

**Comparison of the metabolic physiology of exploited
and unexploited populations of red roman
(*Chrysolephus laticeps*) along the south coast of South
Africa.**

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By

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Abstract

Anthropogenic-induced climate change and exploitation pose threat to many marine fishes on which a vast majority of people around the world depend. Rapid changes in sea surface temperature have a direct impact on the physiology of ectothermic organisms such as fish, potentially resulting in changes to population distribution, abundance, and demographics. In the face of climate change, the impacts of increasing temperature variability on fish populations may be exacerbated by exploitation. Understanding how the resilience of exploited populations is affected by climate change is critical to predict how fishes will respond in the future. This study aimed to augment our knowledge on the impact of exploitation and thermal variability on fishes by comparing the thermal physiology of an exploited and unexploited population of the resident, reef-dwelling, *Chrysoblephus laticeps*. Twenty live fish were collected from the exploited, Cape St Francis and 18 fish from the unexploited, Goukamma Marine Protected Area and transported to the laboratory. The metabolic performance, in terms of standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) of individual *C. laticeps* were estimated repeatedly at 10 °C, 16 °C and 21 °C. Linear mixed effects models were used to examine the relationship between temperature, population, and metabolic rate and a 'cvequality' test analysis was used to compare the variance structure of the metabolic rate regression model for each population. Overall, the findings of this study show that *Chrysoblephus laticeps* from the unexploited population maintains a significantly higher aerobic scope (AS) across all temperature treatments (10, 16 and 21 °C) when compared with those from the exploited population. In addition, the maximum metabolic rate (MMR) of individuals from the unexploited population was significantly higher than that of individuals from the exploited population, but there was no evidence to suggest that variability was significantly different between the populations. On the other hand, the individuals from an exploited population had a significantly higher standard metabolic rate (SMR) at high temperatures of 21 °C, while the unexploited population had a low SMR at these high temperatures, but a high SMR at 10 °C. Despite these differences there was no significant variation in the SMR between the two populations.

The findings of this study confirm previous work on different exploited and unexploited populations of *C. laticeps* and together these findings suggest that hook and line exploitation lead to reduced physiological phenotypic diversity and reduced physiological performance in exploited fish populations. These findings emphasise the importance of incorporating the

physiological information to develop viable fisheries management tools in the context of climate change. This study also highlights the effectiveness of MPAs in conserving high-performance physiological phenotypes to maintain phenotypic diversity in fish populations. Future research should aim to evaluate the efficacy of existing MPAs in preserving the physiological diversity of important hook and line fisheries species, while fisheries managers should consider augmenting their approaches through the incorporation of well-designed MPA's to promote physiological diversity. This will be critical to advance the development of sustainable management practices, not only in a South African context but globally, where oceanic and coastal environmental conditions are expected to rapidly change in the future.

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Preface

This thesis consists of an introduction (Chapter 1), study sites and species profile (Chapter 2), methods and materials (Chapter 3), results (Chapter 4), discussion and conclusion (Chapter 5).

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Declaration

I, Xolani Prince Nabani, hereby declare that the work described in this thesis was carried out in the Department of Ichthyology and Fisheries Science at Rhodes University, under the supervision of Professor Warren Potts, Professor Amber Childs, Dr Cuen Muller and Mrs Lauren Bailey. The components of this thesis comprise original work by the author and have not been submitted to any other institution.

Signed: 

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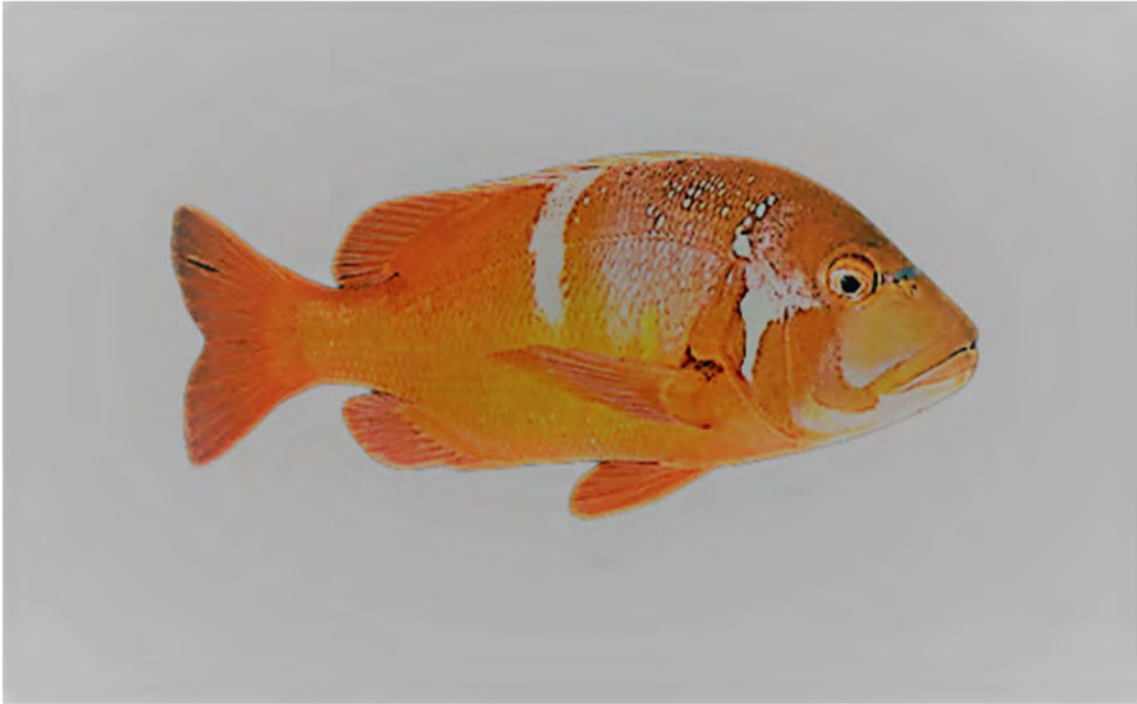
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Abbreviations

AS	Aerobic scope
CT _{max}	Critical thermal maximum
CT _{min}	Critical thermal minimum
CSF	Cape St Francis
DEB	Dynamic energy budget
DO	Dissolved oxygen
FIE	Fisheries-induced evolution
FishID	Fish identification code
GKM	Goukamma Marine Protected area
MTE	Metabolic theory of ecology
MMR	Maximum metabolic rate
$\dot{M}O_2$	Oxygen consumption rate
MPA(s)	Marine protected area(s)
OCLTT	Oxygen capacity-limited thermal tolerance
PE	Port Elizabeth
RMR	Routine metabolic rate
SMR	Standard Metabolic rate
SST	Sea surface temperature
TNP	Tsitsikamma National Park
T _{opt,AS}	Optimum temperature, where aerobic scope is maximal
VIE	Visible implant elastomer

Chapter 1: Introduction



A red roman seabream, *Chrysolephus laticeps*

1.1 Climate change and exploitation

Anthropogenic-induced climate change alters physico-chemical parameters in the marine environment through ocean acidification, increase in extreme weather events, ocean warming and variability, thus directly and indirectly placing fish populations under pressure (Hoegh-Guldberg and Bruno 2010, Howes et al. 2015, Johnson and Layman 2020). The impacts of long-term mean changes in sea surface temperatures have been well documented, however, the short-term localised variabilities which threatens fish populations the most have recently received a considerable attention (Potts et al. 2015, Bates et al. 2018, Bates et al. 2019, Duncan et al. 2019a).

Temperature is one of the main parameters with a direct effect on fish physiological processes (Potts et al. 2015, Schulte 2015, Little et al. 2020). Ectothermic organisms such as fish are very sensitive to changes in environmental temperature with even small changes having a considerable impact on their reproduction (Pankhurst and Munday 2011, Potts et al. 2014), growth and development (Pörtner and Peck 2010). Increasing temperatures may also reduce the size of adult fish because larger fishes in warm temperatures cannot balance the oxygen supply and oxygen demand (Audzijonyte et al. 2016). However, temperatures beyond an individual's thermal limit, may lead to damage at the tissue level, hypoxia or mortality (Pörtner and Peck 2010). At a population level, phenotypic variability among individuals will be essential to ensure that there are sufficient individuals that will be resilient to changes in temperature (Bates et al. 2013, Ward et al. 2016). In the Anthropocene, the persistence of phenotypic variability within fish populations may be compromised by exploitation which can exacerbate the negative impacts of climate change on fish populations (Kjesbu et al. 2014, Morrongiello et al. 2019).

Persistent exploitation through fishing tends to reduce fish population size, lead to size truncation, loss of large females and decrease in genetic diversity (Rijnsdorp et al. 2010, Pinsky and Palumbi 2014, van Overzee and Rijnsdorp 2015). The truncation of the age structure through the removal of the oldest fishes by exploitation has negative consequences as a long adult lifespan provides a buffer to periodic recruitment failure (Planque and Freadou 1999, Perry et al. 2010), which is likely to be more frequent as ocean temperatures warm (Potts et al. 2014). The size structure of populations is also expected to change, where exploited populations will likely have more small adults which invest most of their energy on reproduction and less on growth (Buxton 1990, Kuparinen and Merilä 2007, Audzijonyte et al.

2016). Furthermore, exploitation has been shown to exert selective pressure on targeted fish, which over time leads to reduced genetic diversity in exploited populations (Pinsky and Palumbi 2015). Substantially, to understand the resilience of fish populations to future environmental changes, exploitation must also be considered. It has become very clear that exploitation and climate change act synergistically (Perry et al. 2010, Niiranen et al. 2013) as passive gear has been shown to remove large, mature and high-performing individuals from the population (Alós et al. 2012, Duncan et al. 2019a).

1.2 Fish physiology and conservation

One area that has not been well considered in fisheries management is fisheries-induced evolution (FIE). For example, the vulnerability of individuals to certain fishing gears is dependent on phenotypic characteristics including life history, behaviour and physiology (Law 2000, Uusi-Heikkilä et al. 2008, Auer et al. 2018), all of which are interlinked. Theoretically, the bolder, physiologically fitter individuals will be captured first by passive fishing gears, which may lead to FIE if the physiological traits are passed on to the subsequent generations (Arlinghaus et al. 2017, Hollins et al. 2018). Duncan et al. (2019a) provided the first empirical evidence for this by showing that exploitation removed high-performance metabolic phenotypes from the population, while Muller (2021) showed that larvae from an unexploited *Chysoblephus laticeps* population were more resilient to ocean acidification compared to the exploited population. This is most concerning as the reduction in these phenotypes is likely to limit the population potential for acclimatization and adaptation to climate change impacts.

As high-performance phenotypes are generally thought to be more resilient to changing environmental conditions (Duncan et al. 2019a), it is likely that exploitation may reduce the resilience of fish populations to the impacts of climate change. Understanding how resilient exploited fish populations are to the impacts of climate change is critical for our understanding and the prediction of their future responses. The incorporation of physiological information into fisheries management decisions (Metcalf et al. 2012) will be critical for maintaining resilient fisheries in the Anthropocene and remains a major challenge for the developing world, where fisheries management and physiological research are less developed.

Mechanistic and quantitative approaches are currently used to understand and predict the effect of environmental changes on fishes. The concepts applied include the Metabolic Theory of

Ecology (MTE) (Brown et al. 2004), the Dynamic Energy Budget (DEB) (Kooijman and Kooijman 2010) and the oxygen- and capacity-limited thermal tolerance (OCLTT) (Pörtner and Knust 2007). The OCLTT is currently the most used (albeit most debated (Jutfelt et al. 2018) mechanistic approach and is an extension of Frederick Fry's (1947) metabolic approach aimed at understanding fish physiological responses to environmental stressors (Horodysky et al. 2015). Central to the OCLTT is the quantification of aerobic scope (AS), which is the difference between an individual's standard metabolic rate (SMR) and maximum metabolic rate (MMR) and accounts for the energy available for an individual's performance (Sandblom et al. 2014, Clark et al. 2013a). Aerobic scope seems to be the most used physiological metric for quantifying the metabolic response of fishes and can be used to predict the future response of fish populations to climate variability and changes.

Despite the rapid development of concepts, few studies have applied these to successfully examine the impact of exploitation on the resilience of fishes to these changes. However, Duncan et al (2019a) compared the SMR, MMR and AS curve of a population of a highly resident reef fish (*Chrysoblephus laticeps*) in a heavily exploited area with that of an unexploited area, the Tsitsikamma National Park (TNP) marine protected area (MPA), the oldest MPA in South Africa. They found that the unexploited population had a higher aerobic scope over a range of ecologically relevant temperatures and metabolic diversity was greater when compared to the exploited population. A related study from the same locations but conducted in the field has shown similar trends, where the field metabolic rate of fish from the exploited population was lower than those from the unexploited population, particularly at extreme temperatures (Skeeles 2019). However, since these studies only included a single exploited and unexploited site and Duncan et al (2019a) examined the differences at the population level and not at the level of the individual, additional research is needed to understand the general applicability of these findings. Therefore, it is necessary to explore other MPAs to have a greater validity of the baseline reference physiological information.

1.3 Aim of thesis and Objectives

The broader aim of this thesis is to augment our knowledge on the impact of exploitation on the physiology of fishes by comparing the aerobic scope of individuals and the populations of *C. laticeps* from an additional exploited (Cape St Francis) and unexploited (Goukamma Marine Protected Area) area.

To achieve this the thesis is divided into five chapters: Chapter 1 provides a general introduction and the aim of the thesis. Chapter 2 provides a brief description of the exploited and unexploited site, as well as the model species profile. Chapter 3 describes the methods and materials used and statistical analyses approach taken to analyse the results of this study. Chapter 4 presents the findings of this study, while chapter 5 discusses the findings in the context of previous work and the implications of the study. The latter chapter also makes recommendations for future research in this area.

Chapter 2: Study sites and species profile



Andrew Meiklejohn (left) and Xolani Nabani (right) landing live red roman fish at Goukamma Marine Protected area (Image credit: Dr Cuen Muller).

2.1 Study sites

2.1.1 Climate change in South African context

To achieve the aim of this study, it was paramount to understand the climatic conditions of the South African coast since environmental thermal variability has a direct influence on the physiology of fish. The South African coast has two distinct major currents, the Benguela Current is a northward flowing ocean current, extending from around Cape Point to the Angola-Benguela Front, which is situated around southern Angola and the Agulhas Current (Figure 2.1), which is a southward flowing current extending from the north of KwaZulu-Natal Province to the tip of the Agulhas Bank (Figure 2.1) in South Africa (Emanuel et al. 1992, Demarcq et al. 2003, Spalding 2007, Roberson et al. 2017). The coast of South Africa influenced by the Benguela current is relatively colder, with an average temperature of 12-14 °C, on the other hand the coast characterised by the Agulhas temperature is relatively warmer, with an average temperature of 17-18 °C (Smit et al. 2013). The sites selected for the present study fall within the southern Cape, which is dominated by the Agulhas Current.

The southern Cape coast of South Africa has highly variable climatic conditions associated with both cooling and warming events (Rouault et al. 2010). The cooling of sea surface temperatures is driven by the south-easterly and easterly winds which intensify and cause upwelling events, while warming is driven by the intensification of the Agulhas current which carries warm tropical waters south-wards (Rouault et al. 2010, Goschen and Schumann 2011, Roberson et al. 2017). These highly variable climatic conditions are expected to become more frequent and intense along the south coast of South Africa (Rouault et al. 2010). This may impact the resilience of highly resident species distributed along these regions of intense cooling and warming of sea surface temperatures.

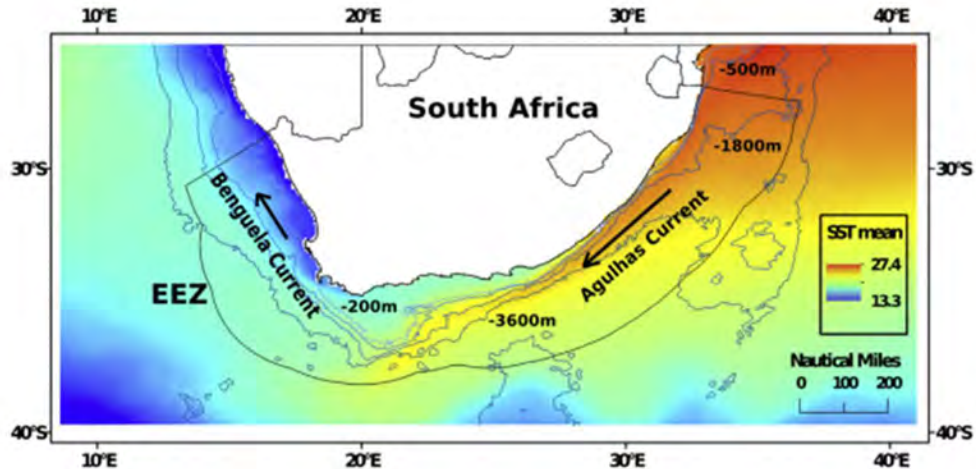


Figure 2.1: Agulhas Current and Benguela Current, with ocean depth (m) and sea surface temperature (°C) along the coastal region of South Africa (taken from Roberson et al. 2017).

2.1.2 Goukamma MPA and Cape St Francis

For this study, one unexploited site (Goukamma MPA) and one exploited site (Cape St Francis) were selected as sampling locations for fish collection. Goukamma MPA is located on the south of South Africa (34°04' S, 22°84' E) between Gerick's Point and Buffels Bay. The MPA is one of the largest MPAs in South Africa, established in 1990 to protect marine coastal ecosystems (Götz 2005, Molewa 2017). It covers a total area of approximately 40 km and a length of 18 km along the shore (Götz 2005). The MPA has been highly effective in protecting fish populations and has a positive spill-over effect (Kerwath et al. 2013). The MPA protects a diverse range of species, especially the resident species, and the spill-over of sparids, particularly *C. laticeps* to the adjacent exploited waters has been observed (Götz 2005, Kerwath et al. 2013). The MPA is in relatively close proximity (approximately 120 km apart) to Cape St Francis, the exploited site selected for this study.

Cape St Francis is one of the traditional fishing grounds along the south coast of South Africa, with chokka squid fishing being the most dominant commercial fishing activity taking place in the area (Roberts 2005, Voogt 2014). Although squid fishery is dominant, commercial, recreational and small-scale fishing for linefish (fish captured using hook and line) occurs in the area and is done by the local community and people who visit Cape St Francis on vacations (Voogt 2014). In terms of fishing effort, *Chrysoblephus laticeps* catches between 1985 and 2016 were higher in Cape St Francis compared with the area surrounding the Goukamma marine protected area (Figure 2.2a).

From an environmental perspective, the two sites are both situated in the warm-temperate region of the coast and consequently have comparable environmental conditions, including wind-driven upwelling (Figure 2.2b) and a considerable influence from the warm Agulhas Current. Data collected at between 20 and 27 m depth between February and August (2022) suggests that the thermal regime of the two areas are similar (Figure 2.3).

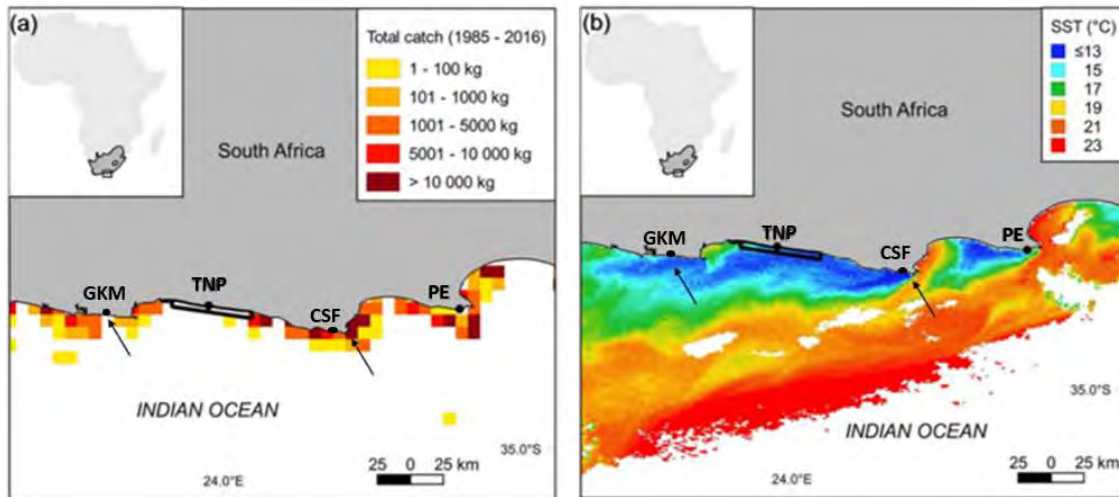


Figure 2.2: Unexploited Goukamma MPA (GKM) and exploited Cape St Francis (CSF) site (indicated by arrows) and a) reported catches of *Chrysoblephus laticeps* from 1985 – 2016 (modified map from Duncan et al. 2019a) and b) an example of one upwelling event occurring in both study sites (modified map from Duncan et al. 2019a), colours are MODIS Terra satellite sea surface temperature depicting an upwelling event on 04-03-2010 taken from Smit et al. (2013).

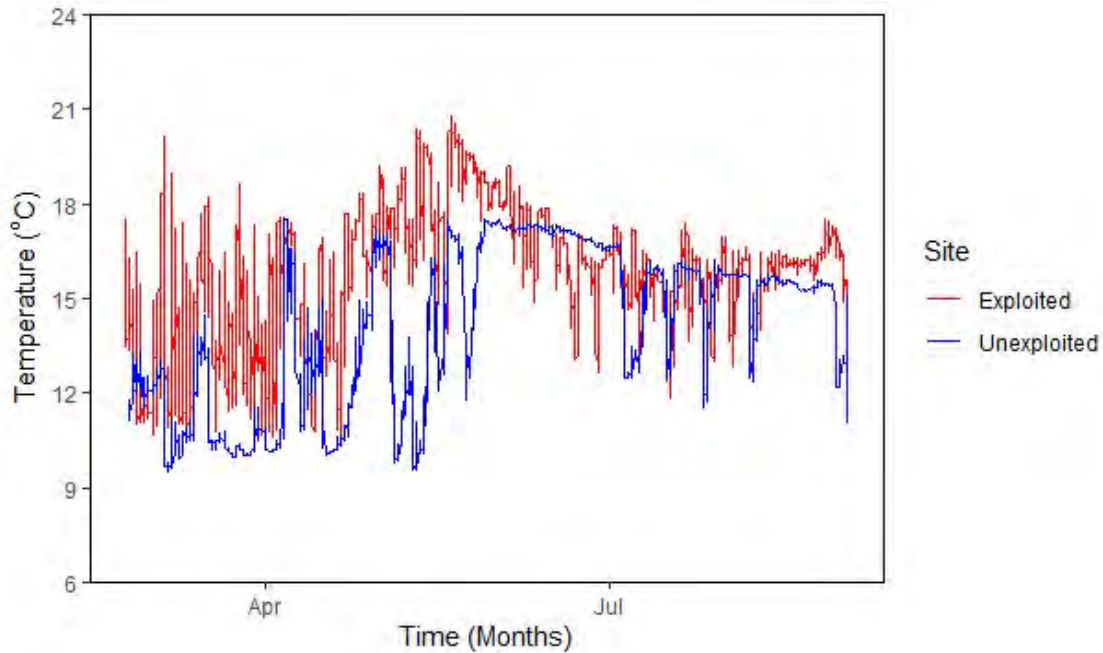


Figure 2.3: Temperature variability in Goukamma MPA (Unexploited) and Cape St Francis site (Exploited) from February to August 2022, temperature recorded at depths of 27 m (Unexploited site) and 20 m (Exploited site).

2.2 Species Profile

To achieve the aim of this study, not only was it necessary to explore marine protected areas and exploited sites other than the Tsitsikamma National Park and Noordhoek, respectively, but also to select the same species that has been a model to build baseline reference physiological information for South Africa (Duncan et al. 2019a). The red roman, *Chrysoblephus laticeps*, is an endemic South African seabream species that belongs to the family Sparidae. It is distributed along the coast of the Western Cape and Eastern Cape provinces of South Africa (Buxton 1984, Götz and Kerwath 2013). Adult *C. laticeps* inhabit inshore and offshore reefs to about 100m in depth, with juveniles inhabiting subtidal reefs to about 30m in depth. The eggs and larvae have been found off coastal shelves through most of the adult distribution (Buxton 1989, Götz et al. 2008). The species feeds mainly on crustaceans, echinoderms and cephalopods (Buxton 1984). It is highly resident species (Kerwath et al. 2007, Götz et al. 2008) and benefits from spatial protection (Kerwath et al. 2008). *Chrysoblephus laticeps* is a protogynous hermaphroditic fish, changing sex from female to male and reproducing in summer between October and January (Buxton 1990). *Chrysoblephus laticeps* is a commercially exploited linefish species, and currently the species is declared “near threatened” on the IUCN red list (Mann et al. 2014). The

species is hardy and well suited for laboratory experiments (Davis 1996, Duncan et al. 2019a) and therefore it is a suitable species to achieve the aim of this study.

Chapter 3: Methods and Materials



An intermittent-flow respirometer chamber housed in a water bath with fresh seawater during flush period.

3.1 Fish Collection:

Eighteen live red roman were collected from the Goukamma MPA in May 2022 and 20 from the exploited site (Cape St Francis) in October 2021 using hook and line at depths between 12 and 30 m. After capture, fish were vented using a hypodermic needle (16 gauge) to prevent barotrauma-related mortality. After venting, the fish were placed into one of two 250 L PVC tanks with fresh seawater and transported back to the shore and transferred into a large cylindrical holding tank (1 000 L) which was supplied with fresh seawater using a submersible pump. Oxygen was bubbled into the tanks during transportation to the South African Institute of Aquatic Biodiversity's (SAIAB) Aquatic Ecophysiology Research Laboratory (AERP) at the Department of Ichthyology and Fisheries Science (DIFS), Rhodes University.

3.2 Housing system and fish welfare:

Once at the AERP, fish were housed in one of two cylindrical holding tanks (5 900 L each) connected to a marine recirculating system with a total volume of 1 400 L. The system comprised a protein skimmer (UltraZap, Red Devil DC 5000s pump), a bubble bead filter (BBF-200-COMP, Wilpet Koi Products) for filtration of dirt particles, ultraviolet sterilizers (UVS-30, Wilpet Koi Products) to clear seawater and destroy small pathogens, a fluidised biological filter (750 L slime tank, SuperActiFlo Media) and a sump (750 L slimline). Water temperature was maintained by heat element (1.5 kW titanium hotrod) connected to temperature controller (STC-1000) and wall-mounted heat pump (AquaHeat) connected to an adjustable temperature controller (STC-1000). Tanks were aerated by an air blower (2.2 kW) located outside the laboratory, this was done to maintain oxygen saturation at 100%. Fish were acclimated at 16 °C for a period of two weeks before the start of the experiments. The photoperiod was set at 9.5 hours of light and 14.5 hours of dark. Water quality parameters, including pH, dissolved oxygen, ammonia, nitrite and nitrate concentrations were monitored twice daily.

Fish were fed a diet of frozen/thawed squid every two days, feeding rates were controlled due to the positive relationship between food availability and standard metabolic rate (Auer et al. 2016). For the purpose of individual identification, each individual was tagged after being exposed to the first temperature treatment (16 °C) and the mass of fish was measured soon after tagging. To do this, each fish was immersed into a water bath with clove oil sedative solution (40mg/L). Once fish were sedated (i.e., confirmed by the loss of equilibrium), a visible implant

elastomer (VIE) tag (Northwest Marine Technology, USA) was injected sub-dermally using an insulin syringe. The location of the injection and colour of the VIE tags was varied amongst individuals to allow for individual identification. Fish were placed in a water bath to ensure that they recovered from sedation and tagging stress and returned to the housing tanks after they had recovered.



Figure 3.1: *Chrysoblephus laticeps* tagging using Visible Implant Elastomer (VIE) for the purpose of individual identification.

3.3 Experimental set-up:

Intermittent-flow respirometers were used in the laboratory following experimental procedure by Duncan et al. (2019a). Four cylindrical respirometers (45 cm length and 29cm diameter) made from thick-walled Perspex were contained in glass water-baths and shielded from each other and from external disturbance by covering the sides of water-baths with black plastic sheeting. Each respirometer consisted of a flush pump (saltwater submersible pump) inlet which pumps water into the respirometer chamber after each measurement (closed) period, a recirculation loop made from an oxygen impermeable clear tubing (Oxygen-impermeable material), a peristaltic pump (Masterflex HV-07522 with 4 multi-channel F/S pump) connected to FireStingO₂ fibre optic oxygen sensor (FSO₂-4, Pro Science GmbH). The oxygen meter was used to take measurements of oxygen concentration from the circulation loop connected to the

respirometer chamber. Pro Oxygen Logger Software (Pro Science GmbH) was used to read measurements taken by the FireSting oxygen sensor every five seconds.

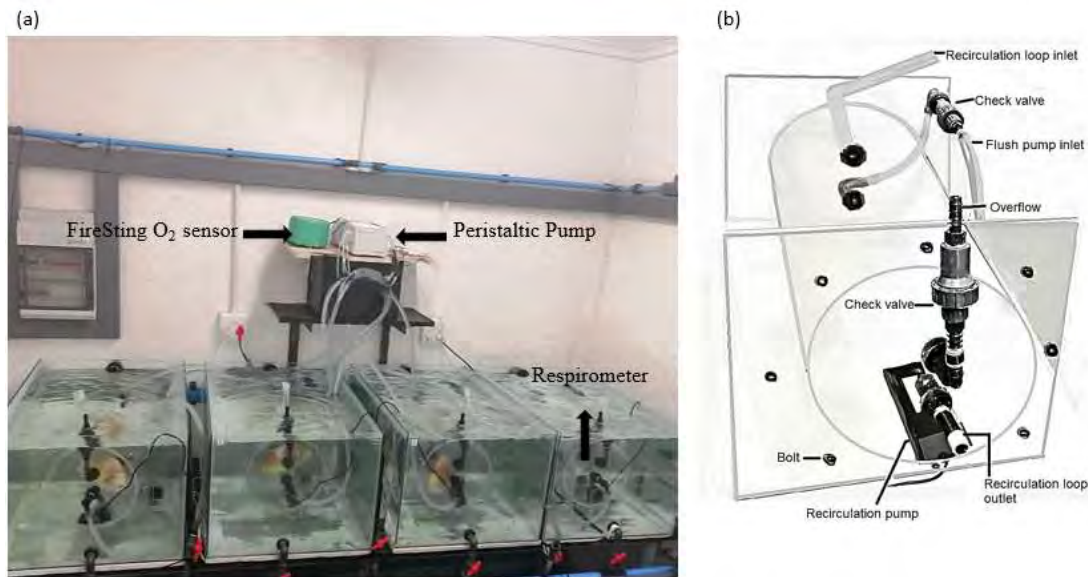


Figure 3.2: Experimental set-up with a) four respirometers, peristaltic pump and oxygen sensor, b) an intermittent flow respirometer design (modified from Bailey 2022).

3.4 Experimental procedure:

Fish were fasted for 36 hours to reduce postprandial effects before the experiments. After the fasting period, fish were placed into each of the four respirometers (four fish at a time) and given 12 hours to acclimate to the respirometer at 16 °C and 24 hours to acclimate to the new temperature and respirometer at 10 and 21 °C. During this time temperature was either increased or decreased from 16 °C by one degree per hour until the test temperature was reached. This rate of change was used as it simulated a typical extreme upwelling or downwelling experienced by these fish in the wild.

After acclimation, the rate of oxygen consumption ($\dot{M}O_2$) was recorded every five seconds over a five-minute measurement period, followed by a 15-minute flush period at 16 °C. At high temperatures of 21 °C, the measurement period was reduced to three minutes, followed by a 17-minute flush period to account for reduced oxygen solubility. The $\dot{M}O_2$ measurements for SMR were taken at night between from 1am and 5am when the fish were less active, this was done also to ensure that the SMR is not underestimated since the background respiration was measured only after the MMR measurements. Following SMR measurements, each fish was removed from respirometers and placed in a tank with fresh seawater. The individual was then

hand-chased for 10 minutes until exhaustion and exposed to air for 30 seconds before being returned to the respirometer when $\dot{M}O_2$ measurements began immediately for eight minutes to estimate the MMR. After the first eight minutes, the flush phase was turned on again and fish were left in respirometers for four hours until their metabolic rate had stabilised. Following this, individuals were removed from the respirometers. The blank respirometers were closed and the $\dot{M}O_2$ was measured for three hours after each MMR measurements to account for any background respiration. For the background rate, the measurement and flush period was the same as the treatment measurements (at 16, 10 and 21 °C).

3.5 Data handling and statistical analysis:

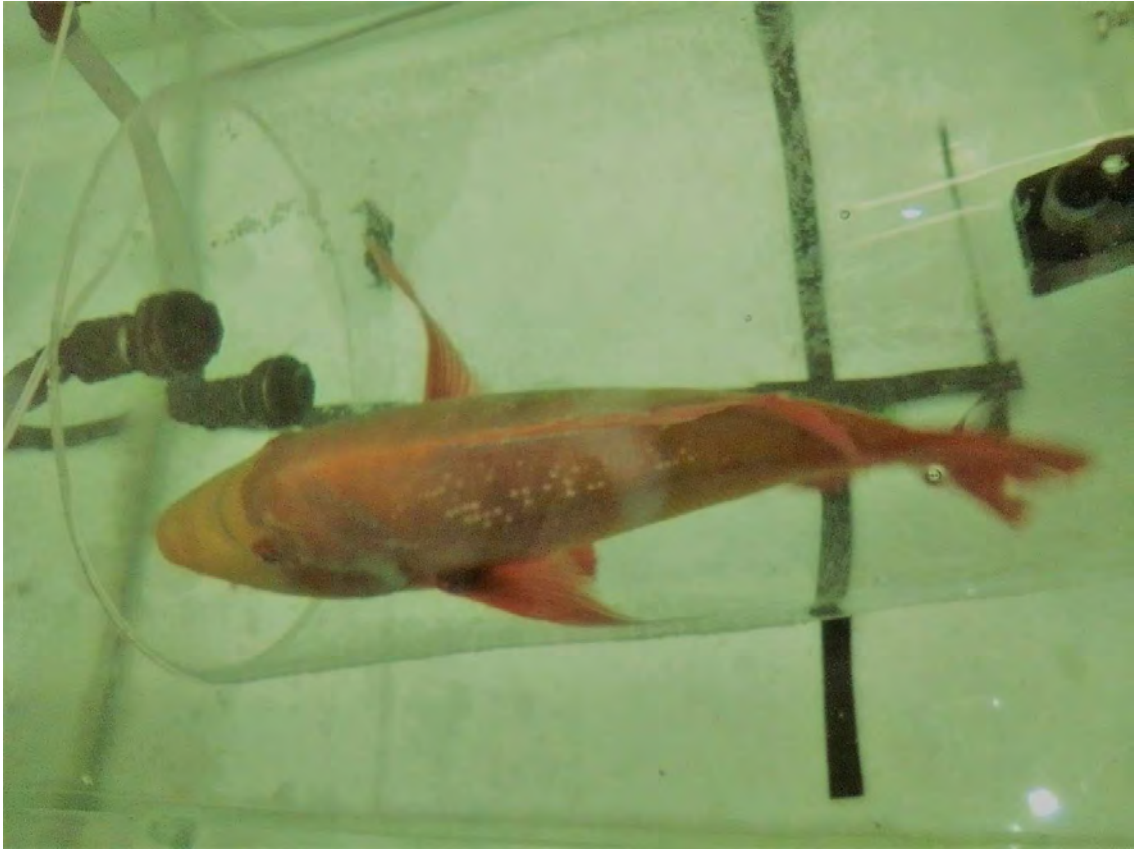
For SMR, 10 traces of measurements (when the flush was closed) were taken and the first 60 seconds were excluded from the analysis, this period was a buffer (a mixing period after the end of each flush period). Due to data noise observed during data analysis, particularly at 10 °C only 15 fish from the unexploited site and 12 fish from the exploited site were included in the analyses. One measurement period of eight minutes was taken to estimate MMR with 180 seconds window width and the first 60 seconds were excluded. The MMR estimate was selected by observing the first and subsequent measurement phases and the single greatest oxygen decline was chosen. After the SMR and MMR were estimated, an aerobic scope was calculated by subtracting SMR from MMR.

$$AS = MMR - SMR$$

The `respR` package was used to estimate SMR and MMR in RStudio software (Harianto et al. 2019), a quality threshold of $R^2 \geq 0.9$ was used to filter a linear decline in oxygen. For each temperature, the bottom 20% was used as an estimate for SMR (Chabot et al. 2016). The microbial respiration was accounted for by averaging three measurement periods and subtracting them from the MMR and SMR data. The SMR and MMR rates were converted into meaningful units and the mass of each fish was included ($O_2 \text{ mg. min}^{-1} \cdot \text{kg}^{-1}$). Using the ‘`lme4`’ package (Bates et al. 2015) in RStudio, linear mixed effects models (LME) with second order polynomial regression were used to model the effect of temperature and site (exploited vs unexploited) on the metabolic rate of *C. laticeps*. Temperature, its quadratic form, and site, together with the interaction between the two were included as fixed effects, with metabolic rate as the response variable. Temperature and fish ID were included in the random effects

structure, with temperature as the random slope and fishID as random intercept (Harrison et al. 2018). Linear mixed effects models were used to account for homoscedascity and repeated measures of individual fish (Bolker et al. 2009, Zuur et al. 2009). Model assumptions were checked using residual diagnostic plots using the package “*DHARMA*” package. The SMR and MMR data were $\log_{10}(x)$ transformed to meet model assumptions. The test of coefficient of variations test was performed using the package ‘*cvequality*’ (Marwick and Krishnamoorthy 2019). This was done to compare the spread of measurements between the exploited and unexploited population as refers to differences in phenotypic variability.

Chapter 4: Results



Red roman, *Chrysoblephus laticeps* in an intermittent-flow respirometry chamber.

4.1 Standard metabolic rate (SMR):

The SMR of *C. laticeps* from the exploited site ranged from 0.057 to 0.361, 0.484 to 3.120 and 0.901 to 3.661 $O_2 \text{ mg. min}^{-1} \cdot \text{kg}^{-1}$ at 10, 16 and 21 °C respectively, while for the unexploited the range was 0.052 to 0.703, 0.515 to 2.844 and 0.779 to 3.504 $O_2 \text{ mg. min}^{-1} \cdot \text{kg}^{-1}$ at 10, 16 and 21 °C respectively (Appendix Table 1). There was an increase in the SMR of *C. laticeps* with temperature in both populations (Figure 4.1). The SMR was higher in fish from the unexploited site at 10 °C, but lower at the warmer test temperatures (Figure 4.1). First term and second term temperatures had a significant effect on the SMR (p -value < 0.001, Table 4.1), but there was no influence of site (population) or the interaction between site and temperature (population-temperature) interaction on the SMR (Table 4.1).

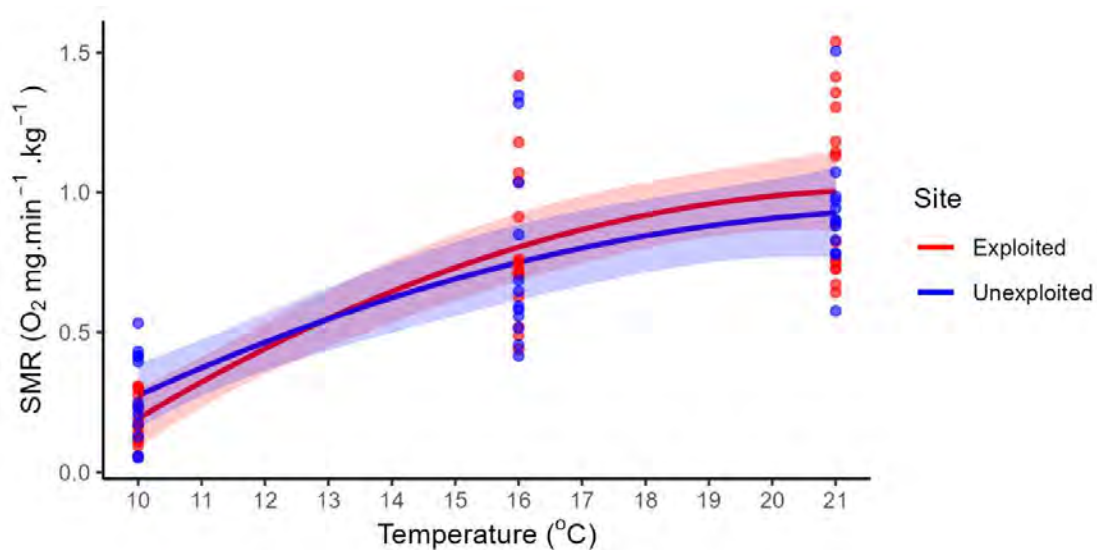


Figure 4.1: Linear mixed effects models for the standard metabolic rate (SMR) of exploited, Cape St Francis (red) and unexploited, Goukamma MPA (blue) populations of *Chrysoblephus laticeps* across different temperatures (10, 16 and 21 °C), with second order polynomial regression and shaded regions representing 95% confidence intervals.

Table 4.1: Linear mixed effect model output with second order polynomial regression modelling the effect of temperature on the log-transformed standard metabolic rate (SMR) of *Chrysoblephus laticeps* from the exploited and unexploited populations. Significant p values in bold.

Predictors	Log1p(SMR)			
	Estimates	SE	t value	P
(Intercept)	0.67	0.04	15.70	<0.001
Temperature [1st degree]	3.03	0.31	9.77	<0.001
Temperature [2nd degree]	-0.72	0.27	-2.66	0.010
Site [Unexploited]	-0.02	0.06	-0.26	0.794
Temperature [1st degree] * Site [Unexploited]	0.60	0.46	-1.28	0.204
Temperature [2nd degree] * Site [Unexploited]	0.21	0.41	0.52	0.605
Random Effects				
σ^2	0.04			
τ_{00} FishID	0.01			
τ_{11} FishID.Temperature	0.00			
ρ_{01} FishID	-1.00			
ICC	0.23			
N _{FishID}	27			
Observations	81			
Marginal R ² / Conditional R ²	0.658 / 0.737			
AIC	124.894			

There was low variability in the SMR of individuals from the exploited and unexploited population of *C. laticeps* at 10 °C, but distinct variability at 16 °C and 21 °C (Figure 4.2). The test of coefficient of variance showed that there was no significant difference in the SMR variation between the sites at any of the test temperatures (Table 4.2).

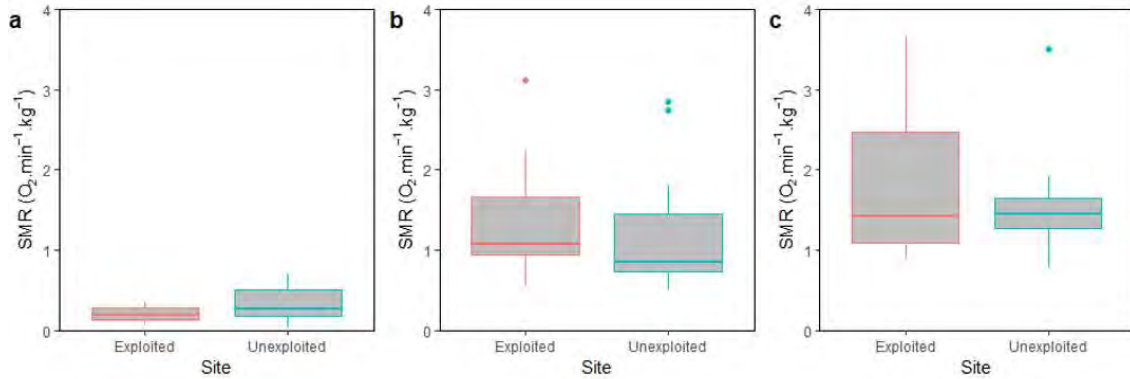


Figure 4.2: Box plot of the raw data standard metabolic rate (SMR) ($\text{O}_2 \text{ mg. min}^{-1} \cdot \text{kg}^{-1}$) of *C. laticeps* individuals from exploited and unexploited populations measured at three temperature treatment a) 10 °C, b) 16 °C and c) 21 °C.

Table 4.2: Summary of tests on the equality of coefficient of variations in the standard metabolic rate (SMR) between the two populations (exploited and unexploited) of *Chrysoblephus laticeps* across all test temperatures.

Temperature	Test type	Test statistic	p-value
(a) 10 °C	<i>D' AD</i> asymptotic	0.952	0.329
(b) 16 °C	<i>D' AD</i> asymptotic	0.376	0.540
(c) 21 °C	<i>D' AD</i> asymptotic	0.181	0.671

4.2 Maximum metabolic rate (MMR):

The MMR of *C. laticeps* from the exploited population ranged from 2.511 to 5.823, 2.854 to 8.265 and 3.102 to 7.197 O₂ mg. min⁻¹ .kg⁻¹ at 10, 16 and 21 °C respectively, while the MMR for the unexploited population of *C. laticeps* ranged from 3.286 to 5.001, 2.133 to 7.799 and 4.498 to 10.182 O₂ mg. min⁻¹ .kg⁻¹ at 10, 16 and 21 °C respectively (Appendix Table 1). There was an increase in the MMR of *C. laticeps* with temperature in both populations. The MMR of *C. laticeps* from the exploited population was lower than the MMR of *C. laticeps* from the unexploited population across all test temperatures (Figure 4.3), but particularly at the highest temperature where the MMR of the exploited population declined from 16 °C. First term temperature had a significant effect on MMR (p-value < 0.001, Table 4.3), second term temperature had a significant effect on MMR (p-value = 0.004) and site had a significant effect on MMR (p-value = 0.039, Table 4.3). The first and second term site-temperature interaction did not have a significant effect on MMR.

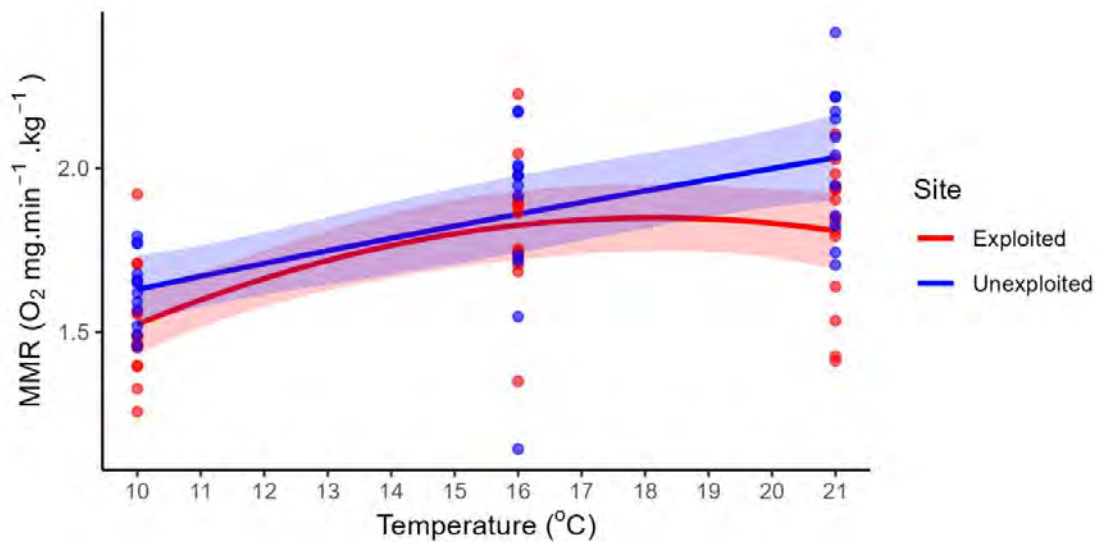


Figure 4.3: Linear mixed effects models for the maximum metabolic rate (MMR) of exploited, Cape St Francis (red) and unexploited, Goukamma MPA (blue) populations of *Chrysoblephus laticeps* across different temperatures (10, 16 and 21 °C), with second order polynomial regression and shaded regions representing 95% confidence intervals.

Table 4.3: Linear mixed effect model output with second order polynomial regression modelling the effect of temperature on the log-transformed maximum metabolic rate (MMR) of *Chrysoblephus laticeps* from the exploited and unexploited populations, with significant p values in bold.

Predictors	Log1p(MMR)			
	Estimates	SE	Statistic	P
(Intercept)	1.72	0.04	41.82	<0.001
Temperature [1 st degree]	1.09	0.22	4.93	<0.001
Temperature [2 nd degree]	-0.62	0.21	-3.00	0.004
Site [Unexploited]	0.12	0.06	1.97	0.053
Temperature [1 st degree] * Site [Unexploited]	0.40	0.33	1.20	0.071
Temperature [2 nd degree] * Site [Unexploited]	0.58	0.31	1.85	0.078
Random Effects				
σ^2	0.02			
τ_{00} FishID	0.00			
τ_{11} FishID.Temperature	0.00			
ρ_{01} FishID	1.00			
ICC	0.02			
N _{FishID}	27			
Observations	81			
Marginal R ² / Conditional R ²	0.522 / 0.532			
AIC	274.688			

There was low variability in the MMR of individuals from the exploited and unexploited population of *C. laticeps* at 10 °C, but high variability in the MMR of *C. laticeps* from the unexploited site when compared to the MMR of *C. laticeps* from the exploited at 16 °C and 21 °C (Figure 4.4). The test of coefficient of variance showed that there was no significant difference in the MMR variation between the exploited site and unexploited sites at any of the test temperatures (Table 4.4).

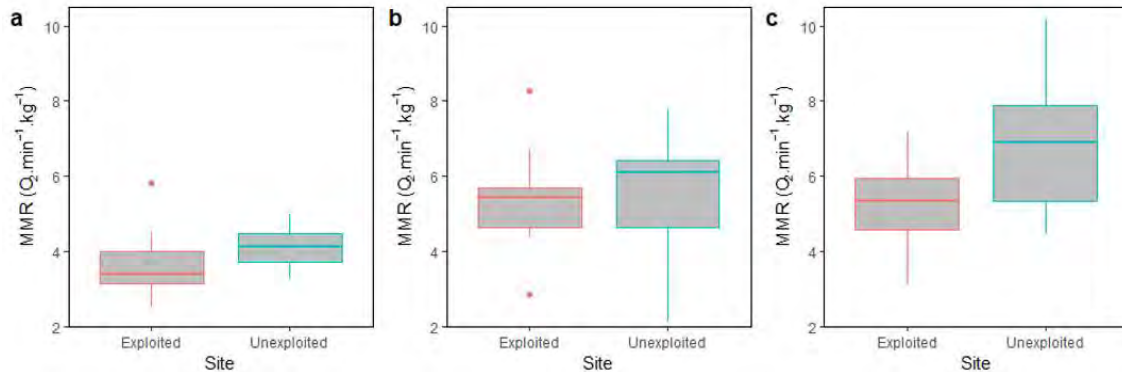


Figure 4.4: Box plot of the raw data maximum metabolic rate (MMR) ($O_2 \text{ mg} \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$) of *C. laticeps* individuals from exploited and unexploited populations measured at three temperature treatment a) 10 °C, b) 16 °C and c) 21 °C.

Table 4.4: Summary of tests on the equality of coefficient of variations in the maximum metabolic rate (MMR) between the two populations (exploited and unexploited) of *Chrysoblephus laticeps* across all test temperatures.

Temperature	Test type	Test statistic	p-value
(a) 10 °C	Asymptotic	2.648	0.104
(b) 16 °C	Asymptotic	0.569	0.451
(c) 21 °C	Asymptotic	0.427	0.836

4.3 Aerobic scope (AS)

The AS of *C. laticeps* from the exploited population ranged from 2.396 to 5.462, 1.713 to 5.202 and 1.880 to 5.688 O₂ mg. min⁻¹ .kg⁻¹ at 10, 16 and 21 °C respectively, while the AS for the unexploited population of *C. laticeps* ranged from 2.736 to 4.681, 1.323 to 6.462 and 8.543 to 10.182 O₂ mg. min⁻¹ .kg⁻¹ at 10, 16 and 21 °C respectively (Appendix Table 1). There was an increase in the AS of *C. laticeps* with temperature in the unexploited population, but the AS assumed a bell-shaped curve in the exploited population (Figure 4.5). Second term temperature had a significant effect on AS (p-value = 0.037, Table 4.5), site had a significant effect on AS (p-value = 0.011, Table 4.5) and first term site-temperature interaction had a significant effect on AS (p-value = 0.026, Table 4.5). However, first term temperature and second term site-temperature interaction did not have a significant effect on AS (Table 4.5).

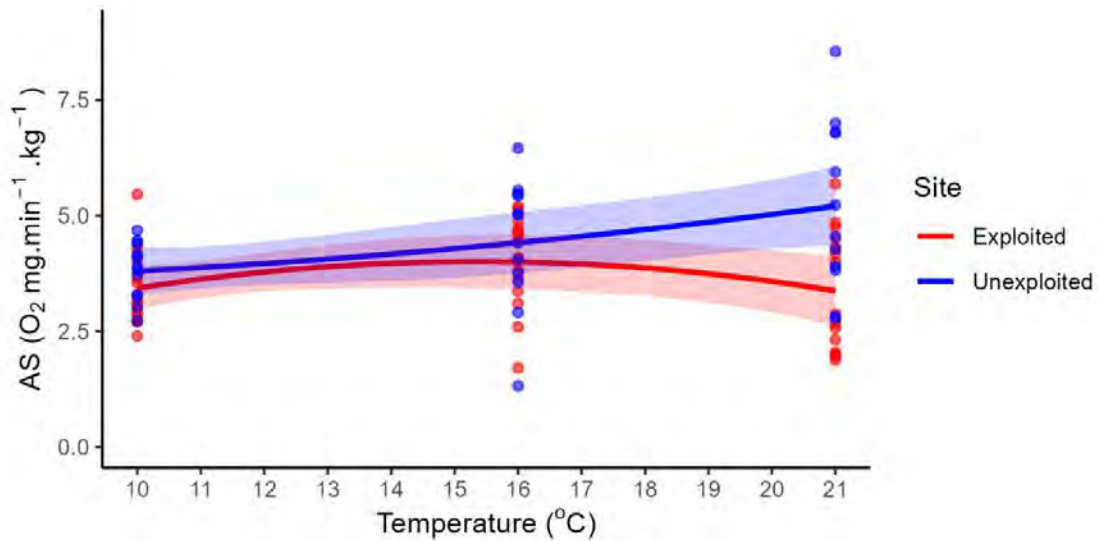


Figure 4.5: Linear mixed effects models for the aerobic scope (AS) of exploited, Cape St Francis (red) and unexploited, Goukamma MPA (blue) populations of *Chrysoblephus laticeps* across different temperatures (10, 16 and 21 °C), with second order polynomial regression and shaded regions representing 95% confidence intervals.

Table 4.5: Linear mixed effect model output with second order polynomial regression modelling the effect of temperature on the aerobic scope (AS) of *Chrysoblephus laticeps* from the exploited and unexploited populations, with significant p values in bold.

		AS			
Predictors		Estimates	SE	t value	P
(Intercept)		3.60	0.22	16.20	<0.001
Temperature [1 st degree]		-0.09	1.53	-0.06	0.956
Temperature [2 nd degree]		-2.54	1.20	-2.12	0.037
Site [Unexploited]		0.87	0.33	2.62	0.011
Temperature	[1 st degree] * Site [Unexploited]	5.22	2.29	2.28	0.026
Temperature	[2 nd degree] * Site [Unexploited]	3.18	1.79	1.77	0.081
Random Effects					
σ^2		0.79			
τ_{00} FishID		0.54			
τ_{11} FishID.Temperature		0.01			
ρ_{01} FishID		-1.00			
N FishID		27			
Observations		81			
Marginal R ² / Conditional R ²		0.326 / NA			
AIC		250.933			

There was low variability in the AS of individuals from the exploited and unexploited population of *C. laticeps* at 10 °C, but high variability in the AS of *C. laticeps* from the

unexploited population when compared to the AS of *C. laticeps* from the exploited population at 16 and 21 °C (Figure 4.6). The test of coefficient of variance showed that there was no significant difference in the AS variation between the exploited site and unexploited sites at any of the test temperatures (Table 4.6).

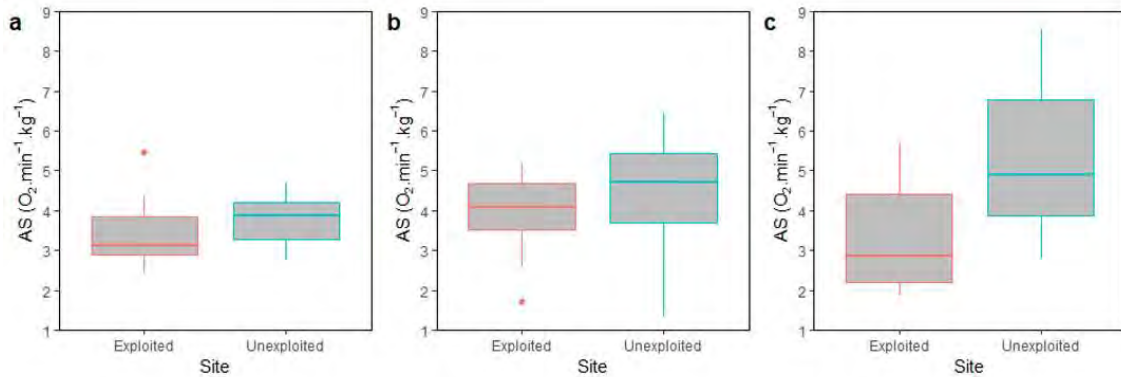


Figure 4.6: Box plot of the raw data aerobic scope (AS) ($\text{O}_2 \text{ mg. min}^{-1} \cdot \text{kg}^{-1}$) of *C. laticeps* individuals from exploited and unexploited populations measured at three temperature treatment a) 10 °C, b) 16 °C and c) 21 °C.

Table 4.6: Summary of tests on the equality of coefficient of variations in the aerobic scope AS between the two populations (exploited and unexploited) of *Chrysoblephus laticeps* across all test temperatures.

Temperature	Test type	Test statistic	p-value
(a) 10 °C	Asymptotic	1.572	0.210
(b) 16 °C	Asymptotic	0.676	0.411
(c) 21 °C	Asymptotic	0.069	0.793

Chapter 5: Discussion



Live red roman, *Chrysolephus laticeps* in an intermittent-flow respirometry chamber.

5.1 Overview

Overall, this study showed that the *Chrysoblephus laticeps* from the unexploited population had a statistically significantly higher aerobic scope across all treatment temperatures when compared to the exploited population. However, the exploited population of *C. laticeps* had a high SMR at higher temperature and lower SMR at lower temperature when compared to the unexploited population. There were no significant differences in the coefficient of variations between the two populations. These findings suggest that although there is still a great deal of physiological variability within the exploited population, which may promote adaptation at a population level, the significantly higher MMR and AS at average (16 °C) and warm temperatures (21 °C) suggests that individuals from unexploited populations may be more resilient to the expected warming predicted for the region. These results also provide further evidence to suggest that passive gear fishing removes high thermal performance phenotypes from populations (Duncan et al 2019a), and this has considerable implications for how we manage our fish populations for resilience in the Anthropocene.

Despite the collection of physiology information from different exploited and unexploited sites, the findings of this study agreed with that of Duncan et al. (2019a) who showed that *C. laticeps* in the Tsitsikamma National Park had a broader aerobic scope and was composed of individuals with higher performance phenotypes when compared to the heavily exploited population from Noordhoek, Port Elizabeth. The present study found that the AS of *C. laticeps* population from the unexploited Goukamma Marine Protected Area was significantly different than the exploited population in Cape St Francis with rates typically higher at all measured temperatures. However, the approach of this study was slightly different to that of Duncan et al. (2019a) in that the present study measured the metabolic rate (SMR, MMR and AS) of the same individuals at all temperature treatment (10, 16 and 21 °C) in a repeated measures design, while Duncan et al. (2019a) did not measure the metabolic rate of each individual across all test temperatures. Nevertheless, the same trends are observed, both studies show that the MMR and SMR of *C. laticeps* increase with increase in temperature and that there is a considerable divergence in the MMR and AS at higher temperatures, with unexploited populations having a higher MMR and AS when compared to the exploited populations (Figure 5.1a and b). This does not only support the findings of Duncan et al (2019a), but also provides further evidence that hook and line fishing has an impact on the thermal physiology of a population.

While this research was conducted in controlled laboratory conditions, laboratory findings have also been reflected in the wild, where the unexploited population was found to have a higher field metabolic rate (FMR) and high levels of acceleration when compared to the exploited population (Skeeles 2019, Mlotshwa 2023). Skeeles (2019) found that the *C. laticeps* from the unexploited, Tsitsikamma National Park had a greater FMR across temperatures they experienced in the wild compared to the exploited Port Elizabeth population (Figure 5.1c). Mlotshwa (2023), conducted the same field experiments as Skeeles (2019) at the same study sites selected in the present study (Goukamma Marine Protected area and Cape St Francis) and found that the *C. laticeps* from the unexploited population maintained high levels of acceleration across temperatures experienced by fish in the wild when compared to the exploited population (Figure 5.1d). When combined, the findings of the present study and those of Duncan et al (2019a), Skeeles (2019) and Mlotshwa (2023) suggest that it is highly likely that the unexploited populations of *C. laticeps* will be comparatively more resilient to future changes in the environment. When this is coupled with the findings by Muller et al. (2020) who found that the larvae from unexploited populations were more tolerant to environmental stress, it appears that these traits are passed to the next generation and that individuals from unexploited populations will provide future generations with the phenotypes necessary to adapt to a changing environment.

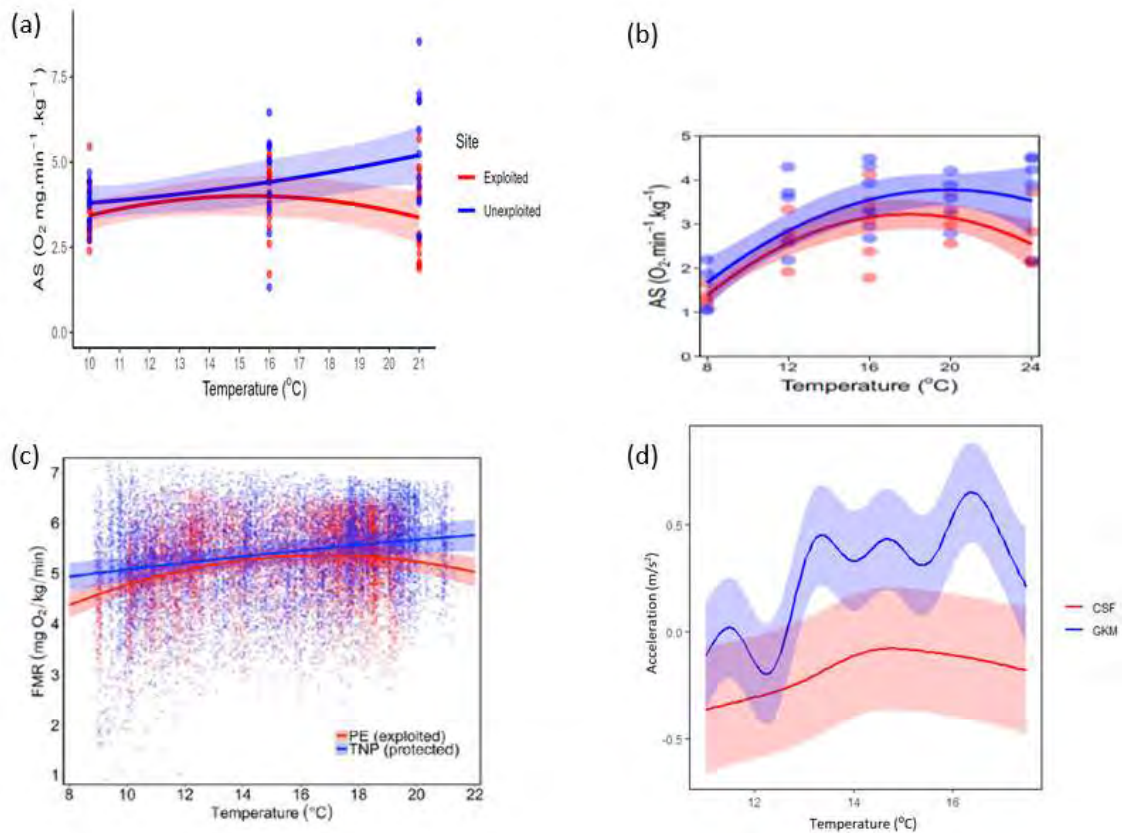


Figure 5.1: a) Aerobic scope of *C. laticeps* from the exploited Cape St Francis (CSF) and unexploited Goukamma Marine Protected Area (GKM) populations across different test temperatures, b) Aerobic scope of *Chrysoblephus laticeps* from the exploited Port Elizabeth (PE) and unexploited Tsitsikamma National Park (TNP) populations across different test temperatures (Duncan et al. 2019a), c) field metabolic rate of *C. laticeps* from the exploited PE and unexploited TNP populations across different temperatures experienced by fish in the wild (Skeeles 2019), d) acceleration activities of *C. laticeps* from the exploited CSF and unexploited GKM populations across different temperatures experienced by fish in the wild (Mlotshwa 2023).

In an exploited population, individuals with a high-performance aerobic scope phenotype may be removed from the population as they are at risk for capture through passive gear (Klefoth et al. 2017, Lennox et al. 2017, Hollins et al. 2018, Duncan et al. 2019a). Boldness and exploration in fishes is often associated with high aerobic scope (Lennox et al. 2017, Hollins et al. 2018, Bailey et al. 2022), and this could explain why passive-gear fishing alters the phenotypic diversity of exploited populations by removing high-performance phenotypic individuals. In the case of *C. laticeps*, it can be assumed that the targeting of high-performance phenotypes

has been long occurring in the exploited populations, leading to a reduction in both aerobic scope and the diversity of physiological phenotypes. Laboratory experiments conducted by Bailey (2022) on the *C. laticeps* showed that there is a link between metabolic phenotype and behaviour, where individuals with a broader aerobic scope were found to be more aggressive. This is concerning because exploitation may lead to physiological plastic changes and possibly over time may lead to fisheries-induced evolution (FIE), particularly since Muller (2020) showed that these traits are heritable.

Oxygen and temperature are among parameters that greatly influence the SMR, MMR and AS in fishes and are said to be fundamental in determining metabolic performance and fitness (Reemeyer and Rees 2019, Rubalcaba et al. 2020). As temperatures increase, the metabolic rate of fish increases (SMR, MMR and AS). While the SMR increases exponentially, MMR and AS generally increases from lower temperatures until a peak, after which they decline (Healy and Schulte 2012, Gräns et al. 2014). There are exceptions, however, some species have been observed to maintain a high AS even at temperatures beyond their ecologically relevant temperature (Norin et al 2014, Gräns et al. 2014). In the present study, the SMR, MMR and AS increased with temperature and began to decrease at the highest test temperature (21 °C) (Figure 4.1, 4.3, 4.5). With increase in temperature, the solubility of oxygen in water declines, this is often accompanied by an increase in the oxygen demand in fishes at a tissue level (Pörtner and Knust 2007, Deutsch et al. 2015, Salin et al. 2016). Although oxygen may not be a limiting factor at cold temperatures, a reduced metabolic rate (SMR, MMR, AS) is often observed. Indeed, a low SMR, MMR and AS was observed at the lowest test temperatures (10 °C) in this study (Figure 4.1,4.3 and 4.5). One of the reasons for this could be the reduced cardiac contractility which is due to a reduced flux of ions essential to generate force in the heart (Salin et al. 2016, Keen et al. 2017).

At higher temperatures, aerobic respiration may be limited by oxygen when oxygen supply does not match the demand, thus the AS and performance of an individual fish may decrease (Pörtner and Farrel 2008, Seibel et al. 2021). However, the decrease in performance due to a mismatch in oxygen supply and demand may apply to some but not all fish species (Clark et al. 2013a, b, Jutfelt et al. 2018, Lefevre et al. 2021). Although the OCLTT hypothesis which assumes that aerobic scope decreases at either side of optimal temperature ($T_{opt,AS}$) is not universal, it can be valuable and still apply to a species that has a $T_{opt,AS}$ within their ecologically relevant temperatures and may experience highly variable thermal conditions

(Eliason et al. 2011, Pörtner et al. 2017). Therefore, the OCLTT hypothesis is well-suited for application in the case of *C. laticeps*.

The results of this study showed that there was no difference in the SMR between the unexploited and exploited populations at the average temperature, but there were no clear differences at the lowest temperature (Figure 4.1b, Figure 4.4). At the lower temperature, the unexploited site had a high SMR and the variability within the population was a little higher compared to the exploited site. The interpopulation differences observed at the lower temperature could be the result of exploitation. Fish with a high SMR have high food demands and may need to search for food at lower temperatures. Fish with a high SMR tend to have a high physiological performance within a population and their extended foraging bouts can make them more likely to encounter fishing gear (Metcalf et al. 2016), increasing their vulnerability to capture. The reduced SMR in the exploited population suggests that the resilience of the exploited population of *C. laticeps* to future climate change may be compromised when the predicted intensity and frequency of upwelling events associated with cold temperatures persist within their home-range.

On the other hand, the differences in the MMR were very clear at the average (16 °C) and highest (21 °C) temperatures (Figure 4.2b; Figure 4.5). The unexploited population had a higher MMR with higher variability compared to the exploited population. Since the *C. laticeps* population in Goukamma is spatially protected (Kerwath et al 2008, Götz et al. 2008), exploitation does not exert selective pressure on this population. The selective removal of individuals with a higher MMR in the exploited area is the most likely explanation for these differences and this could explain the higher MMR exhibited by the unexploited population. These results suggest that the unexploited population is more likely to have individuals that can cope with the thermal variability associated with a future marine environment.

Overall, the differences between populations were less pronounced at the coldest temperature and there was less variability in both SMR and MMR at this temperature. This may be because these fish are nearer their low thermal tolerance limit than their upper limit. A previous study conducted by Alison et al. (2021) found that the CT_{min} of Fransmadam *Boopsoidea inornate*, a closely related seabream species found in the same area was closer to the conditions found during upwelling events than their CT_{max} was to the warmest temperatures experienced in the wild. They concluded that marine cold spells in the region are more likely to have negative

consequences for the species than marine heat waves. It is therefore possible that the predicted increase in the frequency and intensity of upwelling events predicted for the region may pose a greater threat to *C. laticeps* than warm water intrusions or fronts (Rouault et al. 2010, Goschen et al. 2012, Duncan et al 2019b, 2020).

5.2 Marine protected areas and conservation physiology

This study further extends our understanding of how MPAs play an important role in conserving certain physiological traits that may lead to resilience of fish populations to environmental stressors. This study showed that the unexploited population of *C. laticeps* had a high AS compared to the exploited population. This finding illustrates how MPAs may play an important role in protecting individuals with greater energetic budget, which could make fish populations more resilient in a changing environment. Ultimately, the protection of high-performance phenotypes within fish populations should be a goal to ensure the survival and resilience of fish populations to climate change impacts (Carr et al. 2017, Duncan et al. 2019b). In terms of fisheries management, MPAs are one of the most viable management tools, providing a wide variety of benefits, these include diversity conservation, restoration of population structure and size (Carr et al. 2017, Davies et al. 2017). Therefore, in the face of climate change, the promulgation of appropriately placed and well-designed MPAs is vital as they enhance the resilience of fish population to environmental thermal changes (McLeod et al. 2009, Carr et al. 2017, Roberts et al. 2017, Duncan et al. 2019a, 2020).

The success of MPAs in managing fisheries and conserving diversity requires proper planning and careful selection of areas to be protected. Despite the complexity of the marine environment, there are areas predicted to be more resilient to future climate change (Green et al. 2014). Duncan et al. (2020) used a mechanistic model to identify areas where *C. laticeps* may be negatively affected by the predicted future climate change in the South African coast. They identified, the areas around the Goukamma Marine Protected area, Amathole MPA and Bird Island MPA to be areas where *C. laticeps* populations are expected to be more vulnerable to future climate change (Duncan et al. 2020). This highlights not only the importance of these MPA's for promoting resilience of *C. laticeps*, but also stresses the importance of maintaining the integrity of these valuable areas. Duncan et al. (2020) also predicted a contraction of *C. laticeps* distribution in the west and east edges of the current distribution. This is concerning as a shrinking distribution can have negative consequences for the population size of the

species. Consequently, the newly established Robben Island and Amathole expansion MPAs, which are situated on the boundary of the western and eastern distribution of the species, respectively (Kirkman et al. 2021) may be critical areas for the protection of the species.

5.3 Caveats of the study

The primary limitation of this study is that sample collection and experiments were conducted at different times, starting with individuals from the exploited site, followed by individuals from the unexploited site (end of 2021 and beginning of 2022 respectively). This was due to COVID-19 restrictions and delays in ethical clearance approval, we were not able to collect fish early in 2021 because the ethical clearance was approved late, and the COVID-19 restrictions were still in place, and this hindered sample collection. In addition, since fishes were collected from a vessel, there were few window periods where sea conditions were conducive for fishing. However, given that the patterns found between other exploited and unexploited regions were similar both in the laboratory (Duncan et al. 2019) and in-situ (Skeeles 2019, Mlotshwa 2023) it is unlikely that this had a large impact on the findings. Furthermore, the specimens were acclimated for two weeks at the same temperature thus, this ensured that all specimens had a similar recent thermal history and in terms of collection, the same selective gear was used to collect samples from both sites (exploited and unexploited).

5.4 Further recommendations and conclusions

The marine environment is very complex and climate change drives dynamic changes in both physical and chemical composition of water bodies (Hoegh-Guldberg and Bruno 2010). However, this study only focused on thermal variability as a single environmental parameter. Munday et al. (2009) showed how additive effects of ocean acidification and thermal warming increase mortality of *Ostorhinchus doederleini* and *Ostorhinchus cyanosoma*. Future research should aim to examine the combined effects of multiple environmental stressors such as changing temperature and pH. Understanding the impacts that environmental changes and anthropogenic activities have on the physiology and genetics of individuals and populations will assist in predicting the future persistence of fish populations in a changing environment. Incorporating physiological information into fisheries management frameworks will assist in developing viable management tools. For example, bioclimatic envelope models can be used to predict the future distribution and resilience of fish populations in a climate change context (Deutsch et al. 2015, Evans et al. 2015, Townhill et al. 2017). For example, in a South African

context, Duncan et al. (2020) incorporated physiological information into species distribution models to predict how *C. laticeps* distribution may be constrained by low oxygen supply in the west coast and high oxygen demand in the east coast. They used physiological information collected through conducting laboratory experiments to investigate the tolerance of *C. laticeps* to hypoxia across different temperature treatments (8 to 24 °C), highlighting the importance of physiological data and its contribution to mechanistic species distribution models.

In conclusion, the present study contributes to the limited baseline physiological reference information for South African linefish in the face of climate change. It shows how fishing may have negative impacts on physiological diversity of linefish species and how MPAs promulgated at appropriate areas can enhance resilience of fish populations to future climate change. In addition, the present study examined physiological information at an individual level, showing the value of using repeated measures to understand the consequences of the selective removal of individuals through exploitation.

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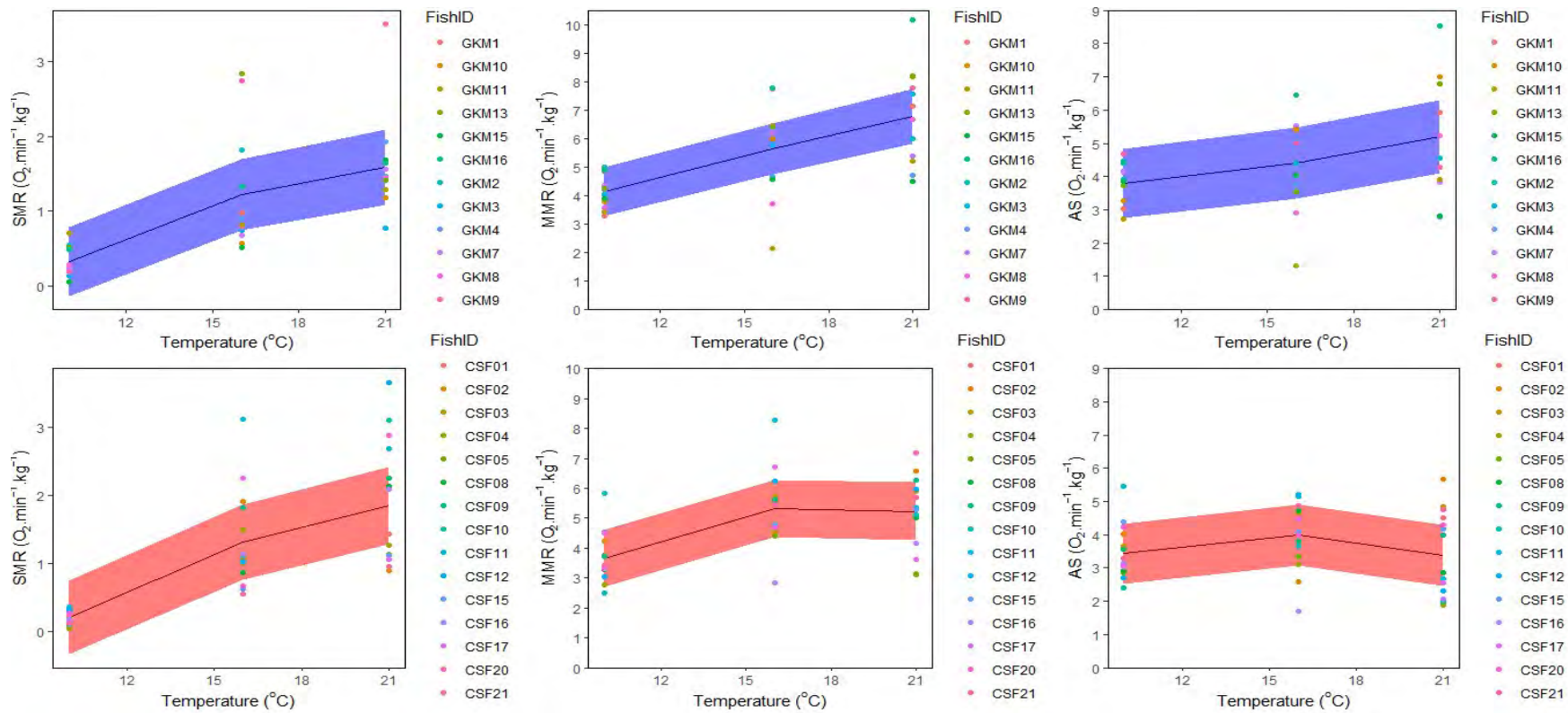
Appendix:

Appendix Table 1: Raw data of the Standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS)) (O_2 mg. $min^{-1}.kg^{-1}$) indices with treatment temperature, sampling site (exploited and unexploited), fish identification code (FishID) and fish mass (kg).

Temperature	Site	FishID	Mass			
			(kg)	MMR	SMR	AS
10	Exploited	CSF01	1,1067	3,42961	0,34639	3,08322
10	Exploited	CSF02	0,3002	4,24115	0,21229	4,02886
10	Exploited	CSF03	0,7252	3,75846	0,10063	3,65783
10	Exploited	CSF04	0,6358	2,76499	0,05726	2,70773
10	Exploited	CSF05	1,3834	3,04600	0,19295	2,85305
10	Exploited	CSF08	0,6203	3,27604	0,35268	2,92337
10	Exploited	CSF09	0,3510	3,73453	0,18477	3,54976
10	Exploited	CSF10	0,7712	2,51085	0,11531	2,39554
10	Exploited	CSF11	0,5062	5,82253	0,36081	5,46172
10	Exploited	CSF12	0,3310	3,03203	0,31699	2,71504
10	Exploited	CSF15	0,9078	4,52575	0,14944	4,37631
10	Exploited	CSF16	0,6905	3,31953	0,17811	3,14142
10	Exploited	CSF17	0,3315	3,32027	0,26802	3,05225
10	Exploited	CSF20	0,4216	4,51248	0,25983	4,25265
10	Exploited	CSF21	0,9485	3,41430	0,12881	3,28549
10	Unexploited	GKM1	0,9200	3,28641	0,25935	3,02706
10	Unexploited	GKM2	0,8750	5,00142	0,54021	4,46121
10	Unexploited	GKM3	0,5850	4,04549	0,13695	3,90853
10	Unexploited	GKM4	0,6350	4,20227	0,05181	4,15045
10	Unexploited	GKM7	1,0500	4,34631	0,23026	4,11605
10	Unexploited	GKM8	1,1450	3,56038	0,28052	3,27986
10	Unexploited	GKM9	1,0250	4,86736	0,18669	4,68067
10	Unexploited	GKM10	1,0650	3,78379	0,51588	3,26791
10	Unexploited	GKM11	1,2700	3,43946	0,70334	2,73612
10	Unexploited	GKM13	0,5150	4,24497	0,50897	3,73599
10	Unexploited	GKM15	0,9850	3,90323	0,06005	3,84318
10	Unexploited	GKM16	0,7350	4,88615	0,48396	4,40219

16	Exploited	CSF01	1,1067	5,61371	1,03519	4,57852
16	Exploited	CSF02	0,3002	4,50820	1,91381	2,59439
16	Exploited	CSF03	0,7252	5,73694	1,08436	4,65258
16	Exploited	CSF04	0,6358	4,59274	1,49159	3,10115
16	Exploited	CSF05	1,3834	4,38789	1,02598	3,36191
16	Exploited	CSF08	0,6203	5,58526	0,87265	4,71261
16	Exploited	CSF09	0,3510	5,63940	1,82628	3,81312
16	Exploited	CSF10	0,7712	4,76766	1,12350	3,64416
16	Exploited	CSF11	0,5062	8,26514	3,12002	5,14511
16	Exploited	CSF12	0,3310	6,24090	1,03867	5,20224
16	Exploited	CSF15	0,9078	4,72698	0,62913	4,09786
16	Exploited	CSF16	0,6905	2,85440	1,14187	1,71253
16	Exploited	CSF17	0,3315	6,72408	2,25231	4,47178
16	Exploited	CSF20	0,4216	4,68376	0,68159	4,00216
16	Exploited	CSF21	0,9485	5,43999	0,55134	4,88865
16	Unexploited	GKM1	0,9200	6,45880	0,98436	5,47445
16	Unexploited	GKM2	0,8750	6,22614	1,81504	4,41110
16	Unexploited	GKM3	0,5850	5,79005	0,74678	5,04327
16	Unexploited	GKM4	0,6350	4,66529	0,90822	3,75707
16	Unexploited	GKM7	1,0500	6,21996	0,67257	5,54739
16	Unexploited	GKM8	1,1450	3,69640	0,78939	2,90701
16	Unexploited	GKM9	1,0250	7,76006	2,74161	5,01846
16	Unexploited	GKM10	1,0650	6,00452	0,57564	5,42888
16	Unexploited	GKM11	1,2700	2,13304	0,80985	1,32319
16	Unexploited	GKM13	0,5150	6,40727	2,84369	3,56358
16	Unexploited	GKM15	0,9850	4,56853	0,51538	4,05315
16	Unexploited	GKM16	0,7350	7,79877	1,33722	6,46155
21	Exploited	CSF01	1,1067	5,93945	1,43023	4,50922
21	Exploited	CSF02	0,3002	6,58936	0,90104	5,68832
21	Exploited	CSF03	0,7252	5,91463	1,06943	4,84520
21	Exploited	CSF04	0,6358	3,15865	1,27890	1,87975
21	Exploited	CSF05	1,3834	3,10213	1,14076	1,96137
21	Exploited	CSF08	0,6203	5,00709	2,13791	2,86918

21	Exploited	CSF09	0,3510	6,26007	2,26066	3,99940
21	Exploited	CSF10	0,7712	5,10187	3,10781	1,99405
21	Exploited	CSF11	0,5062	5,35164	2,68787	2,66377
21	Exploited	CSF12	0,3310	5,98189	3,66147	2,32042
21	Exploited	CSF15	0,9078	5,29345	1,11822	4,17523
21	Exploited	CSF16	0,6905	4,14816	2,09444	2,05371
21	Exploited	CSF17	0,3315	3,63424	1,06730	2,56694
21	Exploited	CSF20	0,4216	7,19746	2,88423	4,31323
21	Exploited	CSF21	0,9485	5,71005	0,95645	4,75360
21	Unexploited	GKM1	0,9200	7,12324	1,17889	5,94435
21	Unexploited	GKM2	0,8750	6,01123	1,46325	4,54799
21	Unexploited	GKM3	0,5850	7,58405	0,77870	6,80534
21	Unexploited	GKM4	0,6350	4,71059	1,92352	2,78707
21	Unexploited	GKM7	1,0500	5,39086	1,56742	3,82344
21	Unexploited	GKM8	1,1450	6,68302	1,45016	5,23286
21	Unexploited	GKM9	1,0250	7,78004	3,50354	4,27650
21	Unexploited	GKM10	1,0650	8,18142	1,18741	6,99401
21	Unexploited	GKM11	1,2700	5,19850	1,29334	3,90516
21	Unexploited	GKM13	0,5150	8,19749	1,41220	6,78529
21	Unexploited	GKM15	0,9850	4,49755	1,67860	2,81895
21	Unexploited	GKM16	0,7350	10,18150	1,63874	8,54276



Appendix Figure 1: Linear mixed effects models with second order polynomial regression and fish ID as random factor for unexploited (blue) and exploited (red) *C. laticeps* population. The different coloured points represent the standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) ($\text{mg. } O_2 \cdot \text{min}^{-1} \cdot \text{kg}^{-1}$) for each individual fish, the lines and shaded regions are fitted models with 95% confidence interval.

Appendix Table 2: Summary statistics (minimum, maximum, mean and standard deviation) of fish mass (kg) and standard metabolic rates (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) ($\text{O}_2 \text{ mg. min}^{-1}.\text{kg}^{-1}$) for each temperature ($^{\circ}\text{C}$) and site.

Temperature ($^{\circ}\text{C}$)	Site	Summary- Stat	Mass (kg)	MMR	SMR	AS
10	CSF	Min	0,300	2,511	0,057	2,396
		Max	1,383	5,823	0,361	5,462
		Mean	0,669	3,647	0,215	3,432
		Stdv	0,317	0,840	0,098	0,810
	GKM	Min	0,515	3,286	0,052	2,736
		Max	1,270	5,001	0,703	4,681
		Mean	0,900	4,131	0,330	3,801
		Stdv	0,237	0,575	0,213	0,610
16	CSF	Min	0,300	2,854	0,484	1,713
		Max	1,383	8,265	3,120	5,202
		Mean	0,673	5,291	1,267	4,024
		Stdv	0,307	1,192	0,705	0,959
	GKM	Min	0,515	2,133	0,515	1,323
		Max	1,270	7,799	2,844	6,462
		Mean	0,900	5,644	1,228	4,416
		Stdv	0,237	1,636	0,812	1,398
21	CSF	Min	0,300	3,102	0,901	1,880
		Max	1,383	7,197	3,661	5,688
		Mean	0,669	5,226	1,853	3,373
		Stdv	0,317	1,230	0,903	1,282
	GKM	Min	0,515	4,498	0,779	2,787
		Max	1,270	10,182	3,504	8,543
		Mean	0,900	6,795	1,590	5,205
		Stdv	0,237	1,701	0,669	1,819