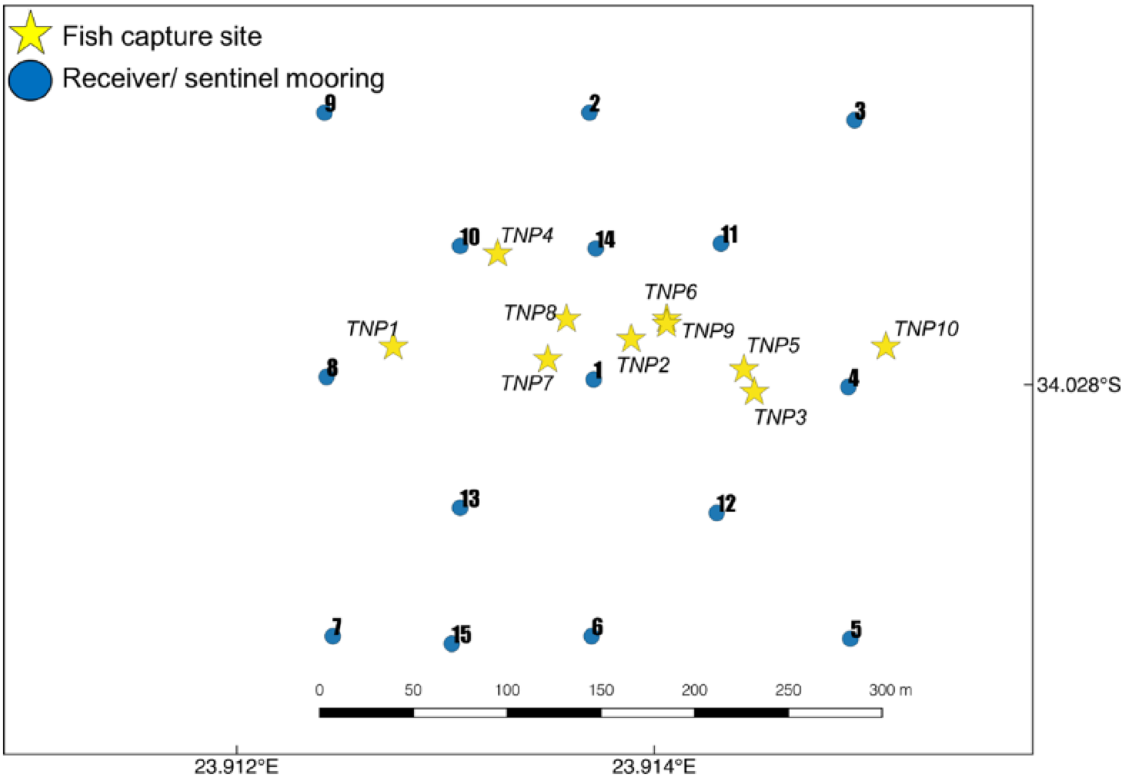


Fig 4.4: Map of the distribution of the acoustic receivers and the capture site of the ten *Chrysopbelphus laticeps* (stars) tagged in the Port Elizabeth (red dots) and Tsitsikamma National Park (blue dots) study sites. Details of sentinel tag or receiver moorings (1–15) in each site can be found in Appendix 3. Individual fish details can be found in Table 4.2.

Table 4.2: Acoustic accelerometer transmitter number (ID code), fish length (FL), total number of detections, number of days detected (no. days), number of monitoring days (mon. days) and the catch location coordinates for *Chrysoblephus laticeps* individuals caught in the Port Elizabeth (PE) and Tsitsikamma National Park (TNP) sites. Italics and * indicate fish excluded from analysis.

Site	**Fish ID**	**Id Code**	**FL (mm)**	**Total detections**	**No. days**	**Mon. days**	**Coordinates South**	**East**
PE	PE1	4386	360	26044	86	90	-34.05141	25.55032
PE	PE2	4384	290	45859	93	93	-34.05021	25.54916
PE	PE3	4412	330	73532	88	88	-34.0514	25.55037
PE	PE4	4418	270	98488	88	88	-34.05093	25.55158
PE	PE5	4396	392	114052	88	88	-34.05062	25.55091
PE	PE6	4408	262	10130	32	87	-34.05043	25.55175
PE	PE7	4416	320	135458	88	88	-34.05145	25.5508
PE	PE8	4392	365	2723	75	88	-34.05112	25.54717
PE	PE9	4402	305	2078	80	87	-34.05112	25.54717
PE	PE10	4400	292	58671	86	86	-34.05133	25.55005
TNP	TNP1	4414	270	26549	46	46	-34.02785	23.91275
TNP	TNP2	4406	350	64562	91	91	-34.02782	23.91389
TNP	TNP3*	*4404*	*335*	*43*	*1*	*1*	*-34.02803*	*23.91448*
TNP	TNP4	4398	325	76627	90	92	-34.02748	23.91325
TNP	TNP5	4410	390	83319	93	93	-34.02794	23.91443
TNP	TNP6	4394	295	48019	92	92	-34.02774	23.91406
TNP	TNP7*	*4390*	*270*	*7*	*1*	*1*	*-34.0279*	*23.91349*
TNP	TNP8	4382	370	29083	93	93	-34.02774	23.91358
TNP	TNP9*	*4388*	*325*	*652*	*8*	*30*	*-34.02776*	*23.91406*
TNP	TNP10	4380	340	66326	93	93	-34.02785	23.91511

4.2.3 Data processing

Data for each acoustic transmitter were processed individually. Times of detection were corrected for potential time drift using the VUE software (VEMCO Bedford, Nova Scotia). The first 24 hours of data were excluded (Brownscombe *et al.*, 2017) and duplicate recordings by several receivers bar the first detection were removed. Data were then filtered to only include acceleration recordings below 1.5 m/s^2 (as discussed in Chapter 3). Acceleration values were subsequently averaged every half hour in order to link these values by date and time to their corresponding water temperature. Data were categorized into day (06:00–17:59) or night (18:00–05:59) based on the average sunrise and sunset times during the experimental months (February to May 2019).

Daytime data were considered to estimate the FMR and thus used for analysis. This was because the laboratory calibration was conducted in the daytime and since exploitation for this species occurs during the day, the daytime analyses also provides information to understand the relationship between fish and fishers. As mass of the fish could not be measured on the boat we used a standard allometric length-weight conversion (Mass = $51.892e^{0.0903*Fork\ Length}$; r^2 = 0.97) calculated from the laboratory specimens to estimate mass. From the filtered data that included temperature, acceleration, site and fish mass, the FMR of each data point was estimated using the equation developed from the modelling process in Chapter 3:

$$\mathrm{FMR} = -0.705 + 0.413 * (\text{site TNP}) + 5.972 * (\text{acceleration}) + 0.164 * (\text{temperature}) - 1.114 * (\text{mass}) - 0.133 * (\text{acceleration} : \text{temperature})$$

(Equation 3.2, Chapter 3)

To ensure direct comparison of the impact of temperature on fish from the two areas, all FMR data were mass standardized. This was done by dividing FMR by mass using the mass-scaling exponent of 0.82 for maximum metabolic rate (MMR) of *C. laticeps*, which was estimated from fish from the same populations (Duncan *et al.,* 2019a).

4.2.4 Statistical Analysis

4.2.4.1 Experimental temperature regime

Temperature profiles from each site were plotted to examine whether or not the two populations experienced similar thermal conditions during the experimental period. Major upwelling events (characterised by a minimum of 5°C cooling within 24 hours) were identified to assess whether these were in synchrony between sites.

4.2.4.2 Temperature and population effects on FMR

To test for differences in the relationship between temperature and FMR between the two sites, a second order polynomial linear mixed effects model was run, with population (exploited/protected) as an interaction term, using the nlme package (Pinheiro *et al.,* 2017) in R version 3.3.3 (R Core Team 2017). The random effects structure combined fish ID (to account for repeated measures of each individual fish) and temperature as the random intercept and slope, respectively. Because residual variance decreased with temperature and potentially differed between sites, a variance structure with the combination of temperature and population as variance covariates was incorporated into the model (Zuur *et al.,* 2009). Temporal autocorrelation within individuals was accounted for by using an autocorrelation structure which included individual fish as a grouping factor and a continuous time covariate (Pinero and Bates, 2000). The model was validated using the procedure suggested by Zuur *et al.,* (2009).

4.2.4.3 Inter-individual variation in the FMR and temperature relationship

To assess and compare the relationship between FMR and temperature among individuals, a second order polynomial relationship was plotted for each fish, with FMR as the dependent variable and temperature as the independent variable, using ggplot2 (Wickham, 2006). To quantify cold temperature limits on FMR (detailed in Chapter 3), a piecewise linear breakpoint analysis was conducted by plotting the natural logarithm of FMR against temperature (1000/K, from 18°C down to the coldest temperature experienced) for each individual fish, using the segmented package (Muggeo 2003, 2008).

4.3 Results

4.3.1 Experimental temperature regime

Fish in the PE and TNP populations experienced similar thermal conditions during the experiment. The mean temperature in PE was 15.52°C ± 3.01 (range: 8.89–19.84°C) compared to 15.00°C ± 3.63 (range: 8.84–21.53°C) in TNP (Figure 4.5). Temperature variability was prevalent, and several major upwelling events occurred simultaneously.

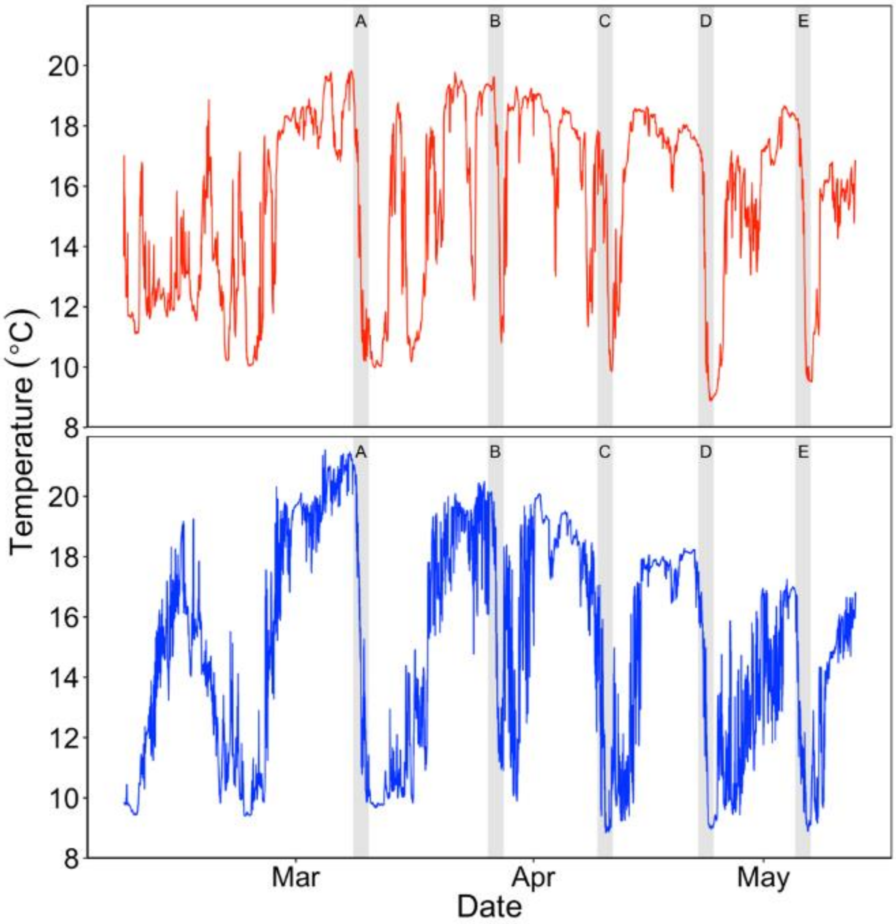


Figure 4.5: Temperature time series (every half hour) profiles from the centre of the PE array (red, depth = 14 m) and the TNP array (blue, depth = 18 m) over the three-month experimental period. Examples of coinciding upwelling events are shaded in grey and labelled respectively.

4.3.2 V13AP Detections

Ninety seven percent and 81 % of sentinel transmitter transmissions were detected by the nearest receiver (70 m) in PE and TNP, respectively. These results suggest that the overall detection efficiency of both acoustic arrays was sufficient in detecting tagged fish. All 13 receivers were retrieved from PE and a total of 567 035 acceleration estimates were obtained from the 10 individuals (Table 4.2). Each fish provided acceleration recordings through the majority of the observed temperatures (at least 3°C above and below environmental mean) and thus were included in analysis. Two of the 13 TNP receivers were lost and a total of 395 187 acceleration estimates were obtained from the 11 receivers (Table 4.2). The acceleration recordings for two fish (TNP3 and TNP7) were uncharacteristically low and it was assumed that these individuals did not survive after the surgical procedure (Figure 4.6). In addition, because the limited acceleration estimates obtained for fish TNP9 were over a narrow thermal range, this individual was also excluded from the subsequent analyses (Table 4.2, Figure 4.6). After six weeks, the acceleration estimates of TNP1 became extremely low and it was also assumed that this fish had died. A total of ten and seven fish were therefore used for analysis from PE and TNP, respectively.

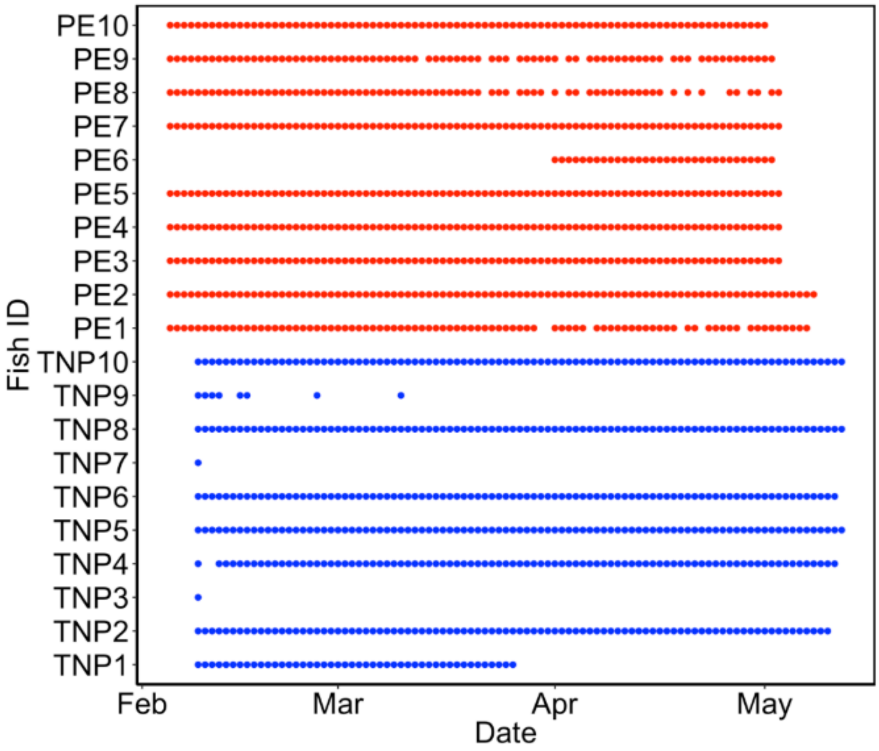


Figure 4.6: Abacus plot representing the days a tagged *Chrysoblephus laticeps* was detected by any of the receivers in the Port Elizabeth (PE, red) or Tsitsikamma National Park (TNP, blue) acoustic arrays over the three-month (February–May 2019) experimental period.

4.3.3 Temperature and population effects on FMR

The FMR of the TNP population had a positive linear relationship with temperature, whereas a bell-shaped relationship was evident for the PE population, with a reduced FMR observed at high and low temperatures (Figure 4.7). Both temperature and the quadratic temperature term had a significant effect on the FMR of *C. laticeps* (p-value = 0.000, Table 4.3). While population (exploitation/protection) did not significantly influence the FMR of *C. laticeps* (p-value = 0.145, Table 4.3), there was a significant interaction effect between population and the quadratic temperature term (p-value = 0.000, Table 4.3). Based on this interaction and modelled FMR (Figure 4.7), it appears that the FMR of the PE population was significantly reduced when temperature deviated towards extremes.

Table 4.3: Linear mixed effects modelling results for day time field metabolic rate (FMR) of *Chrysoblephus laticeps* from the Port Elizabeth (PE, exploited) and Tsitsikamma National Park (TNP, protected) populations, presented as a quadratic function of temperature (Temp), with exploitation/protection (Population) as an interaction term. AIC is Akaike information criterion, SE refers to standard error, DF indicates the degrees of freedom and significant *p*-values are highlighted in bold.

Effect	Estimate	SE	DF	t-value	*p*-value
Intercept	5.185	0.086	22511	60.160	**0.000**
Population	0.204	0.134	15	1.524	0.145
Temp	25.469	6.450	22511	3.950	**0.000**
Temp^2	-17.061	1.919	22511	-8.892	**0.000**
Population: temp	3.885	9.930	22511	0.391	0.6957
Population: temp^2	15.776	2.366	22511	6.668	**0.000**
AIC	44569.5				

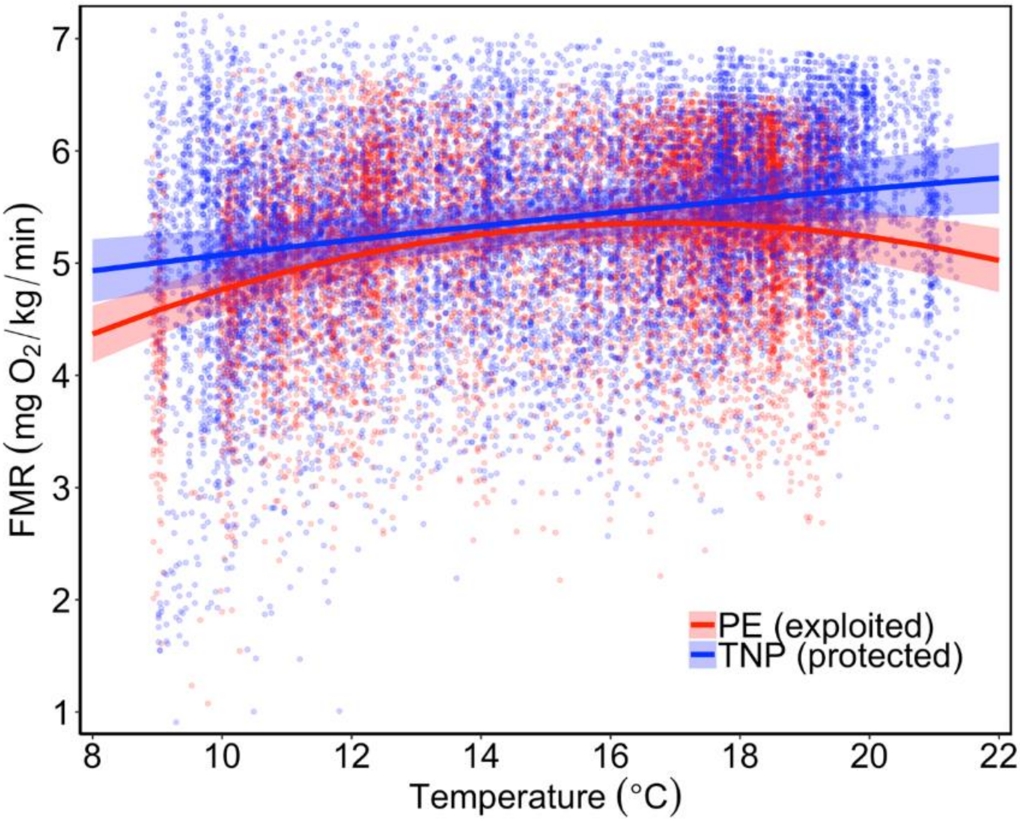


Figure 4.7: Linear mixed effects model fits (solid line) and recorded data points (dots) of field metabolic rate (FMR) for exploited (PE, red) and protected (TNP, blue) populations of *Chrysoblephus laticeps* across the thermal range observed during the experiment. Shaded areas represent 95% confidence intervals.

4.3.4 Intra-population variation in the relationship between FMR and temperature

There was a noticeable variation in the relationship between FMR and temperature within populations (Figure 4.8, Appendix 4). The relationship between FMR and temperature for the majority (90%) of the individuals from the exploited PE population assumed a typical bell-shaped curve, with decreases in FMR at the thermal extremes (hereon termed standard thermal performance (STP) phenotypes). In contrast, a single individual from this population exhibited a negative linear relationship between FMR and temperature (PE9, Figure 4.8, Appendix 4). In the protected TNP population, the shape of the FMR curve of four of the seven (57%) individuals was similar to those from the exploited population, while the remaining three had an elevated FMR at the thermal extremes (TNP1, TNP2 and TNP10, Figure 4.8, Appendix 4) (hereon termed high thermal performance (HTP) phenotypes).

There was a depression (indicated by the breakpoint and subsequent negative slope) in the FMR at cooler temperatures for all individuals from the exploited population (Figure 4.9). In contrast, a breakpoint in the FMR was only recognised at cooler temperatures for four of the seven (57%) individuals from the unexploited TNP population. The temperature at which this depression occurred was above 12°C for half of the exploited population (PE2, PE3, PE5, PE9 and PE10, Figure 4.11), whilst only occurring above 12°C in two fish (29%) from the protected population (TNP6 and TNP8, Figure 4.9). The remaining three fish from the protected population with no depression (TNP1, TNP2 and TNP10, Figure 4.9), were those HTP individuals which maintained FMR at temperature extremes (Figure 4.8).

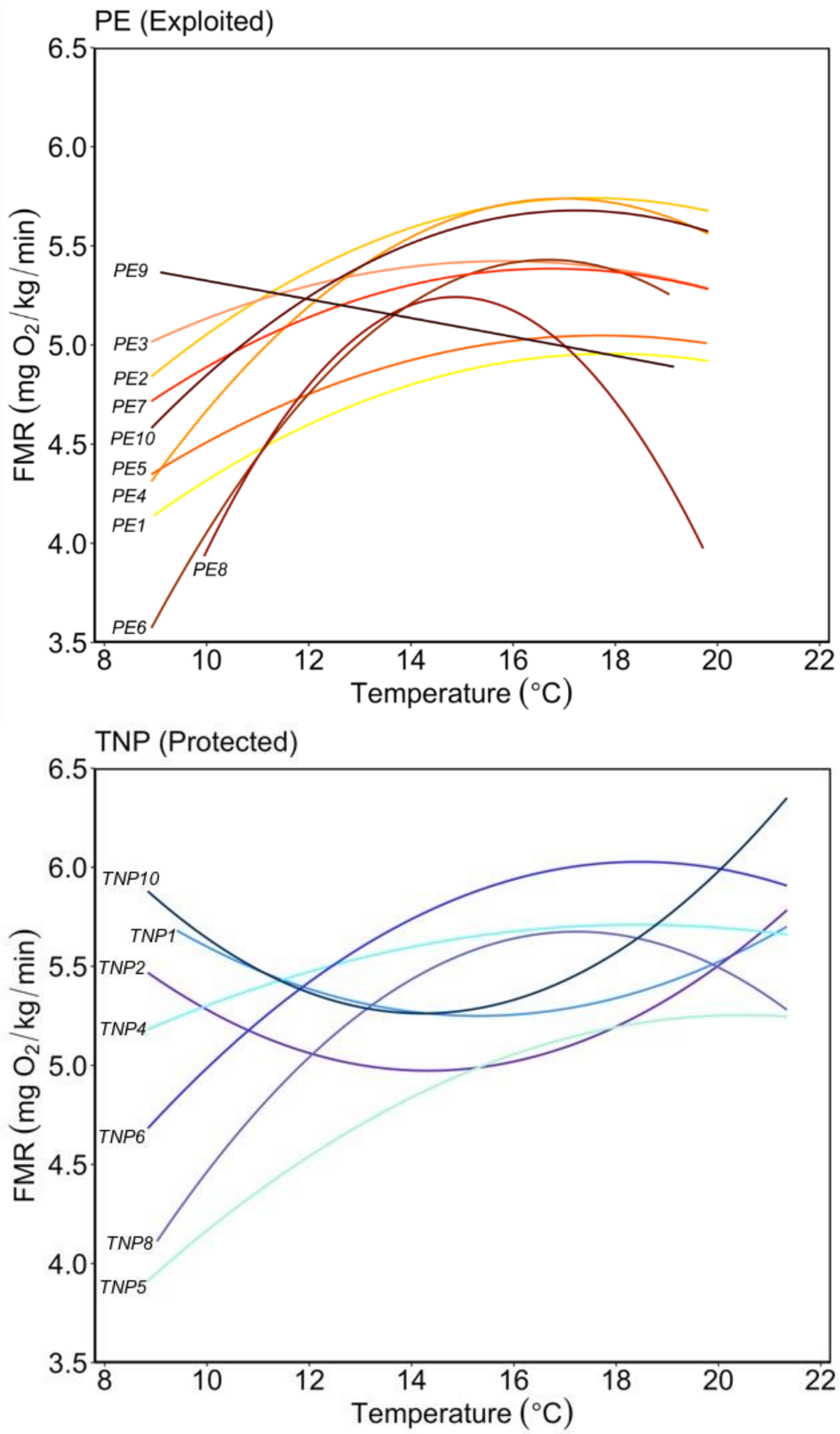
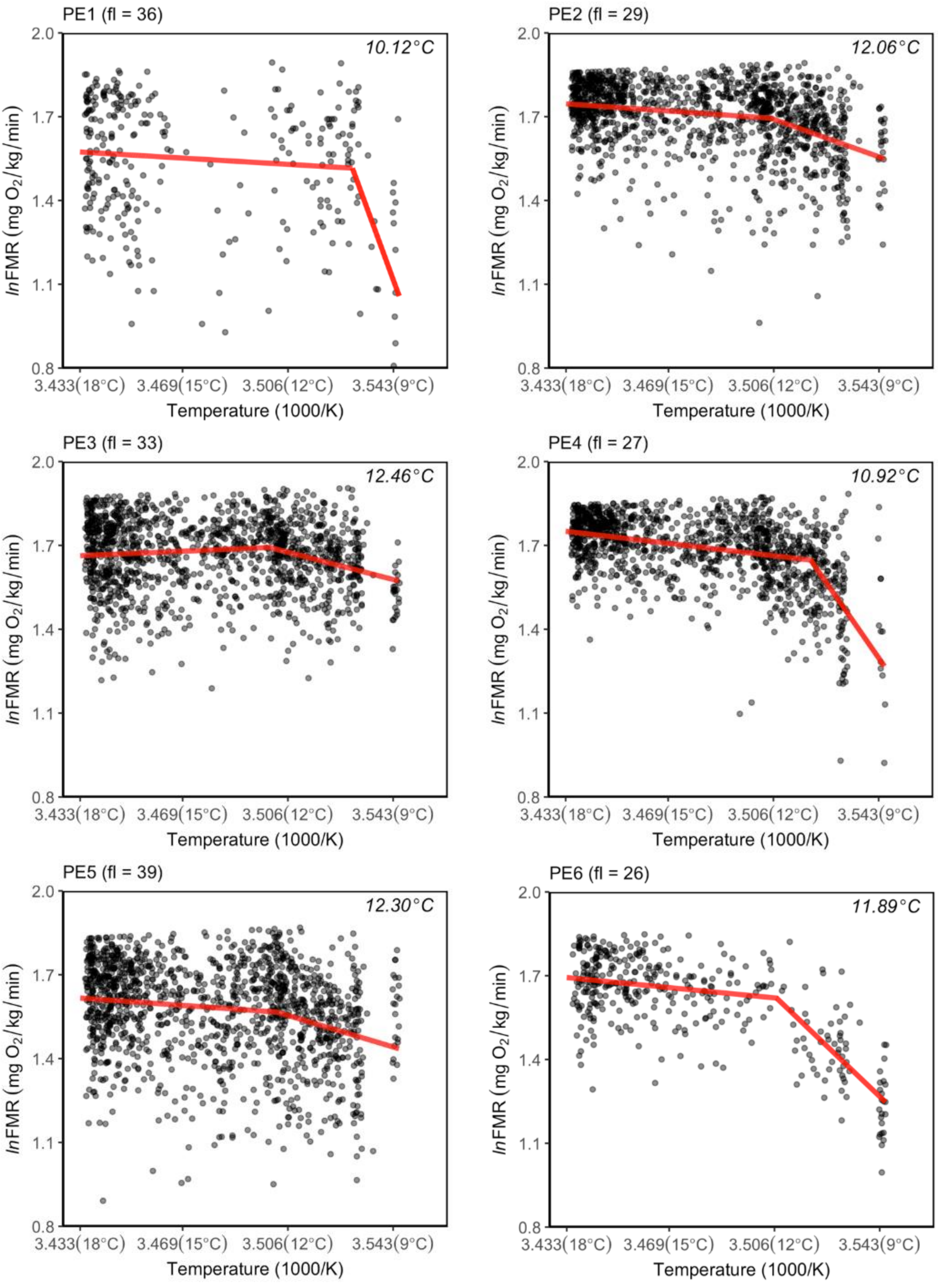
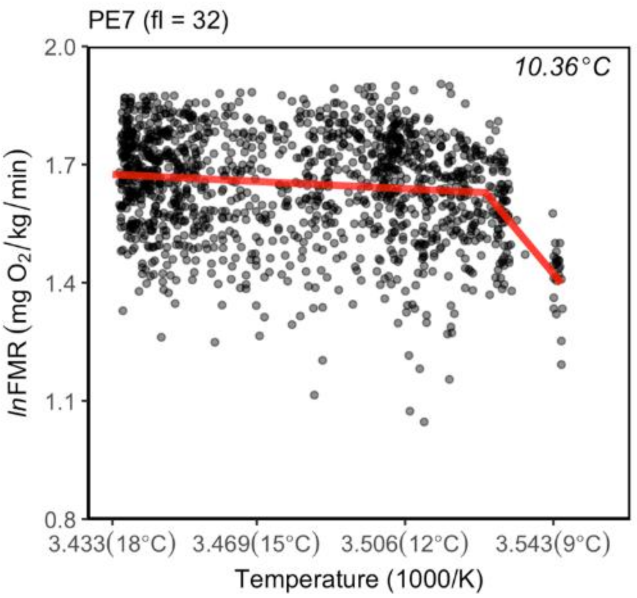
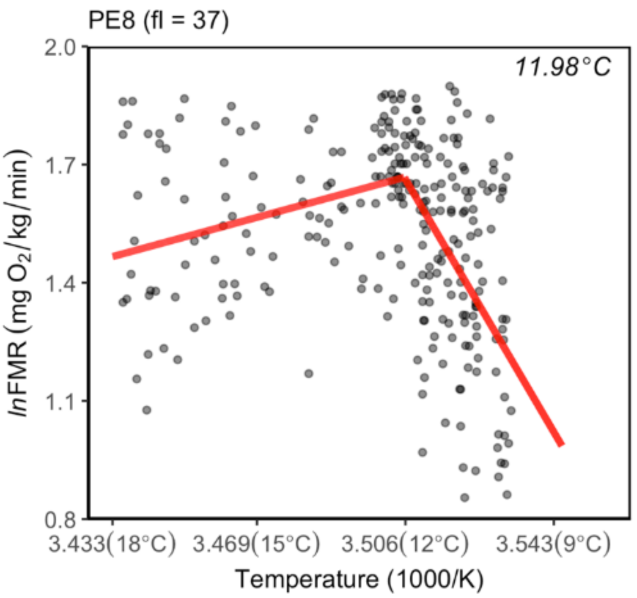
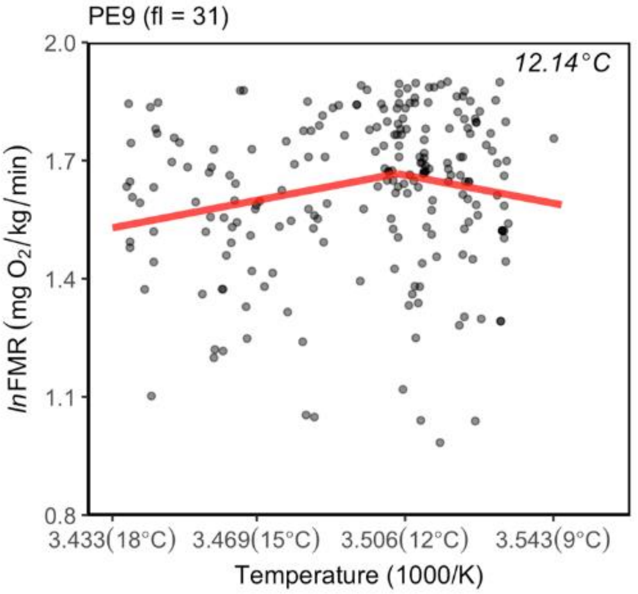


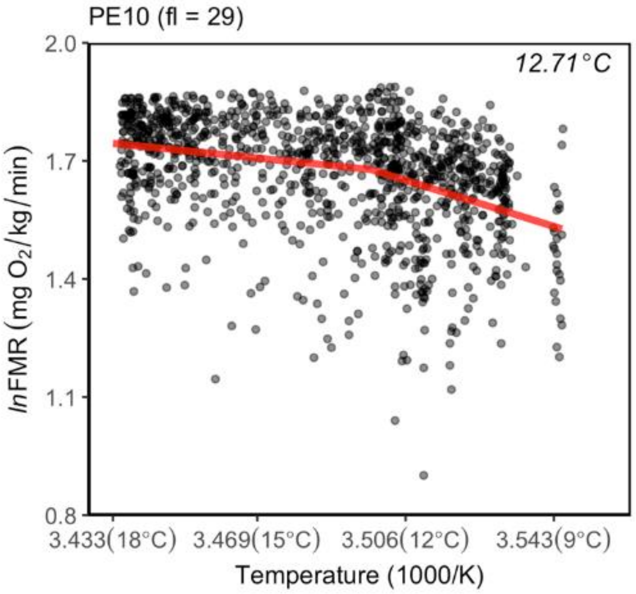
Figure 4.8: Best fit second order polynomial relationship for the field metabolic rate (FMR) of individual *Chrysoblephus laticeps* from the exploited (PE, coral colour theme) and protected (TNP, aqua colour theme) populations across temperatures experienced in the field. (Separate individual plots in Appendix 4.)

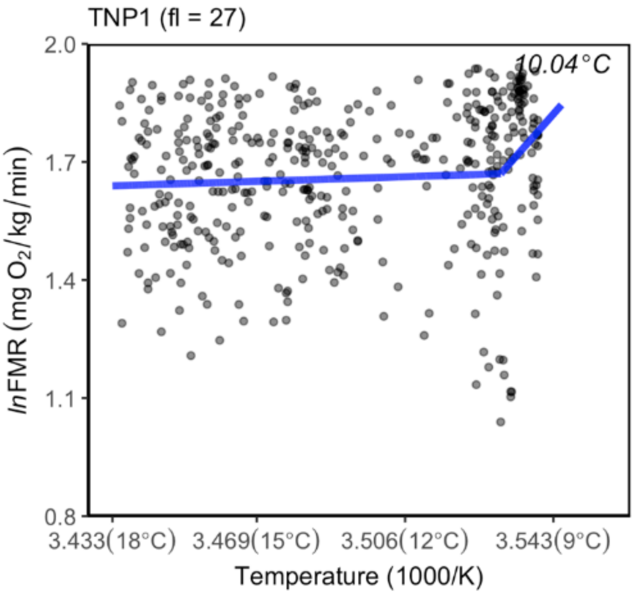

PE1 (fl = 36)
10.12°C
PE2 (fl = 29)
12.06°C
PE3 (fl = 33)
12.46°C
PE4 (fl = 27)
10.92°C
PE5 (fl = 39)
12.30°C
PE6 (fl = 26)
11.89°C
lnFMR (mg O2/kg/min)
2.0
1.7
1.4
1.1
0.8
3.433(18°C)
3.469(15°C)
3.506(12°C)
3.543(9°C)
Temperature (1000/K)

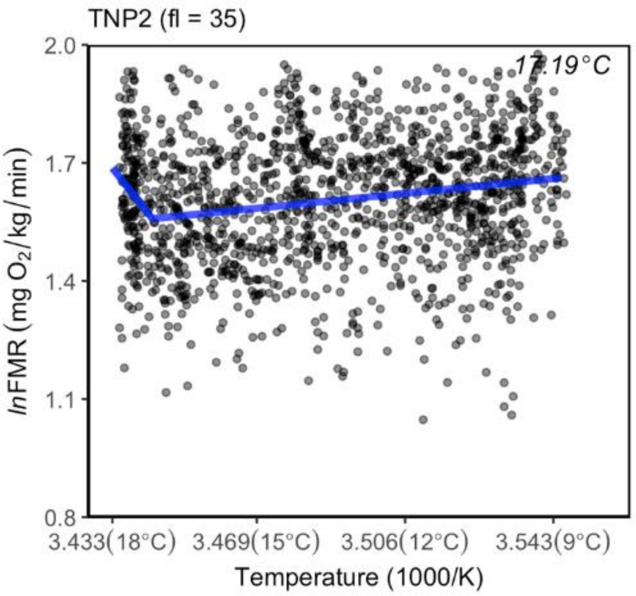

PE7 (fl = 32)
10.36°C
lnFMR (mg O$_2$/kg/min)
2.0
1.7
1.4
1.1
0.8
3.433(18°C)
3.469(15°C)
3.506(12°C)
3.543(9°C)
Temperature (1000/K)


PE8 (fl = 37)
11.98°C
lnFMR (mg O$_2$/kg/min)
2.0
1.7
1.4
1.1
0.8
3.433(18°C)
3.469(15°C)
3.506(12°C)
3.543(9°C)
Temperature (1000/K)


PE9 (fl = 31)
12.14°C
lnFMR (mg O$_2$/kg/min)
2.0
1.7
1.4
1.1
0.8
3.433(18°C)
3.469(15°C)
3.506(12°C)
3.543(9°C)
Temperature (1000/K)


PE10 (fl = 29)
12.71°C
lnFMR (mg O$_2$/kg/min)
2.0
1.7
1.4
1.1
0.8
3.433(18°C)
3.469(15°C)
3.506(12°C)
3.543(9°C)
Temperature (1000/K)


TNP1 (fl = 27)
10.04°C
lnFMR (mg O$_2$/kg/min)
2.0
1.7
1.4
1.1
0.8
3.433(18°C)
3.469(15°C)
3.506(12°C)
3.543(9°C)
Temperature (1000/K)


TNP2 (fl = 35)
17.19°C
lnFMR (mg O$_2$/kg/min)
2.0
1.7
1.4
1.1
0.8
3.433(18°C)
3.469(15°C)
3.506(12°C)
3.543(9°C)
Temperature (1000/K)

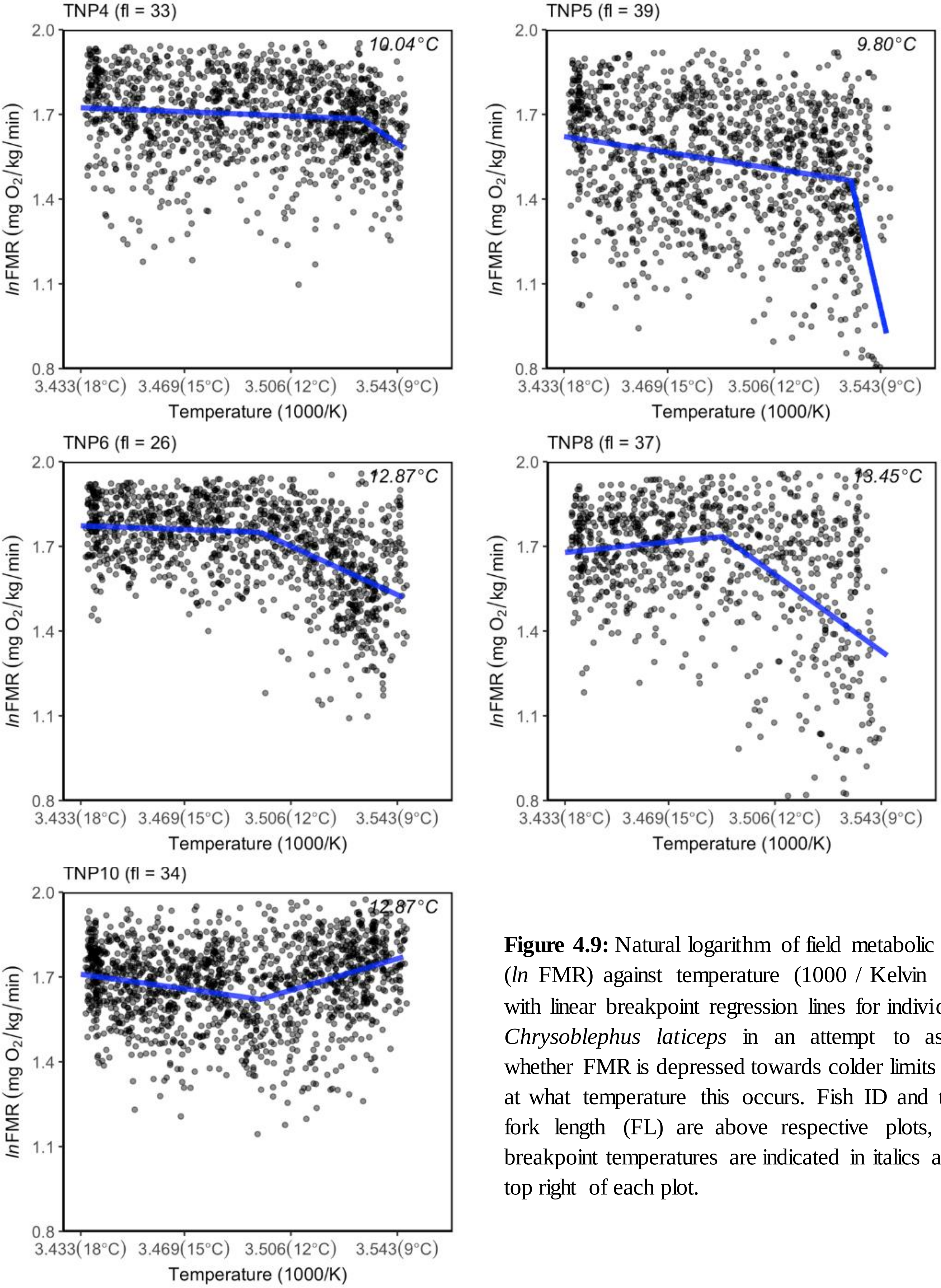


Figure 4.9: Natural logarithm of field metabolic rate (*ln* FMR) against temperature (1000 / Kelvin (K)) with linear breakpoint regression lines for individual *Chrysoblephus laticeps* in an attempt to assess whether FMR is depressed towards colder limits and at what temperature this occurs. Fish ID and their fork length (FL) are above respective plots, and breakpoint temperatures are indicated in italics at the top right of each plot.

4.4 Discussion

The results of this chapter suggest that the exploited *C. laticeps* population have a reduced ability to maintain normal activity levels and limited intra-population variability at thermal extremes compared to the unexploited population. Furthermore, individuals from the exploited population appeared to be more affected by cold temperatures, as most individuals appeared to have a depressed energy output when exposed to cold extremes. These findings suggest that exploitation by passive-fishing could reduce the energetic performance of a wild population, and therefore the resilience of exploited *C. laticeps* to thermal variability.

The inter-population differences in FMR at thermal extremes may be underpinned by differences in their physiological capacity. Duncan *et al.,* (2019a) found that individuals belonging to the exploited population (PE) had a significantly lower aerobic scope across all temperatures, but particularly at the thermal extremes, compared to individuals from the unexploited population (TNP). A lower metabolic scope suggests that exploited fish populations could lack the physiological capacity to expend energy on fitness-related activities (feeding and reproduction) (Metcalfe *et al.,* 2016, Pörtner *et al.,* 2017). The reduced FMR of the exploited population at thermal extremes observed in this study not only supports the findings by Duncan *et al.,* (2019a) but suggests that their laboratory results could be reflected in the behaviour of the fish in the wild. Because the FMR in this study was derived from acceleration, and acceleration underlies activities such as feeding and reproduction, it can be assumed that reductions in FMR may compromise these activities at thermal extremes. This could ultimately lead to a decline in population fitness.

To date, the fitness consequences of contrasting metabolic characteristics at the population level have been poorly studied. There is currently little agreement on how metabolic rate determines growth and reproduction (Neubauer and Andersen, 2019), although it has been suggested that individuals with high metabolic rates may have increased foraging rates, social dominance and overall competitiveness (Killen *et al.*, 2016, Behrens *et al.*, 2018). A recent paper by Neubauer and Andersen (2019) used a trait-based eco-physiological modelling approach to derive general predictions of temperature impacts on fish physiology, performance and ecology. One of their conclusions is that the metabolic scope begins to limit performance at thermal extremes. Based on the findings of this study, it is possible that the exploited (PE) population may, when exposed to increased thermal extremes from a changing climate, grow more slowly and suffer higher rates of natural mortality, causing a reduction in overall performance compared to the unexploited population (TNP).

The superior physiological performance by the unexploited population during sub-optimal temperatures (Figure 4.7) may be attributed to the greater levels of inter-individual variation in the relationship between FMR and temperature (Figure 4.8). The high FMR values of the HTP-phenotypic individuals from the unexploited population suggests that they had more energy available for general activities (Metcalfe *et al.*, 2016) (TNP1, TNP2 and TNP10, Figure 4.8), particularly as temperatures departed further from the environmental mean. This phenomenon was absent in the exploited population except for one individual (PE9, Figure 4.8). Although higher FMRs at thermal extremes may appear to be unusual, a similar pattern has been observed in the activity of *A. vulpes* (Brownscombe *et al.*, 2014). Our findings are congruent with those of Duncan *et al.*, (2019), who found greater variance in the aerobic scope of the protected population, particularly towards cold and warm boundaries. As metabolic rate is plastic (Norin and Metcalfe, 2019, Reveillon *et al.*, 2019), the modification of an individual's thermal performance from the population norm may be underpinned by the presence of phenotypic plasticity (Schulte *et al.*, 2011, Whitney *et al.*, 2016). It appears that the protected population has a higher level of phenotypic plasticity in their energetic response to thermal variability. This is further supported by recent research which suggests that the capacity to express behavioural plasticity is positively linked with high metabolic scope phenotypes (Biro *et al.,* 2018). While acknowledging the small sample size, if our sample specimens are a true representation of their respective population, then the lack of plasticity within the exploited population may be detrimental for future climate resilience.

Although Bates *et al.,* (2018) advocate the importance of understanding the effects of temperature variability, the colder side of climate change remains largely neglected (Szekeres *et al.,* 2016). This is a concern as the projected increase in temperature variability (Solomon *et al.,* 2007, Bates *et al.,* 2018) means localized cold events are predicted to become more frequent (Szekeres *et al.,* 2016, Duncan *et al.,* 2019b). Cold spells and extreme upwelling events have had detrimental impacts on coastal species along the South African coast, with mass mortalities (including *C. laticeps*) documented as early as the 1980's (Hanekom *et al.,* 1989). An acute decrease in ambient temperature which causes physiological stress is termed *cold shock*, and results in cascading behavioural and physiological responses such as metabolic depression (Donaldson *et al.,* 2008). In this context, it is alarming that the entire exploited population, yet only 56 % of the protected population, show signs of this decline in their FMR at cold temperatures (Figure 4.9). The onset of these metabolic cold shock symptoms in the exploited population seem to appear even at warmer temperatures (> 12°C) (Figure 4.9). These findings are similar to those of Duncan *et al.,* (2019a), who observed a break in the linear relationship between temperature and standard metabolic rate of the exploited population (PE) at 12.7°C. A reason for the cold-driven reduction of FMR may be the increased metabolic cost to accelerate at cold temperatures, presented in Chapter 3. In corroboration, Speers-Roesch *et al.,* (2018) demonstrated that energy-savings in the cunner *Tautogolabrus adsepersus* at cold extremes stemmed from reducing activity. In a population with a reduced plasticity to cold shock, exhibiting potential effects even at warmer temperatures, cold temperatures may be a hindrance for the future performance of exploited *C. laticeps*.

Assessing resilience to climate variability largely entails looking at the capacity of a population to maintain structure and functioning in the face of future disturbance (Folke, 2004). Underlying this capacity is the distribution of phenotypes and the degree of phenotypic plasticity within the population (Bernhardt and Leslie, 2013, Norin *et al.*, 2016). Populations with metabolic plasticity are likely to be more resilient to changing environments, such as those with increasing thermal instability (Seebacher *et al.*, 2015, Norin and Metcalfe, 2019). This is particularly relevant for resident species that are less likely to shift to areas with more desirable conditions. Thus, the reduced variability in physiological phenotypes (Duncan *et al.*, 2019a), and the FMR response to thermal variability by *C. laticeps* in the exploited area, may constrain their resilience. The HTP-phenotypic individuals from the unexploited population are expected to be more competitive in a future climate regime because of a probable selective force for such phenotypes. Although research into the transgenerational characteristics of metabolic rates and plasticity is challenging (Donelson *et al.*, 2017), it has been shown that metabolic traits in fish can evolve (Auer *et al.*, 2018) and are heritable (Munday *et al.*, 2017). Therefore, while the HTP traits in the unexploited population may maintain the adaptive potential of the population, the reduced variability and STP attributes suggests that exploited populations may have limited adaptive potential to increasing thermal variability.

The absence of HTP phenotypes and plasticity within the exploited population could be an outcome of passive fishing selection (Hollins *et al.*, 2018). Traits including boldness and aggression have been related to vulnerability to passive fisheries (Walsh *et al.*, 2006, Biro and

Post, 2008, Klefoth *et al.,* 2017). Physiological characteristics linked to vulnerability have also been associated with elevated cardiac (Cooke *et al.,* 2007) and metabolic scopes (Redpath *et al.,* 2010). These phenotypic traits result in more frequent encounters with fishing gear through elevated activity and curiosity (Hollins *et al.,* 2018). Therefore, as passive fisheries are not temperature-regulated, the HTP phenotypes present in the protected population may have been removed from the exploited population during encounters with fishers at sub-optimal temperatures. With exploitation occurring over many generations, the aforementioned phenotypic traits may have been weaned out of the population. While acknowledging the small sample size, the results of this study suggest that the effects of passive-fisheries may impact the resilience of *C. laticeps* to climate variability.

Although all efforts were made to test the effects of exploitation and temperature on the FMR of *C. laticeps*, it is acknowledged that other factors may have contributed towards our results. Food availability has been known to alter metabolic rates (Auer *et al.,* 2016), and as protected areas are better likely to preserve species richness and diversity (Roberts *et al.,* 2017), food accessibility is likely to differ between the two sites. However, if this did have an impact, we would have expected to see a difference in overall FMR between sites (a significant population term in Table 4.3), which is not the case as differences only occurred towards extreme temperatures. Divergent levels of competition can also affect energy expenditure (for example, Delong *et al.,* 2013). The higher species richness in TNP, and hence competition, could therefore be a contributing factor to the greater plasticity seen in the protected population. This is because some individuals may choose to capitalize on less competitive, sub-optimal conditions (such as during extreme temperatures) over their counterparts. Although an indirect effect, this would prove to be a benefit for protective management, and highlights the need for research involving the link between competition and metabolic rates in fish.

Landscape characteristics can also influence energetic costs (Shepard *et al.,* 2013). For example, Brownscombe *et al.,* (2017) distinctly illustrated the effects of habitat type on energy expenditure in *A. vulpes*. We are confident that the reef environments between our sites were similar but a finer look into the habitat and bathymetry of each site will aid in understanding the spatiotemporal energy expenditure of this species. This will be a step towards assessing whether fish from either population thermoregulate using behaviour such as taking to caves as refuge (Nay *et al.,* 2015, Habary *et al.,* 2017). The results of this study appear to show expected temperature-metabolic patterns such as performance curves with a bell shape, suggesting that although we have correlated FMR with temperature, a large proportion of FMR values are likely to be temperature-driven.

Only including acceleration values below 1.5 m/s^2 as a consequence of straight-line swimming calibrations was a major limitation of this study. Consequently, a total 57 % of acceleration estimates from the field were excluded illustrating the ecological significance of this shortfall. However, since analysis was standardized between the two populations, a comparison of the relationship between FMR and temperature, albeit at low acceleration rates, was still possible. Future analysis will therefore explore the relationship between acceleration values (without filtering below 1.5 m/s^2) and temperature. Although the estimates of FMR appeared to be realistic, despite the 1.5 m/s^2 cut-off in the validation, they were on the upper edge (4–6 mg O_2/kg/min) of the aerobic scope estimates for the same populations (Duncan *et al.,* 2019a). It is possible that the higher FMR values could be attributed to the elevated energetic cost of life in the natural environment. However, this could also be a consequence of rotational locomotion and the impact of ocean swell (such as studied by Marcoux and Korsmeyer, 2019), which may have resulted in overestimates of acceleration (and FMR). While this bias is less likely in low energy environments, the impact of water movements on the estimates of acceleration in high energy environments should be assessed.

Another caveat associated with using accelerometer transmitters is the trade-off challenges of increased battery and memory with limited recorded parameters and reduced frequencies, which currently restricts fine-scale analysis of behaviour and field metabolism with acoustic accelerometers (Cooke *et al.,* 2016). In addition, perhaps more critically, when examining the impact of temperature on FMR, a temperature sensor should be incorporated into the acoustic accelerometer transmitters, especially those recording movement on two axes. As data storage tags with heart rate, acceleration and temperature features do exist (as used by Clarke *et al.,* 2010), the simultaneous inclusion of these parameters in future acoustic transmitters will enhance the analyses of the physiological responses of fish to their natural environment. This would be especially beneficial in assessing post-anaerobic effects on metabolic rate (Cooke *et al.,* 2016). The monetary cost associated with this equipment is another challenge, especially in developing nations, as it impedes researchers from being able to scale up their sample sizes, something that was evident in this study.

On a global scale, regardless of gear used, fisheries induce some form of selective mortality which may influence the resilience of fish in the Anthropocene. Thus, research on the relevance of our findings in other species, fisheries and environments is required. In addition, the selective effects of different gear (for example, capture fisheries) on the physiology of fish is currently an under studied issue. For example, are populations subjected to the removal of shoaling fish by trawl fisheries, left with high performance phenotypes that do not rely on the energy saving associated with schooling (Nadler *et al.,* 2016)? By comparing the wild energy expenditure of an exploited and unexploited population of *C. laticeps* over a three-month period of high temperature variability, we were able to assess individual energetic responses to temperature gradients, enabling us to infer population trends. There is evidently less plasticity in the energetic response of individuals in the exploited population, that as a whole, appear to be more sensitive to sub-optimal and cold temperatures. If these differences in population phenotypes are consistent throughout each population, driven by exploitation, heritable and linked to increased fitness, then in the context of future climate variability and increasing periods of sub-optimal temperatures, it is likely that exploitation can influence the resilience of *C. laticeps* to temperature variability.

Chapter 5: General Discussion

A *Chrysoblephus laticeps* displaying all of its beauty in a typical South African reef scene (image credit: Steve Benjamin)

5.1 Marine protected areas promote climate resilience for *Chrysoblephus laticeps*

To the best of my knowledge, this study is the first to use acoustic accelerometer transmitters and a calibration procedure to assess the wild energetic response of a resident marine species to high levels of thermal variability. In addition, by comparing the energetic response between an exploited and protected population, this study provided novel findings which may better illuminate the implications of the selective nature of passive-fishing on the climate resilience of fishes. In their natural environment, it appears that the energetic output of the exploited population is constrained in cold and warm extremes. The study also found a greater level of inter-individual variability in the FMR-temperature relationship within the protected population. There was a higher proportion of high thermal performance phenotypes that maintain energy expenditure at sub-optimal/extreme temperatures in the unexploited fish compared with the exploited population, which is dominated by individuals with standard thermal performance phenotypes. This chapter explores the potential anthropogenic and climate change impacts on the future of HTP phenotypes. This is particularly relevant as the effects of climate change at population, community and ecosystem levels are largely an outcome of processes acting on individuals (Perry *et al.*, 2010), and there is increasing recognition of the need to understand individual variability for a cohesive ecosystems-based approach to fisheries management (Ward *et al.*, 2016).

Foremost, this study improves understanding of the mechanisms driving the resilience of fishes to a changing environment. The results of this study, in combination with those of Duncan *et al.*, (2019a) contribute towards the contentious debate over the ecological applicability of the aerobic scope metric. The elevated high-performance metabolic-scope laboratory phenotypes within TNP, and the reduction of these respective individuals in PE (Duncan *et al.*, 2019a), are reflected in the proportion of HTP and STP phenotypes found in the same populations in the wild. This finding may suggest that aerobic scope could indeed accurately represent the energetic capacity of an individual in the field, and can therefore aid in understanding the physiological resilience of fish to temperature change. However, there is a mismatch between the temperature at which FMR and aerobic scope curves peak (even with the 1.5 m/^{s2} acceleration cut-off) (see Duncan *et al.,* 2019a for comparison) which supports the apprehension behind using the pinnacle of aerobic scope (ToptAS) as an optimum temperature for performance for a species (Clark *et al.,* 2013). Moving forward, the study of Duncan *et al.,* (2019a) and this study provide substantial evidence for the presence of fish with high metabolic-scope and elevated field energetic characteristics in the TNP MPA and the lack thereof in the exploited area. This has potentially far reaching implications for the way in which we view exploitation and how we adapt to maintain resilient fisheries in the Anthropocene (Figure 5.1).

On a global scale, fisheries exploitation is increasing to meet the protein demand of an exponentially growing human population (FAO, 2014). Unchanged, this will continue to reduce trait diversity in populations (Enberg *et al.,* 2012, Cooke *et al.,* 2017) and amplify the effects of climate change stressors (Perry *et al.,* 2010). The lack of thermal physiological diversity and HTP phenotypes within the exploited population of *C. laticeps,* and potentially other species that are targeted using the same capture techniques, is a concern. The prevalence of STP phenotypes in exploited populations may well result from the loss of HTP fish to passive harvesting. Based on these findings, the energetic advantage of HTP individuals at thermal extremes makes these individuals susceptible to fishing pressure regardless of temperature, and thus they are more likely to be harvested. However, the behavioural and vulnerability traits of HTP fish still need to be assessed to further understand this potential mechanism (Figure 5.1). A lack of diversity in the thermal physiological traits of populations could lead to reduced resilience due to the dominance of STP individuals and their poor energetic capacity at thermal extremes (Figure 5.1, pathway X). This could further hinder the sustainability of the fishery as an increased occurrence of STP individuals might have an impact on catchability, with more vulnerable individuals dominating exploited fish populations (Biro and Post, 2008, Arlinghaus *et al.*, 2017, Cooke *et al.*, 2017).

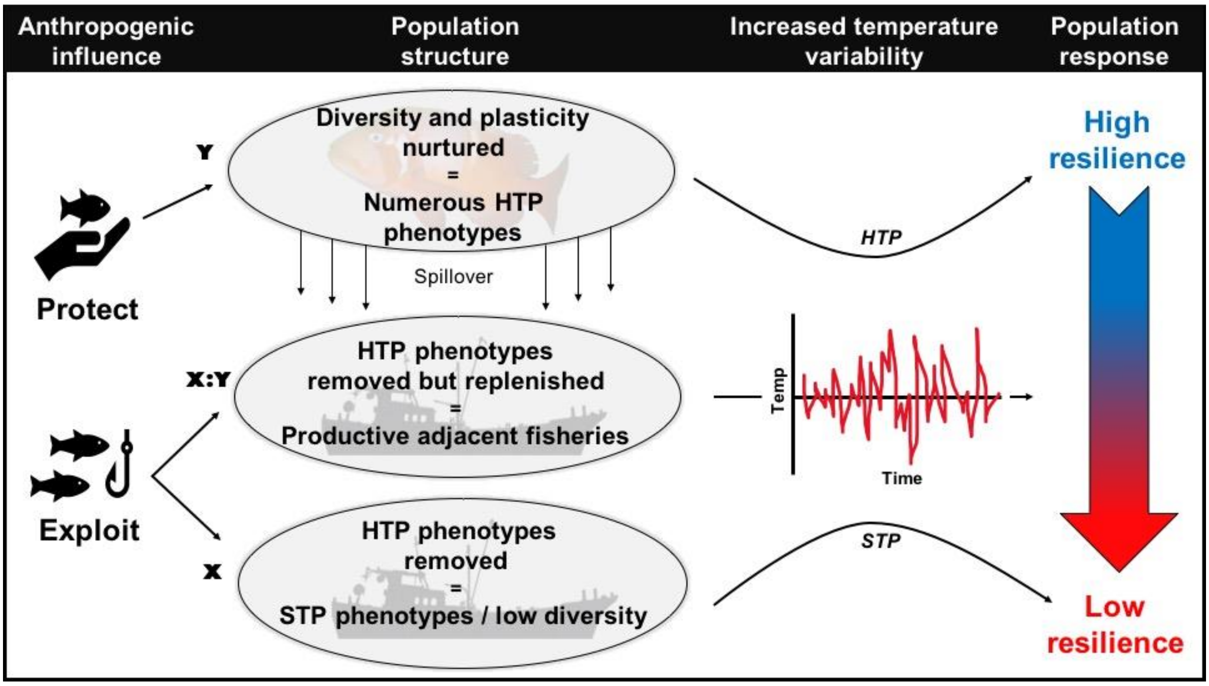


Figure 5.1: Conceptual depiction of the impacts of protection and exploitation on the population structure (in terms of physiological trait diversity) of *Chrysoblephus laticeps*, and the potential outcomes in terms of resilience as these populations progress through a future of increasing thermal variability. HTP signifies the high thermal performance phenotypes discussed in Chapter 4 where energy expenditure is maintained at sub-optimal temperatures. STP indicates standard thermal performance phenotypes where energy output is decreased at thermal extremes. Different pathways caused by anthropogenic impacts and their consequences in a future of temperature variability are indicated by X, Y and X:Y, which is the interaction between the two.

The greater physiological diversity and high number of HTP individuals in the near-pristine population within TNP highlights the importance of protective management. Marine protected areas (MPA), formally created as a means for marine conservation (Agardy, 1994), now appear globally as a tool for fisheries management (McLeod *et al.*, 2009). In this chapter, MPAs are referred to as no-take-reserves; they are the most effective protected areas as all extractive activities are prohibited (Sala and Giakoumi, 2018). Their direct biological benefits have been well studied, leading to positive effects on biomass, numerical density, size of individuals and species richness (reviewed in Lester *et al.*, 2009). In addition, MPAs preserve life-history characteristics such as age-at-maturity, age-at-sex-change and a balanced sex ratio, all of which have been identified in the study area and species (Buxton 1993, Gotz *et al.*, 2008). These heritable traits can spread through dispersal of larvae and adults into adjacent exploited areas, and thus maintain productivity and population continuity (Planes *et al.*, 2009, Kerwath *et al.*, 2013).

Only recently have MPAs been recognized for their potential to mitigate effects of climate change on marine ecosystems (Roberts *et al.*, 2017, although Bates *et al.*, 2019 better discuss their associated complexity). The greater reproductive output of larger populations can act as a buffer against environmental perturbation (Roberts *et al.*, 2017), whilst the preservation of individual trait diversity can increase chances of survival and hence population resilience as surroundings change (Bernhardt and Leslie, 2013). Evidence for the increased diversity of the thermal physiological traits of *C. laticeps* within Africa's oldest MPA, presented in this study and in that of Duncan *et al.*, (2019a), substantiates the climate change-mitigating potential of these areas. The larger numbers of HTP phenotypes within TNP can ensure persistence under future selection pressures, rendering resilience as the area is subjected to increasing thermal variability (Duncan *et al.*, 2019b). Future research still needs to assess whether these phenotypes are heritable, associated with beneficial life-history strategies, and consistently occur in other protected populations. Protective management is an anthropogenic influence which can foster physiological trait diversity and HTP individuals in a population, increasing probable population resilience in an inevitable future of rising thermal variability (Figure 5.1, pathway Y).

South Africa's population of *C. laticeps* and its dependent fishing industry are confronted with a future of increasing temperature variability, and to remain sustainable, biological and socio-economic resilience must be prioritised. From the perspective of the industry, resilience is underpinned by the maintenance of predictable catch rates (Perry *et al.,* 2010). Efficient spatial planning of MPAs is key in maintaining socio-economic sustainability as well as biological rigidity (Le Cornu *et al.,* 2018). By safeguarding HTP phenotypes in well positioned areas, productivity within adjacent fisheries can remain stable in an unpredictable future from the spillover of adults and larvae with HTP physiological traits to other areas (Figure 5.1, pathway X:Y). In another study on *C. laticeps,* Kerwath *et al.,* (2013) showed that the 40 km^2 Goukamma MPA, situated 100 km from TNP, effectively doubled catch-per-unit-effort (CPUE) in adjacent fisheries 10 years after being established. Over a similar timeframe, extreme upwelling events have increased in the area (Duncan *et al.,* 2019b). Therefore, the rise in productivity of adjacent fisheries at a time of increased thermal variability could suggest a contribution by the overflow of individuals with HTP traits from the adjacent MPA. The biological and socio-economic benefits derived from an abundance of HTP individuals may already be present along South Africa's coast.

By understanding the potential mechanism driving resilience to increased thermal variability, it may be possible, through the design of MPA networks, to further increase the resilience of *C. laticeps* populations to future thermal variability. When considering this, and the significance of MPA networks, the future of *C. laticeps* and the respective fishery looks more optimistic as we progress through the Anthropocene. Within 2019, 20 new Marine Protected

Areas proposed by the South African Minister of Environmental Affairs were formally gazetted. Five percent of South African marine ecosystems are now protected compared to a previous 0.4% before 2019. Across *C. laticeps'* core distribution there is efficient coverage by numerous MPAs, despite only a few being no-take zones (Figure 5.2). The adequately spaced Table Mountain National Park, Addo Elephant Park, Tsitsikamma National Park and De Hoop provide the largest coverage, with the latter two being exclusively restricted zones (Figure 5.2). Between these are well-dispersed smaller MPAs such as Walker Bay, Stilbaai, Goukamma and Sardinia Bay, providing additional intermittent protection. When combining results of enhanced HTP phenotypic diversity in protected areas with the efficient spatial coverage of MPAs in *C. laticeps*' core distribution, adequate levels of resilience to impending temperature change may result. Although TNP, South Africa's largest MPA, is situated in the core of the distribution of *C. laticeps*, the general MPA protection around the country may also provide protection for other species with similar life histories (such as resident or long-lived species). However, it is likely that the positioning of the MPA network, in relation to distribution of a species, is critical for the efficacy of protection. Ultimately, in South Africa (and globally), fisheries management should consider conservation physiology, and the positioning of MPAs should be evaluated in light of the core distribution of the major fisheries species and their life history tactics, particularly with regards to their dispersal capabilities.

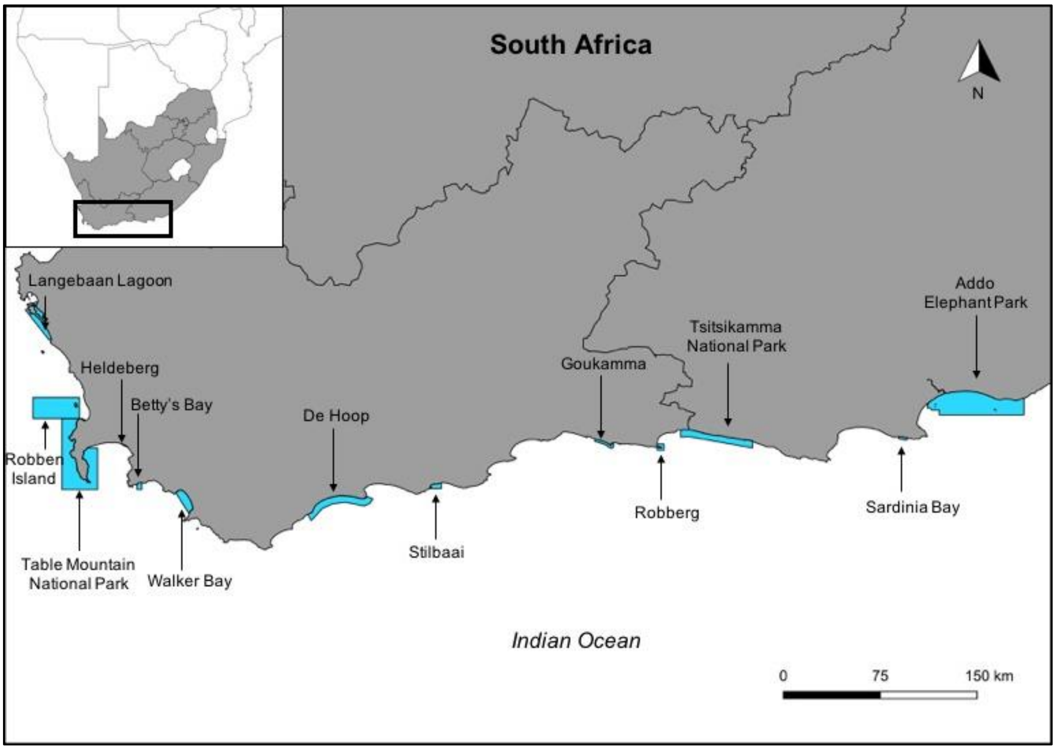


Figure 5.2: South African marine protected areas (MPA's, light blue) across the core distribution of *Chrysoblephus laticeps*. Note the dispersed large MPA's (Table Mountain National Park, De Hoop, Tsitsikamma National Park and Addo elephant Park) with efficiently-positioned smaller intermittent MPA's (Walker Bay, Stilbaai, Goukamma, Sardinia Bay) providing an efficient network of protective coverage for *C. laticeps* and similar species.

Before concluding this thesis, some uncertainties of this study must be addressed. Foremost, the differences observed between the exploited and unexploited site are attributed to differing historical fisheries pressures. However, because of a limited site comparison, the observed population differences could stem from other unaccounted factors including a difference in local adaptations to thermal environments (e.g., Eliason *et al.* 2011). Thus, to truly substantiate such findings and reduce some uncertainty, a more robust approach would be to compare multiple sites for exploited and unexploited populations. Further, the small sample sizes raise uncertainty that the individuals selected are a true representative of the population. Whilst increasing the sample size of such experiments comes with an associated monetary cost, a reduced uncertainty within a studied population can have more of a significant impact for management and conservation decisions.

Regardless of these uncertainties, the alignment of the findings of this study with those of Duncan *et al.,* (2019a) suggests that the results are robust and therefore this thesis provides a fundamental example of the applicability of conservation physiological research. Mckenzie *et al.,* (2016) reviewed the four major issues around this field of study that emerged from meetings under the European Union's Cooperation in Science and Technology (COST) Action FA1004 *Conservation Physiology of Marine Fishes* (2011–2015; http://fish-conservation.nu). This research strongly aligns with two of these issues, namely, "i) the state of basic physiological knowledge for marine fishes and how this might be applied directly towards conservation goals" and "iii) how biotelemetry and biologging studies can contribute to conservation research" (Mckenzie *et al.*, 2016). This study therefore contributes to the basic physiological knowledge of a marine fish by elucidating the natural-state energy expenditure of a resident Sparid in response to *in situ* thermal variability. By comparing this response in a protected and exploited population, this study has demonstrated that appropriate protective management may preserve the thermal physiological diversity of fishes, thus integrating our research with conservation goals. Finally, as the methods entailed the use of acoustic accelerometry, this study provides empirical evidence of the usefulness of biotelemetry for conservation research.

References

Agardy, M.T. 1994. Advances in marine conservation: the role of marine protected areas. *Trends in ecology & evolution* 9: 267-270.

Algera, D.A., Brownscombe, J.W., Gilmour, K.M., Lawrence, M.J., Zolderdo, A.J. and Cooke, S.J. 2017. Cortisol treatment affects locomotor activity and swimming behaviour of male smallmouth bass engaged in paternal care: A field study using acceleration biologgers. *Physiology & Behavior* 181: 59-68.

Arlinghaus, R., Laskowski, K.L., Alós, J., Klefoth, T., Monk, C.T., Nakayama, S. and Schröder, A. 2017. Passive gear-induced timidity syndrome in wild fish populations and its potential ecological and managerial implications. *Fish and Fisheries* 18: 360-373.

Auer, S.K., Salin, K., Rudolf, A.M., Anderson, G.J. and Metcalfe, N.B. 2016. Differential effects of food availability on minimum and maximum rates of metabolism. *Biology Letters* 12: p.20160586.

Auer, S.K., Dick, C.A., Metcalfe, N.B. and Reznick, D.N. 2018. Metabolic rate evolves rapidly and in parallel with the pace of life history. *Nature Communications* 9: 14.

Baker, R. R. (1978). *The Evolutionary Ecology of Animal Migration*. New York: Holmes and Meyer.

Baker, R., Barnett, A., Bradley, M., Abrantes, K. and Sheaves, M. 2019. Contrasting Seascape Use by a Coastal Fish Assemblage: a Multi-methods Approach. *Estuaries and Coasts* 42: 292-307.

Barnett, A., Payne, N.L., Semmens, J.M. and Fitzpatrick, R. 2016. Ecotourism increases the field metabolic rate of whitetip reef sharks. *Biological Conservation* 199: 132-136.

Bates, A.E., Barrett, N.S., Stuart-Smith, R.D., Holbrook, N.J., Thompson, P.A. and Edgar, G.J. 2014. Resilience and signatures of tropicalization in protected reef fish communities. *Nature Climate Change* 4: 62-67.

Bates, A.E., Helmuth, B., Burrows, M.T., Duncan, M.I., Garrabou, J., Guy-Haim, T., Lima, F., Queiros, A.M., Seabra, R., Marsh, R. and Belmaker, J. 2018. Biologists ignore ocean weather at their peril. *Nature 560: 299-301*.

Bates, A.E., Cooke, R.S., Duncan, M.I., Edgar, G.J., Bruno, J.F., Benedetti-Cecchi, L., Côté, I.M., Lefcheck, J.S., Costello, M.J., Barrett, N. and Bird, T.J. 2019. Climate resilience in marine protected areas and the 'Protection Paradox'. *Biological Conservation* 236: 305-314.

Behrens, J.W., Svendsen, J.C., Neuenfeldt, S., Andersen, N.G. and van Deurs, M. 2018. Individual variation in aerobic scope affects modeled vertical foraging migration in Atlantic cod Gadhus morhua, but only in moderate hypoxia. *Marine Ecology Progress Series* 599: 201-208.

Bernhardt, J.R. and Leslie, H.M. 2013. Resilience to climate change in coastal marine ecosystems. *Annual Review of Marine Science* 5: 371-392.

Binder, T.R., Wilson, A.D., Wilson, S.M., Suski, C.D., Godin, J.G.J. and Cooke, S.J. 2016. Is there a pace-of-life syndrome linking boldness and metabolic capacity for locomotion in bluegill sunfish? *Animal Behaviour* 121: 175-183.

Biro, P.A. and Post, J.R. 2008. Rapid depletion of genotypes with fast growth and bold personality traits from harvested fish populations. *Proceedings of the National Academy of Sciences* 105: 2919-2922.

Biro, P.A., Garland Jr, T., Beckmann, C., Ujvari, B., Thomas, F. and Post, J.R. 2018. Metabolic scope as a proximate constraint on individual behavioral variation: effects on personality, plasticity, and predictability. *The American Naturalist* 192: 142-154.

Blake, R.W. 2004. Fish functional design and swimming performance. *Journal of Fish Biology* 65: 1193–1222.

Boisclair, D. and Leggett, W.C. 1989. The importance of activity in bioenergetics models applied to actively foraging fishes. *Canadian Journal of Fisheries and Aquatic Sciences 46*: 1859-1867.

Bouyoucos, I.A., Montgomery, D.W., Brownscombe, J.W., Cooke, S.J., Suski, C.D., Mandelman, J.W. and Brooks, E.J. 2017. Swimming speeds and metabolic rates of semi-captive juvenile lemon sharks (Negaprion brevirostris, Poey) estimated with acceleration biologgers. *Journal of Experimental Marine Biology and Ecology* 486: 245-254.

Brander, K. 2010. Impacts of climate change on fisheries. *Journal of Marine Systems* 79: 389-402.

Brodie, S., Taylor, M.D., Smith, J.A., Suthers, I.M., Gray, C.A. and Payne, N.L. 2016. Improving consumption rate estimates by incorporating wild activity into a bioenergetics model. *Ecology and evolution* 6: 2262-2274.

Brouwer, S.L. and Buxton, C.D. 2002. Catch and effort of the shore and skiboat linefisheries along the South African Eastern Cape coast. *African Journal of Marine Science* 24: 341-354.

Brown, J.H., Gillooly, J.F., Allen, A.P., Savage, V.M. and West, G.B. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771-1789.

Brown, D.D., Kays, R., Wikelski, M., Wilson, R. and Klimley, A.P. 2013. Observing the unwatchable through acceleration logging of animal behavior. *Animal Biotelemetry* 1: 20.

Brownscombe, J.W., Gutowsky, L.F., Danylchuk, A.J. and Cooke, S.J. 2014. Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. *Marine Ecology Progress Series* 505: 241-251.

Brownscombe, J.W., Cooke, S.J. and Danylchuk, A.J. 2017. Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Oecologia* 183: 689-699.

Bruce, B., Bradford, R., Foster, S., Lee, K., Lansdell, M., Cooper, S. and Przeslawski, R. 2018. Quantifying fish behaviour and commercial catch rates in relation to a marine seismic survey. *Marine Environmental Research* 140: 18-30.

Buxton, C. D. 1987. Life history changes of two reef fish species in exploited and unexploited marine environment in South Africa. Rhodes University, PhD thesis. 229 pp.

Buxton, C.D., 1990. The reproductive biology of Chrysoblephus laticeps and C. cristiceps (Teleostei: Sparidae). *Journal of Zoology* 220: 497-511.

Buxton, C.D. 1993. Life-history changes in exploited reef fishes on the east coast of South Africa. *Environmental Biology of Fishes* 36: 47-63.

Claireaux, G., Couturier, C. and Groison, A.L. 2006. Effect of temperature on maximum swimming speed and cost of transport in juvenile European sea bass (Dicentrarchus labrax). *Journal of Experimental Biology* 209: 3420-3428.

Clark, T.D., Sandblom, E., Hinch, S.G., Patterson, D.A., Frappell, P.B. and Farrell, A.P. 2010. Simultaneous biologging of heart rate and acceleration, and their relationships with energy expenditure in free-swimming sockeye salmon (Oncorhynchus nerka). *Journal of Comparative Physiology B* 180: 673-684.

Clark, T.D., Sandblom, E. and Jutfelt, F. 2013. Aerobic scope measurements of fishes in an era of climate change: respirometry, relevance and recommendations. *Journal of Experimental Biology* 216: 2771-2782.

Cooke, S.J., Suski, C.D., Ostrand, K.G., Wahl, D.H. and Philipp, D.P. 2007. Physiological and behavioral consequences of long-term artificial selection for vulnerability to recreational angling in a teleost fish. *Physiological and Biochemical Zoology* 80: 480-490.

Cooke, S.J. and O'Connor, C.M. 2010. Making conservation physiology relevant to policy makers and conservation practitioners. *Conservation Letters* 3: 159-166.

Cooke, S.J., Sack, L., Franklin, C.E., Farrell, A.P., Beardall, J., Wikelski, M. and Chown, S.L. 2013. What is conservation physiology? Perspectives on an increasingly integrated and essential science. *Conservation Physiology* 1: p.cot001.

Cooke, S.J., Brownscombe, J.W., Raby, G.D., Broell, F., Hinch, S.G., Clark, T.D. and Semmens, J.M. 2016. Remote bioenergetics measurements in wild fish: opportunities and challenges. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 202: 23-37.

Cruz-Font, L., Shuter, B.J. and Blanchfield, P.J. 2016. Energetic costs of activity in wild Lake Trout: A calibration study using acceleration transmitters and positional telemetry. *Canadian journal of fisheries and aquatic sciences* 73: 1237-1250.

Davis, J. A. 1996. Investigations into the larval rearing of two South African sparid species. Rhodes University, MSc thesis. 147 pp.

DeLong, J.P., Hanley, T.C. and Vasseur, D.A. 2014. Competition and the density dependence of metabolic rates. *Journal of Animal Ecology* 83: 51-58.

Deutsch, C., Ferrel, A., Seibel, B., Pörtner, H.O. and Huey, R.B. 2015. Climate change tightens a metabolic constraint on marine habitats. *Science* 348: 1132-1135.

Dillon, M.E., Woods, H.A., Wang, G., Fey, S.B., Vasseur, D.A., Telemeco, R.S., Marshall, K. and Pincebourde, S. 2016. Life in the frequency domain: the biological impacts of changes in climate variability at multiple time scales. *Integrative and comparative biology* 56: 14-30.

Donaldson, M.R., Cooke, S.J., Patterson, D.A. and Macdonald, J.S. 2008. Cold shock and fish. *Journal of Fish Biology* 73: 1491-1530.

Donelson, J.M., Salinas, S., Munday, P.L. and Shama, L.N. 2018. Transgenerational plasticity and climate change experiments: Where do we go from here?. *Global Change Biology* 24: 3-34.

Duncan, M.I., Bates, A.E., James, N.C. and Potts, W.M. 2019a. Exploitation may influence the climate resilience of fish populations through removing high performance metabolic phenotypes. *Scientific reports 9*: 1-10.

Duncan, M.I., James, N.C., Bates, A.E., Goschen, W.S. and Potts, W.M. 2019b. Localised intermittent upwelling intensity has increased along South Africa's south coast due to El Niño–Southern Oscillation phase state. *African Journal of Marine Science* 41: 325-330.

Eliason, E.J., Clark, T.D., Hague, M.J., Hanson, L.M., Gallagher, Z.S., Jeffries, K.M., Gale, M.K., Patterson, D.A., Hinch, S.G. and Farrell, A.P. 2011. Differences in thermal tolerance among sockeye salmon populations. *Science 332*: 109-112.

Enberg, K., Jørgensen, C., Dunlop, E.S., Varpe, Ø., Boukal, D.S., Baulier, L., Eliassen, S. and Heino, M. 2012. Fishing-induced evolution of growth: concepts, mechanisms and the empirical evidence. *Marine Ecology* 33: 1-25.

FAO. 2014. The State of World Fisheries and Aquaculture. Food and Agriculture Organization of the United Nations.

Ferrari, M.C., Munday, P.L., Rummer, J.L., McCormick, M.I., Corkill, K., Watson, S.A., Allan, B.J., Meekan, M.G. and Chivers, D.P. 2015. Interactive effects of ocean acidification and rising sea temperatures alter predation rate and predator selectivity in reef fish communities. *Global change biology* 21: 1848-1855.

Folke, C., Carpenter, S., Walker, B., Scheffer, M., Elmqvist, T., Gunderson, L. and Holling, C.S. 2004. Regime shifts, resilience, and biodiversity in ecosystem management. *Annu. Rev. Ecol. Evol. Syst.* 35: 557-581.

Frölicher, T.L., Fischer, E.M. and Gruber, N. 2018. Marine heatwaves under global warming. *Nature* 560: 360 -364.

Fry, F.E.J. 1947. Effects of the environment on animal activity. *Publ. Out. Fish. Res. Lab.* 55: 1-62.

Gannon, R., Taylor, M.D., Suthers, I.M., Gray, C.A., van der Meulen, D.E., Smith, J.A. and Payne, N.L. 2014. Thermal limitation of performance and biogeography in a free-ranging ectotherm: insights from accelerometry. *Journal of Experimental Biology* 217: 3033-3037.

Gjelland, K.Ø. and Hedger, R.D. 2013. Environmental influence on transmitter detection probability in biotelemetry: developing a general model of acoustic transmission. *Methods in Ecology and Evolution* 4: 665-674.

Gleiss, A.C., Dale, J.J., Holland, K.N. and Wilson, R.P. 2010. Accelerating estimates of activity-specific metabolic rate in fishes: testing the applicability of acceleration data-loggers. *Journal of Experimental Marine Biology and Ecology* 385: 85-91

Goolish, E.M. 1991. Aerobic and anaerobic scaling in fish. *Biological Reviews 66*: 33-56.

Goschen, W.S. and Schumann, E.H. 2011. The physical oceanographic processes of Algoa Bay, with emphasis on the western coastal region. *South African Environmental Observation Network (SAEON) and the Institute of Maritime Technology (IMT). IMT document number: PO106-10000-730002*.

Goschen, W.S. and Schumann, E.H. 1995. Upwelling and the occurrence of cold water around Cape Recife, Algoa Bay, South Africa. *South African Journal of Marine Science* 16: 57-67.

Götz, A., Kerwath, S.E., Attwood, C.G. and Sauer, W.H. 2008. Effects of fishing on population structure and life history of roman Chrysoblephus laticeps (Sparidae). *Marine Ecology Progress Series* 362: 245-259.

Götz, A. and Kerwath, S. 2013. Roman (*Chrysoblephus laticeps*). P. 357 in Mann, B. Q. (ed.). *Southern African Marine Linefish Species Profiles* (Special publication). Oceanographic Research Institute, Durban.

Habary, A., Johansen, J.L., Nay, T.J., Steffensen, J.F. and Rummer, J.L. 2017. Adapt, move or die–how will tropical coral reef fishes cope with ocean warming? *Global change biology* 23: 566-577.

Halsey, L.G., Shepard, E.L.C., Quintana, F., Laich, A.G., Green, J.A. and Wilson, R.P. 2009. The relationship between oxygen consumption and body acceleration in a range of species. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 152: 197-202.

Hanekom, N., Hutchings, L., Joubert, P.A. and Van Der Byl, P.C.N. 1989. Sea temperature variations in the Tsitsikamma Coastal National Park, South Africa, with notes on the effect of cold conditions on some fish populations. *South African Journal of Marine Science 8*: 145-153.

Heino, M. and Godø, O.R. 2002. Fisheries-induced selection pressures in the context of sustainable fisheries. *Bulletin of Marine Science* 70: 639-656.

Heino, M., Pauli, B.D. and Dieckmann, U. 2015. Fisheries-induced evolution. *Annual review of ecology, evolution, and systematics* 46: 461-480.

Helmuth, B. 2009. From cells to coastlines: how can we use physiology to forecast the impacts of climate change? *Journal of Experimental Biology 212*: 753-760.

Hessenauer, J.M., Vokoun, J.C., Suski, C.D., Davis, J., Jacobs, R. and O'Donnell, E. 2015. Differences in the metabolic rates of exploited and unexploited fish populations: a signature of recreational fisheries induced evolution? *PloS one* 10: p.e0128336.

Hollins, J., Thambithurai, D., Koeck, B., Crespel, A., Bailey, D.M., Cooke, S.J., Lindström, J., Parsons, K.J. and Killen, S.S. 2018. A physiological perspective on fisheries-induced evolution. *Evolutionary applications* 11: 561-576.

Holt, R.E. and Jørgensen, C. 2015. Climate change in fish: effects of respiratory constraints on optimal life history and behaviour. *Biology letters* 11: p.20141032.

Horodysky, A.Z., Cooke, S.J. and Brill, R.W. 2015. Physiology in the service of fisheries science: why thinking mechanistically matters. *Reviews in fish biology and fisheries* 25: 425-447.

Ibarz, A., Felip, O., Fernández-Borràs, J., Martín-Pérez, M., Blasco, J. and Torrella, J.R. 2011. Sustained swimming improves muscle growth and cellularity in gilthead sea bream. *Journal of Comparative Physiology B* 181: 209-217.

International Union for Conservation of Nature (IUCN), 2016. IUCN Resolutions, Recommendations and other Decisions.

Johansen, J.L. and Jones, G.P. 2011. Increasing ocean temperature reduces the metabolic performance and swimming ability of coral reef damselfishes. *Global Change Biology* 17: 2971-2979.

Jørgensen, C., Enberg, K., Dunlop, E.S., Arlinghaus, R., Boukal, D.S., Brander, K., Ernande, B., Gårdmark, A.G., Johnston, F., Matsumura, S. and Pardoe, H. 2007. Ecology: managing evolving fish stocks. *Science* 318: 1247-1248.

Jørgensen, C., Ernande, B. and Fiksen, Ø. 2009. Size-selective fishing gear and life history evolution in the Northeast Arctic cod. *Evolutionary Applications* 2: 356-370.

Jutfelt, F., Norin, T., Ern, R., Overgaard, J., Wang, T., McKenzie, D.J., Lefevre, S., Nilsson, G.E., Metcalfe, N.B., Hickey, A.J. and Brijs, J. 2018. Oxygen-and capacity-limited thermal tolerance: blurring ecology and physiology. *Journal of Experimental Biology* 221: p.jeb169615.

Kerwath, S.E., Götz, A., Attwood, C.G., Cowley, P.D. and Sauer, W.H.H. 2007a. Movement pattern and home range of roman Chrysoblephus laticeps. *African Journal of Marine Science 29*: 93-103.

Kerwath, S.E., Götz, A., Attwood, C.G., Sauer, W.H.H. and Wilke, C.G. 2007b. Area utilisation and activity patterns of roman Chrysoblephus laticeps (Sparidae) in a small marine protected area. *African Journal of Marine Science* 29: 259-270.

Killen, S.S., Marras, S., Ryan, M.R., Domenici, P. and McKenzie, D.J. 2012. A relationship between metabolic rate and risk-taking behaviour is revealed during hypoxia in juvenile European sea bass. *Functional Ecology* 26: 134-143.

Killen, S.S., Glazier, D.S., Rezende, E.L., Clark, T.D., Atkinson, D., Willener, A.S. and Halsey, L.G. 2016. Ecological influences and morphological correlates of resting and maximal metabolic rates across teleost fish species. *The American Naturalist* 187: 592-606.

Klefoth, T., Skov, C., Kuparinen, A. and Arlinghaus, R. 2017. Toward a mechanistic understanding of vulnerability to hook-and-line fishing: Boldness as the basic target of angling-induced selection. *Evolutionary applications* 10: 994-1006.

Kuparinen, A. and Merilä, J. 2007. Detecting and managing fisheries-induced evolution. *Trends in ecology & evolution* 22: 652-659.

Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine Science* 57: 659-668.

Le Cornu, E., Doerr, A.N., Finkbeiner, E.M., Gourlie, D. and Crowder, L.B. 2018. Spatial management in small-scale fisheries: A potential approach for climate change adaptation in Pacific Islands. *Marine Policy* 88: 350-358.

Lear, K.O., Whitney, N.M., Brewster, L.R., Morris, J.J., Hueter, R.E. and Gleiss, A.C. 2017. Correlations of metabolic rate and body acceleration in three species of coastal sharks under contrasting temperature regimes. *Journal of Experimental Biology* 220: 397-407.

Lennox, R.J., Aarestrup, K., Cooke, S.J., Cowley, P.D., Deng, Z.D., Fisk, A.T., Harcourt, R.G., Heupel, M., Hinch, S.G., Holland, K.N. and Hussey, N.E. 2017a. Envisioning the future of aquatic animal tracking: technology, science, and application. *BioScience* 67: 884-896.

Lennox, R.J., Alós, J., Arlinghaus, R., Horodysky, A., Klefoth, T., Monk, C.T. and Cooke, S.J. 2017b. What makes fish vulnerable to capture by hooks? A conceptual framework and a review of key determinants. *Fish and Fisheries* 18: 986-1010.

Lester, S.E., Halpern, B.S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B.I., Gaines, S.D., Airamé, S. and Warner, R.R. 2009. Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384: 33-46.

Marcoux, T.M. and Korsmeyer, K.E. 2019. Energetics and behavior of coral reef fishes during oscillatory swimming in a simulated wave surge. *Journal of Experimental Biology* 22: p.jeb191791.

McBryan, T.L., Anttila, K., Healy, T.M. and Schulte, P.M. 2013. Responses to temperature and hypoxia as interacting stressors in fish: implications for adaptation to environmental change. *Integrative and comparative biology* 53: 648-659.

McKenzie, D.J., Axelsson, M., Chabot, D., Claireaux, G., Cooke, S.J., Corner, R.A., De Boeck, G., Domenici, P., Guerreiro, P.M., Hamer, B. and Jørgensen, C. 2016. Conservation physiology of marine fishes: state of the art and prospects for policy. *Conservation physiology* 4: p.cow046.

McLeod, E., Salm, R., Green, A. and Almany, J. 2009. Designing marine protected area networks to address the impacts of climate change. *Frontiers in Ecology and the Environment* 7: 362-370.

McNamara, J.M. and Houston, A.I. 1996. State-dependent life histories. *Nature* 380: 215-221.

Metcalfe, J.D., Wright, S., Tudorache, C. and Wilson, R.P. 2016. Recent advances in telemetry for estimating the energy metabolism of wild fishes. *Journal of Fish Biology* 88: 284-297.

Mori, T., Miyata, N., Aoyama, J., Niizuma, Y. and Sato, K., 2015. Estimation of metabolic rate from activity measured by recorders deployed on Japanese sea bass Lateolabrax japonicus. *Fisheries science* 81: 871-882.

Muggeo, V. M. R. 2003. Estimating regression models with unknown break-points. *Statistics in Medicine* 22: 3055–3071.

Muggeo, V. M. R. 2008. segmented: An R package to fit regression models with broken-line relationships. *R News* 8:20–25.

Munday, P.L., Crawley, N.E. and Nilsson, G.E. 2009. Interacting effects of elevated temperature and ocean acidification on the aerobic performance of coral reef fishes. *Marine Ecology Progress Series* 388: 235-242.

Munday, P.L., Donelson, J.M. and Domingos, J.A. 2017. Potential for adaptation to climate change in a coral reef fish. *Global change biology* 23: 307-317.

Murchie, K.J., Cooke, S.J., Danylchuk, A.J. and Suski, C.D. 2011. Estimates of field activity and metabolic rates of bonefish (Albula vulpes) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent-flow respirometry. *Journal of Experimental Marine Biology and Ecology* 396: 147-155.

Nadler, L.E., Killen, S.S., McClure, E.C., Munday, P.L. and McCormick, M.I. 2016. Shoaling reduces metabolic rate in a gregarious coral reef fish species. *Journal of Experimental Biology* 219: 2802-2805.

Nay, T.J., Johansen, J.L., Habary, A., Steffensen, J.F. and Rummer, J.L. 2015. Behavioural thermoregulation in a temperature-sensitive coral reef fish, the five-lined cardinalfish (Cheilodipterusquinquelineatus). *Coral Reefs* 34: 1261-1265.

Neubauer, P. and Andersen, K.H. 2019. Thermal performance of fish is explained by an interplay between physiology, behaviour, and ecology. *Conservation Physiology*.

Norin, T., Malte, H. and Clark, T.D. 2014. Aerobic scope does not predict the performance of a tropical eurythermal fish at elevated temperatures. *Journal of Experimental Biology* 217: 244-251.

Norin, T., Malte, H. and Clark, T.D. 2016. Differential plasticity of metabolic rate phenotypes in a tropical fish facing environmental change. *Functional Ecology* 30: 369-378.

Norin, T. and Metcalfe, N.B. 2019. Ecological and evolutionary consequences of metabolic rate plasticity in response to environmental change. *Philosophical Transactions of the Royal Society B* 374: p.20180180.

Ortega-Cisneros, K., Yokwana, S., Sauer, W., Cochrane, K., Cockcroft, A., James, N.C., Potts, W.M., Singh, L., Smale, M., Wood, A. and Pecl, G. 2018. Assessment of the likely sensitivity to climate change for the key marine species in the southern Benguela system. *African journal of marine science* 40: 279-292.

Ottersen, G., Hjermann, D.Ø. and Stenseth, N.C. 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (Gadus morhua) stock. *Fisheries oceanography* 15: 230-243.

O'Toole, A.C., Murchie, K.J., Pullen, C., Hanson, K.C., Suski, C.D., Danylchuk, A.J. and Cooke, S.J. 2011. Locomotory activity and depth distribution of adult great barracuda (Sphyraena barracuda) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters. *Marine and Freshwater Research* 61: 1446-1456.

Papastamatiou, Y.P., Watanabe, Y.Y., Bradley, D., Dee, L.E., Weng, K., Lowe, C.G. and Caselle, J.E. 2015. Drivers of daily routines in an ectothermic marine predator: hunt warm, rest warmer? *PLoS One* 10: p.e0127807.

Patterson, D.A., Cooke, S.J., Hinch, S.G., Robinson, K.A., Young, N., Farrell, A.P. and Miller, K.M. 2016. A perspective on physiological studies supporting the provision of scientific advice for the management of Fraser River sockeye salmon (Oncorhynchus nerka). *Conservation physiology* 4.

Payne, N.L., Gillanders, B.M., Seymour, R.S., Webber, D.M., Snelling, E.P. and Semmens, J.M. 2011. Accelerometry estimates field metabolic rate in giant Australian cuttlefish Sepia apama during breeding. *Journal of Animal Ecology* 80: 422-430.

Perry, R.I., Cury, P., Brander, K., Jennings, S., Möllmann, C. and Planque, B. 2010. Sensitivity of marine systems to climate and fishing: concepts, issues and management responses. *Journal of Marine Systems* 79: 427-435.

Pinheiro, J.C. and Bates, D.M. 2000. Linear mixed-effects models: basic concepts and examples. *Mixed-effects models in S and S-Plus* 3-56.

Pinheiro, J., Bates, D., DebRoy, S. and Sarkar, D. 2016. R Core Team (2016) nlme: linear and nonlinear mixed effects models. R package version 3.1-128. *Bioinformatics* 26: 1463-1464.

Planes, S., Jones, G.P. and Thorrold, S.R. 2009. Larval dispersal connects fish populations in a network of marine protected areas. *Proceedings of the National Academy of Sciences* 106: 5693-5697.

Planque, B., Fromentin, J.M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I. and Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate?. *Journal of Marine Systems* 79: 403-417.

Pörtner, H.O. and Knust, R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315: 95-97.

Pörtner, H.O. and Farrell, A.P. 2008. Physiology and climate change. *Science* 322: 690-692.

Pörtner, H.O. 2012. Integrating climate-related stressor effects on marine organisms: unifying principles linking molecule to ecosystem-level changes. *Marine Ecology Progress Series* 470: 273-290.

Potts, W.M., Götz, A. and James, N. 2015. Review of the projected impacts of climate change on coastal fishes in southern Africa. *Reviews in fish biology and fisheries* 25: 603-630.

Redpath, T.D., Cooke, S.J., Suski, C.D., Arlinghaus, R., Couture, P., Wahl, D.H. and Philipp, D.P. 2010. The metabolic and biochemical basis of vulnerability to recreational angling after three generations of angling-induced selection in a teleost fish. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 1983-1992.

Réveillon, T., Rota, T., Chauvet, É., Lecerf, A. and Sentis, A. 2019. Repeatable inter-individual variation in the thermal sensitivity of metabolic rate. *Oikos*.

Rhein M, Rintoul SR, Aoki S, Campos E, Chambers D, Feely RA, Gulev S, Johnson GC, Josey SA, Kostianoy A, Mau- ritzen C, Roemmich D, Talley LD, Wang F (2013) Observations: ocean. In: Stocker TF, Qin D, Plattner G-K, Tignor M, Allen SK, Boschung J, Nauels A, Xia Y, Bex V, Midgley PM (eds) Climate change 2013: the physical science basis. Contribution of working group I to the fifth assessment report of the intergovernmental panel on cli- mate change. Cambridge University Press, Cambridge, pp 255–316.

Roberts, C.M., O'Leary, B.C., McCauley, D.J., Cury, P.M., Duarte, C.M., Lubchenco, J., Pauly, D., Sáenz-Arroyo, A., Sumaila, U.R., Wilson, R.W. and Worm, B. 2017. Marine reserves can mitigate and promote adaptation to climate change. *Proceedings of the National Academy of Sciences* 114: 6167-6175.

Robson, A.A., Halsey, L.G. and Chauvaud, L. 2016. Feet, heat and scallops: what is the cost of anthropogenic disturbance in bivalve aquaculture?. *Royal Society Open Science* 3: p.150679.

Rome, L.C. 1990. Influence of temperature on muscle recruitment and muscle function in vivo. *American Journal of Physiology-Regulatory, Integrative and Comparative Physiology* 259: 210-222.

Rome, L.C. 1995. Influence of temperature on muscle properties in relation to swimming performance. In *Biochemistry and Molecular Biology of Fishes* 5: 73-99.

Rouault, M., Pohl, B. and Penven, P. 2010. Coastal oceanic climate change and variability from 1982 to 2009 around South Africa. *African Journal of Marine Science* 32: 237-246.

Rupia, E.J., Binning, S.A., Roche, D.G. and Lu, W. 2016. Fight-flight or freeze-hide? Personality and metabolic phenotype mediate physiological defence responses in flatfish. *Journal of Animal Ecology* 85: 927-937.

Sala, E. and Giakoumi, S. 2017. No-take marine reserves are the most effective protected areas in the ocean. *ICES Journal of Marine Science* 75: 1166-1168.

Schlegel, R.W., Oliver, E.C., Wernberg, T. and Smit, A.J. 2017. Nearshore and offshore co-occurrence of marine heatwaves and cold-spells. *Progress in oceanography* 151: 189-205.

Schulte, P.M., Healy, T.M. and Fangue, N.A. 2011. Thermal performance curves, phenotypic plasticity, and the time scales of temperature exposure. *Integrative and Comparative Biology* 51: 691-702.

Schumann, E.H., Cohen, A.L. and Jury, M.R. 1995. Coastal sea surface temperature variability along the south coast of South Africa and the relationship to regional and global climate. *Journal of Marine Research* 53: 231-248.

Schumann, E.H. 1999. Wind-driven mixed layer and coastal upwelling processes off the south coast of South Africa. *Journal of Marine Research 57*: 671-691.

Seebacher, F., Tallis, J.A. and James, R.S. 2014. The cost of muscle power production: muscle oxygen consumption per unit work increases at low temperatures in Xenopus laevis. *Journal of Experimental Biology* 217: 1940-1945.

Seebacher, F., White, C.R. and Franklin, C.E. 2015. Physiological plasticity increases resilience of ectothermic animals to climate change. *Nature Climate Change* 5: 61.

Shepard, E.L., Wilson, R.P., Rees, W.G., Grundy, E., Lambertucci, S.A. and Vosper, S.B. 2013. Energy landscapes shape animal movement ecology. *The American Naturalist* 182: 298-312.

Shipley, O.N., Brownscombe, J.W., Danylchuk, A.J., Cooke, S.J., O'Shea, O.R. and Brooks, E.J. 2018. Fine-scale movement and activity patterns of Caribbean reef sharks (Carcharhinus perezi) in the Bahamas. *Environmental Biology of Fishes* 101: 1097-1104.

Solomon, S., Qin, D., Manning, M., Averyt, K., Marquis, M. and Tignor, M.M. eds. 2007. *Climate change 2007-the physical science basis: Working group I contribution to the fourth assessment report of the IPCC* (Vol. 4). Cambridge university press.

Somero, G.N. 2012. The physiology of global change: linking patterns to mechanisms. *Annual Review of Marine Science* 4: 39-61.

Speers-Roesch, B., Norin, T. and Driedzic, W.R. 2018. The benefit of being still: energy savings during winter dormancy in fish come from inactivity and the cold, not from metabolic rate depression. *Proceedings of the Royal Society B: Biological Sciences* 285: p.20181593.

Stehfest, K.M., Lyle, J.M. and Semmens, J.M. 2015. The use of acoustic accelerometer tags to determine seasonal changes in activity and catchability of a recreationally caught marine teleost. *ICES Journal of Marine Science* 72: 2512-2520.

Struthers, D.P., Gutowsky, L.F., Enders, E.C., Smokorowski, K.E., Watkinson, D.A., Silva, A.T., Cvetkovic, M., Bibeau, E. and Cooke, S.J. 2017. Factors influencing the spatial ecology of Lake Sturgeon and Walleye within an impounded reach of the Winnipeg River. *Environmental Biology of Fishes* 100: 1085-1103.

Svendsen, M.B.S., Bushnell, P.G. and Steffensen, J.F. 2016. Design and setup of intermittent-flow respirometry system for aquatic organisms. *Journal of Fish Biology 88*: 26-50.

Szekeres, P., Eliason, E.J., Lapointe, D., Donaldson, M.R., Brownscombe, J.W. and Cooke, S.J. 2016. On the neglected cold side of climate change and what it means to fish. *Climate Research* 69: 239-245.

Teske, P.R., Forget, F.R.G., Cowley, P.D., Von der Heyden, S. and Beheregaray, L.B. 2010. Connectivity between marine reserves and exploited areas in the philopatric reef fish Chrysoblephus laticeps (Teleostei: Sparidae). *Marine Biology* 157: 2029-2042.

Todgham, A.E. and Stillman, J.H. 2013. Physiological responses to shifts in multiple environmental stressors: relevance in a changing world. *Integrative and comparative biology* 53: 539-544.

Tomlinson, S., Arnall, S.G., Munn, A., Bradshaw, S.D., Maloney, S.K., Dixon, K.W. and Didham, R.K. 2014. Applications and implications of ecological energetics. *Trends in ecology & evolution* 29: 280-290.

Vasseur, D.A., DeLong, J.P., Gilbert, B., Greig, H.S., Harley, C.D., McCann, K.S., Savage, V., Tunney, T.D. and O'Connor, M.I. 2014. Increased temperature variation poses a greater risk to species than climate warming. *Proceedings of the Royal Society B: Biological Sciences* 281: p.20132612.

Walsh, M.R., Munch, S.B., Chiba, S. and Conover, D.O. 2006. Maladaptive changes in multiple traits caused by fishing: impediments to population recovery. *Ecology letters* 9: 142-148.

Ward, T.D., Algera, D.A., Gallagher, A.J., Hawkins, E., Horodysky, A., Jørgensen, C., Killen, S.S., McKenzie, D.J., Metcalfe, J.D., Peck, M.A. and Vu, M. 2016. Understanding the individual to implement the ecosystem approach to fisheries management. *Conservation Physiology* 4.

Wickham, H. 2016. ggplot2: elegant graphics for data analysis. *Springer*.

Wikelski, M. and Cooke, S.J. 2006. Conservation physiology. *Trends in Ecology & Evolution* 21: 38-46.

Wilson, R.P., White, C.R., Quintana, F., Halsey, L.G., Liebsch, N., Martin, G.R. and Butler, P.J. 2006. Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *Journal of Animal Ecology* 75: 1081-1090.

Wilson, S.M., Hinch, S.G., Eliason, E.J., Farrell, A.P. and Cooke, S.J. 2013. Calibrating acoustic acceleration transmitters for estimating energy use by wild adult Pacific salmon. *Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology* 164: 491-498.

Wilson, A.D., Brownscombe, J.W., Sullivan, B., Jain-Schlaepfer, S. and Cooke, S.J. 2015. Does angling technique selectively target fishes based on their behavioural type? *PLoS One* 10: p.e0135848.

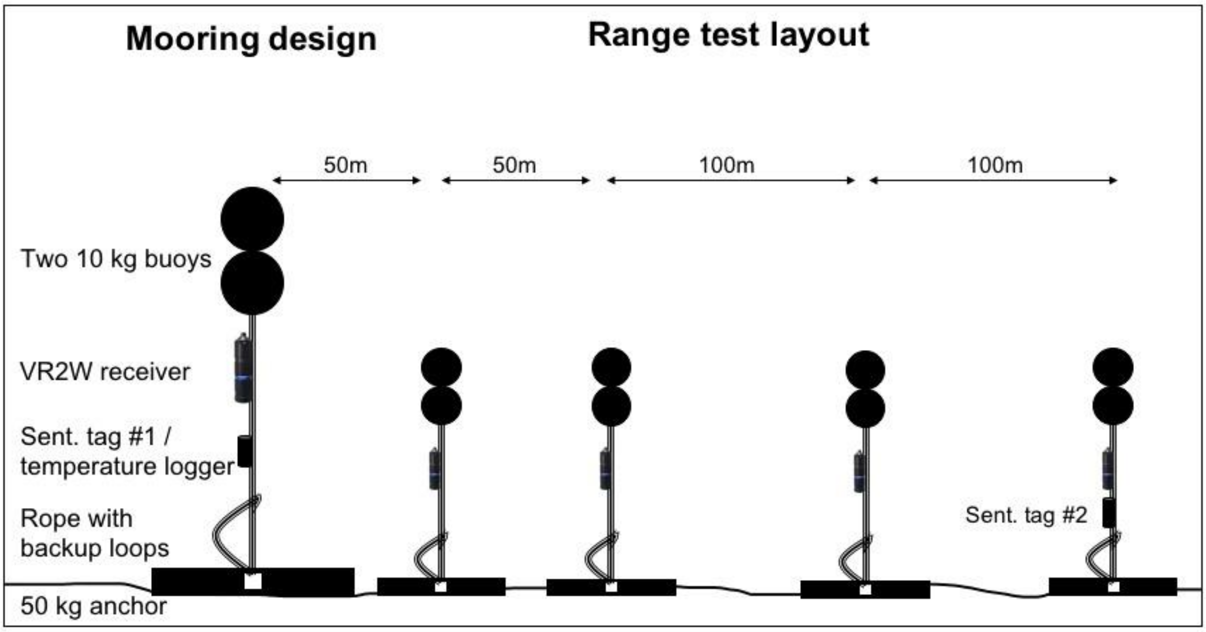
Wright, S., Metcalfe, J.D., Hetherington, S. and Wilson, R. 2014. Estimating activity-specific energy expenditure in a teleost fish, using accelerometer loggers. *Marine Ecology Progress Series* 496: 19-32.

Yasuda, T., Komeyama, K., Kato, K. and Mitsunaga, Y. 2012. Use of acceleration loggers in aquaculture to determine net-cage use and field metabolic rates in red sea bream Pagrus major. *Fisheries Science* 78: 229-235.

Zuur, A., Ieno, E.N., Walker, N., Saveliev, A.A. and Smith, G.M. 2009. *Mixed effects models and extensions in ecology with R*. Springer Science & Business Media.

Appendices

Appendix 1: A schematic of the mooring design used to keep receivers in one place within the water column and the basic layout of the range test utilized at both sites.



Appendix 2: Coordinates and depth details of deployed moorings forming the two fine-scale arrays. Visual identification of corresponding mooring numbers can be seen in Figure 4.4.

Site	Mooring number	Depth (m)	East	South	Comments
PE	1	14	25.55045	-34.05135	Temp. logger
PE	2	14	25.55046	-34.05033	
PE	3	16	25.55181	-34.0503	
PE	4	16	25.55174	-34.05133	
PE	5	19	25.55168	-34.05237	
PE	6	18	25.5505	-34.05235	
PE	7	18	25.54919	-34.05242	
PE	8	15	25.54922	-34.05133	
PE	9	10	25.54919	-34.05027	
PE	10	13	25.54985	-34.05083	
PE	11	14	25.55106	-34.05082	
PE	12	17	25.55109	-34.05183	
PE	13	14	25.54973	-34.05172	
PE	14	14	25.55045	-34.0508	Sent. tag no. 65163
PE	15	18	25.54983	-34.05234	Sent. tag no. 65165
TNP	1	18	23.91371	-34.02798	Temp. logger
TNP	2	13	23.91369	-34.02692	
TNP	3	10	23.91496	-34.02695	
TNP	4	12	23.91493	-34.02801	
TNP	5	23	23.91494	-34.02901	
TNP	6	23	23.9137	-34.029	
TNP	7	23	23.91246	-34.029	
TNP	8	19	23.91243	-34.02797	
TNP	9	13	23.91242	-34.02692	
TNP	10	15	23.91307	-34.02745	
TNP	11	13	23.91432	-34.02744	
TNP	12	22	23.9143	-34.02851	
TNP	13	22	23.91307	-34.02849	
TNP	14	15	23.91372	-34.02746	Sent tag no. 65164
TNP	15	23	23.91303	-34.02903	Sent. tag no. 65166

Appendix 3: A poster to inform local fisherman about tags they may potentially find in red roman within the Port Elizabeth area. This was greatly received by the angling community with close to 500 shares on Facebook.

ATTENTION

All FISHERS

If you catch a *Red Roman* with a scar on it's belly like the one in the photo below:

PLEASE

Keep the fish and the tag that will be inside and call either

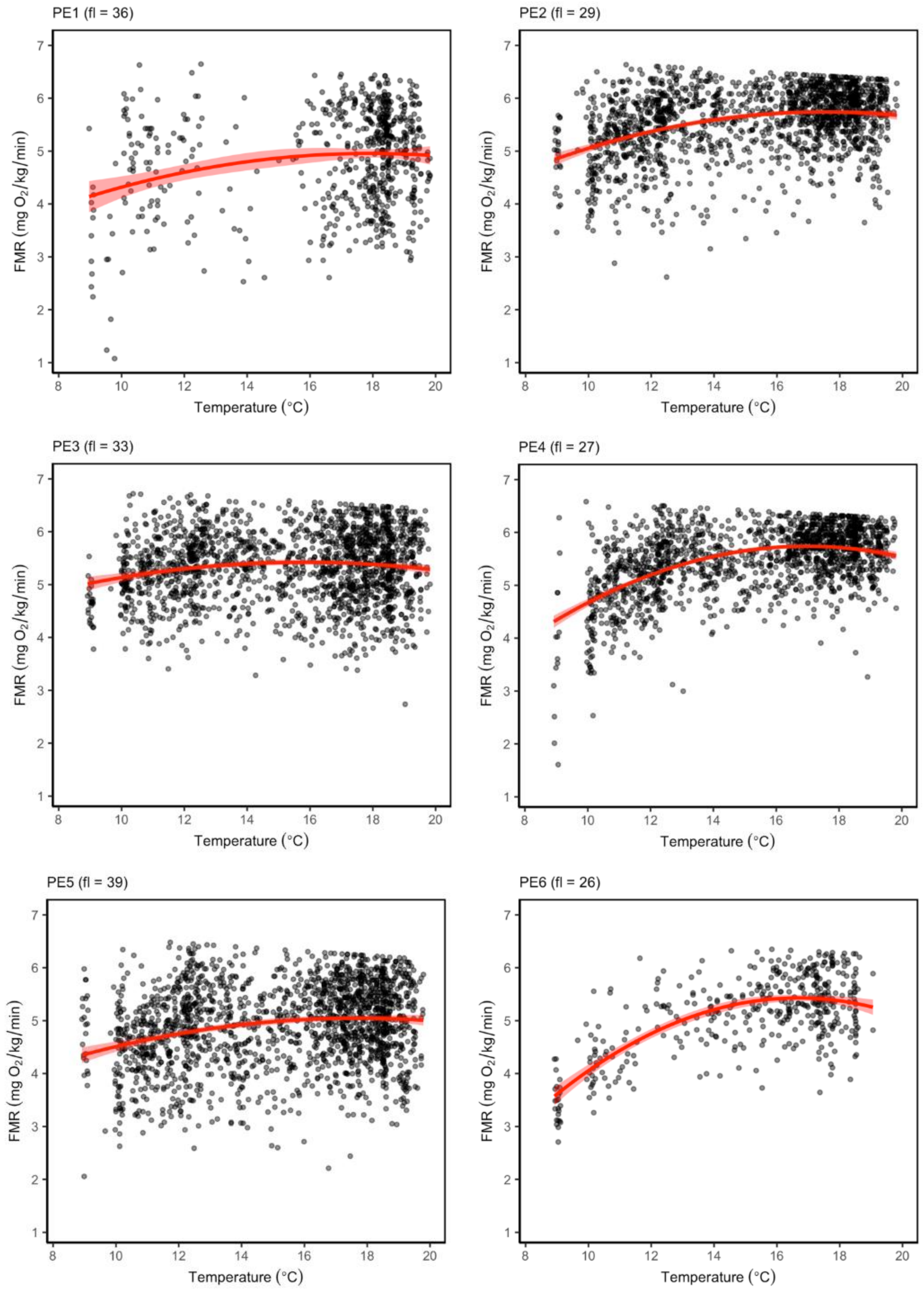
Mike on 0723681481 or

Amber on 0761947094.

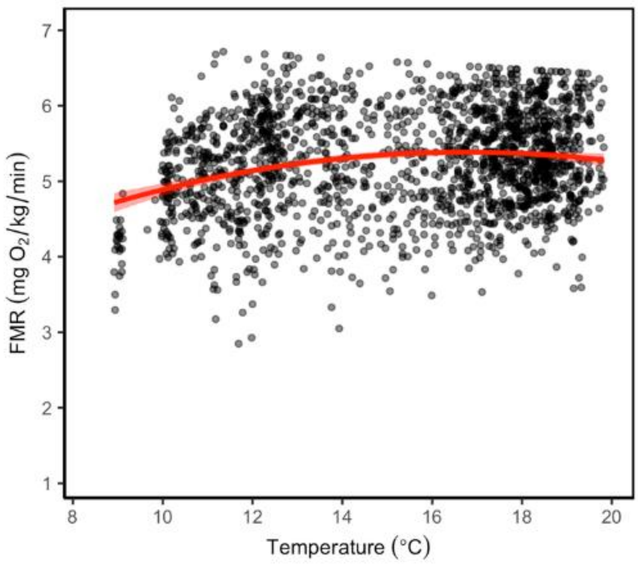
(small reward for lost tags)

Thank you fellow fishers, this will help a tremendous amount towards my Masters research

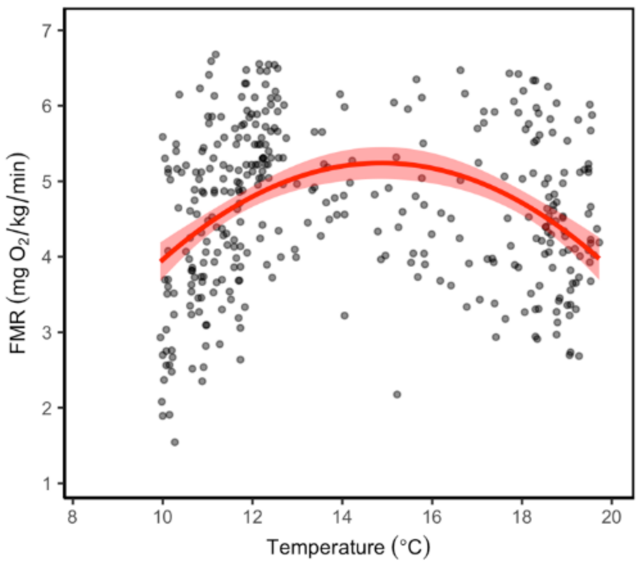
Appendix 4: Best fit second order polynomial relationship (line) and recorded data points (black dots) of the field metabolic rate (FMR) for each individual *Chrysoblephus laticeps* across experienced temperatures in the field. Shaded areas represent 95% confidence intervals.


PE1 (fl = 36)
PE2 (fl = 29)
PE3 (fl = 33)
PE4 (fl = 27)
PE5 (fl = 39)
PE6 (fl = 26)
FMR (mg O₂/kg/min)
Temperature (°C)
1
2
3
4
5
6
7
8
10
12
14
16
18
20

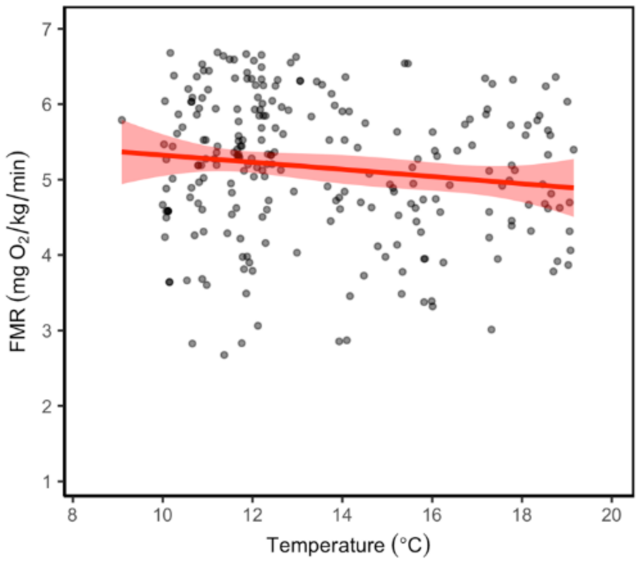
PE7 (fl = 32)



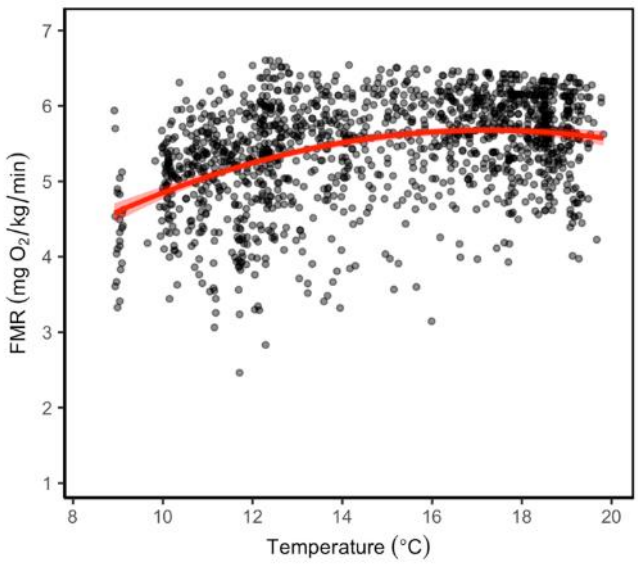
PE8 (fl = 37)



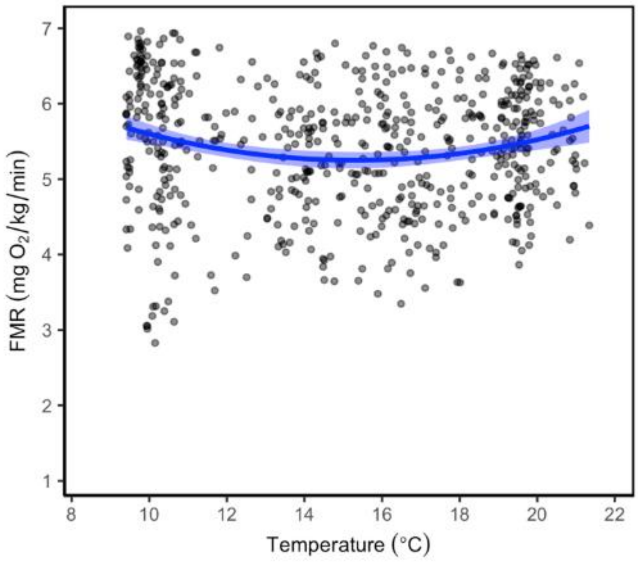
PE9 (fl = 31)



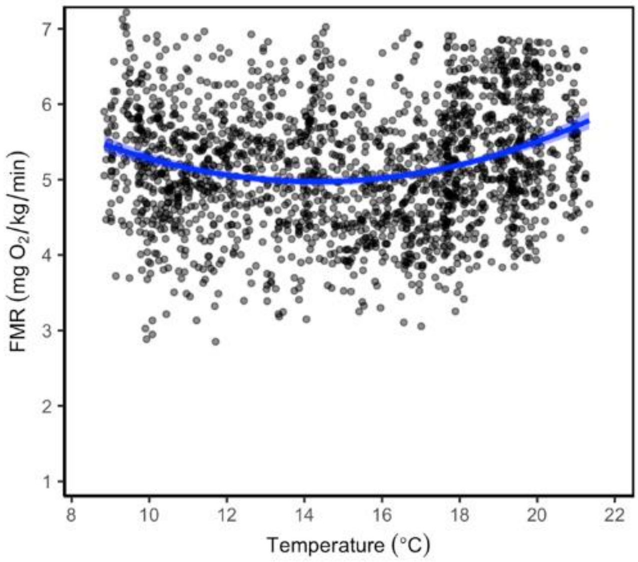
PE10 (fl = 29)



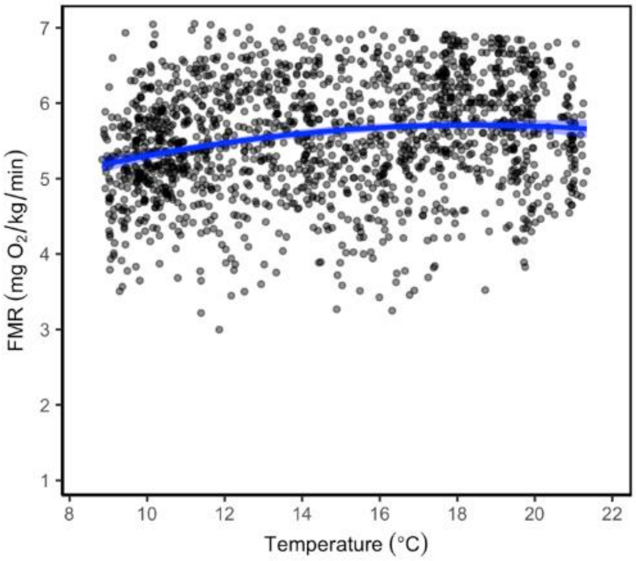
TNP1 (fl = 27)



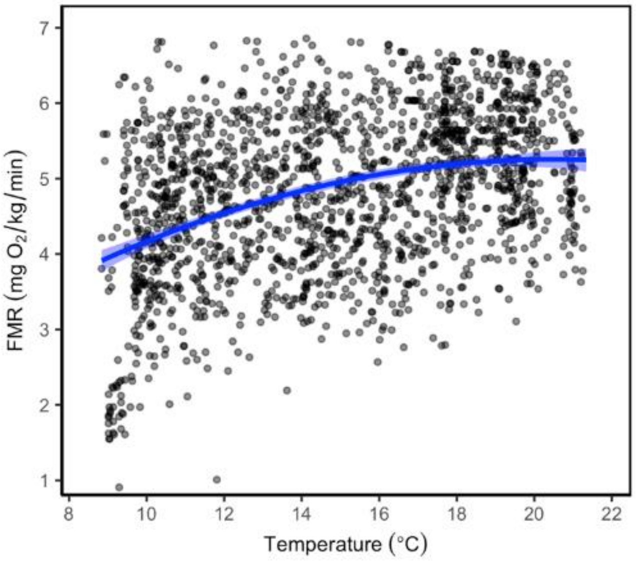
TNP2 (fl = 35)



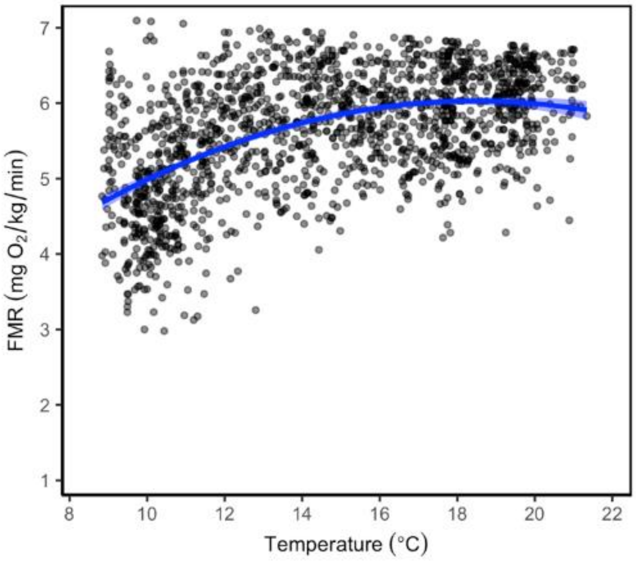
TNP4 (fl = 33)



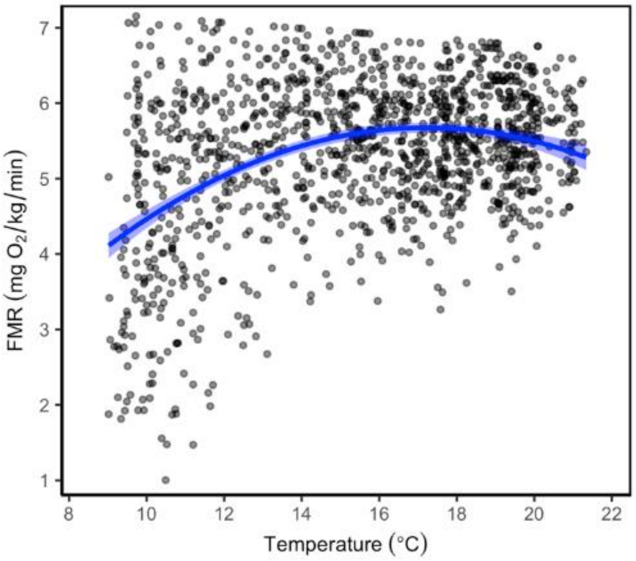
TNP5 (fl = 39)



TNP6 (fl = 30)



TNP8 (fl = 37)



TNP10 (fl = 34)