The effects of temperature and exploitation on the behaviour of red roman *Chrysoblephus laticeps* (Sparidae) at baited video stations

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ABSTRACT

Marine environments are experiencing rapidly increasing temperatures, sea levels and acidification and higher frequencies and magnitudes of extreme weather events as a result of climate change. In the Agulhas Ecoregion of South Africa, there has been an increase in the frequency and intensity of upwelling events. Upwelling events result in rapid and large decreases in water temperature which can persist for several days. Variation in water temperature is known to impact the metabolic rate of fish (which are ectotherms) and in turn their activity patterns. To promote fitness related traits, the metabolic rate of fish is maximised at a specific temperature range. Outside of this optimal temperature range, the capacity of fish to perform aerobically declines. Therefore, it is expected that an increase in upwelling may place the fish under significant physiological stress.

The effects of climate change can be compounded by the effects of fisheries-induced evolution; the microevolution of a fish population due to the artificial selection of certain biological traits by fishing practices. Passive fishing gears preferentially remove large (older) and bold individuals, causing reductions in population size, genetic diversity and fecundity as well as size and age truncation and the loss of large, bold and dominant phenotypes in fish populations. These demographic changes affect the adaptive capacity of fish and exploited populations are expected to be less resilient to climate variability and long-term temperature change.

The resilience of fish is largely dependent on their physiological attributes, particularly their metabolic rate. Theoretically, fish with broader aerobic scope (defined as the difference between an individual's maximum metabolic rate and standard metabolic rate) will be more tolerant to the impacts of climate change as they have energy available for adaptation. Recent respirometry and accelerometry studies suggest that populations of the endemic southern African linefish *Chrysoblephus laticeps* (red roman) from inside marine protected areas (MPAs) have higher metabolic rates and broader aerobic scope compared to those found outside of MPAs, particularly at thermal extremes. As *C. laticeps* are highly resident it is possible that fish populations protected within well-established MPAs may be more resilient to the physiological stresses caused by upwelling if they are able to maintain their activity levels despite changing temperatures.

Behaviour is a proxy that can be used to infer metabolism as behaviours have associated metabolic costs and benefits. Behaviour is also a trait that can be altered by passive fishing practices which preferentially extract more active and bold individuals. Given this context, the aim of this thesis was to determine the effects of short-term thermal variability on the population structure and behaviour of *C. laticeps* and whether these effects differed between protected and exploited populations.

Baited remote underwater stereo-video systems (stereo-BRUVs) were used to observe *C. laticeps* inside two MPAs (Tsitsikamma and Goukamma) and at two exploited sites (Port Elizabeth and Cape St. Francis) over the temperature range 10-18 °C. The relative abundance, size and relevant behaviours of *C. laticeps* were recorded. The relative abundance (MaxN) of *C. laticeps* was not significantly higher inside the MPAs compared to the exploited sites. The size of *C. laticeps* did not vary significantly by protection level either. However, the mean size of *C. laticeps* was considerably smaller at Port Elizabeth compared to the three other locations. There was a notable absence of large *C. laticeps* size classes at Port Elizabeth.

The effect of water temperature on relative abundance was only seen in the exploited areas, where temperature and abundance were positively correlated. This was not the case in the protected areas where *C. laticeps* abundance remained roughly consistent. Generally, the effect of temperature on all measured behaviours was consistent across protection levels. An exception was that the feeding rate at Tsitsikamma MPA was significantly higher than at Cape St. Francis at temperatures below 11.5 °C. Temperature had a significant effect on the time taken for the first individual to appear in the field of view. This time shortened with increasing temperature, regardless of protection level. This was likely a result of the metabolic constraints placed on individuals by low waters temperatures and individuals would be able to pursue the bait more readily at higher temperatures. However, there was no evidence of greater metabolic scope from the *C. laticeps* individuals observed in the MPAs, relative to the exploited areas.

Individual size and the presence of conspecifics were also found to significantly influence behaviour. Generally, size had a positive relationship with behaviour, with larger individuals more likely to feed on the bait, chase other fish from the bait (only in the MPAs) and spend more time in the field of view. The higher displays of aggression in MPAs may be an indication of fishing practices having removed bold and dominant individuals at the exploited sites. The probability of fleeing and the feeding rates of individuals increased with increasing numbers of conspecifics, suggesting that *C. laticeps* behaviour is influenced by intraspecific competition.

Overall, this thesis did not find strong evidence that *C. laticeps* from MPAs performed better than *C. laticeps* from exploited areas, even at low temperatures. Behavioural responses to temperature were highly variable across locations and this may be attributed to high behavioural phenotypic diversity among individuals. Environmental stressors, such as temperature changes, can illicit very different behavioural responses among individuals in a population. It is also possible that *C. laticeps* from the exploited areas have the same genetic predispositions to physiological stress as the individuals in the MPAs due to spillover and larval recruitment from the MPAs. Indeed, genetic studies find that all *C. laticeps* population in South African represent a single well-mixed genetic stock. It is likely that greater sampling effort is required to resolve the patterns in behaviour between exploited and protected populations. Nonetheless, given the influence of size on behaviour, the smaller size of *C. laticeps* at Port Elizabeth may be cause for concern regarding the vulnerability of future populations to ongoing climate change.

Chrysoblephus laticeps photographed on South African reefs. Two juveniles are pictured on the left and an adult on the right. Photo credit: Peter Southwood.

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Pictured are some of the people who played a pivotal supporting role during my thesis and some noteworthy moments with them throughout my academic journey.

DECLARATION

I, Bontle Boitumelo Mataboge, declare that the components of this thesis comprise original work by the author and this thesis has not been submitted to any university other than Rhodes University, Grahamstown, South Africa.

The research carried out in this thesis was approved by and in line with the standards of the Rhodes University Animal Research Ethics Committee (RU-AREC). Ethics approval number: 2021-4946-6024.

CHAPTER 1

1 GENERAL INTRODUCTION

1.1 CONCEPTUAL BACKGROUND

There is strong scientific agreement and evidence that marine environments are changing as a result of anthropogenic climate change (Hoegh-Guldberg & Bruno 2010, Lima & Wethey 2012, Cai et al. 2014, 2015, IPCC 2019). This change is driven by global increases in carbon dioxide (CO_2) emissions as a result of fossil fuel usage (Doney et al. 2012, IPCC 2019). The past century has seen warming of the ocean's upper layers (Levitus et al. 2009, IPCC 2019), as well as significant increases in ocean acidification, marine heat waves, average sea surface temperatures and average sea levels (Caldeira & Wickett 2003, Fabry et al. 2008, Potts et al. 2015, Oliver et al. 2018, IPCC 2019, Grab et al. 2019, Antão et al. 2020).

Temperature is arguably the most important factor influencing the physiology of ectotherms (Paaijmans et al. 2013). The body temperature of ectotherms has a significant effect on their aerobic performance, as it affects the rate of virtually all physiological processes (Huey & Kingsolver 1993, Forster et al. 2012). An ectotherm's aerobic performance is maximised at a specific temperature range to promote fitness-related traits (Huey & Kingsolver 1993, Fossette et al. 2012, Paaijmans et al. 2013, Clark et al. 2013). These traits include, foraging and feeding activity, reproductive behaviour and inter- and intraspecific interactions (Hutchison & Maness 1979, Peck 2002, Angilletta et al. 2002, Clark et al. 2013). When temperatures fall outside of this optimal temperature range, an ectotherm's aerobic performance declines (Huey & Kingsolver 1993, Nguyen et al. 2011, Paaijmans et al. 2013, Clark et al. 2013).

Marine ectotherms are considered particularly vulnerable to the impacts of climate change (Pinsky et al. 2019). The local extinction rate of species due to warming is double in the oceans when compared to land (Pinsky et al. 2019). This could be attributed to the higher upper thermal limits of terrestrial ectotherms, particularly at higher latitudes (Sunday et al. 2011). In addition, the greater variation in microclimate and prevalence of thermal refugia on land may promote increased survival by terrestrial ectotherms (Pinsky et al. 2019, Antão et al. 2020). Understanding the adaptive capacity of marine life to temperature changes is essential in the context of ongoing and projected climate change.

Marine ectotherms experience different temperature ranges depending on the biogeographic region in which they live (Sunday et al. 2011, Nguyen et al. 2011, Peck et al. 2014). Seasonal temperature variation is lower near the equator and poles (Sunday et al. 2011, Peck et al. 2014). As a consequence, studies find that tropical and polar ectotherms are generally less resilient to warming and have narrower breadths of thermal tolerance than those from temperate regions (Sunday et al. 2011, Peck et al. 2014, Vinagre et al. 2016, Antão et al. 2020). This suggests that tropical and polar species may be more vulnerable to ocean warming (Peck 2002, Nguyen et al. 2011, Peck et al. 2014). Polar species are vulnerable to warming as many of them are stenothermal, with considerably low upper lethal temperatures (Somero & DeVries 1967, Peck 2002). Tropical species live very close to their upper thermal limits and thus cannot tolerate much further warming (Nguyen et al. 2011, Morley et al. 2017). Furthermore, regions close to the equator and the poles are experiencing faster rates of warming compared to global averages (Liu et al. 2005, Rayfuse 2007, IPCC 2019). In the long-term, temperature changes are expected to shift distributions of animals as they migrate to thermally favourable environments (Berggren et al. 2009, Feehan et al. 2009).

An ectotherm's depth distribution may also impact its tolerance to temperature changes (Nguyen et al. 2011). Intertidal species experience large deviations from the daily mean temperature, while subtidal species experience smaller deviations (Nguyen et al. 2011). Consequently, intertidal ectotherms demonstrate the greatest acclimatisation to short-term temperature variability compared to ectotherms from more thermally stable habitats, such as the subtidal benthic habitats on the continental shelf (Hilton et al. 2010, Nguyen et al. 2011). Intertidal ectotherms are, however, more vulnerable to chronic warming (Nguyen et al. 2011, Vinagre et al. 2016). Intertidal habitats (such as rocky shores) experience very high daily maximum temperatures and as such, intertidal species live very close to their upper thermal limits and cannot tolerate much further warming (Nguyen et al. 2011, Vinagre et al. 2016). Subtidal ectotherms living in locations influenced by wind-induced upwelling can also experience rapid and large fluctuations in temperature (Hyun & He 2010, Malan et al. 2019). These drastic drops in temperature caused by upwelling can result in the deaths of cold-stunned fish (e.g. Hanekom et al. 1989). In the temperate Tsitsikamma National Park Marine Protected Area mortalities of subtidal reef fish associated with an upwelling event in the 1980s were recorded in 14 species, with most of the affected individuals being juveniles (Hanekom et al. 1989). This suggests that subtidal fish species may be more sensitive to temperature changes if shallower and warmer refugia is unavailable.

The effects of climate change can be compounded by the effects of fishing on the demographics of fish populations (Brander 2010, Perry et al. 2010). This is due to fisheries-induced evolution; the microevolution of a fish population due to the artificial selection of certain biological traits by fishing practices (Law 2000, Jørgensen et al. 2007, Landi et al. 2015). Passive fishing gears, which are those that aren’t associated with gear movements and/or pursuit of the target species (e.g. gill nets, longlines), rely on the behaviour of the target fish towards the gear for the capture of fish (Bjordal 2002). Consequently, passive fishing gears preferentially remove large (older) and bold individuals, causing substantial changes to fish genetic and population structure (Perry et al. 2010, Heino et al. 2015, Colefax et al. 2016). Such changes include reduced population sizes, size and age truncation, reduced fecundity and the loss of large, bold and dominant phenotypes (Law 2000, Perry et al. 2010, Alós et al. 2016, Monk et al. 2021). These demographic changes affect the adaptive capacity of fish and exploited populations are expected to be less resilient to climate variability and long-term temperature change (Brander 2010, Perry et al. 2010, Planque et al. 2010, Heino et al. 2015). Consequently, marine protected areas (MPAs) have been proposed as a conservation strategy to promote climate change resilience (McLeod et al. 2009, Roberts et al. 2017, Wilson et al. 2020).

The sparid *Chrysoblephus laticeps* is a Southern African reef caught using passive gears, specifically hook and line (Götz & Kerwath 2013). Recent research has found that *C. laticeps* within MPAs are able to achieve higher metabolic rates compared to *C. laticeps* populations from exploited sites (Duncan et al. 2019, Skeeles 2019). Metabolic rate is an objective measure which is used to understand the energy costs of an animal's activities (Metcalfe et al. 2016). Animals with high aerobic scope, defined as the difference between an individuals' maximum metabolic rate and standard metabolic rate, are presumed to have energy available for activities beyond survival and maintenance (Fry 1947, Clark et al. 2013, Pörtner et al. 2017). Duncan et al. (2019) and Skeeles (2019) found that protected *C. laticeps* populations maintained elevated metabolic rates and had broader metabolic scope, across a wide of range temperatures (8-24 °C) compared to exploited *C. laticeps* populations. These differences between the populations were more pronounced at thermal extremes (Duncan et al. 2019, Skeeles 2019). This was attributed to the prevalence of high thermal performance phenotypes in the unexploited populations (Duncan et al. 2019). Based on these findings, Duncan et al. (2019) proposed that protected *C. laticeps* populations might be more resilient to the impacts of climate change than exploited populations, if they can maintain their activity levels despite changing temperatures or have energy available for adaptation. To measure metabolism, Duncan et al. (2019) and Skeeles (2019) employed respirometry and accelerometry.

Behaviour can also be used as a proxy for metabolism as behaviours have associated metabolic costs and benefits (Clark et al. 2013, Metcalfe et al. 2016). Moreover, behaviour can also be affected by fishing practices (Colefax et al. 2016, Pauli & Sih 2017, Rhoades et al. 2019). Alós et al. (2012) found that passive fishing techniques preferentially extract more active individuals. Rhoades et al. (2019) found that feeding rates of several temperate reef fish species (rock basses, mail-cheeked fish, surfperches, greenlings and wrasses) were higher in older MPAs compared to newer MPAs or partial-take areas. Feeding rates still differed even after accounting for differences in fish abundances and size across all sites, with individuals from older MPAs having double the feeding rate of similarly sized conspecifics from newer MPAs or partial-take areas (Rhoades et al. 2019). The presence of divers disrupted the feeding of fish in the newer MPAs or partial-take areas but not in the older MPAs (Rhoades et al. 2019).

What is highlighted, is that behaviour is an important component in understanding the effects of fisheries-induced evolution (Uusi-Heikkilä et al. 2008, Pauli & Sih 2017, Rhoades et al. 2019). However, there are very few studies which measure the effects of exploitation on the behaviour of fish assemblages. Many studies on the effectiveness of MPAs have emphasised the recovery of fish population numbers and sizes within MPAs (Yemane et al. 2004, Götz 2005, Kerwath et al. 2008, Götz et al. 2011, Sanguinetti 2013, Dickens 2015). As differences in fish behaviour can persist long after the recovery of densities to pre-exploitation levels (Rhoades et al. 2019), this could lead to underestimating the effects of fisheries-induced evolution and overestimating the recovery effects of protection. As such, it is important to identify and understand the behaviour of different fish populations within protected and exploited contexts.

Underwater video methods, such as baited remote underwater stereo-video systems (stereo-BRUVs) are increasingly popular techniques used to sample aquatic environments (e.g. Cappo et al. 2006, Ellender et al. 2012, Becker et al. 2013, Bernard et al. 2014). This is because stereo-BRUVs are a non-extractive method that can be used for assessing the abundance, diversity, size and behaviour of fish (He 2003, Cappo et al. 2006, Harvey et al. 2007, Ellender et al. 2012, Becker et al. 2013). Typically stereo-BRUVs are used to assess fish assemblage structure (Cappo et al. 2006, Harvey et al. 2007, Bernard et al. 2014, Whitmarsh et al. 2017). However, there is potential to use stereo-BRUVs to quantify fish behaviour.

1.2 RATIONALE

In the Agulhas Ecoregion of South Africa, the water temperature has undergone significant changes in the past couple of decades (Malan et al. 2019, Jury 2020). On average there has been warming of coastal waters in the Agulhas Ecoregion, with sea surface temperatures increasing rapidly (Malan et al. 2019, Jury 2020). At the same time, sea temperatures have become more variable in the summer months due to upwelling during these months (Goschen & Schumann 2011). An increase in upwelling-favourable (easterly) winds and a stronger Agulhas current has led to increasing frequency and intensity of upwelling events (Goschen et al. 2015, Malan et al. 2018, 2019, Jury 2020). While many of South Africa's coastal fishes are broadly tolerant of temperature fluctuations, it is expected that the warmer temperatures and the increasing intensity of upwelling events will place fish under significant physiological stress (Roessig et al. 2004, Bernhardt & Leslie 2013, Potts et al. 2015).

The response of fish populations to the stresses caused by upwelling could vary dependant on protection. The findings of Duncan et al. (2019), that the aerobic scope of *C. laticeps* is higher within MPAs compared to heavily fished areas, suggest that passive fishing has selected for *C. laticeps* populations comprised of less physiologically fit individuals. Consequently, *C. laticeps* within well-established MPAs may be more resilient to physiological stresses of upwelling and better able to cope with climate change.

Baited remote underwater stereo-video systems (stereo-BRUVs) can detect local changes in fish assemblage structure resulting from short-term changes in water temperature (Westera et al. 2009, Watson & Harvey 2009). As fish are thermoconformers (Forster et al. 2012, Paaijmans et al. 2013), the low temperatures brought on by upwelling may result in reduced abundance and greater levels of lethargy in the fish. Using behaviour as an indicator of activity levels, it will be possible to quantify the impacts of temperature change on fish populations from stereo-BRUVs videos. More specifically, stereo-BRUVs can be used to determine the impacts of upwelling on the behaviour of *C. laticeps* populations inside and outside of MPAs. This novel use of a relatively new technology would provide unique insights into understanding how passive gear fishing may alter the behaviour of fish populations and whether MPAs support fish populations that are more resilient to temperature fluctuations, given ongoing climate change.

1.3 RESEARCH AIMS

The aim of this thesis is to improve our understanding of how a history of exploitation will influence the behaviour of fishes in a rapidly changing climate. To do this the natural behaviour of fish in exploited and unexploited populations of *Chrysoblephus laticeps* in a thermally variable environment will be compared.

1.3.1 RESEARCH OBJECTIVES

The thesis aims will be achieved through the following objectives:

(1) Conduct a pilot study to determine if season has an effect on the behaviour of *C. laticeps*. The results of this pilot study will be used to inform the main study's sampling approach.
(2) Determine the suitability of stereo-BRUVs data for quantifying behavioural metrics related to the activity of *C. laticeps*. This objective will be carried out in the pilot study.
(3) Conduct an uncontrolled field experiment to compare the behaviour of *C. laticeps* at different water temperatures inside and outside of two well-established marine protected areas in the Agulhas Ecoregion of South Africa.

1.4 THESIS OUTLINE

This thesis is separated into five chapters. The first chapter is a general introduction to the main topics covered in the thesis. The aims and objectives of the study are stated and an outline of the thesis structure is then provided.

Chapter 2 is a systematic literature review. This provides an unbiased evaluation of the literature on selected topics relevant to the research aims. The focal topics of the reviewed were (1) the study species, *C. laticeps* and (2) the use of stereo-BRUVs in behavioural studies.

Chapter 3 presents the results from the pilot study. The pilot study was conducted to (1) test the suitability of stereo-BRUVs to assess the behaviour of *C. laticeps*, (2) develop and refine the ethogram to be used in the behavioural analyses and (3) test for seasonal differences in behaviour to inform the sampling program of the main study.

Chapter 4 contains the main research chapter. This chapter estimated population parameters and quantified behaviour of *C. laticeps*, using methods informed by the systematic review and pilot study chapters. The purpose of this chapter was to test the effect of both temperature and protection/exploitation on the abundance, size and behaviour of *C. laticeps.*

Chapter 5, the final chapter contains a synthesis of all key findings of this research, gives concluding remarks and highlights future research priorities.

CHAPTER 2

2 CURRENT KNOWLEDGE OF *CHRYSOBLEPHUS LATICEPS* AND THE USE OF RUVS TO STUDY FISH BEHAVIOUR: A SYSTEMATIC REVIEW

2.1 INTRODUCTION

Chrysoblephus laticeps is a Sparid endemic to the temperate regions of southern Africa (Götz & Kerwath 2013). *Chrysoblephus laticeps* has been well researched due to its importance to local linefisheries, a common passive fishing technique used in South Africa (Buxton 1989, 1990, Hecht & Tilney 1989, Götz & Kerwath 2013). *Chrysoblephus laticeps* is a good choice for a study species because there is extensive literature to compare and contextualise the findings of this thesis' research. The objective of the first section of the review is to provide a comprehensive synthesis of all research into *C. laticeps* and identify any knowledge gaps. This first section will have a specific focus on *C. laticeps* behaviour, fisheries-induced evolution and conservation through marine protected areas (MPAs).

The objective of the second section of this review is to establish the feasibility of remote underwater video systems (RUVs) for studies of behaviour. Laboratory studies are not suitable to study behaviour as the behaviours observed in captivity may not reflect natural behaviours. Thus, there is potential for using RUVs to study fish behaviour. This is because RUVs cause little disturbance and are non-extractive (Cappo et al. 2006, Harvey et al. 2007, Bernard 2012, Bernard et al. 2014), allowing for *in situ* studies of behaviour. Accordingly, the second section of this review will search for and assess all research in which RUVs were used for behavioural studies.

Traditional literature reviews are susceptible to bias during the identification, selection and synthesis of studies (Haddaway et al. 2015). To mitigate against bias, systematic reviews follow rigorous methodologies that aim to maximise transparency, objectivity, and repeatability (Moher et al. 2009, Haddaway et al. 2015). The purpose of this review is to objectively assess the literature and provide details of processes of searching, selecting and synthesising of information. The focal topics of this review are (1) the study species *C. laticeps* and (2) the use of RUVs in behavioural studies.

2.2 METHODS

2.2.1 REVIEW PROTOCOL

PRISMA: Preferred Reporting Items for Systematic Reviews and Meta-Analysis (Moher et al. 2009) was used as the basis for creating protocols for this review. The PRISMA protocol is comprehensive and includes 27 items that can be considered (Moher et al. 2009), however only 14 of these were considered relevant for this review (Table 2.1).

Table 2.1: The item numbers from the PRISMA (Moher et al. 2009) included in this systematic review

Section	Topic	Item no.	Description
Title	Title	1	Identifying the report as a systematic review
Introduction	Rationale	3	Reasons for the review
	Objectives	4	Explicit statement of questions being addressed by the review
Methods	Protocol	5	Indicate if a review protocol exists and where it can be accessed
	Eligibility criteria	6	Specify criteria used to determine eligibility of a study
	Information sources	7	Describe all information sources in the search and date last searched
	Search	8	Present full electronic search strategy, including any limits used, such that it could be repeated
	Study selection	9	State the process for selecting studies (screening, eligibility and inclusion in the systematic review)
	Risk of bias across studies	15	Specify any assessment of risk of bias that may affect the cumulative evidence
Results	Study selection	17	Give numbers of studies screened, assessed for eligibility and included in the review
	Study characteristics	18	For each study, present characteristics for which data were extracted
Discussion	Summary of evidence	24	Summarise the main findings including the strength of evidence for each main outcome
	Limitations	25	Discuss limitations at study and outcome level and at review level
	Conclusions	26	Provide a general interpretation of the results in the context of other evidence and implications for future research

2.2.2 INFORMATION SOURCES

Google Scholar was chosen as the database for the literature search. In comparison to Scopus, International Scientific Indexing (ISI) and Web of Science, Google Scholar finds the highest number of citations, the highest proportion of grey literature, has extensive book coverage, includes non-English results and is free (Harzing 2010, Pellack 2019, Martín-Martín et al. 2019). Results from any year were included during the searches, while citations and patents were excluded from the search results.

The South African National ETD (e-theses & dissertations) Portal (http://www.netd.ac.za) was used to search for unpublished (grey) literature from South Africa. The South African National ETD Portal is an online repository containing over 137 000 theses and dissertations from 23 South African universities.

2.2.3 LIMITATIONS

While a robust approach was followed, this review does have some publication bias. For instance, information presented at conferences is unlikely to be discovered unless the conference proceedings are published. Research undertaken for theses may not be discovered if students do not publish the results of their studies (i.e. in journals, reports) or their thesis is not uploaded to a website which is publicly accessible.

2.3 KNOWLEDGE OF *CHRYSOBLEPHUS LATICEPS*

2.3.1 SEARCH AND STUDY SELECTION

A Google scholar search on 29 April 2020 for “Chrysoblephus laticeps” produced 473 results. On the same day a Google scholar search for “*Chrysophrys laticeps*” produced 88 results, a search for “*Chrysoblephus algoensis*” produced three results, a search for “*Chrysophrys algoensis*” produced five results and a search for “*Chrysophrys pugicephalus*” produced two results. These four species names were searched as they are synonyms for *Chrysoblephus laticeps*. Search results containing the terms “*Chrysoblephus laticeps*”, “*Chrysophrys laticeps*”, “*Chrysoblephus algoensis*”, “*Chrysophrys algoensis*”, “*Chrysophrys pugicephalus*”, “*C. laticeps*”, “*C. algoensis*”, “*C. pugicephalus*”, “roman seabream”, “red roman” or “roman” in any part of their text were selected for abstract reading. Without duplication, a total of 205 abstracts were read.

An advanced search of the terms “*Chrysoblephus”* or “*laticeps*” in the South African National ETD Portal on the 4th May 2020 yielded 22 results. Advanced searches for the terms “*Chrysophrys*” and *“laticeps*,” “*Chrysoblephus*” and “*algoensis*” as well as “*Chrysophrys*” and “*pugicephalus*” yielded no results. After removing duplicates from the results all abstracts were read and this amounted to 19 abstracts.

Publications were included in the review if *C. laticeps* formed part of any analysis in the study. If this could not be discerned from the abstract, the methods section was read as well. Furthermore, only original/primary research was included in the review (i.e. systematic reviews, reference lists or any other secondary source were excluded during the selection process). In total 114 publications were included in the review.

To better understand the trends in research, each publication was allocated to one or two of the following six themes:

1) Taxonomy & systematics

Publications that report species descriptions, taxonomic revision or relationships between species. Includes publications in which molecular techniques were used to investigate phylogeny, population genetics or classification of *C. laticeps*.

2) Biology

Publications that investigated physiology, life history, reproduction, age and growth, diet and feeding, egg and larval studies, distribution, tagging and movement, abundance and population dynamics of *C. laticeps*. Included publications investigating methods of collecting biological data.

3) Ecology

Publications that did not focus on *C. laticeps* solely but assessed ecosystems as a whole. Such studies largely focused on trophic relationships and species distributions, densities, biomasses and habitat usage.

4) Mariculture

Publications investigating mariculture systems or the mariculture suitability of *C. laticeps*.

5) Management & fisheries

Publications that focused on the management of *C. laticeps*. These included stock assessments, catch statistics, economic, socio-economic and MPA studies. Also included publications in which taxonomic, systematic, biological and ecological data of *C. laticeps* were used to make management and policy recommendations.

6) Other

Publications that could not be attributed to any of the five above-mentioned themes. Only one publication was categorised as other. It was an archaeological study of shell middens, in which remains of *C. laticeps* were found.

2.3.1 RESULTS

2.3.1.1 SUMMARY STATISTICS

The 114 publications included in the review spanned the years 1830-2020. The majority (71%) of publications were peer-reviewed articles, 21% were theses and other publication types (books, book chapters, conference proceeding and reports) comprised the remaining 8%. A large proportion of journal articles (43%) were published in the African Journal of Marine Science (which was known as the South African Journal of Marine Science until its name change in 2003).

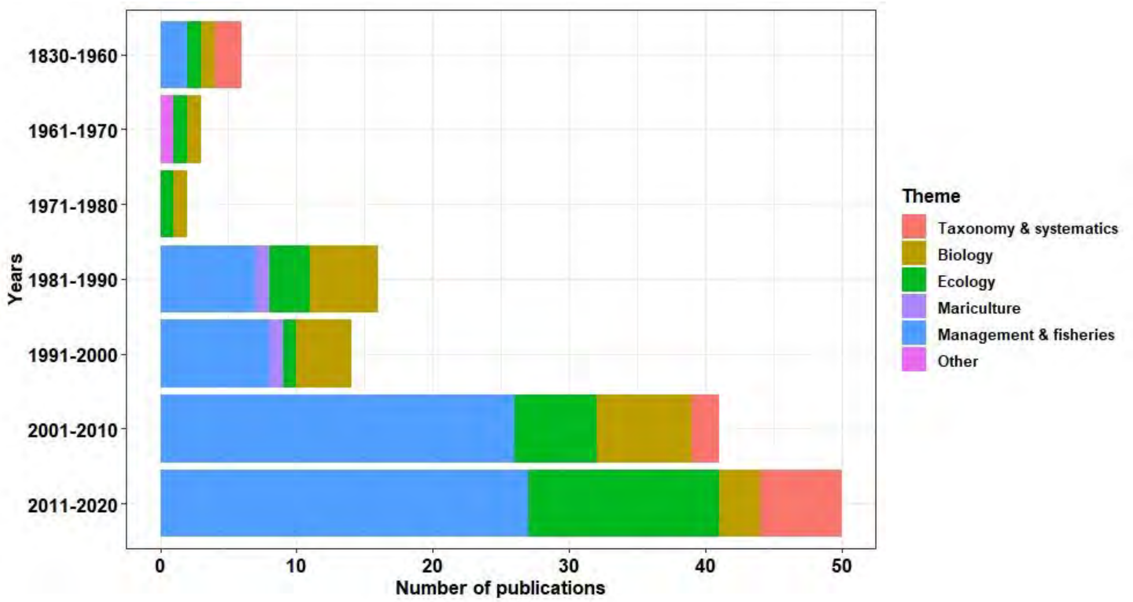

Figure 2.1: Trends in research on *Chrysoblephus laticeps* from 1830 – 2020.

2.3.1.2 TRENDS IN RESEARCH

Prior to 1981, there was little research published on *C. laticeps* (Figure 2.1). However, since then there has been a significant increase in the number of publications concerning *C. laticeps*, with the bulk of research taking place in the last two decades (Figure 2.1). Early studies of *C. laticeps* focused on its taxonomy and biology. However, since the 2000's studies have focused on *C. laticeps* in the context of fisheries and management (Figure 2.1). The bulk of publications have used *C. laticeps* as an indicator species in ecological, MPA and fisheries studies (Figure 2.1). Mariculture studies were very few, although the findings of Davis (1996) imply that *C. laticeps* would be a suitable mariculture candidate.

The majority of MPA studies were undertaken in the Tsitsikamma National Park MPA (Figure 2.2). This could be because it is South Africa's oldest MPA and therefore ideal for studying long-term effects of protection on species. Furthermore, choosing Tsitsikamma MPA as a study site affords one a large archive of comparative studies. The second and third most-studied MPAs were the Goukamma and Table Mountain National Park MPAs, respectively (Figure 2.2).

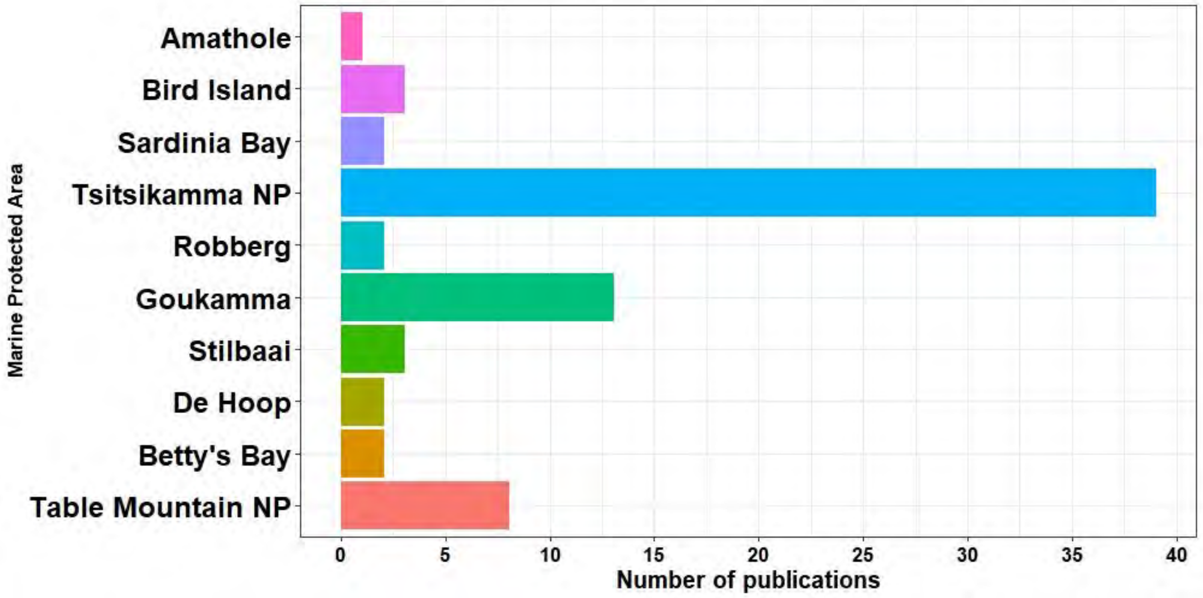

Figure 2.2: Geographical distribution of marine protected area research on *Chrysoblephus laticeps* as revealed through a systematic literature review. NP = National Park.

A total of 12 publications, the first published in 2012, made use of remote underwater stereo-video systems (stereo-RUVs) or baited remote underwater stereo-video systems (stereo-BRUVs) to study *C. laticeps*. All the studies that included stereo-RUVs or stereo-BRUVs took place in MPAs (namely, Tsitsikamma, Stilbaai, Betty's Bay and Table Mountain National Park) and were in the categories ecology and management & fisheries.

2.3.1.3 CURRENT UNDERSTANDING OF *C. LATICEPS* BIOLOGY AND ECOLOGY

Chrysoblephus laticeps also known as “red roman” or “roman seabream” is an endemic southern African sparid, occurring from Namibia to Port St. Johns (Smith 1938, Götz & Kerwath 2013). *Chrysoblephus laticeps* is most common on reef habitats down to 100 m (Penrith 1972a, Buxton & Smale 1989, Burger 1990, Gotz et al. 2008, Schmidt 2018). Mark-recapture and acoustic telemetry studies find *C. laticeps* to be highly resident, occupying a small home range of between 1-3km^2 (Buxton & Allen 1989, Griffiths & Wilke 2002, Kerwath et al. 2007a, 2007b).

Chrysoblephus laticeps is long lived and slow growing, reaching fifty percent maturity at approximately 184 mm fork length (FL) and an age of 3.5 years (Götz 2005). The maximum recorded age of a *C. laticeps* individual is 19 years (Götz 2005). *Chrysoblephus laticeps* is a protogynous hermaphrodite and changes sex from female to male between 250 mm and 425 mm FL, with sex change occurring throughout the year (Penrith 1972b, Buxton 1989, 1993). *Chrysoblephus laticeps* is monandric; all individuals develop into females in their early life and all functional males are derived from functional females (Penrith 1972b, Buxton 1989). Apart from size, *C. laticeps* do not display external sexual dimorphism (Penrith 1972b).

Comparisons of abundance on different habitats found *C. laticeps* to be significantly more abundant on high relief/rugorosity reefs (Penrith 1972a, Buxton 1987, Buxton & Smale 1989, Smith 2005). Juvenile *C. laticeps* are common in shallower waters less than 12 m and the abundance of adult *C. laticeps* significantly increases with increasing depth (Buxton 1987, Buxton & Smale 1989, Burger 1990, Lechanteur & Griffiths 2001, Sanguinetti 2013, Heyns-Veale et al. 2016, Roberts et al. 2016). The abundance of *C. laticeps* increases with increasing temperature (within its range) and they are most abundant in waters warmer than 13 °C (Buxton 1987, Buxton & Smale 1989, Burger 1990, Lechanteur & Griffiths 2001, Schmidt 2018). At low water temperatures, particularly during upwelling events, *C. laticeps* are not easy to detect but they can be found hiding in caves on reefs (Buxton 1987, Lechanteur 1999, Lechanteur & Griffiths 2001). Laboratory studies find that active ovaries of *C. laticeps* may regress as a result of exposure to cold water (Davis 1996) and that *C. laticeps* can go into "cold shock" at temperatures below 8 °C (Duncan 2018). Cold shock refers to the sub-lethal effects or death caused by exposure to extremely low temperatures (Donaldson et al. 2008).

Chrysoblephus laticeps is a benthic carnivore that feeds on a variety of reef-associated prey, such as molluscs, crinoids, decapods, ophiuroids and asteroidea (Buxton 1984, 1987, Lechanteur 1999, Lechanteur & Griffiths 2003). There is an ontogenetic shift in the diet of *C. laticeps*. Small *C. laticeps* (100-200 mm FL) consume large numbers of small prey types which they ingest whole (Buxton 1984, 1987). Large *C. laticeps* (>200 mm FL) consume fewer but larger prey types, which are crushed or ingested whole (Buxton 1984, 1987).

Chrysoblephus laticeps was once an important component of commercial catches (Hecht & Tilney 1989, Griffiths 2000). However, in recent decades due to declining stocks, the contribution of *C. laticeps* to the commercial catch is very small (Buxton 1987, Bennett et al. 1994, Booth & Hecht 1998, Attwood & Farquhar 1999, Griffiths 2000, Brouwer & Buxton 2002, Smith 2005). Catches of *C. laticeps* were highest between the years 1927–1931 but then decreased to 12% of these levels between 1986–1998 (Griffiths 2000). Although *C. laticeps* is still targeted by recreational ski boat fishers, it only makes a small (1-14%) contribution to their catch (Brouwer & Buxton 2002, Smith 2005, Pradervand & Hiseman 2006).

There have been few behavioural studies of *C. laticeps.* During diving surveys, Penrith (1972a) observed *C. laticeps* swimming in groups of 3-6 individuals, with an individual occasionally swimming away to feed. Individuals would feed quickly, possibly as a result of being mobbed by other individuals from the group (Penrith 1972a). Penrith (1972a) observed the territorial nature of *C. laticeps*. Antagonistic behaviour of *C. laticeps* has also been noted in BRUVs footage (De Vos 2012, Sanguinetti 2013). Courtship and spawning behaviour of *C. laticeps* has been observed in holding tanks by Buxton (1987, 1990) and Davis (1996).

Chrysoblephus laticeps is often used as an indicator species to assess the effects of exploitation on linefish species and the effectiveness of MPAs. Several publications have investigated fisheries-induced evolution in *C. laticeps*. Most studies found that the abundance of *C. laticeps* is significantly greater inside protected areas compared to exploited sites (Buxton 1987, Buxton &

Smale 1989, Lechanteur 1999, Smith 2005, Götz 2005, Bennett 2007, Götz et al. 2008b, 2009, Sanguinetti 2013, Roberson et al. 2015). However, there is not the same level of agreement with regards to size differences between protected and exploited populations of *C. laticeps*. Some studies found a significant differences in the mean size of *C. laticeps* between protected and exploited areas (Götz 2005, Bennett 2007, Götz et al. 2008b, 2009), whilst other studies did not (Buxton 1987, Buxton & Smale 1989). This could be related to the time since protection as it is the earliest studies (Buxton 1987, Buxton & Smale 1989) which did not find significant differences in the mean size. Nonetheless, all studies found significant differences in length frequency distributions between exploited and unexploited populations of *C. laticeps*. *Chrysoblephus laticeps* in protected areas had a greater proportion of large individuals (Buxton 1987, Buxton & Smale 1989, Lechanteur 1999, Smith 2005, Götz 2005, Bennett 2007, Götz et al. 2008b, 2009). Maximum recorded sizes of *C. laticeps* are also considerably larger in protected areas than exploited areas (Buxton & Smale 1989, Lechanteur 1999, Smith 2005, Bennett 2007, Götz et al. 2008b, 2009).

Genetic studies of *C. laticeps* from seven sites along its distribution (False Bay, Struisbaai, Alphard Banks, Plettenberg Bay, Tsitsikamma MPA, Bird Island MPA and Port Alfred) did not find not significant genetic structure in these populations (Teske et al. 2010, Wright et al. 2015). That is, individuals from the same site are not more closely related to each other than they are to individuals from different sites and all sites had similar levels of genetic diversity (Teske et al. 2010, Wright et al. 2015). This indicates that all *C. laticeps* populations across southern Africa's coast represent a single, well-mixed stock. Teske et al. (2010) suggest that larval dispersal may account for the high levels of genetic mixing found in populations of *C. laticeps*.

Exploitation does appear to have an effect on the physiology of *C. laticeps*. A laboratory study by Duncan et al. (2019) found that exploitation had a significant effect on the metabolic rates of *C. laticeps*. Protected populations had higher maximum (aerobic) metabolic rates (MMR) compared to exploited populations (Duncan et al. 2019). Protected populations also had greater aerobic scope (AS), which is the difference between an individual's standard metabolic rate (SMR) and MMR (Duncan et al. 2019). These findings were consistent over a temperature range of 8 to 24

°C (Duncan et al. 2019), implying that at any given temperature protected populations of *C. laticeps* can achieve greater rates of oxygen consumption compared to their exploited counterparts.

Skeeles (2019) found that field metabolic rates (FMR), the metabolic rate of a free-living *C. laticeps*, differed between exploited and unexploited populations. At thermal extremes the FMR of exploited populations were much lower than their protected counterparts (Skeeles 2019). During upwelling events, the metabolic rate of individuals in the exploited population began to decline earlier (at temperatures from 12.7 °C and below), whereas this was not observed in individuals from the unexploited population (Skeeles 2019). These findings suggest that there is a positive relationship between metabolic rate and capture vulnerability in passive-gear fisheries (Duncan et al. 2019).

Temperature variability is prevalent in the Agulhas Ecoregion and major ephemeral upwelling events are not uncommon (Duncan 2018). The findings of Duncan et al. (2019) and Skeeles (2019) suggest that protected populations of *C. laticeps* may be less sensitive to temperature changes compared to exploited populations. Lechanteur (1999) found that the abundance of *C. laticeps* was 2.5 times greater within MPAs compared to adjacent exploited sites in cold water (12-13 °C) and two times greater in warmer water (13-16.5 °C). Collectively these findings indicate the potential for MPAs to conserve *C. laticeps* individuals that are more resilient to temperature changes. Despite this, Duncan et al. (2019) found that aerobic scope of *C. laticeps* was reduced at 8 °C regardless of whether the individual was from an exploited or protected population. While *C. laticeps* populations within MPAs may be more resilient to temperature increases, these protected populations may not be as resilient to the lowest temperatures associated with upwelling.

2.4 CAN RUVS BE USED TO STUDY FISH BEHAVIOUR?

2.4.1 SEARCH AND STUDY SELECTION

A 16 April 2020 Google Scholar search for “stereo bruv behaviour” produced 440 results. A 20 April 2020 Google scholar search for “stereo ruv behaviour” produced 115 results. All search results were screened by title; only titles which contained the words “behaviour,” “behaviours” and “behavioural” were selected for abstract reading. A Google Scholar search for “stereo bruv behavior” on the 16th April 2020 produced 342 results. A Google Scholar search on the 20th April for “stereo ruv behavior” produced 220 results. Again, titles containing the words “behavior,” “behaviors” and “behavioural” were selected for abstract reading.

A Google Scholar search for “bruv aggression” produced 257 results. A Google scholar search for “bruv predation” produced 493 results. A Google scholar search for “bruv chase” produced 132 results. A Google scholar search for “bruv flee” produced 112 results. All these searches occurred on the 22nd April 2020. If the title of or abstract of a search result contained the words “bruv” and “predation” or “chase” or “flee,” it was selected for abstract reading.

Without duplication, a total of 61 abstracts were read. Only studies in which some form of remote underwater video system was used to make behavioural observations or measure other metrics related to behaviour (e.g. time to first sighting in video) were included in the review. If this could not be discerned from the abstract, the methods section was then read. Furthermore, only original/primary research was included in the review (i.e. systematic reviews, reference lists or any other secondary source were excluded during the selection process). In total 35 publications were included in the review.

2.4.2 RESULTS

2.4.2.1 SUMMARY STATISTICS

The majority of the 35 publications (74%) were peer-reviewed articles, 20% were theses and other publication types (conference proceeding and reports) comprised the remaining 6%. All studies were fairly recent, with the oldest study published in 2008 (Figure 2.3).

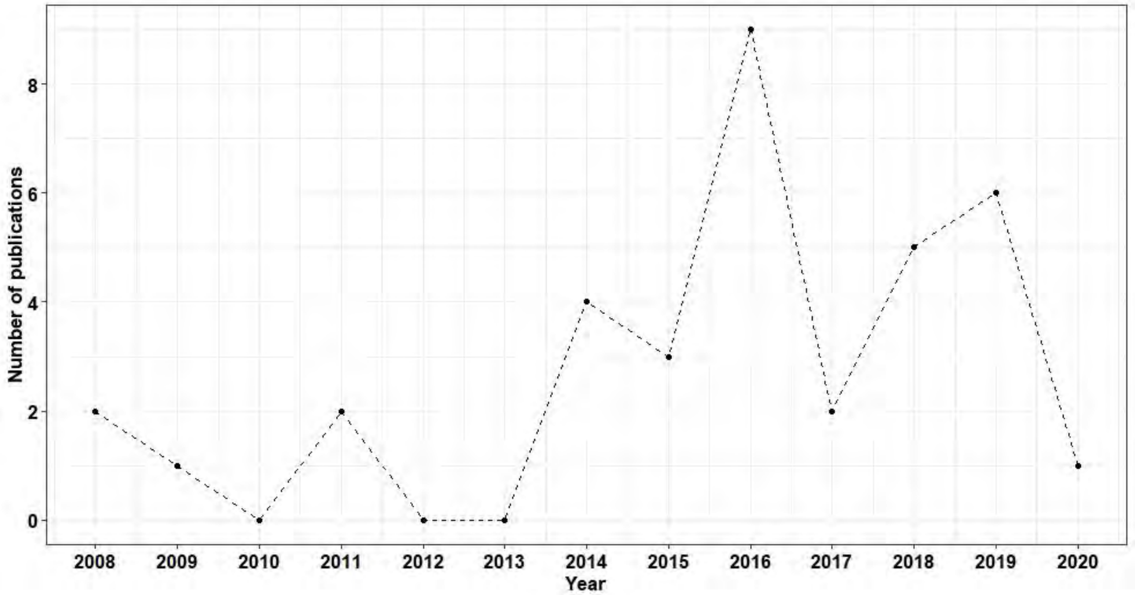

Figure 2.3: The number of behavioural studies using remote underwater video per year from 2008.

Behaviours such as social interactions (Witkowski et al. 2016), avoidance (Whitehead 2014), feeding (Zintzen et al. 2011, Barley et al. 2016, Reeds et al. 2018), schooling (Santana-Garcon et al. 2014), mating (Birt et al. 2019), swimming (Ryan 2016), responses to other fish (Phenix et al. 2019, Finucci et al. 2019, Shea et al. 2020) and sponging (a behaviour displayed by dolphins in which they carry sponges on their rostra to help forage prey items they otherwise are unable to access), (Tyne 2008) were investigated. Responses to human-related behaviours were also investigated in some studies, such as responses to marine noise, scuba divers and shark shields

(Kempster et al. 2016, Roberts et al. 2016, Bradley et al. 2017). A plurality of publications (34%) researched sharks and the rest of the publications studied reef fishes, eels, sea turtles, crabs, hagfishes, catfishes, dolphins and molluscs. The majority of studies (76%) made use of baited systems (BRUVs) while 24% made use of non-baited systems (RUVs).

The majority of studies (58%) were conducted in Oceania with a plurality of study sites (39%) located in Australia. Notably, there were no studies conducted in South America and only three studies conducted in Asia (Figure 2.4). Study sites in Europe were limited to western European countries (Figure 2.4). In Africa, studies were conducted in southern Africa or island nations in the Indian Ocean (Figure 2.4).

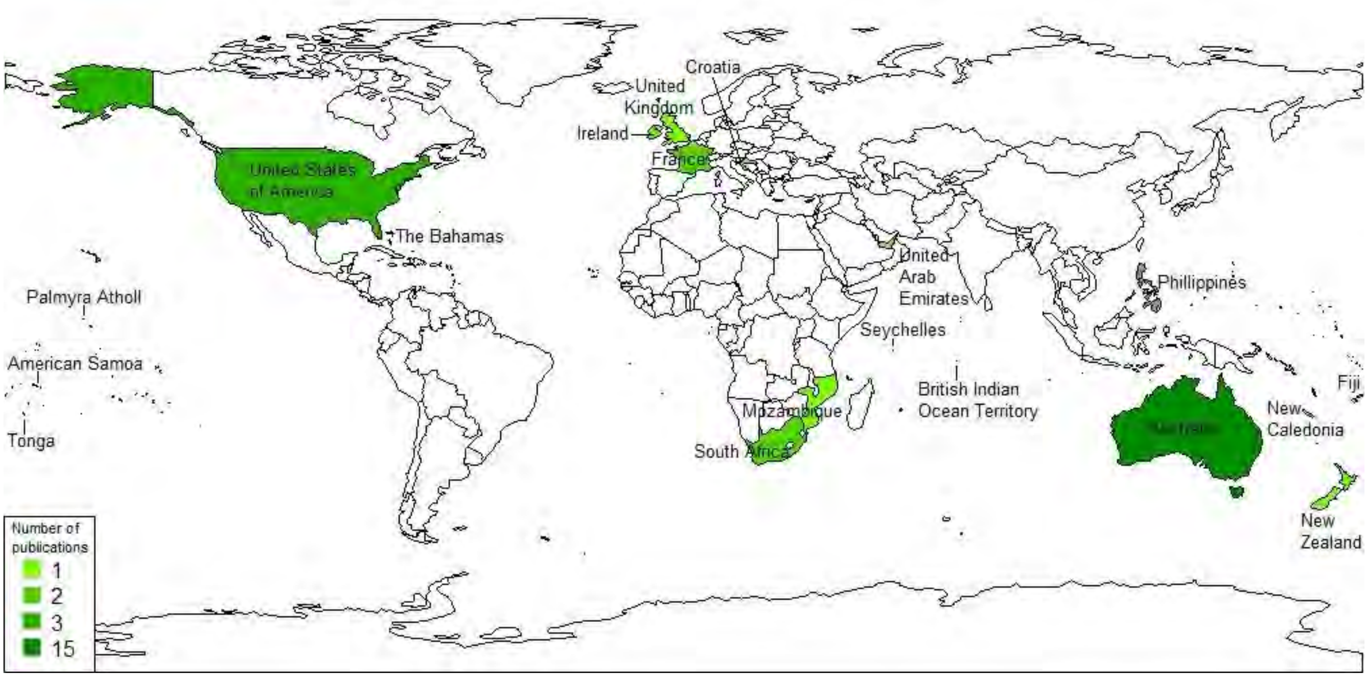

Figure 2.4: Geographic location of studies in which remote underwater video systems were used to study behaviour.

2.4.2.2 KNOWLEDGE

Several studies demonstrated the utility of remote underwater video techniques for observing short-term (seconds) behaviour. Some of the simplest behaviours to measure were the time taken for a species to appear in the field of view and the time taken to reach MaxN (the maximum number of individuals of a species present in a single frame). These metrics have featured in studies by Bassett & Montgomery (2011), Kruschel et al. (2016), Colefax et al. (2016), Coghlan et al. (2017), Phenix et al. (2019) and Finucci et al. (2019). Coghlan et al. (2017) found that the abundance of target species (seven ray-finned fish species) was higher and peaked at an earlier time in areas closed to fishing as opposed to exploited areas. In contrast, the abundance and time to peak abundance of species not targeted by fisheries did not vary between fished and unfished areas (Coghlan et al. 2017).

Baited remote underwater video systems (stereo-BRUVs) have been used to assess agonistic interactions. Experimental studies have found that at high conspecific densities, large individuals outcompete smaller conspecifics for bait (Gerlotto & Fréon 1992, Webster 2004). Studies utilising BRUVs have also observed agonistic interactions (mainly chase-flee), particularly among predatory fishes (Ebner et al. 2009, Finucci et al. 2019). Large, aggressive individuals were observed chasing conspecifics and other species from the bait, as well as effectively guarding the bait (Ebner et al. 2009, Finucci et al. 2019).

Colefax et al. (2016) investigated the feeding hesitation and feeding rank of target and non-target species in areas of varying fishing intensity. Feeding hesitation refers to the time taken from the initial presence of a species in the field of view until the same species first feeds on the bait. Feeding rank refers to the order in which species fed on the bait. Target species showed greater feeding hesitation and lower feeding rank in highly fished areas. The inverse was true for less intensely fished areas. Furthermore, in target species large individuals did not exert feeding dominance in the presence of conspecifics, regardless of angling intensity. Instead mid-sized individuals were generally the first individuals to feed. These results may be attributed to either "learning" of cautious behaviour by target fish or the fisheries-induced selection of more timid behaviour (Colefax et al. 2016). In intensely fished areas non-target species had higher feeding rank compared to less intensely fished areas, however, feeding hesitation did not vary between the angling intensity regimes (Colefax et al. 2016).

A few studies have also used RUVs to estimate swimming speeds and changes in trajectory of fish and sharks (Santana-Garcon et al. 2014, Beyan et al. 2015, Ryan 2016). If the frame rate of the video is known, speed can be measured by the distance travelled by an individual over a set number of frames. However, mono-RUVs should not be used to calculate swimming speeds. Speed is more precisely measured in the three dimensional (3D) plane than the 2D plane (Niu et al. 2018). Thus, stereo-RUVs, for estimating swimming speeds as they make use of two calibrated cameras in combination with software (e.g. EventMeasure) to create a 3D measurement space (Ryan 2016).

Overall, RUVs are a viable tool for conducting *in situ* behavioural studies. Branconi et al. (2019) studied the behaviour of the humbug damselfish (*Dascyllus aruanus*) using two methods of data collection; behavioural scoring directly by a scuba diver and remotely using a video camera. The damselfish were fed in the water column significantly less in the presence of a diver (Branconi et al. 2019). This could be because the damselfish perceived the diver as a competitor or threat. Given that the presence of a diver can influence fish behaviour, RUVs may be better suited for behavioural studies.

However, the experimental design must be well thought out to ensure that appropriate study sites, focal species and sampling procedures are applied. For instance, there may be diurnal and nocturnal differences in activity and abundance of fishes or seasonal behavioural patterns related to spawning activity (Ebner et al. 2009, Witkowski et al. 2016). Additionally, camera resolution affects taxonomic identification (Ebner et al. 2009), so high camera resolutions should be employed to extract as much detail from the video footage as possible. Lastly, horizontal-facing cameras are also recommended as opposed to downward facing cameras, as they have a greater and deeper field of view (Ebner et al. 2009, Coghlan et al. 2017).

2.5 CONCLUSIONS

Chrysoblephus laticeps has been extensively studied, with its research increasing in recent years. The effects of exploitation on various aspects of the biology and ecology of *C. laticeps* have been investigated by several researchers (see Figure 2.5). Fishing has resulted in lower abundances, as well as size and age truncation of exploited *C. laticeps* populations. Exploitation can also reduce the physiological fitness of *C. laticeps*. Notably, genetic differences do not exist between exploited and protected *C. laticeps* populations. The study of *C. laticeps* behaviour remains a major research gap. Furthermore, research into the effects of temperature on *C. laticeps* is limited to a few publication based on laboratory findings (Figure 2.5).

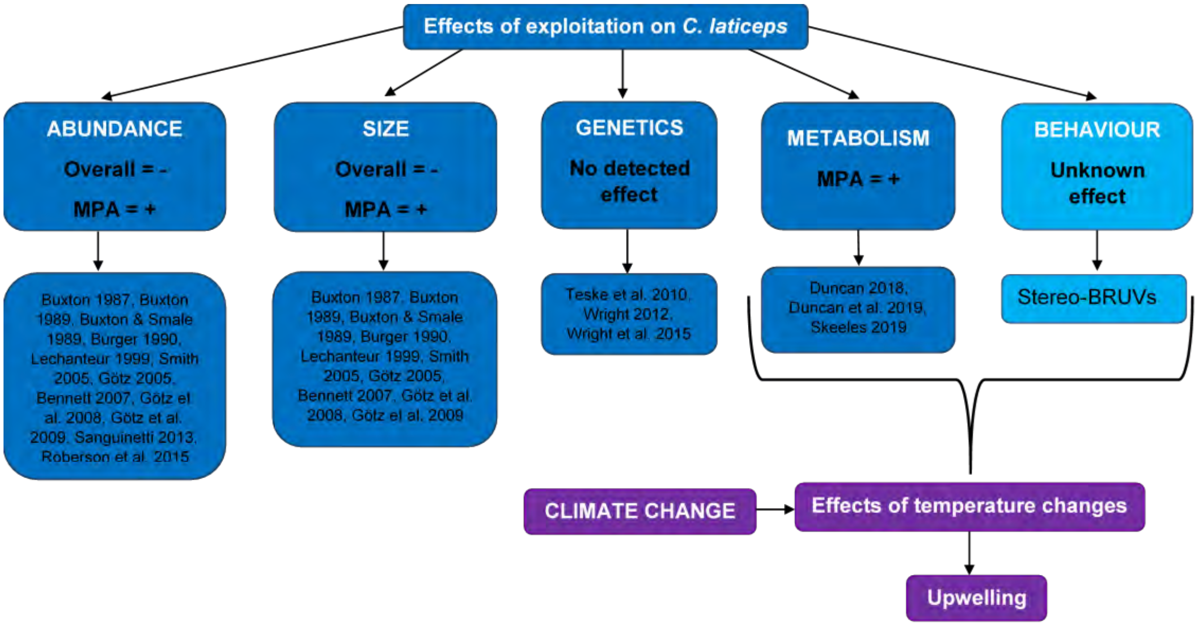

Figure 2.5: Schematic diagram showing a summary of literature investigating the effects of fisheries on *Chrysoblephus laticeps*. Overall refers to the effect of fishing on *C. laticeps* populations as a whole. MPA (marine protected area) refers to the effect of protection on *C. laticeps* populations. A negative sign (-) represents a negative effect (i.e. declining over time) and a positive sign (+) represents a positive effect (i.e. recovery or maintenance of pre-exploitation conditions). Dark blue = known information, light blue = unknown information to be addressed in this thesis. Curly bracket represents studies that investigate the effect of both fishing and temperature changes on *C. laticeps*.

Many studies have used RUVs to study a wide variety of behaviours in animals of varying taxonomic groups and trophic levels. The behaviours studied can be simple, such as the time taken to appear in the field of view or the time taken to feed. The behaviours studied can also be complex, such as mating rituals, schooling behaviour or responses to marine noise. Bait has a positive effect on the abundance of piscivores and carnivores, so non-baited systems would allow fish to be sampled under near-natural conditions (Harvey et al. 2007, Bernard & Götz 2012). However, a much higher number of non-baited samples is required to obtain data with the same statistical power as baited systems (Harvey et al. 2007, Bernard & Götz 2012). This makes baited systems more efficient and cost-effective to use, especially when investigating carnivorous species. Accordingly, baited systems (stereo-BRUVs) are more suitable to study the behaviour of *C. laticeps*. This systematic review reveals that there is broad scope for the behavioural analysis of *C. laticeps* using stereo-BRUVs. Such a study would provide unique insights into the biology and adaptive capacity of *C. laticeps* and would represent novel use of stereo-BRUVs data in South Africa.

CHAPTER 3

3 PILOT STUDY: ON THE SUITABILITY OF STEREO-BRUVS FOR MEASURING *CHRYSOBLEPHUS LATICEPS* BEHAVIOUR IN THE WILD AND TESTING FOR SEASONAL DIFFERENCES IN BEHAVIOUR.

3.1 INTRODUCTION

Chrysoblephus laticeps is a resident reef fish with the bulk of its distribution along South Africa's temperate south coast (Buxton & Allen 1989, Duncan et al. 2020). This core distribution of *C. laticeps* occurs within a thermally variable upwelling zone (Goschen & Schumann 2011, Malan et al. 2019). The thermal variability is highest in summer months (November to February), due to the prevalence of alternating easterly and westerly winds that drive upwelling and downwelling, respectively (Goschen & Schumann 2011). This can result in water temperature changes of greater than 10^{o}C over a couple of hours (Lutjeharms et al. 2000, Goschen et al. 2012). On the other hand, thermal variability is lowest in winter, due to the absence of upwelling favourable wind directions (Goschen & Schumann 2011). This coincides with the optimal temperature conditions for the metabolic performance of *C. laticeps* (Duncan et al. 2019).

Summer also coincides with the spawning season of *C. laticeps*, based on gonado somatic indices (GSI), (Buxton 1990). In fish GSI is used as an indicator of reproductive activity, as GSI increases with gonadal maturation, peaks when gonads are ripe and decreases after spawning (Anderson & Gutreuter 1983, Rizzo & Bazzoli 2020, Blincow et al. 2020). In *C. laticeps*, the GSI of both male and females is highest in the summer months, between October and February (Buxton 1990). While *C. laticeps* is resident and does not undertake spawning migrations, it is possible that its behavioural patterns may vary seasonally (Griffiths & Wilke 2002, Kerwath et al. 2007b). For instance, Kerwath et al. (2007b) found that during the spawning season female C. *laticeps* utilise a much greater area compared to other times of the year.

For planning the sampling programme to address the main aim of this thesis, data collection in summer and winter would be necessary to cover the contrasting temperature dynamics. Collection of data during optimal temperature conditions would be facilitated by sampling in winter, while sampling in, above optimal (warmer) and below optimal (colder) temperatures would be facilitated by sampling in summer. However, before implementing this sampling plan it is important to test whether the behaviour of *C. laticeps* is dependent on season or comparable across seasons. If *C. laticeps* activity levels differ between seasons, then sampling should take place during summer only, to sample across as much greater temperature variability. In addition to collecting new stereo-BRUVs data, a large amount of historical stereo-BRUVs datasets are potentially available for use in this study. However, these datasets contain samples collected in both summer and winter. Thus, it is important to know whether stereo-BRUVs data collected in summer and winter are comparable. If so, both historical winter and summer datasets can be included in the main study. If behaviour does differ by season, a statistical method that accounts for the effect of season can be applied in the statistical analysis.

The systematic review (Chapter 2) revealed that several metrics from stereo-BRUVs footage can be used to describe fish behaviour, such as the time to appear in the field of view, feeding on bait, etc. However, not all may be suitable to describe the behaviour of *C. laticeps* relating to metabolic performance. Based on theory related to ectotherms and evidence from physiological studies (Duncan et al. 2019, Skeeles 2019), it is expected that the activity levels of *C. laticeps* will depend on water temperature, with more energy available for activity at optimal temperatures than above and below optimal temperatures. It is necessary to develop a suite of easily measurable behavioural indices specifically for *C. laticeps* to capture its activity levels. The software BORIS (Friard & Gamba 2016) can potentially be used for quantifying behavioural metrics of *C. laticeps.* BORIS is a free, open-source software for logging/coding behavioural observations from video or audio (Friard & Gamba 2016). Thus, BORIS can be used to create an ethogram and testing the practicality of quantifying the behaviours listed in the ethogram for *C. laticeps* using stereo-BRUV footage.

3.1.1 AIMS

The aims of this pilot study were to identify appropriate metrics for describing the behaviour of *Chrysoblephus laticeps* using stereo-BRUVs and to determine whether there are seasonal differences in the behaviour of *C. laticeps* across comparable temperatures.

3.2 METHODS

3.2.1 STUDY AREA

To address the aims of this pilot-study, research was carried out using data collected from an established marine protected area (MPA) within the centre of the *C. laticeps* distribution, the Tsitsikamma National Park MPA. Reproductively active *C. laticeps* of both sexes occur within this MPA (Bennett et al. 2009). Reproduction is a likely cause for season differences in behaviour, so the presence of reproductively active *C. laticeps* is essential for this study.

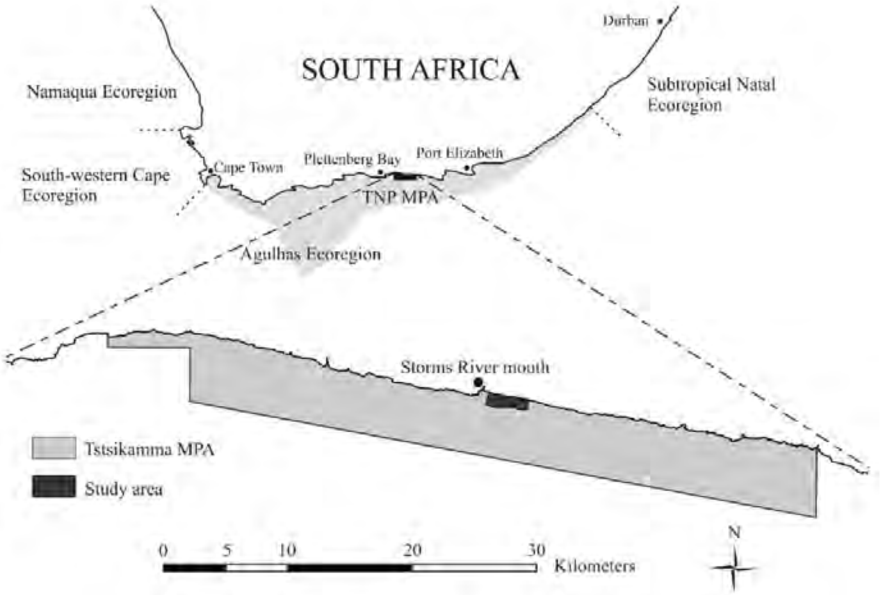

Figure 3.1: The location of the Tsitsikamma National Park (TNP) Marine Protected Area (MPA) in South Africa, with the position of the Rheeders Reef complex (study area) within the TNP MPA.

The Tsitsikamma MPA is situated in the Agulhas Ecoregion (Figure 3.1). Established in 1964, it is South Africa’s oldest MPA (Attwood et al. 1997). It extends 5.6 km offshore and spans 60 km of coastline, from the mouth of the Groot River to Nature’s Valley, making it one of South Africa’s largest coastal no-take MPAs (Molewa 2016, MPA Forum South Africa 2021a). The purpose of this MPA is to protect vulnerable fish species that are of commercial importance, allowing stock recovery and to provide an appropriate reference environment for research and monitoring (Attwood et al. 1997, Molewa 2016). Tsitsikamma MPA is considered one of South Africa's best examples of a pre-exploitation inshore ecosystem (Buxton 1993, Bernard & Götz 2012). Rheeders reef, the study site, is a large and diverse reef complex (Bernard & Götz 2012) situated in the centre of Tsitsikamma MPA (Figure 3.1).

3.2.2 SAMPLING METHOD

Historical stereo-BRUVs data sets collected during four separate sampling trips (February 2013, September 2013, February 2014, and July 2014) using stereo-BRUVs were obtained from the South Africa Institute for Aquatic Biodiversity's (SAIAB) existing stereo-BRUVs repository. The stereo-BRUVs used consisted of two video cameras (Canon Legria HFM 506 or Canon HF M56 HD) in an underwater housing (Figure 3.2). Between the two cameras is an LED light in an underwater housing (Figure 3.2). The cameras were mounted 70 cm apart on a horizontal basebar within a stainless steel frame and converged inwardly at 8° allowing for a field of view of up to 10 m overlapping from 0.5 m in front of the cameras (Figure 3.2). A pole, known as the bait arm, extended perpendicularly from the mid-point between the two cameras, with a bait canister (Figure 3.2) attached 1.5 m from the cameras.

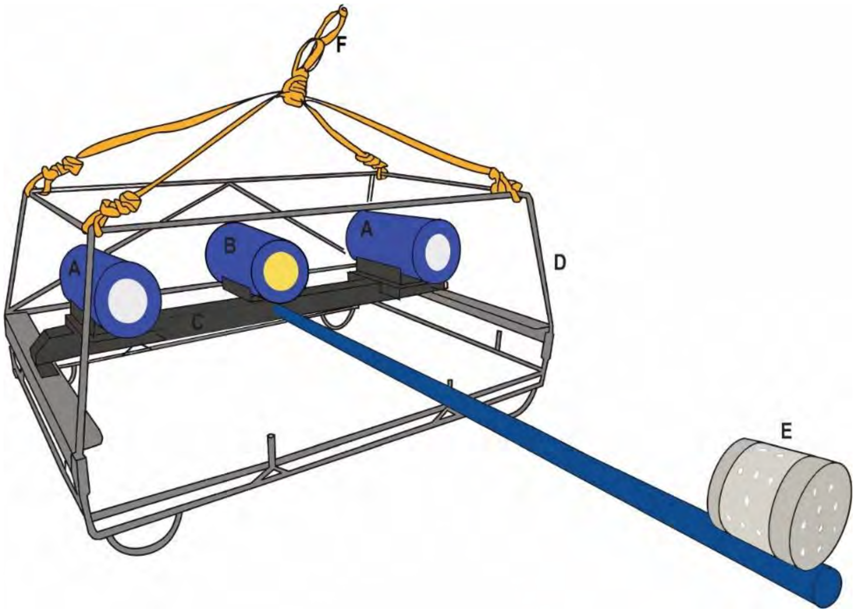

Figure 3.2: Drawing of the baited remote underwater stereo-video system. Underwater housings for HD video cameras (A), underwater housing for blue LED lighting (B), basebar (C), the system's frame (D), bait canister (E) and rope attachment for buoys during deployment and retrieval (F). Drawing by Dr Elodie Heyns.

Prior to and following each sampling field trip, each camera pair was calibrated in their mounted positions. A calibration cube and the software CAL (seagis.com.au) was used to calibrate each camera system, following the procedures recommended by Harvey & Shortis (1998). The calibration procedure measures the base separation, camera orientations and lens distortions that are unique to each stereo camera pair. This enables accurate photogrammetric length measurements to be made from video samples collected by each camera pair (Langlois et al. 2020).

For each sample in the repository, a stereo-BRUVs was deployed onto the sea floor to record footage for a minimum of 60 minutes. Approximately one kilogram of crushed pilchard (*Sardinops sagax*) bait was used for each deployment. Pilchards were used as they are the most effective and cost-efficient bait type to sample reef fish in South Africa (Halse 2016). The stereo-BRUVs were only deployed to a maximum depth of 50 m and the depth at which each sample was collected was recorded. Depth (m) was measured using a GPS linked echo-sounder attached to the boat. Depth is defined as distance from the sea surface to the ocean floor at the point where the stereo-BRUVs was deployed. The bottom water temperature (^{o}C) during the deployment was measured with HOBO Onset temperature loggers mounted on the stereo-BRUVs frame.

3.2.3 SAMPLING APPROACH

A stratified random sampling approach was followed on each of the sampling trips. Using existing bathymetric maps (Bennett 2007, Bernard 2012), Rheeders reef was subdivided into a grid with cells of 300 m^2. The co-ordinates at the centre of each cell were taken as the potential sampling site. For the stratification, each potential sampling site was classified according to depth (Shallow: <16 m; Mid: 16-31 m; Deep: 31-50 m) and reef profile (variation in reef height within the field of view = High: >1 m; Low: <1 m). Co-ordinates of potential sampling sites were put into a random sequence generator in Excel and an even number were selected for each strata combination. The sampling procedure was further randomised by the sequence in which the sites were sampled during the day.

3.2.4 SAMPLE SELECTION

A select subset of samples from the historical datasets (February 2013, September 2013, February 2014, and July 2014) were used in the pilot study. The samples were selected based on the following criteria:

(a) The presence of *C. laticeps* in the video: only samples in which at least one *C. laticeps* appears in the field of view during the 60 minutes deployment were included.
(b) Depth: only samples within depths 14-25 m were included.
(c) Temperature: only samples with temperatures 14-19 °C were included. This was to separate the effect of temperature from the seasonal effect.
(d) Habitat type: only samples deployed on reef were included.

The rationale for this selection criteria was to select samples with *C. laticeps* at their preferred depth, temperature and habitat type. A total of 28 samples were included in the pilot study: nine summer samples and 19 winter samples. While every effort was made to select a balanced number of samples, most samples available from the summer months in the historic datasets fell outside the threshold selection criteria for water temperature. Details of each samples' date of collection, coordinates, depth and temperature can be found in APPENDIX 1 at the end of the thesis.

3.2.5 VIDEO ANALYSIS

For each stereo-BRUVs sample, the time taken for the first *C. laticeps* to (1) arrive in the field of view and (2) feed on the bait was recorded. The time for the first *C. laticeps* to arrive was defined as the time between the stereo-BRUVs settling on the sea floor and the first frame in which a *C. laticeps* individual appears in the field of view. The time for the first *C. laticeps* to feed was taken as the time between the first *C. laticeps* individual appearing in the field of view and the first frame in which a *C. laticeps* individual takes a bite at the bait canister and, as such, is independent of the time to arrive.

The EventMeasure (stereo) software version 3.54 (SeaGIS Pty Ltd.) was used to estimate the relative abundance of *C. laticeps* and measure the lengths of individuals. Relative abundance was measured as "MaxN", which is defined as the maximum number of *C. laticeps* individuals identified in a single video frame during the 60 minute deployment (Langlois et al. 2020). Length measurements (fork length) of each *C. laticeps* individual from the MaxN frame were made. Length was derived from point-to-point fork length measurements facilitated by the stereo-camera calibration files.

A range of behavioural observations were made on the individuals recorded in the MaxN frame using the software BORIS version 7.6.1 (Friard & Gamba 2016). First, an ethogram was developed to determine and quantify the behaviour of *C. laticeps* individuals. Six different behaviours were defined and categorised as either a point or a state event as required by the BORIS interface. Point events are behaviours which have an occurrence but no duration. Their resulting output is a count of how many times the behaviour occurred. State events have a duration, with a start and an end. Their resulting output is a count (in seconds) of how long the behaviour occurred. Five behaviours were point events: feeding on bait, aggressive feeding, aggressive displays, fleeing and spawning and are described in Table 3.1. One behaviour was a state event: time spent in the field of view was and is described in Table 3.1.

Table 3.1: List of behaviours expected to be displayed by *Chrysoblephus laticeps* from the baited remote underwater stereo-video system samples.

Category	**Behaviour**	**Definition**	**Unit of measurement**	**Data type**
Feeding	Feeding on bait	Focal fish is observed feeding, the head is inclined towards the bait canister and the jaws are in contact with the bait canister.	Individual	Count of events per individual
	Aggressive feeding	Focal fish is observed feeding, taking 3 or more consecutive “bites” of the bait canister within 3 seconds.	Individual	Count of events per individual
Agonistic	Aggressive displays	Focal fish chases or bites another fish.	Individual	Count of events per individual
	Flee	Focal fish quickly swims away from another fish in response to received aggressive displays.	Individual	Count of events per individual
Reproductive	Spawning	Focal fish displays the sequence of courtship and spawning behaviours described by Buxton (1990) and Davis (1996).	Individual	Count of events per individual
Persistence	Time in field of view	Start – first frame focal fish appears in. End - last frame focal fish appears in.	Individual	Time in seconds
Response time	Time to arrive	First frame in which a *C. laticeps* appears.	Sample	Time in seconds
	Time to 1st feeding	First frame in which a *C. laticeps* feeds on the bait.	Sample	Time in seconds

The behaviour of each individual from the MaxN frame was then observed. At the MaxN frame of each video sample, each *C. laticeps* individuals was labelled from 1 – MaxN (see Figure 3.3 for an example). For each individual, the footage was rewound to the first frame in which it appeared. The behaviour of the individual was then observed and coded using the defined ethogram, until the last frame in which it was observed. Lastly, the number of co-occurring species during each observation period was recorded.

Figure 3.3: The MaxN (relative abundance) frame of *Chrysoblephus laticeps* in a baited remote underwater stereo-video system sample. Each individual *C. laticeps* was labelled from 1 – MaxN (which in this example is 5).

Table 3.2 Full list of explanatory variables used in the statistical analyses.

Covariate	Definition	Values
Sample	The unique code given to each sample.	28 unique sample codes
Season	The season in which samples were collected. spring/summer samples = summer and autumn/winter samples = winter.	Summer ; Winter
Depth	The distance from the sea surface to the ocean floor at the point where the stereo-BRUVs was deployed.	14 - 26 m
Temperature	Average temperature during the 60 minute stereo-BRUV deployment.	14.24 - 18.39 °C
MaxN	MaxN of *C. laticeps* in the video sample.	2 - 10
Co-occurring species	Number of co-occurring species while the individual *C. laticeps* was in field of view.	0 - 11
Size	Length of individual *C. laticeps.*	150.617 - 459.476 mm

3.2.6 STATISTICAL ANALYSES

All statistical analyses were conducted in R version 4.0.3 (R Core Team 2018) using the RStudio version 1.2.1335 interface (*RStudio: Integrated Development Environment for R* 2018).

The behavioural response variables represent two core types of data based on the unit of measurement (Table 3.1). The behaviours ‘time to arrive’ and ‘time to first feeding’ were both measured at the sample level, while the remaining behaviours were measured for individual fish, nested within each sample. As multiple individual fish were recorded from a sample this creates dependency in the data. Consequently, mixed effect models, with sample included as a random effect, were used to analyse patterns in the individual level behavioural response data. This dependency was not present for the behaviours recorded at the sample level and these responses were analysed using appropriate generalised regression techniques.

Prior to modelling, detailed exploratory data analyses were conducted following the protocol by Zuur et al. (2010). The purpose of the data exploration was to understand the nature of the data. This protocol includes checking for collinearity and interactions between covariates (see Table 3.2 for the full list), outliers in the data, zero-inflation, normality of the response variables, spatial patterns and the balance of the data. The error distribution (family) used in each model was based on the type of response variable and over-dispersion parameters (i.e. Poisson for count data where the mean is equal to the variance, negative binomial for count data where the variance is greater than the mean, Tweedie for continuous data and binomial for presence/absence data).

For the sample level response variables, the exploratory analysis revealed no non-linear trends in the response variables relative to the predictors and as a result generalised linear models (GLMs) were used. However, for both ‘time to arrive’ and ‘time to first feeding’, the Poisson residuals were over dispersed and the chosen GLM was fitted with the negative binomial distribution (Table 3.3: Model 1 and Model 2). The negative binomial GLMs were fitted using the MASS package (Venables & Ripley 2002).

For the individual level response variables, data exploration revealed that *C. laticeps* size showed a positive relationship with the presence of most behaviours. Further, the *C. laticeps* measured in summer (mean size 321.3 ± 74.1 mm) were significantly (two-sample t-test with all assumptions met: $t = 2.26$, $p = 0.03$) bigger than those measured in winter (mean size 267.8 ±

69.5 mm), (Figure 3.4). Therefore, individual *C. laticeps* size was included in the models to account for its effect on *C. laticeps* behaviour when testing the effect of season.

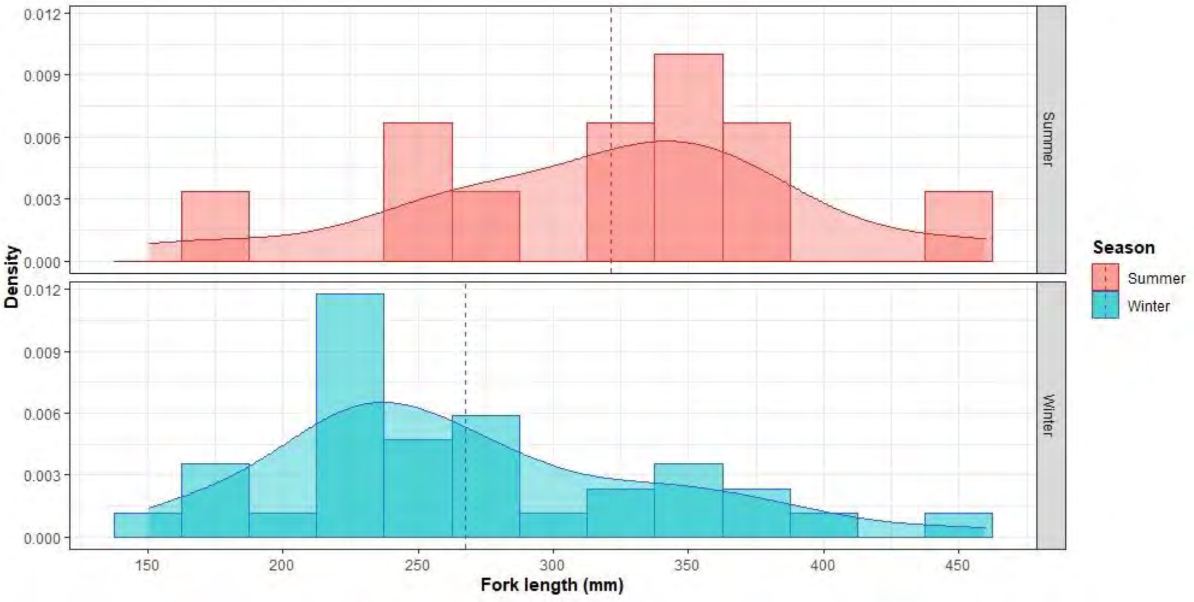

Figure 3.4: Length frequency distribution of *Chrysoblephus laticeps* measured from Tsitsikamma marine protected area in summer and winter of 2013 and 2014. The dashed line represents the mean fork length for each season.

Data exploration also revealed that the effect of size on behaviour was non-linear and so generalised additive mixed effect models (GAMMs) were used to investigate behaviour. The GAMMs were fitted using the MGCV package (Wood 2011, 2017). The sample code was included as a random effect using the bs= “re” term in the MGCV package (Wood 2008). Season was included as a parametric coefficient while the remaining covariates, excluding sample, (see Table 3.2) were fitted with thin plate spline smooth terms (Wood 2008).

The behaviours ‘feed on bait’, ‘aggressive feeding’ and ‘aggressive displays’ had high zero-inflation (>75%). Thus, the data were converted to presence/absence and GAMMs were fitted with the binomial distribution (Table 3.3: Models 3-5). The behaviour ‘fleeing’ could not be modelled as there were only three measured individuals that displayed this behaviour. The sizes of the three *C. laticeps* individuals which fled ranged from 234-340 mm FL. Notably, two of these individuals had both fed on the bait and fed aggressively. To investigate 'time spent in the field of view', a GAMM was fitted with the Tweedie distribution (Table 3.3: Model 6).

Table 3.3: Covariates included in the best-fit generalised linear models (GLMs) and generalised additive mixed models (GAMMS) applied to investigate behaviour of *Chrysoblephus laticeps*. 's' = smooth terms, 'k' = knots, 'bs' = basis spline, 're' = random effect.

Model	**Type**	**Error distribution**	**Best-fit structure**	**Excluded explanatory variables**
1	GLM	Negative binomial	Time to arrive ~ Season	Depth, Temperature, MaxN
2	GLM	Negative binomial	Time to feed ~ Temperature + Season	Depth, MaxN
3	GAMM	Binomial	Feed on bait ~ s(Size, k=6) + s(Co-occurring species, k=3) + s(Sample, bs="re") + Season	Depth, Temperature
4	GAMM	Binomial	Aggressive feeding ~ s(Depth, k=3) + s(Size, k=6) + s(Co-occurring species, k=3) + s(Temperature, k=3) + s(Sample, bs="re") + Season	MaxN
5	GAMM	Binomial	Aggressive displays ~ s(Size, k=6) + s(Sample, bs="re") + Season	Depth, Co-occurring species, MaxN, Temperature
6	GAMM	Tweedie	Time in field of view ~ s(Size, k=6) + s(Sample, bs="re") + Season	Depth, Co-occurring species, MaxN, Temperature

Automated model selection was carried out with the R package MuMIn using the dredge function (Barton, 2020) to identify the best-fit models (Table 3.3). Here, a full model was fitted (i.e. a model containing all the available covariates, see Table 3.2) and the Akaike Information Criterion (AIC) score was calculated for all possible model formulations (Logan 2010). The model with the lowest AIC score was regarded as the best-fit. The best-fit model was then explored further to determine model fit and the significance of each covariate and its contribution to the model (Zuur et al. 2009). During model selection, season (for GLMs and GAMMs) and the random effect of sample (for GAMMs) were forced to be included in the best-fit model, to ensure that the data dependency and research question could be answered.

Following this, sequential likelihood ratio tests were carried out on the GLMs to determine the significance of each covariate. For the GAMMs, a Wald's test was carried out on each model to determine the significance of each covariate.

To visualise the relationships between the important explanatory variables and the behavioural responses, predicted datasets were created based on the model coefficients. When predicting the effect of season, all other covariates included in the model were set to their mean value. Then, if there were any other significant covariates in the model, their predicted effect was also visualised. Plots were created using ggplot2 (Wickham 2016). Generally, only plots of significant covariates were presented in the results section.

3.3 RESULTS

In total, the behaviour of 141 *C. laticeps* individuals was assessed. Sometimes not all the individuals at MaxN could be measured. This was a result of the fish only appearing in one video of the stereo-pair, the fish being too far away from the camera or the angle of the fish not allowing an accurate measurement to be taken. Out of the 141 individuals whose behaviour was assessed, 46 could be measured (12 in summer and 34 in winter) and included in the individual level behaviour analyses.

3.3.1 TIME TO ARRIVE MODEL

The best-fit model explained little (7.1%) of the observed variability in the time to arrive. Season did not have a significant effect on the time to arrive (sequential likelihood ratio test, *p* = 0.112), while all other covariates were excluded during the model selection process (Table 3.4). While there was a notable difference in the mean time to arrive between summer (mean ± standard deviation: 61.9 ± 87.5 s) and winter (21.6 ± 44.5 s) there was considerable variability around each mean resulting in no statistical difference.

Table 3.4: Results from the sequential likelihood ratio test for the best-fit generalised linear model investigating determinants of *Chrysoblephus laticeps* time to arrive (Table 3.3: Model 1). *df* = Degrees Freedom.

Term	***df***	**Deviance**	**Residual *df***	**Residual deviance**	***p*-value**	
NULL			27	35.491		
Season	1	2.521	26	32.969	0.112	ns

*Significance codes: *** < 0.001; ** < 0.01; * < 0.05;* ns = not significant

TIME TO FEED MODEL

The best-fit model explained 26.5% of the observed variability in the time to feed of *Chrysoblephus laticeps*. Time to feed of *C. laticeps* was not influenced by season (sequential likelihood ratio test, *p* = 0.639, Table 3.5). While there was a notable difference in the mean time to feed between summer (514.4 ± 854.8 s) and winter (123.5 ± 238.4 s) there was considerable variability around each mean resulting in no statistical difference. Temperature did have a significant effect on the time to feed (sequential likelihood ratio test, $p < 0.001$, Table 3.5). The time to feed was longer at colder temperatures and decreased with increasing temperature, regardless of season (Figure 3.5). The time to feed was also more variable at lower temperatures as indicated by the width of the confidence intervals (Figure 3.5B).

Table 3.5: Results from the sequential likelihood ratio test for the best-fit generalised linear model investigating determinants of *Chrysoblephus laticeps* time to feed (Table 3.3: Model 2). *df* = Degrees Freedom.

Term	*df*	Deviance	Residual *df*	Residual deviance	*p*-value	
NULL			25	43.386		
Temperature	1	11.283	24	32.103	< 0.001	***
Season	1	0.219	23	31.884	0.639	ns

*Significance codes: *** < 0.001; ** < 0.01; * < 0.05;* ns = not significant

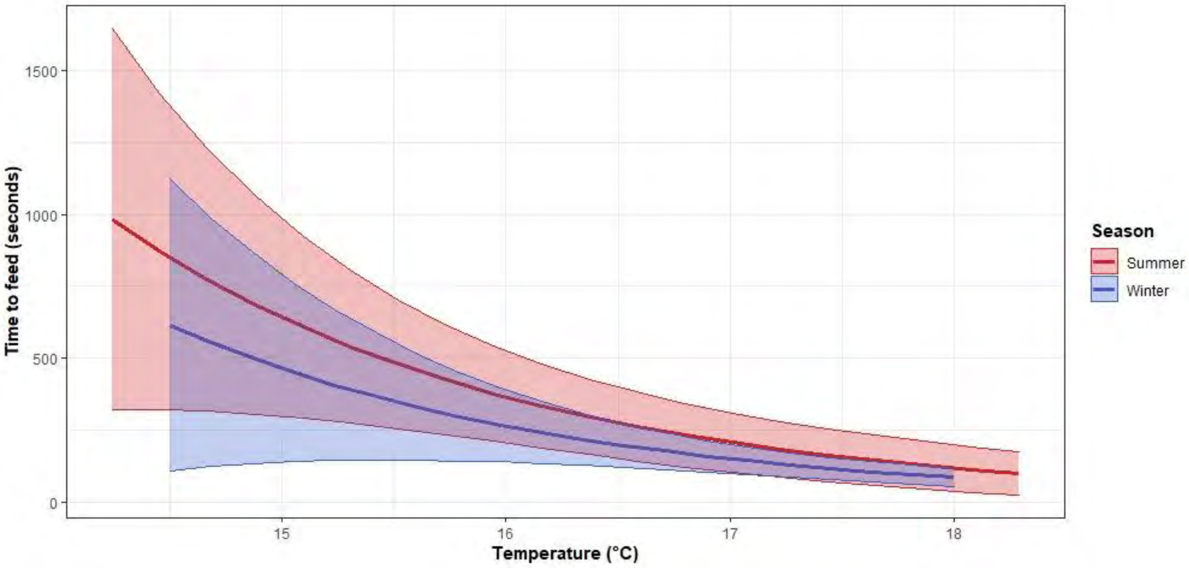

Figure 3.5: Predicted results from the generalised linear model (Table 3.3: Model 2) showing (A) the effect of temperature on the time to feed, holding all other covariates constant and (B) the effect of MaxN on the time to feed, holding all other covariates constant. The shaded area around each trend line represents the approximate 95% confidence interval.

3.3.2 FEED ON BAIT MODEL

The best-fit model explained 27.4% of the observed variability in the probability of feeding on bait. The Wald's test found that neither season (p = 0.371; summer = 0.5 ± 0.52, winter = 0.5 ± 0.51) nor size (p = 0.234) had a significant effect on the probability of feeding, nor did any other covariate (Table 3.6). The prediction plot illustrates that at smaller sizes the probability of feeding is close to 0 and at the largest sizes the probability is close to 1, however, there was a lot of uncertainty around the predicted mean values (Figure 3.6). The random effect of sample was not significant (Table 3.6).

Table 3.6: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of feeding on bait by *Chrysoblephus laticeps* (Table 3.3: Model 3). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Season	1	0.801	0.371	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Size	1.123	4.581	0.234	ns
Co-occurring species	2.946	2.645	0.312	ns
Sample	3.152×10^{-05}	0	0.913	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

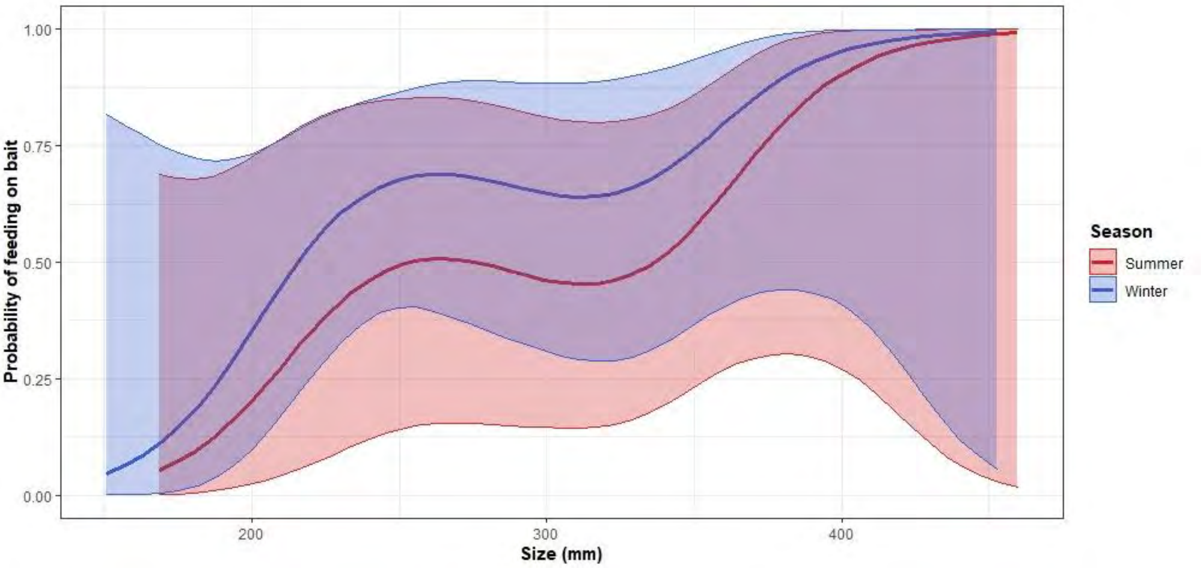

Figure 3.6: Predicted results from the generalised additive mixed model (Table 3.3: Model 3) showing the effect of size on the probability of feeding on bait, holding all other covariates constant. The shaded area around each trend line represents the approximate 95% confidence interval.

3.3.3 AGGRESSIVE FEEDING MODEL

The best-fit model explained 52.2% of the observed variability in the probability of aggressive feeding. Season did not have a significant effect on the probability of aggressive feeding (Wald's test, *p* = 0.088; summer = 0.33 ± 0.49, winter = 0.35 ± 0.49; Table 3.7). Alternatively, the probability of aggressive feeding increased significantly with the size of *C. laticeps* (Wald's test, *p* = 0.006; Table 3.7), however, there was a lot of uncertainty around the predicted mean values (Figure 3.7). The random effect of sample was not significant (Table 3.7).

Table 3.7: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of aggressive feeding (Table 3.3: Model 4). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Season	1	2.904	0.088	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Depth	1.000	1.823	0.177	ns
Size	1.000	7.644	0.006	**
Co-occurring species	1.857	2.178	0.311	ns
Temperature	2.125	5.439	0.132	ns
Sample	$2.447\text{x}10^{-05}$	0	0.540	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

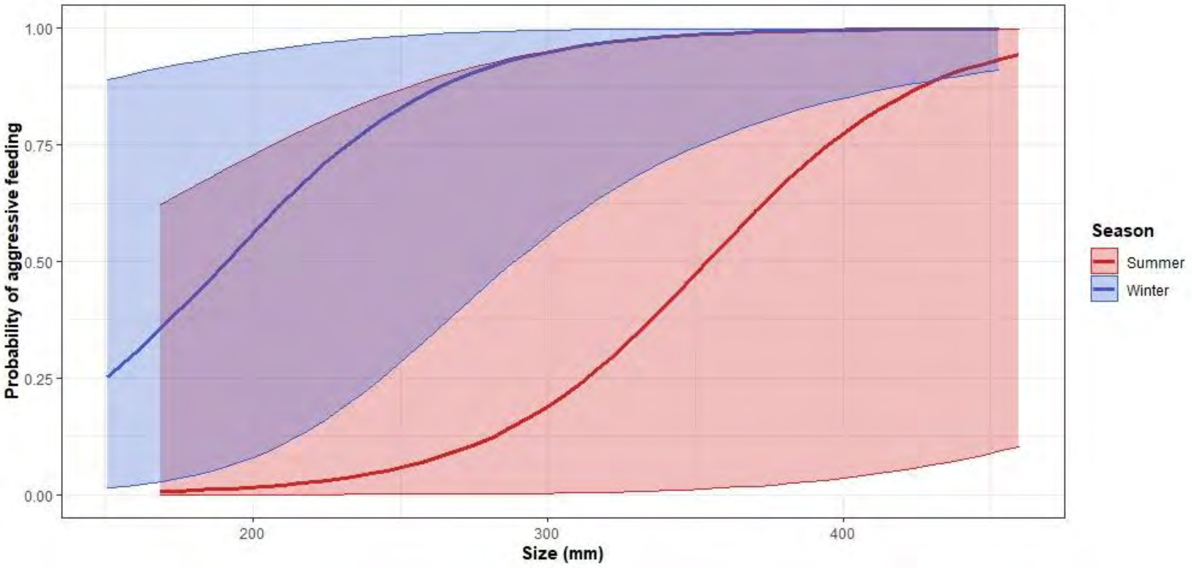

Figure 3.7: Predicted results from the generalised additive mixed model (Table 3.3: Model 4) showing the effect of size on the probability of aggressive feeding, holding all other covariates constant. The shaded area around each trend line represents the approximate 95% confidence interval.

3.3.4 DISPLAYS OF AGGRESSION

The best-fit model explained 26.6% of the observed variability in the probability of *C. laticeps* displaying aggression. The Wald's test found that season did not have a significant effect (p = 0.964; summer = 0.42 ± 0.51, winter = 0.24 ± 0.43) on the probability of displaying aggression

(Table 3.8). *Chrysoblephus laticeps* size had a significant positive effect on the probability of displaying aggression (Wald's test, *p* = 0.003; Table 3.8; Figure 3.8). The random effect of sample was not significant (Table 3.8).

Table 3.8: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of aggressive displays by *Chrysoblephus laticeps* (Table 3.3: Model 5). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Season	1	0.002	0.964	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Size	1.000	8.806	0.003	**
Sample	1.75×10^{-05}	0	0.949	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

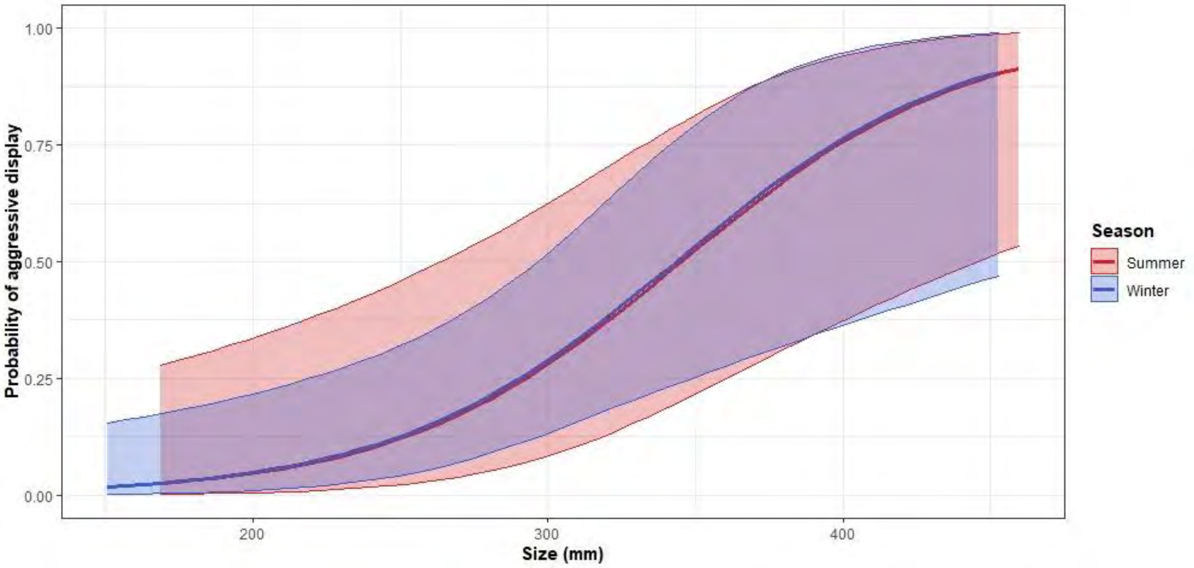

Figure 3.8: Predicted results from the generalised additive mixed model (Table 3.3: Model 5) showing the effect of size on the probability of displaying aggression, holding all other covariates constant. The shaded area around each trend line represents the approximate 95% confidence interval.

3.3.5 TIME IN FIELD OF VIEW

The mean time spent in the field of view was 48 ± 48 seconds in summer and 38 ± 33 seconds in winter. The best-fit model explained little (12.2%) of the observed variability in the time spent in the field of view. While season had no effect (Wald's test, p = 0.775), the time spent in the field of view increased significantly with *C. laticeps* size (Wald's test, p = 0.028; Table 3.9). The time spent in the field did appear to be more variable in larger individuals compared to smaller ones (Figure 3.9). The random effect of sample was not significant (Table 3.9).

Table 3.9: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of time spent in field of view by *Chrysoblephus laticeps* (Table 3.3: Model 6). df = Degrees of freedom; edf = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Season	1	0.083	0.775	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Size	1.123	4.413	0.028	*
Sample	7.534×10^{-05}	0	0.900	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

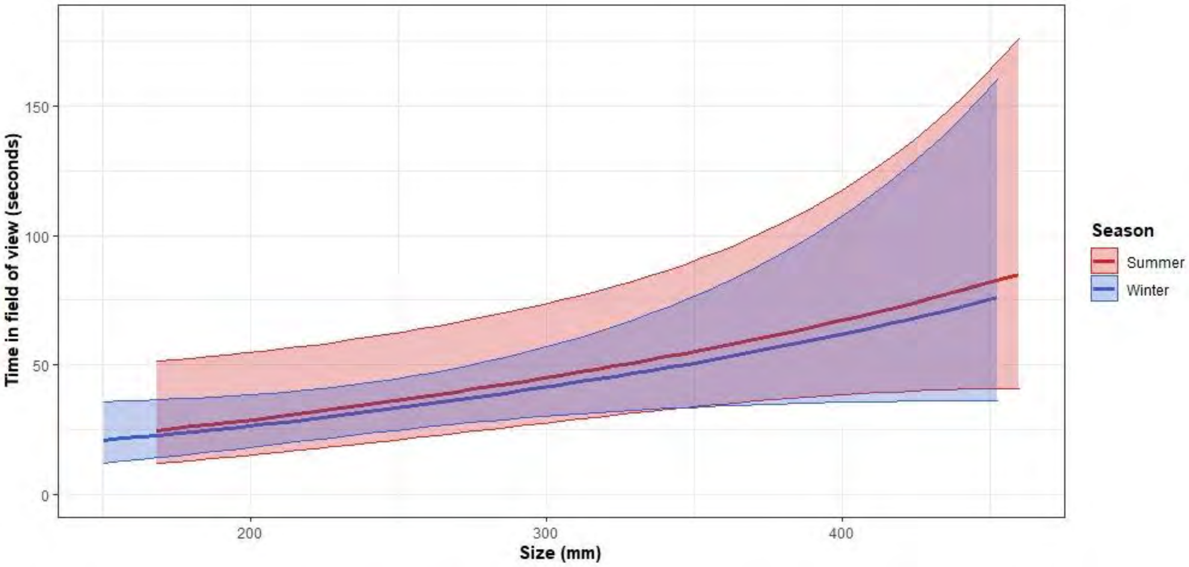

Figure 3.9: Predicted results from the generalised additive mixed model (Table 3.3: Model 6) showing the effect of size on time spent in the field of view, holding all other covariates constant. The shaded area around each trend line represents the approximate 95% confidence interval.

3.4 DISCUSSION

This pilot study aimed to identify appropriate metrics for describing the behaviour of *Chrysoblephus laticeps* using stereo-BRUVs footage and to determine if there were seasonal (summer and winter) differences in the activity of *C. laticeps* across comparable temperatures. The selected behavioural metrics used in this pilot study were suitable and could detect differences in fish behaviour using stereo-BRUVs footage. However, for the behaviours feeding on bait, aggressive feeding, aggressive displays and fleeing this was only possible when considering the presence or absence of behaviours as the data had a high number of zeros and modelling was not possible with the count-based data. Furthermore, the behaviours were identified as being influenced by individual *C. laticeps* size, indicating that size needed to be accounted for in data analysis. Using these behavioural metrics together with *C. laticeps* size, this pilot study did not detect a significant difference in the behaviour of *C. laticeps* between seasons. However, there was considerable variability in the data. In the context of this research, the outcome means sampling can occur across seasons and for the main study archival footage from different seasons can be utilised when comparing the behaviour of fish from exploited and unexploited populations. This is particularly important for this study as it increases the number of available datasets for analysis and potentially reduces uncertainty in the analyses.

This pilot study found that size and temperature most influenced the behaviour of *C. laticeps*. Even though the *C. laticeps* measured in summer were significantly larger than those measured in winter, season did not have a significant effect on behaviour. Generally, size had a positive relationship with behaviour. Larger *C. laticeps* were more likely to feed aggressively (Figure 3.7), display aggression (Figure 3.8) and spend more time in the field of view (Figure 3.9). Larger individuals may have been feeding more aggressively due to having higher energy demands, thus requiring more food than smaller fish (Xu et al. 2007, Davis et al. 2012, Briones et al. 2012). Larger individuals were also more likely to display aggression towards other fish. During video analysis *C. laticeps* individuals were observed chasing both conspecifics and fish of different species. The displays of aggression by larger *C. laticeps* could be due to the territorial nature of males (Penrith 1972a, Buxton 1987). Male *C. laticeps* gather a harem of females for extended periods of time which they aggressively defend (Buxton 1987, Buxton & Garratt 1990). Protecting their harem has energetic costs and could further incentivise males to feed more than smaller females.

Spawning behaviour was not observed in any video and fleeing could not be modelled due to too few fish displaying the behaviour. This suggests that these behaviours might not be reliable indicators to use, or that a much larger dataset is required to effectively sample these behaviours. Only three individuals were observed fleeing and two of these individuals had both fed on the bait and fed aggressively. Possibly these individuals were in competition with other fish over the bait, which resulted in them being chased away. Larger *C. laticeps* spent more time in the field of view than smaller *C. laticeps*. Gerlotto & Fréon (1992) and Webster (2004) have observed larger fish outcompeting smaller conspecifics in BRUVs videos. Thus, the shorter time in the field of view associated with smaller individuals may suggest that they swim away when larger fish are present. On the other hand, the larger individuals are able to remain in the field of view for longer as there are fewer competitors or predators.

Temperature significantly influenced the time taken to feed. Despite selecting samples within a narrow temperature range, some variation in temperature across the sample set was unavoidable as this pilot study was an uncontrolled field survey which used historically collected data. The results showed that the time taken for the first *C. laticeps* to feed was longer at lower temperatures and shorter at higher temperatures. This could be a result of the constraints temperature places on the metabolic rate of fish (Huey & Kingsolver 1993, Clark et al. 2013, Watson et al. 2019). As the metabolic rate of *C. laticeps* increases with increasing temperatures (Duncan et al. 2019), individuals would be able to achieve greater rates of feeding at warmer temperatures. As this data covered a narrow temperature range, this result suggests that the behaviour ‘time to feed’ might be sensitive enough to detect changes in *C. laticeps* activity associated with metabolic activity and fisheries-induced evolution.

Neither MaxN (the abundance of conspecifics) nor the number co-occurring species significantly affected the behaviour of *C. laticeps*. In all models, these variables were either dropped during the model selection process or when they were included, their effect was not significant. This result is important for the main study, where abundance may vary between exploited and unexploited areas, as it suggests that behaviour of *C. laticeps* individuals is independent of abundance at the sample scale. Further, if *C. laticeps* behaviour is not influenced by the presence of other fish, this suggests that if behavioural differences are observed between exploited and protected populations they are not determined by differences in the location-specific fish assemblages.

The random effect of sample was never significant. This suggests that the behaviour of *C. laticeps* was independent of sample, and that the random effect may not be necessary. However, it was deemed important to keep it in the models to account for any variability associated with sample-level dependency. The absence of a significant effect might reflect the generally high variability in the data and may also be linked to the low sample size. If more data from each sample and from more study sites are included, the dependency may be present and as such, the random effect should be considered in the main study.

A limitation of this pilot study is the small sample size from the summer datasets that met the sample inclusion criteria (see section 3.2.4). In summer, most samples fell outside the narrow preferred temperature range. This resulted in an undesirable imbalance of the number of samples between seasons in the analyses and this may have influenced the outcome of the pilot data analysis. This pilot study also revealed the importance of individual *C. laticeps* size and that the behaviour observations were prone to zero-inflation. Given the importance of size in influencing behaviour, only individuals that could be measured were included in the analysis. As a result, a large amount of behavioural data was discarded. Zero-inflation meant that count data had to be converted to absence/presence data. Consequently, the factors determining how frequently an individual fed on bait, aggressively fed, displayed aggression or fled could not be investigated. A larger sample size could address these issues by compensating for the loss of data from excluding unmeasured fish and overcoming zero-inflation. Despite the limitations of this pilot study, it is unlikely that the main finding, which is that behaviour does not vary seasonally, would change with a larger sample size.

3.5 CONCLUSIONS

The behavioural metrics measured were suitable for quantifying the behaviour of *C. laticeps* from stereo-BRUVs footage. The behaviours time to arrive, time to first feeding, time spent in field of view, feeding on bait, aggressive feeding and aggressive displays were found to be suitable for measuring the activity of *C. laticeps*. The behaviour of *C. laticeps* did not vary seasonally. Temperature and size influenced the behaviour of *C. laticeps* the most, with both positively affecting behaviour. The results of the pilot study allow for the inclusion of summer and winter datasets in the main study.

CHAPTER 4

4 THE EFFECTS OF TEMPERATURE AND EXPLOITATION ON THE BEHAVIOUR OF RED ROMAN *CHRYSOBLEPHUS LATICEPS*

4.1 INTRODUCTION

Regional or local temperature variation is often overlooked in climate change studies in favour of investigating long-term and global temperature changes (Bates et al. 2018). However, short-term local temperature variability associated with events such as upwelling may have more of an impact on the survivability of fish populations compared to long-term warming (Allison et al. 2021). Mean annual sea surface temperatures (SST) along South Africa's coast have seen an increase of 0.25 to 0.50 °C per decade since the 1960's, however, there has also been an increase in localised short-term temperature variability due to an increase in marine heat waves and upwelling (Schumann et al. 1995, Rouault et al. 2010, Schlegel & Smit 2016, Jury 2020).

South Africa's coast is divided into three main bioregions; the cool-temperate west coast, warm-temperate south coast and sub-tropical east coast (Figure 4.1). The greatest abundance of *C. laticeps* is found along the warm-temperate south coast (Whitfield 2005, Duncan et al. 2020). Along the south coast, temperature variability is driven by an increase in upwelling which can result in sea temperature decreases of more than 10 °C within a few hours and these low temperatures can persist for several days (Schumann et al. 1995, Schumann 1999, Lutjeharms et al. 2000, Goschen et al. 2012).

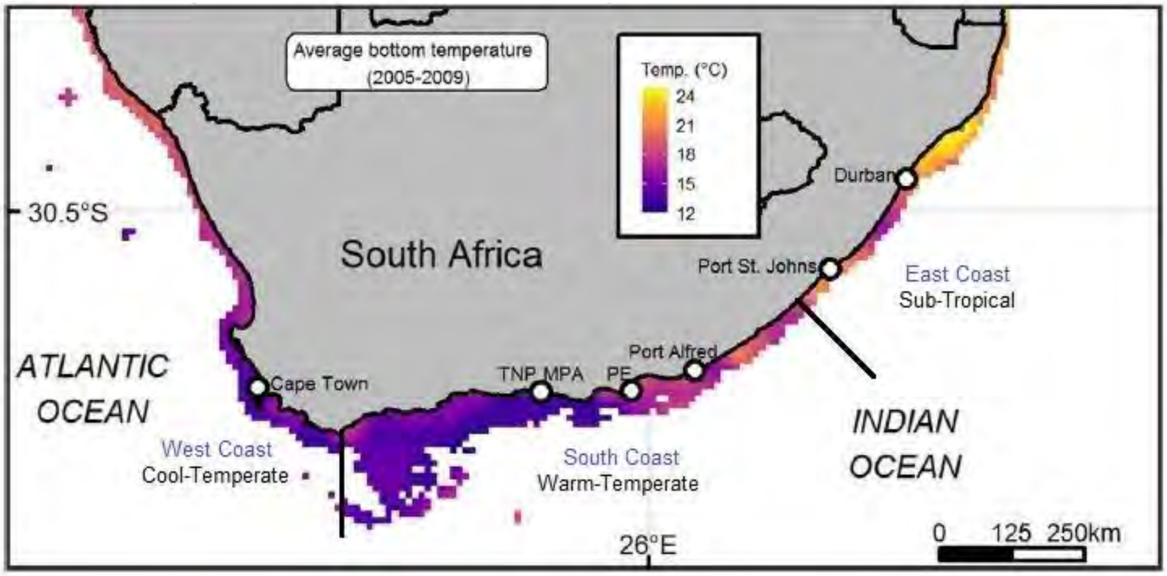

Figure 4.1: Average seafloor ocean temperature (°C) along the coast of Southern Africa between the years 2005-2009. Three major biogeographical zones are delineated by solid black lines and labelled in blue and black text. TNP MPA = Tsitsikamma national park marine protected area; PE = Port Elizabeth. Modified from Duncan et al. (2020).

As temperature has a positive relationship with the metabolic rate of fish, upwelling can be detrimental for fish as it affects their physiological and behavioural performance and can cause death (Roessig et al. 2004, Donaldson et al. 2008, Fossette et al. 2012, Szekeres et al. 2014). Thus, an increase in upwelling intensity and/or frequency is expected to negatively impact the fitness and long-term survival of reef fish (Roessig et al. 2004, Bernhardt & Leslie 2013, Potts et al. 2015). Encouragingly, marine protected areas (MPAs) may conserve fish populations which are able to maintain metabolic function despite an increase in temperature variability (Duncan et al. 2019, Skeeles 2019).

Passive fishing gears, such as hook and line used to catch *C. laticeps,* are known to remove large and bold individuals as these individuals are more likely to feed on the bait and be caught (Law 2000, Arlinghaus et al. 2017). Thus, passive fishing leads to a loss of genetic diversity and size and age truncation within the population (Law 2000, Landi et al. 2015, Kuparinen et al. 2016). In the case of *C. laticeps,* populations within MPAs have been found to be larger in size compared to exploited populations due to protection from fishing (Bennett 2007, Götz et al. 2008b, 2009). Given that the pilot study (Chapter 3) found that size had a positive relationship with behaviours such as aggressive feeding, aggressive displays and the time spent in the field of view, MPAs may support individuals with higher activity levels by conserving large individuals. These individuals may be more tolerant to environmental stressors if they are still able to engage in activities required for maintenance or growth in unfavourable conditions. Duncan et al. (2019) found that across the temperatures 8-24 °C there were fewer individuals in exploited *C. laticeps* populations that demonstrated high metabolic performance compared to protected populations. Additionally, *C. laticeps* within MPAs have been found to achieve significantly higher metabolic rates than their exploited counterparts at temperatures below 8.5 °C (Skeeles 2019). Thus, MPAs may conserve populations of *C. laticeps* which are more resilient to climate change if they are able to forage and defend territory and resources despite changing temperatures.

Importantly, the pilot study identified suitable metrics for describing the behaviour of *C. laticeps* using stereo-BRUVs in order to measure differences in the activity of *C. laticeps*. These behaviours include the time taken for the first individual to arrive and to feed, feeding on the bait, aggressive feeding and displaying aggression. These can be applied to test the effects of both temperature and exploitation on the behaviour of *C. laticeps*.

The effect of exploitation on the behaviour of fish is an often overlooked component regarding fisheries-induced evolution and the use of MPAs in protecting vulnerable fish populations (Uusi-Heikkilä et al. 2008, Pauli & Sih 2017). The majority of studies investigating the effectiveness of MPAs focus on population-based metrics, such as the recovery of fish abundance, diversity and biomass (Yemane et al. 2004, Kerwath et al. 2008, Götz et al. 2011, Sanguinetti 2013, Dickens 2015). Studies which have investigated behaviour found that passive fishing practices preferentially remove more active and bold individuals as they feed more readily on the bait (Alós et al. 2012, Colefax et al. 2016, Pauli & Sih 2017, Rhoades et al. 2019). As a result, exploited populations of target species are more hesitant to feed on bait and this timidity can persist long after the recovery of fish densities to pre-exploitation levels (Colefax et al. 2016, Arlinghaus et al. 2017, Rhoades et al. 2019). Thus, investigating how both exploitation and temperature influence behaviour is useful in understanding the vulnerably of reef fishes to temperature fluctuations and the role that MPAs may play in climate change mitigation.

4.1.1 AIM

The aim of this chapter is to determine how the population structure and activity levels of *Chrysoblephus laticeps* are affected by short-term temperature variability and if the effects differ between established MPAs and areas open to fishing.

4.1.2 OBJECTIVES

(1) Conduct stereo-BRUVs field surveys focusing on *C. laticeps* across a wide range of temperatures in fished and protected areas

(2) Estimate population variables of *C. laticeps* including relative abundance and size structure.

(3) Quantify a selection of activity-based behaviours of *C. laticeps*, informed by the pilot study, using stereo-BRUVs footage.

4.2 METHODS

The findings of Chapter 3 indicated that the methods used in the pilot study could be replicated in the main study. Though, more extensive analyses needed to be undertaken in the main study. The main study will increase number of samples, collect samples from four locations, include additional explanatory variables, sample across a wider range of temperatures and include as many historical stereo-BRUVs datasets as possible. These changes to the study design will improve on the pilot study and enable the primary research questions of this thesis to be addressed.

4.2.1 STUDY AREA

Four study sites along South Africa's south coast were selected with two sites in established MPAs and two in exploited areas (Figure 4.2). Tsitsikamma MPA and Goukamma MPA are both well-established MPAs, with fishing prohibited for more than two decades, and are within close proximity to heavily exploited areas (Figure 4.2). Port Elizabeth and Cape St. Francis have similar environmental conditions and thermal regimes to the two MPAs as well as similar levels of exploitation (Figure 4.2).

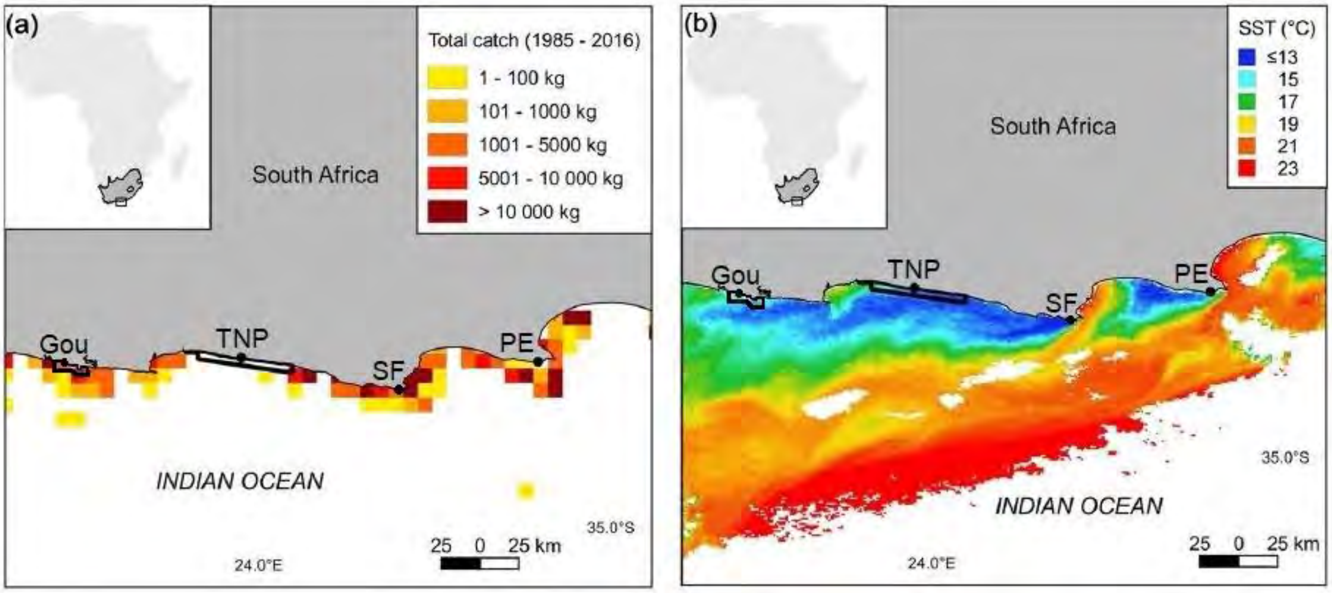

Figure 4.2: Map illustrating the location of study sites in relation to (a) the total reported commercial catch of *Chrysoblephus laticeps* between the years 1985–2016 and (b) sea surface temperatures during an upwelling event on 04/03/2010 as evidence for synchronized upwelling events. Gou = Goukamma marine protected area (MPA), TNP = Tsitsikamma National Park MPA, SF = Cape St. Francis and PE = Port Elizabeth. Modified from Duncan et al. (2019).

Details on the Tsitsikamma MPA study site are given in Chapter 3. Goukamma MPA was established in 1990 (MPA Forum South Africa 2021b). It extends 1.85 km offshore and spans 16 km of coastline, from Buffels Bay to Platbank (Figure 4.2) (Molewa 2017). The purpose of this MPA is to protect and conserve the marine and coastal ecosystem and allow stock recovery of linefish species, including *C. laticeps* (Molewa 2017). The MPA contains a total of 43.8 km^2 of reefs (Götz 2005). The reefs of Goukamma MPA are comparable in depth range and structure to those of the Tsitsikamma MPA (Buxton 1987, Götz 2005).

In Port Elizabeth, the study site selected was the reef complex around the Cape Recife area, to the west of Algoa Bay (Figure 4.2). The physical environment and thermal regime of this frequently fished area is similar to that of the Tsitsikamma and Goukamma MPAs (Buxton 1987, Duncan 2018). The reefs around Cape Recife are also similar to those in Tsitsikamma and Goukamma MPAs in terms of fish assemblage structure (Buxton & Smale 1989, Götz 2005).

In Cape St. Francis, the study site selected was the area of reef between Seal Point and Thyspunt (Figure 4.2). Cape St. Francis and Cape Recife have similar physical environments in terms of annuals patterns of rainfall, wind, currents, upwelling, salinity and productivity (Jury et al. 1993, Jury 2019). Cape St. Francis and Cape Recife also have similar levels of commercial fishing activity (Figure 4.1a), although recreational angling effort appears to be higher in Cape Recife (W. Potts 2021, personal communication, 10 December) as it is situated adjacent to the metropole of Nelson Mandela Bay.

4.2.2 SAMPLING METHOD

As with the pilot study, baited remote underwater stereo-video systems (stereo-BRUVs) were used to carry out the sampling. The sampling method was the same as that described in Chapter 3 (3.2.2 Sampling method).

4.2.3 SAMPLING APPROACH

Historical stereo-BRUVs samples that were included in the analyses were collected during five separate field trips in February 2013 (Tsitsikamma MPA), September 2013 (Tsitsikamma MPA), February 2014 (Tsitsikamma MPA), July 2014 (Tsitsikamma MPA) and April 2015 (Cape Recife, Port Elizabeth). New samples were collected during six separate field trips in May 2019 (Tsitsikamma MPA), June 2019 (Tsitsikamma MPA and Goukamma MPA), October 2019 (Port Elizabeth), January 2020 (Cape St. Francis and Goukamma MPA), February 2020 (Cape Recife, port Elizabeth) and October 2020 (Cape St. Francis).

A stratified random sampling approach was followed. Sampling was restricted to depths of 15-25 m and all samples were either on or in close proximity to available reef habitat. The exact sampling locations were pre-determined using Create Random Points in ArcGIS version 10.4.1, with all points restricted to the known location of reef habitat (using existing bathymetric maps) and the minimum allowed distance set at 500 m from its nearest neighbour within each reef patch. The sampling procedure was further randomised by the sequence in which the sites were sampled during the day.

For each sample a stereo-BRUVs was deployed onto the sea floor to record footage for a minimum of 60 minutes. Approximately one kilogram of crushed pilchard (*Sardinops sagax*) bait was used for each deployment. Pilchards were used as they are the most effective and cost-efficient bait type to sample reef fish in South Africa (Halse 2016). The depths at which each sample was collected was recorded. Depth was measured using a GPS linked echo-sounder attached to the boat. Thus, depth is defined as distance from the sea surface to the ocean floor at the point where the stereo-BRUVs was deployed. The water temperature (in °C) during the deployment of each sample was also recorded. This was done using HOBO Onset temperature loggers which were attached to each stereo-BRUVs.

4.2.4 SAMPLE SELECTION

Samples were selected for analysis after confirming:

a) Habitat type: only samples where the stereo-BRUVs landed on reef were included.
b) The presence of *C. laticeps* in the video; only samples in which at least one *C. laticeps* appears in the field of view during the 60 minutes deployment were included. This was done as the focus of sample selection was getting data to measure the behaviour. Only one sample, from Cape Recife, was discarded as a result of this selection criterion.

Samples from the pilot study from depths between 15-25 m were also included to give a total of 32 samples from Tsitsikamma MPA, 21 from Goukamma MPA, 22 from Cape Recife (Port Elizabeth) and 23 from Cape St. Francis. Details of all included samples' date of collection, coordinates, depth and temperature can be found in APPENDIX 2 at the end of the thesis.

4.2.5 VIDEO ANALYSES

4.2.5.1 RELATIVE ABUNDANCE AND SIZE

The EventMeasure (Stereo) software version 3.54 (SeaGIS Pty Ltd.) was used to estimate the relative abundance of *C. laticeps* and measure the lengths of individuals. Relative abundance was measured as “MaxN”. MaxN is defined as the maximum number of individuals of a given species identified in a single video frame (Langlois et al. 2020). Length measurements (fork length) of each *C. laticeps* individual were taken from the MaxN frame. Length was derived from point-to-point fork length measurements.

4.2.5.2 BEHAVIOUR

For each stereo-BRUVs sample, the time taken for the first *C. laticeps* to (1) arrive in the field of view and (2) feed on the bait was recorded. The time for the first *C. laticeps* to arrive was defined as the time between the stereo-BRUVs settling on the sea floor and the first frame in which a *C. laticeps* individual appears. The time for the first *C. laticeps* to feed was taken as the time between the first *C. laticeps* arriving and the first frame in which a *C. laticeps* takes a bite of the bait canister.

A range of behavioural observations were made using the software BORIS version 7.6.1 (Friard & Gamba 2016). Based on the findings of the pilot study in Chapter 3, six different behaviours were defined and categorised as either a point or a state event as required by the BORIS interface. Point events are behaviours that have an occurrence but no duration. Their resulting output is a count of how many times the behaviour occurred. State events have a duration, with a start and an end. Their resulting output is a time (in seconds) of how long the behaviour occurred. Four behaviours were point events: feeding on bait, chasing, fleeing and spawning (Table 4.1). Although spawning was not observed in the pilot study, this could have been due to the low sample size and for this reason, spawning was included in the analysis.

Two behaviours were state events: feeding duration and time spent in the field of view (Table 4.1). Feeding duration was measured for individuals which fed on the bait more than once and a feeding rate was calculated for individuals which fed more than once (Table 4.1).

Table 4.1: List of behaviours measured from the baited remote underwater stereo-video system samples.

Category	**Behaviour**	**Definition**	**Unit of measurement**	**Data type**
Feeding	Feeding on bait	Focal fish is observed feeding, the head is inclined towards the bait canister and the jaws are in contact with the bait canister.	Individual	Count of events per individual
	Feeding duration	Start – first frame in focal fish feeds on bait End – last frame focal fish feeds on bait	Individual	Time in seconds
	Feeding rate	The number of times the focal fish fed on the bait divided (÷) by its feeding duration.	Individual	Bites per second
Agonistic	Chasing	Focal fish chases another fish.	Individual	Count of events per individual
	Flee	Focal fish quickly swims away from another fish in response to received aggressive displays.	Individual	Count of events per individual
Reproductive	Spawning	Focal fish displays the sequence of courtship and spawning behaviours described by Buxton (1990) and Davis (1996).	Individual	Count of events per individual
Persistence	Time in field of view	Start – first frame focal fish appears in. End - last frame focal fish appears in.	Individual	Time in seconds
Response time	Time to arrive	First frame in which a *C. laticeps* appears.	Sample	Time in seconds
	Time to 1st feeding	First frame in which a *C. laticeps* feeds on the bait.	Sample	Time in seconds

At the MaxN frame of each video sample, each *C. laticeps* was labelled from 1 – MaxN (See Chapter 3, Figure 3.3). For each individual, the footage was rewound to the first frame in which it appeared. The behaviour of the individual was then observed and coded using the defined ethogram, from the first frame the individual appeared to the last frame where it was visible.

Table 4.2: Full list of explanatory variables used in the statistical analyses.

Covariate	Definition	Values
Sample	The unique name given to each sample.	98 unique sample codes
Management	Whether sampled was collected inside or outside an MPA.	MPA; Exploited
Location	The geographical location of where a sample was collected.	Tsitsikamma; Goukamma; Port Elizabeth; Cape St. Francis
Season	The season in which samples were collected.	Spring/Summer; Autumn/Winter
Depth	The distance from the sea surface to the ocean floor at the point where the stereo-BRUV was deployed.	15.0-24.8 m
Temperature	Average temperature during the 60 minute stereo-BRUV deployment.	10.13-17.86 °C
Visibility	The visible distance from the stereo-BRUV that a fish can be accurately identified from both cameras. Estimated using a 3D point in EventMeasure.	843.54 – 4770.23 m
Water column	Portion of field of view showing the pelagic water column relative to the seafloor. Estimated using Vidana (www.marinespatialecologylab.org).	0 – 100%
Reef profile	Defined by the height of visible reef structures: if <1m low profile, if >1m high profile.	Low profile reef; High profile reef
MaxN	MaxN of *C. laticeps* in the video sample.	2 – 19
Size	Length of individual *C. laticeps.*	121.096 – 501.035 mm

4.2.6 STATISTICAL ANALYSES

All statistical analyses were conducted in the R environment version 4.0.3 (R Core Team 2018) using the RStudio version 1.2.1335 interface (*RStudio: Integrated Development Environment for R* 2018). Prior to modelling, detailed exploratory data analyses were conducted following the protocol by Zuur et al. (2010). The purpose of the data exploration was to understand the nature of the data. This protocol includes checking for collinearity and interactions between covariates (see Table 4.2 for the full list), outliers in the data, zero-inflation, normality of the response variables, spatial patterns and the balance of the data.

As in the pilot study, the behavioural response variables represented two core types of data based on the unit of measurement (Table 4.1). 'Time to arrive' and 'time to first feeding' were both measured at the sample level, while the remaining behaviours were measured for individual fish, nested within each sample. As multiple individual fish were recorded from a sample this creates dependency in the data. Consequently, mixed effect models, with sample included as a random effect, were used to analyses patterns in the individual level behavioural response data. This dependency was not present for the behaviours recorded at the sample level and these responses were analysed using appropriate generalised regression techniques.

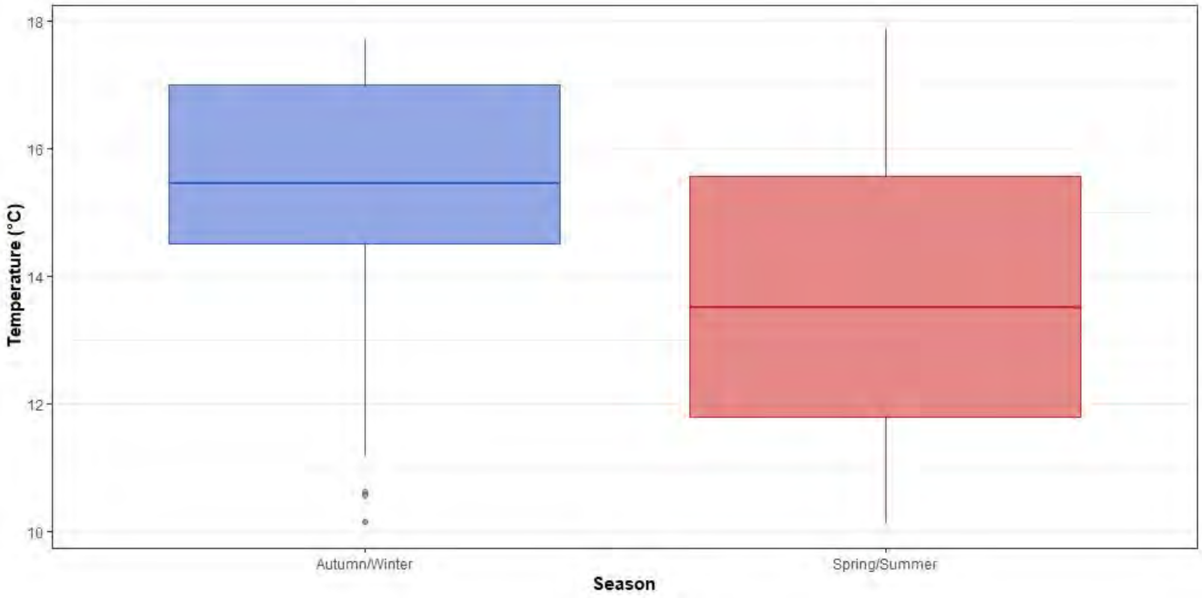

Figure 4.3: The temperature of the baited remote underwater stereo-video system samples included in the analysis, by season. The bold line in each box represents the mean temperature for the season. Circles outside of the boxplot indicate outliers.

The data exploration suggests that there is some covariance between season and temperature. Temperature was more stable in autumn/winter but more variable in spring/summer (Figure 4.3). The mean temperature in autumn/winter was higher (15.11 ± 2.23 °C) than the mean temperature in spring/summer (13.11 ± 2.23 °C). Temperatures below 11 °C in autumn/winter were anomalous. The covariance between season and temperature was therefore considered when interpreting model outputs.

Based on the data exploration GAMs (generalized additive models) and GAMMs (generalised additive mixed effects models) were applied to test the effect of the predictor variables (full list in Table 4.2) on MaxN and behavioural responses (Table 4.1). The GAMs and GAMMs were fitted using the mgcv package (Wood 2011, 2017). The error distribution (family) used in each model was based on the type of response variable and over-dispersion parameters. To investigate MaxN, models were fitted with the Poisson distribution. Tests for over dispersion revealed that the variable was equal to the mean so Poisson was suitable. To investigate 'time to arrive' and 'time to first feeding' models were fitted with the Tweedie distribution. The behaviours 'feed on bait', 'chasing and 'fleeing had high zero-inflation (>65%). Thus, the data were converted to presence/absence and models were fitted with the binomial distribution. For the behaviours 'time in field of view' and 'feeding rate' models were fitted with the Tweedie distribution.

Two sets of models were applied for MaxN and each behavioural response; the first to test if a management scale effect (MPA and exploited) was detectable and the second to test if *C. laticeps* behaviour was better described at the location scale (Tsitsikamma MPA, Goukamma MPA, Cape Recife and Cape St. Francis). This was done as the management level analysis might have hidden location-specific effects. To investigate the effect of management, location included as a random effect in a GAMM, as location was nested within management. The random effect was included using the bs= "re" term in the mgcv package (Wood 2008). To investigate the effect of location, GAMs were applied for the response variables MaxN, time to arrive and time to first feeding, while GAMMs were applied for the individual level response variables. In these models location was included as a main effect and management excluded from the model. For the individual level response variables data exploration revealed that *C. laticeps* size showed a positive relationship with the presence of most behaviours. Thus, individual *C. laticeps* size was included in the models of the BORIS behaviours to account for its effect.

Table 4.3: Structure of models applied to investigate *Chrysoblephus laticeps* MaxN and behaviour. For each response variable and main effect, the model with the lowest AIC score was selected for the next stage of model selection.

Response variable	**Main effect**	**Model**	**Model structure**
MaxN	Management	1	gam(MaxN ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(Temperature) + s(Location, bs="re") + Management)
		2	gam(MaxN ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(Temperature, by = Management, bs="tp") + s(Location, bs="re") + Management)
	Location	1	gam(MaxN ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(Temperature) + Location)
		2	gam(MaxN ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(Temperature, by = Location, bs="tp") + Location)
Y1 = Time to arrive, Time to feed	Management	1	gam(Y1 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(MaxN) + s(Depth) + s(Temperature) + s(Location, bs="re") + Management)
		2	gam(Y1 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(MaxN) + s(Depth) + s(Temperature, by = Management, bs="tp") + s(Location, bs="re") + Management)
	Location	1	gam(Y1 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(MaxN) + s(Depth) + s(Temperature) + Location)
		2	gam(Y1 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(MaxN) + s(Depth) + s(Temperature, by = Location, bs="tp") + Location)
Y2 = Feed on bait, Chasing, Fleeing, Time in field of view, Feeding rate	Management	1	gam(Y2 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(MaxN) + s(Temperature) + s(Size) + s(Sample, bs="re") + s(Location, bs="re") + Management)
		2	gam(Y2 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(MaxN) + s(Temperature, by = Management, bs="tp") + s(Size) + s(Sample, bs="re") + s(Location, bs="re") + Management)
		3	gam(Y2 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(MaxN) + s(Temperature, by = Management, bs="tp") + s(Size, by = Management, bs="tp) + s(Sample, bs="re") + s(Location, bs="re") + Management)
		4	gam(Y2 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(MaxN) + te(Temp, Size, bs="tp")+ s(Sample, bs="re") + s(Location, bs="re") + Management)
	Location	1	gam(Y2 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(MaxN) + s(Temperature) + s(Size) + s(Sample, bs="re") + Location)
		2	gam(Y2 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(MaxN) + s(Temperature, by = Location, bs="tp") + s(Size) + s(Sample, bs="re") + Location)
		3	gam(Y2 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(MaxN) + s(Temperature, by = Location, bs="tp") + s(Size, by = Location, bs="tp) + s(Sample, bs="re") + Location)
		4	gam(Y2 ~ s(Visibility) + s(Water column) + Reef profile + Season + s(Depth) + s(MaxN) + te(Temp, Size, bs="tp")+ s(Sample, bs="re") + Location

A two-stage process was used to identify the best-fit model structure. The first stage aimed to identify the optimal specification of the interaction terms in the GAMs and GAMMs. Interaction terms were added to the full model to determine if the effect of water temperature and size were consistent among locations and management types (Table 4.3). The models including the various interaction terms and a full model without interaction terms were then compared using Akaike Information Criterion (AIC) scores. The model with the lowest AIC score was chosen and used in the model selection process detailed in the following paragraph.

The second stage of model selection was implemented to identify the optimal model structure with the aim to maximize deviance explained and minimise complexity. This was carried out with the R package MuMIn using the dredge function (Bartoń 2020). Here a full model was fitted (i.e. a model containing all the relevant covariates) and comparing the AIC scores for all possible model combinations (Logan 2010). The model with the lowest AIC score was regarded as the best-fit. The best-fit model was then explored further to determine model fit and the significance of each covariate and its contribution to the model (Zuur et al. 2009). Temperature and management or location, were forced to be included in the best-fit model to ensure that the research questions could be answered. Wald’s tests were then carried out on each model to determine the significance of each covariate.

To visualise the relationships between the important explanatory variables and the behavioural responses, predicted datasets were created based on the model coefficients. Model predictions were used as they allow you to predict the value and confidence intervals for the response variable using standard values for the other covariates included in the model (e.g. size) across different levels of a factor (e.g. management) thereby allowing unbiased comparisons. When plotting the effects of management and location all other covariates included in the model were set to their mean value. When plotting the effect of temperature, all other covariates included in the model were set to their mean value. Then, if there were any other relevant significant covariates in the model, their predicted effect was also visualised. Plots were created using ggplot2 (Wickham 2016).

4.3 RESULTS

In total 98 stereo-BRUV samples were included in the analyses (Table 4.4) and the behaviour of 627 *C. laticeps* individuals assessed. Not all the individuals at MaxN could be measured as some fish only appeared in one video of the stereo-pair, were too far away from the camera or the angle of the fish did not allow an accurate measurement to be taken. Out of the 627 individuals whose behaviour was assessed 310 could be measured.

Table 4.4: Distribution of samples and the number of *Chrysoblephus laticeps* measured among the four locations as well as the minimum (min) and maximum (max) temperatures of samples collected at each location.

Location	**Total number of samples**	**Total number of *C. laticeps* measured**	**Min temperature (°C)**	**Max temperature (°C)**
Tsitsikamma MPA	32	82	10.15	17.70
Goukamma MPA	21	103	11.57	16.36
Cape Recife	22	51	11.20	17.86
Cape St. Francis	23	74	10.13	14.80

Spawning behaviour was not observed in any of the videos and could not be modelled. All other behaviours were observed in the videos and had enough observations to be modelled. The model structure and AIC scores of the best-fit models applied to the MaxN and behavioural data is detailed in Table 4.5.

Table 4.5: Covariates included in the best-fit GAMs (generalized additive models) and GAMMs (generalised additive mixed effect models) applied to investigate relative abundance (MaxN) and behaviour of *Chrysoblephus laticeps* following model selection. For each response variable two models were made, with the first testing for an overall Management effect (white background) and the second a Location effect (grey background).

Model	Error distribution	Best-fit structure	AIC score	Excluded explanatory variables
1	Poisson	MaxN ~ s(Depth) + Season + Management + s(Location, bs="re") + s(Temperature, by=Management, bs="tp")	442	Visibility, Water column, Reef profile
2	Poisson	MaxN ~ s(Depth) + s(Temperature, by=Location, bs="tp") + s(Visibility) + Season + Location	439	Water column, Reef profile
3	Tweedie	Time to arrive ~ s(MaxN) + s(Water column) + Season + Management + s(Location, bs="re") + s(Temperature)	965	Visibility, Reef profile, Depth
4	Tweedie	Time to arrive ~ s(MaxN) + s(Water column) + Location + s(Temperature)	966	Visibility, Reef profile, Season, Depth
5	Tweedie	Time to feed ~ s(MaxN) + s(Water column) + Management + s(Location, bs="re") + s(Temperature)	1208	Visibility, Reef profile, Season, Depth
6	Tweedie	Time to feed ~ Reef profile + s(Depth) + Season + Location + s(Temperature)	1209	Visibility, Water column, MaxN
7	Binomial	Feed on bait ~ s(Depth) + s(Size, by=Management, k=4, bs="tp") + s(Visibility) + Management + s(Location, bs="re") + s(Sample, bs="re") + s(Temperature, by=Management, k=4, bs="tp")	342	Water column, Reef profile, Season, MaxN
8	Binomial	Feed on bait ~ s(Size, by=Location, k=5, bs="tp") + s(Visibility) + Location + s(Sample, bs="re") + s(Temperature, by=Location, k=5, bs="tp")	344	Water column, Reef profile, Season, Depth, MaxN
9	Binomial	Chase ~ s(Size) + s(Visibility) + Management + s(Location, bs="re") + s(Sample, bs="re") + s(Temperature)	283	Water column, Reef profile, Depth, Season, MaxN
10	Binomial	Chase ~ s(MaxN) + s(Size, by=Location, k=4, bs="tp") + Location + s(Sample, bs="re") + s(Temperature, by=Location, k=6, bs="tp")	293	Water column, Reef profile, Depth, Season
11	Binomial	Flee ~ s(Depth) + s(MaxN) + s(Size, by=Management, k=6, bs="tp") + Management + s(Location, bs="re") + s(Sample, bs="re") + s(Temperature, by=Management, k=6, bs="tp")	327	Visibility, Water column, Reef profile, Season
12	Binomial	Flee ~ s(MaxN) + s(Size, by=Location, bs="tp") + s(Visibility) + Location + s(Sample, bs="re") + s(Temperature, by=Location, bs="tp")	314	Water column, Reef profile, Depth, Season
13	Tweedie	Feeding rate ~ s(Visibility, k=3) + s(Water column, k=3) + Management + s(Location, bs="re") + s(Sample, bs="re") + s(Temperature, k=6)	456	Reef profile, Depth, Season, MaxN, Size
14	Tweedie	Feeding rate ~ s(MaxN, k=5) + s(Water column, k=3) + Location + s(Sample, bs="re") + s(Temperature, by=Location, k=5, bs="tp")	454	Visibility, Reef profile, Depth, Season, Size
15	Tweedie	Time in field of view ~ s(Depth) + s(MaxN) + s(Size) + s(Water column) + Management + s(Location, bs="re") + s(Sample, bs="re") + s(Temperature)	2916	Visibility, Reef profile, Season
16	Tweedie	Time in field of view ~ s(Size, by=Location, bs="tp") + s(Water column) + Location + s(Sample, bs="re") + s(Temperature, by=Location, bs="tp")	2909	Visibility, Reef profile, Depth, Season, MaxN

4.3.1 SIZE

The mean length of *C. laticeps* was 277.1 mm fork length (FL) within MPAs and 272.4 mm FL in the exploited areas. The size structure of exploited *C. laticeps* populations was similar to that of protected populations (Figure 4.4), and size did not differ significantly between exploited and protected areas (two-sample t-test with all assumptions met: *t* = -0.56, *p* = 0.57). Notably, the largest measured sizes of *C. laticeps* were in the MPAs.

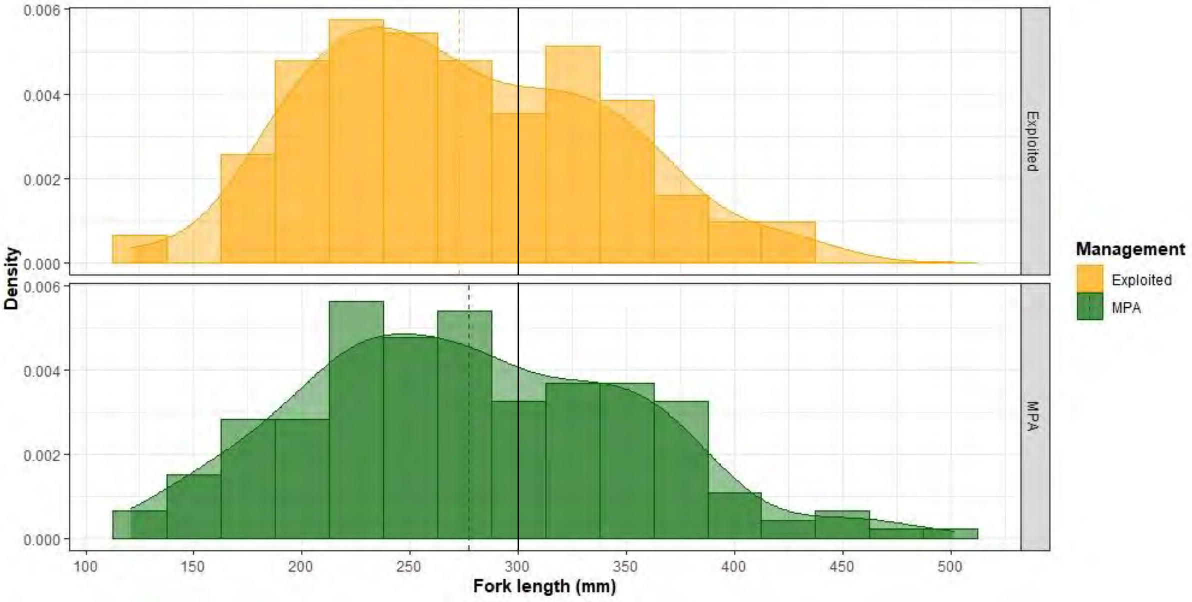

Figure 4.4: Length frequency distribution of *Chrysoblephus laticeps* measured from the marine protected areas (MPA) and at the exploited sites. Dashed line represents the mean fork length. Solid black line represents the minimum landing size of *C. laticeps.*

The mean size of *C. laticeps* was 280.5 ± 73.7 mm FL at Tsitsikamma MPA, 273.9 ± 77.9 mm FL at Goukamma MPA, 254.9 ± 53.8 mm FL at Cape Recife and 284.4 ± 71.9 mm FL at Cape St. Francis. The size structure of *C. laticeps* was similar at Cape St. Francis, Goukamma and Tsitsikamma, although the larger size classes were more common within the two MPAs. Cape Recife had a greater proportion of smaller sized *C. laticeps* (Figure 4.5). Cape Recife also had comparatively fewer largely sized *C. laticeps* than the other three locations, with the largest individual measured being 361.5 mm FL (compared to 437.0 mm FL at Cape St. Francis, 467.4 mm FL at Tsitsikamma and 501.0 mm FL at Goukamma).

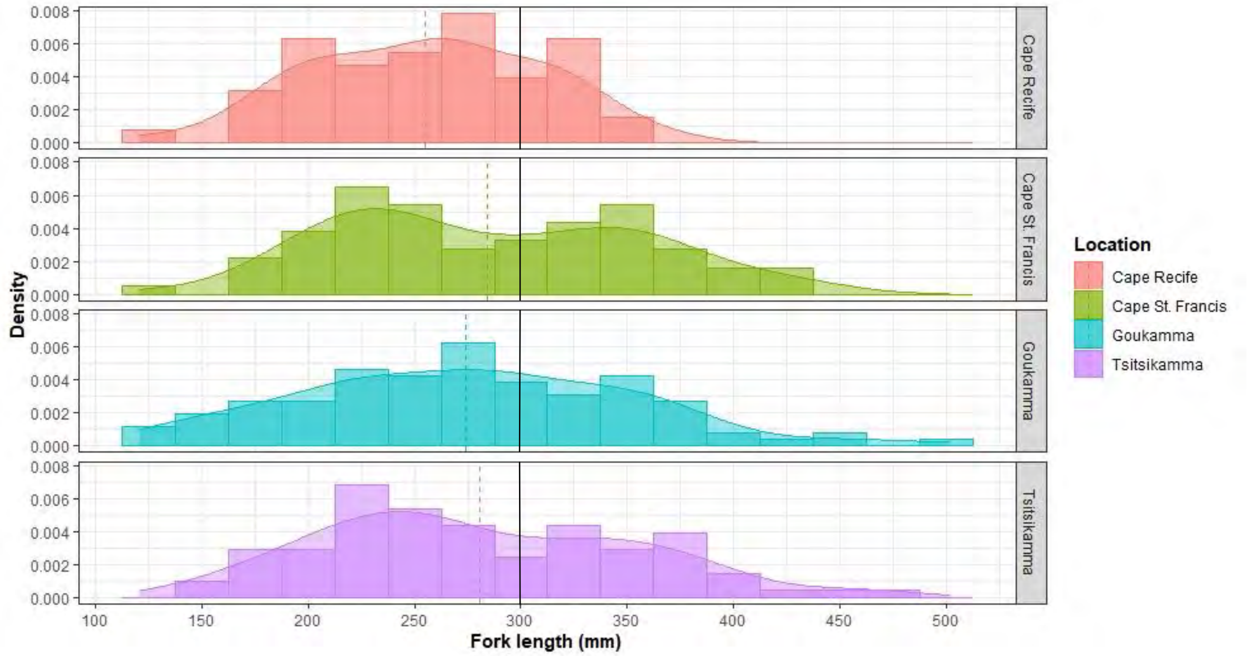

Figure 4.5: Length frequency distribution of *Chrysoblephus laticeps* measured from Cape Recife, Cape St. Francis, Goukamma MPA and Tsitsikamma MPA. Dashed line represents the mean fork length at each Location. Solid black line represents the minimum landing size of *C. laticeps.*

4.3.2 MAXN

The best-fit model investigating the effect of management on MaxN explained 51.8% of the observed variability. The Wald's test found that MaxN was not influenced by management (p = 0.774; Figure 4.6A), with the mean (± standard deviation) MaxN from the raw data being 7.0 (± 3.3) within the MPAs and 5.6 (± 2.7) in the fished areas. In contrast, the random effect of location was significant (Table 4.6) highlighting local scale differences. Temperature did have a significant effect on MaxN, in both the MPA and exploited management zones (Table 4.6). In MPAs, the MaxN increased with increasing temperature until approximately 14 °C, beyond which it steadily declined (Figure 4.6B). In exploited areas MaxN increased with increasing temperature until 16 °C, beyond which it remained fairly consistent (Figure 4.6B). However, with both trends there was considerable uncertainty in the estimates as indicated by the wide confidence intervals (Figure 4.6B).

Table 4.6: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of *Chrysoblephus laticeps* MaxN at the management scale (Table 4.5: Model 1). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Season	1	13.477	<0.001	***
Management	1	0.082	0.774	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Depth	1.000	6.065	0.014	*
Location	1.862	22.648	<0.001	***
Temperature: Management-Exploited	2.007	18.772	<0.001	***
Temperature: Management-MPA	2.925	11.036	0.019	*

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

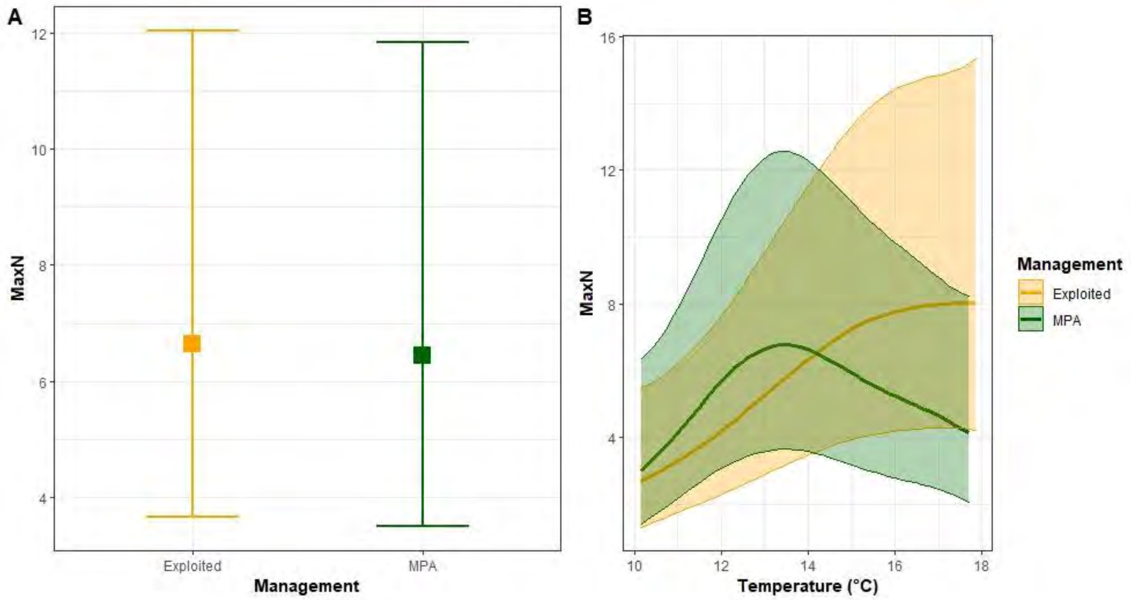

Figure 4.6: Predicted results from the generalised additive mixed model (Table 4.5: Model 1) showing (A) the effect of management on relative abundance (MaxN), holding all other covariates constant and (B) the effect of temperature on MaxN, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

The best-fit model investigating the effect of location on MaxN explained 55.7% of the observed variability. Location had a significant effect on MaxN (Wald's test, p <0.001), with the mean (± standard deviation) MaxN from the raw data being 6.2 (± 2.7) at Tsitsikamma, 8.4 (± 3.6) at Goukamma, 4.8 (± 2.1) at Cape Recife and 6.4 (± 3.0) at Cape St. Francis. Based on the predicted plots (that are based on average water temperature), MaxN was found to be significantly lower at Cape Recife compared to Cape St. Francis and Goukamma, but not Tsitsikamma (Figure 4.7A). In addition, MaxN was predicted to be significantly higher at Cape St. Francis compared to Tsitsikamma and Cape Recife, but not Goukamma (Figure 4.7A). Temperature had a significant effect on MaxN at all locations expect Goukamma (Table 4.7). The effect of temperature on MaxN was most pronounced at Cape St. Francis, with MaxN increasing significantly with increasing temperature (Figure 4.7B). At Cape Recife the rate at which MaxN increased with increasing temperature was much lower (Figure 4.7B). At Tsitsikamma MaxN steadily increased with increasing temperature until about 14°C, beyond which it declined (Figure 4.7B). At Goukamma MaxN decreased slightly with increasing temperature (Figure 4.7B)

Table 4.7: Results of the Wald's test for the best-fit generalised additive model investigating determinants of *Chrysoblephus laticeps* MaxN at the location scale (Table 4.5: Model 2). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value

Parametric terms	***df***	**Chi.sq**	***p-value***	
Season	1	10.77	0.001	**
Location	1	44.89	<0.001	***
Smooth terms	***edf***	**Chi.sq**	***p***	
Depth	1.000	6.737	0.009	**
Temperature: Location-Cape Recife	1.000	5.383	0.020	*
Temperature: Location-Cape St. Francis	1.000	21.798	<0.001	***
Temperature: Location-Goukamma	1.000	0.362	0.548	ns
Temperature: Location-Tsitsikamma	2.453	9.846	0.020	*
Visibility	1.000	2.777	0.096	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

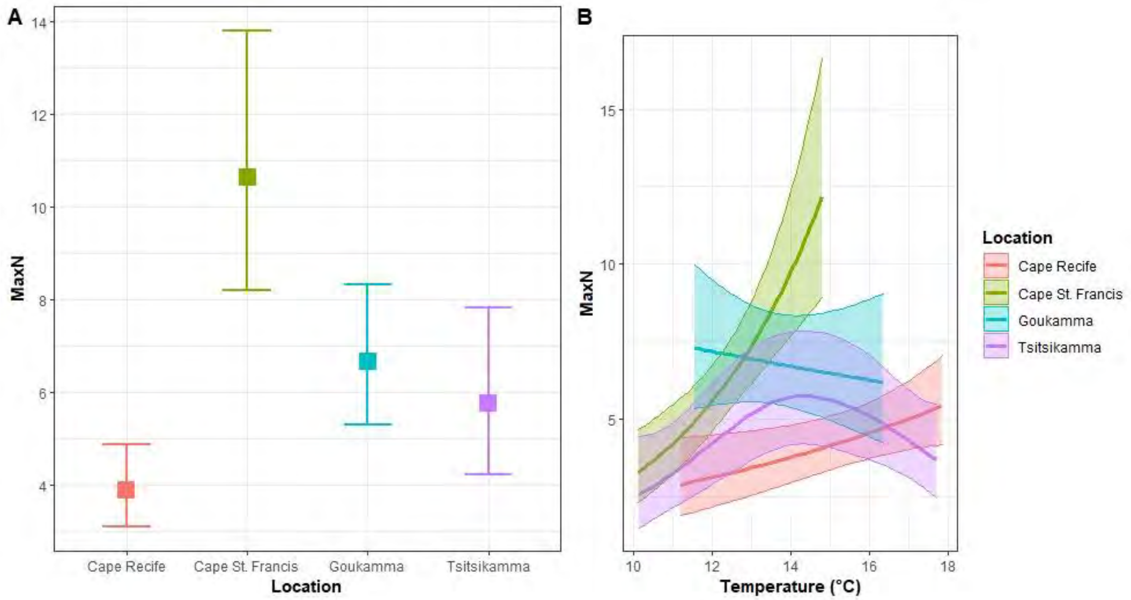

Figure 4.7: Predicted results from the generalised additive model (Table 4.5: Model 2) showing (A) the effect of location on relative abundance (MaxN), holding all other covariates constant and (B) the effect of temperature on MaxN, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

4.3.3 TIME TO ARRIVE

The best-fit model investigating the effect of management on the time to arrive explained 51.6% of the observed variability. Time to arrive was not influenced by management (Wald's test, *p* = 0.894; Table 4.8, Figure 4.8A). While there was a notable difference in the mean time to arrive between MPAs (52.9 ± 70.6 s) and exploited areas (129.1 ± 289.8 s), there was considerable variability around the means and the effect of management was not significant. Temperature did have a significant effect on time to arrive (Wald's test, *p* <0.001). The model selection process excluded the interaction effect between management and temperature, indicating that the effect of temperature was consistent between the management zones (Table 4.3). The time to arrive decreased with increasing temperature until about 14°C, beyond which it was consistent (Figure 4.8B). The relative abundance of *C. laticeps* (MaxN) had a significant negative effect on time to arrive (Wald's test, *p* = 0.015; Figure 4.8C). The random effect of location was not significant (Table 4.8).

Table 4.8: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of time to arrive for *Chrysoblephus laticeps* at the management scale (Table 4.5: Model 3). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Season	1	2.016	0.159	ns
Management	1	0.018	0.894	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
MaxN	1.656	4.384	0.015	*
Water column	3.928	4.298	0.002	**
Location	0.001	0.000	0.528	ns
Temperature	2.595	13.103	<0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

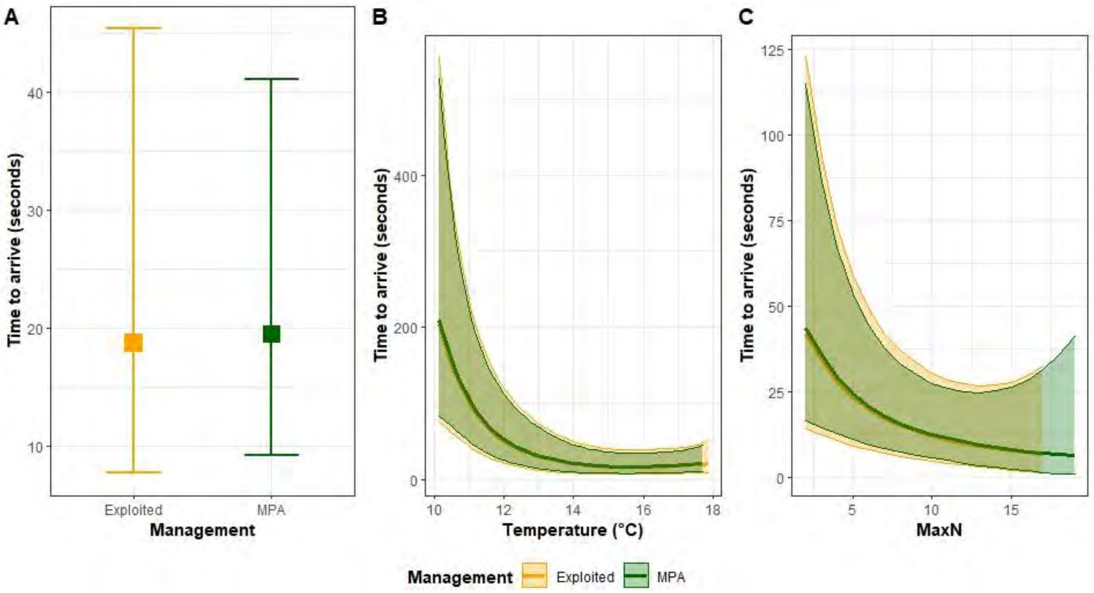

Figure 4.8: Predicted results from the generalised additive mixed model (Table 4.5: Model 3) showing (A) the effect of management on the time to arrive, holding all other covariates constant, (B) the effect of temperature on the time to arrive, holding all other covariates constant and (C) the effect of relative abundance (MaxN) on the time to arrive, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

At the different locations, the mean time to arrive from the raw data was 58.0 ± 78.6 s at Tsitsikamma, 45.2 ± 57.3 s at Goukamma, 53.9 ± 80.6 s at Cape Recife and 201.1 ± 388.1 s at Cape St. Francis. The best-fit model investigating the effect of location on the time to arrive explained 52.4% of the observed variability however, the effect of location did not have a significant effect on the time to arrive (Wald's test, $p = 0.361$; Figure 4.9A). When predicting time to arrive based on standard values for water column, MaxN and temperature the effect of location remained insignificant (Figure 4.9A). Temperature had a significant effect on time to arrive (Wald's test, $p < 0.001$) and was consistent among locations (Interaction excluded from best-fit model; Table 4.3). The time to arrive decreased drastically with increasing temperature until about 13°C, beyond which it fairly consistent (Figure 4.9B). The effect of MaxN on time to arrive was significant (Wald's test, $p = 0.004$) and consistent among locations (interaction excluded from best-fit model; Table 4.3). The time to arrive decreased steadily with increasing relative abundance (MaxN) of *C. laticeps* (Figure 4.9C).

Table 4.9: Results of the Wald's test for the best-fit generalised additive model investigating determinants of time to arrive for *Chrysoblephus laticeps* at the location scale (Table 4.5: Model 4). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Location	3	1.082	0.361	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
MaxN	1.903	4.598	0.004	**
Water column	3.848	8.474	0.001	**
Temperature	2.692	4.598	<0.001	***

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

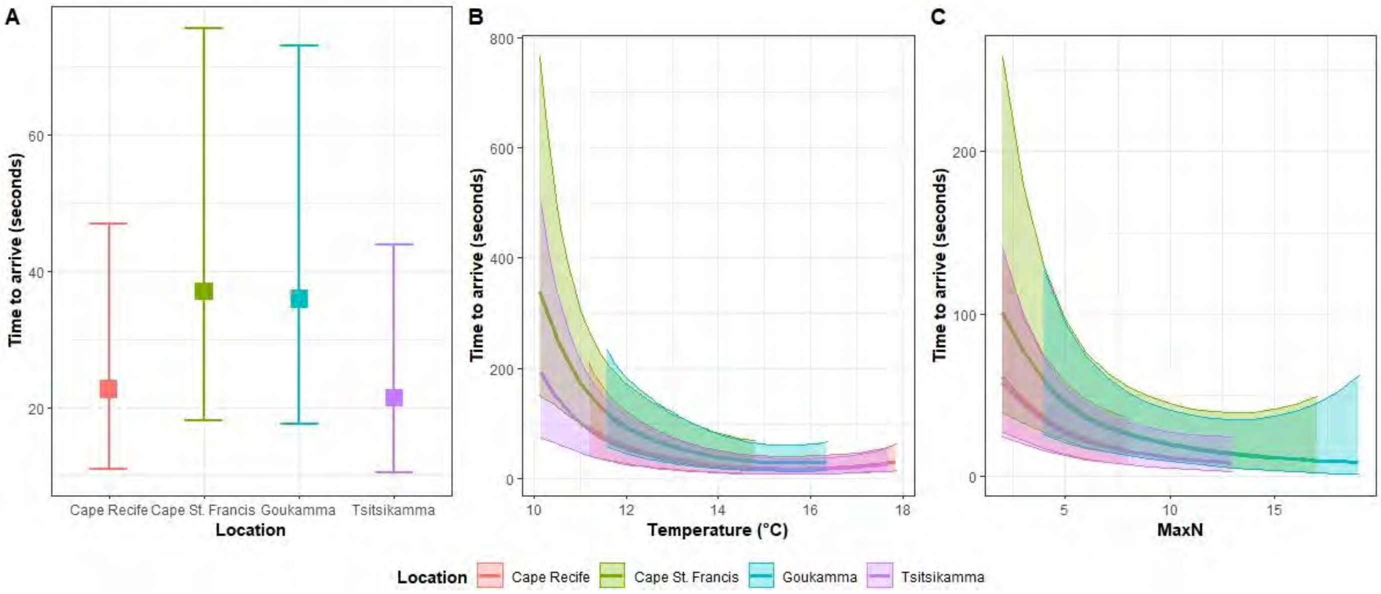

Figure 4.9: Predicted results from the generalised additive model (Table 4.5: Model 4) showing (A) the effect of location on the time to arrive, holding all other covariates constant, (B) the effect of temperature on the time to arrive, holding all other covariates constant and (C) the effect of relative abundance (MaxN) on the time to arrive, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

4.3.4 TIME TO FEED

The best-fit model investigating the effect of management on the time to feed explained 20.6% of the observed variability. Management did not have a significant effect on the time to feed (Wald's test, $p = 0.050$), with the mean time to feed from the raw data being 231.8 ± 426.6 s in MPAs and 306.5 ± 401.8 s in exploited areas. When predicting time to feed based on standardised values for MaxN, water column and temperature there was no clear effect of management, as indicated by the overlapping confidence intervals (Figure 4.10A). Similarly, temperature did not have a significant effect on the time taken to feed (Wald's test, $p = 0.063$; Figure 4.10B). MaxN, the abundance of conspecifics, had a significant effect on time taken to feed (Wald's test, $p = 0.011$). Generally, the time to feed was longer at lower MaxN and decreased as MaxN increased (Figure 4.10C). The model selection process excluded the interaction effect between management and MaxN indicating that the effect of MaxN was consistent between the management zones (Table 4.3). The random effect of location was not significant (Table 4.10).

Table 4.10: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of time to feed by *Chrysoblephus laticeps* at the management scale (Table 4.5: Model 5). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Management	1	3.943	0.050	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
MaxN	3.125	3.397	0.011	*
Water column	1.000	4.618	0.034	*
Location	0.000	0.000	0.866	ns
Temperature	1.000	3.561	0.063	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

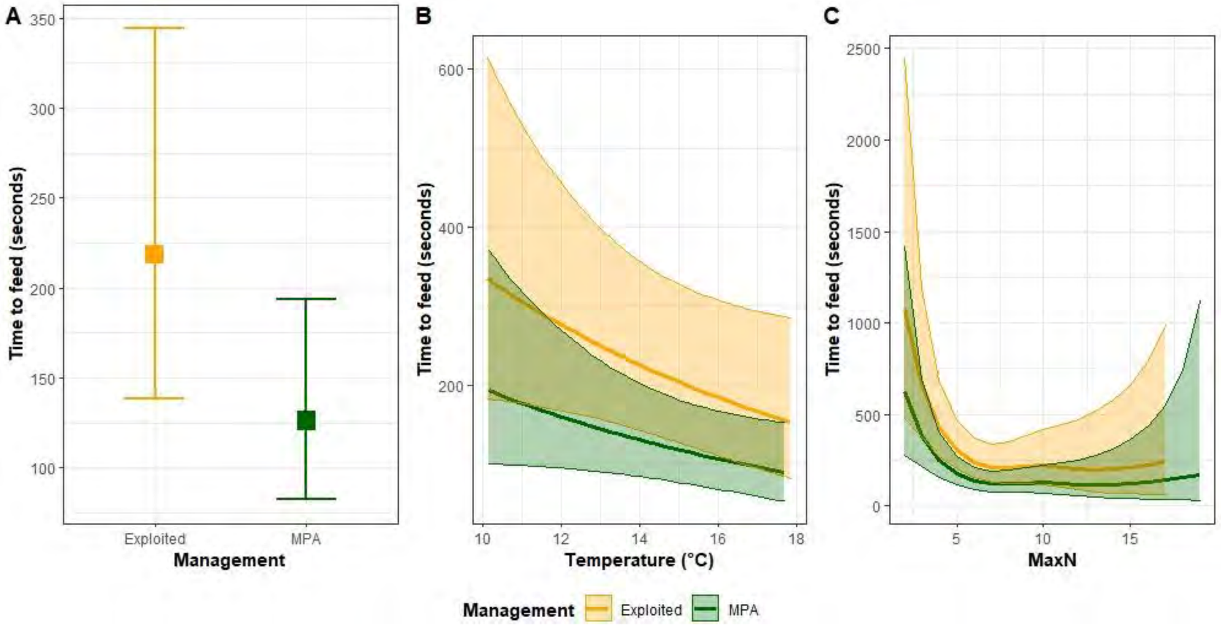

Figure 4.10: Predicted results from the generalised additive mixed model (Table 4.5: Model 5) showing (A) the effect of Management on the time to feed, holding all other covariates constant, (B) the effect of temperature on the time to feed, holding all other covariates constant and (C) the effect of relative abundance (MaxN) on the time to feed, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

The best-fit model investigating the effect of location on time to feed explained 23.5% of the observed variability. Time to feed was not influenced by location (Wald's test, $p = 0.218$; Figure 4.11A), with the mean time to feed from the raw data being 291.8 ± 528.5 s at Tsitsikamma, 143.3 ± 176.5 s at Goukamma, 264.3 ± 324.7 s at Cape Recife and 342.9 ± 462.8 s at Cape St. Francis. The Wald's test found that temperature did not have a significant effect on time to feed ($p = 0.821$, Figure 4.11B).

Table 4.11: Results of the Wald's test for the best-fit generalised additive model investigating determinants of time to feed by *Chrysoblephus laticeps* at the location scale (Table 4.5: Model 6). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Reef profile	1	7.129	0.009	**
Season	1	3.672	0.059	ns
Location	3	1.508	0.218	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Depth	2.889	3.896	<0.001	***
Temp	1.023	0.066	0.821	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

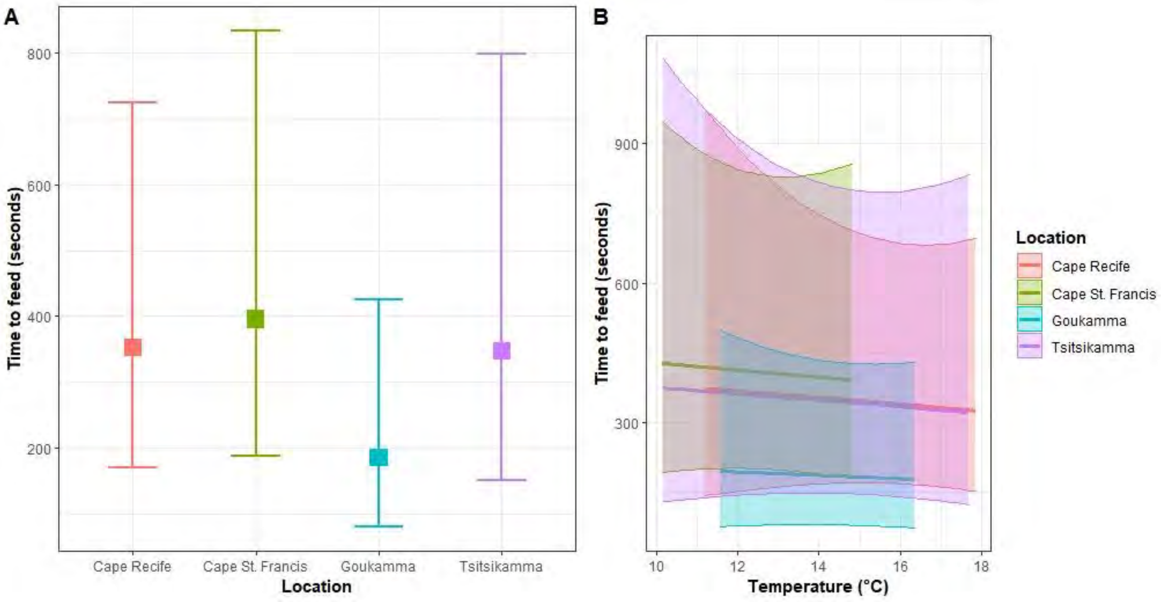

Figure 4.11: Predicted results from the generalised additive model (Table 4.5: Model 6) showing (A) the effect of location on the time to feed, holding all other covariates constant and (B) the effect of temperature on the time to feed, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

4.3.5 FEEDING ON BAIT

The best-fit model investigating the effect of management on the probability of feeding on bait explained 17.9% of the observed variability. Management did not have a significant effect on the probability of feeding on bait (Wald's test, *p* = 0.830; Figure 4.12A), with the mean probability of feeding on bait from the raw data being 0.33 ± 0.47 in MPAs and 0.30 ± 0.46 in exploited areas. The Wald's test found that temperature did not have a significant effect on the probability of feeding on bait, regardless of management type (Table 4.12; Figure 4.12B). Size did have a significant effect on the probability of feeding on bait, and this effect varied across management zones (Table 4.12). Generally, the probability of feeding on bait increased with increasing size (Figure 4.12C). However, within MPAs as size increased beyond 400 mm FL the probability of feeding on bait decreased slightly (Figure 4.12C). The random effects of sample and location were not significant (Table 4.12).

Table 4.12: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of the probability that *Chrysoblephus laticeps* fed on bait at the management scale (Table 4.5: Model 7). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Management	1	0.046	0.830	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Depth	1.000	2.157	0.142	ns
Size: Management-Exploited	2.655	10.696	0.013	*
Size: Management-MPA	2.215	20.646	<0.001	***
Visibility	1.000	9.217	0.002	**
Location	1.517	10.850	<0.001	***
Sample	$2.69\text{x}10^{-04}$	0.000	0.828	ns
Temperature: Management-Exploited	1.644	1.898	0.424	ns
Temperature: Management-MPA	1.000	1.426	0.232	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

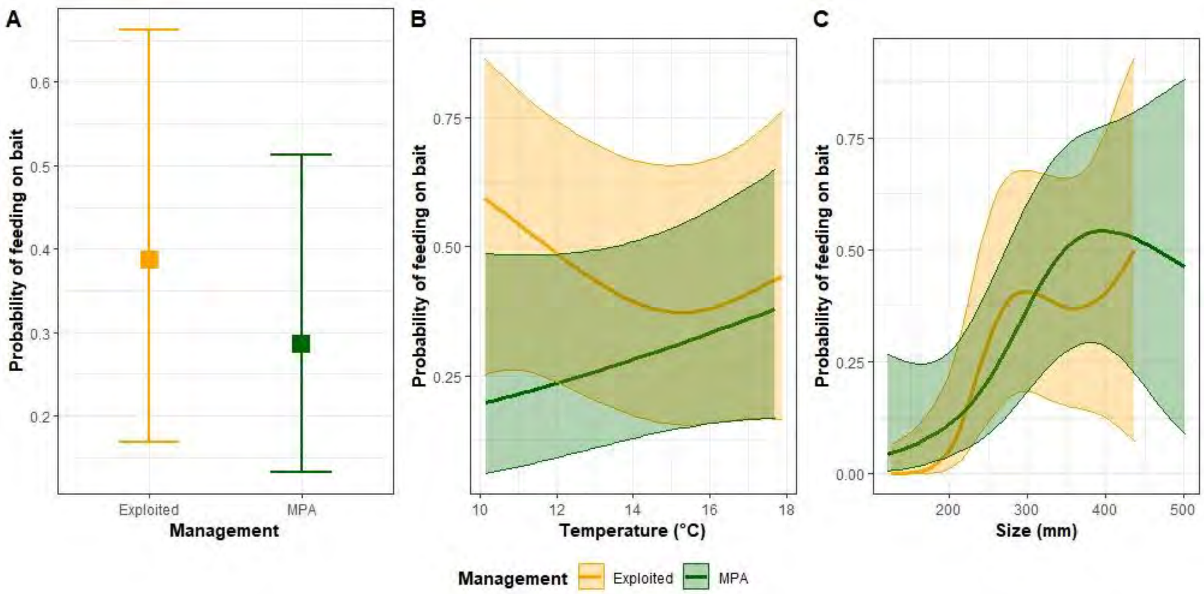

Figure 4.12: Predicted results from the generalised additive mixed model (Table 4.5: Model 7) showing (A) the effect of management on the probability of feeding, holding all other covariates constant, (B) the effect of temperature on the probability of feeding, holding all other covariates constant and (C) the effect of size on the probability of feeding, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

The best-fit model investigating the effect of location on the probability of feeding on bait explained 19.7% of the observed variability. Location had a significant effect on the probability of feeding on bait (Wald's test, *p* = 0.003), with the mean probability of feeding on bait from the raw data being 0.43 ± 0.48 in Tsitsikamma, 0.25 ± 0.43 in Goukamma, 0.33 ± 0.45 in Cape Recife and 0.27 ± 0.45 in Cape St. Francis. Notably, the probability of feeding on bait was significantly higher at Tsitsikamma and Cape Recife compared to Goukamma (Figure 4.13A). The Wald's test found that temperature had a significant negative effect on the probability of feeding on bait at Cape St. Francis (*p* = 0.037; Figure 4.13B). Size had a significant effect on the probability of feeding on bait and this effect varied among the locations (Table 4.13). At Tsitsikamma and Cape St. Francis, the probability of feeding on bait increased with increasing temperature (Figure 4.13C). At Goukamma and Cape Recife, the probability feeding on bait increased with increasing size until 400 mm FL and 300 mm FL respectively, beyond which the probability sharply decreased (Figure 4.13C). The random effect of sample was not significant (Table 4.13).

Table 4.13: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of the probability of feeding on bait at the location scale (Table 4.5: Model 8). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Location	3	13.95	0.003	**
Smooth terms	***edf***	**Chi.sq**	***p***	
Size: Location-Cape Recife	1.987	6.705	0.045	*
Size: Location-Cape St. Francis	1.001	4.848	0.028	*
Size: Location-Goukamma	3.638	18.888	<0.001	***
Size: Location-Tsitsikamma	1.199	5.258	0.027	*
Visibility	1.000	8.567	0.003	**
Sample	0.610	0.616	0.445	ns
Temperature: Location-Cape Recife	1.000	0.036	0.849	ns
Temperature: Location-Cape St. Francis	1.000	4.362	0.037	*
Temperature: Location-Goukamma	1.000	0.419	0.518	ns
Temperature: Location-Tsitsikamma	1.000	0.002	0.966	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

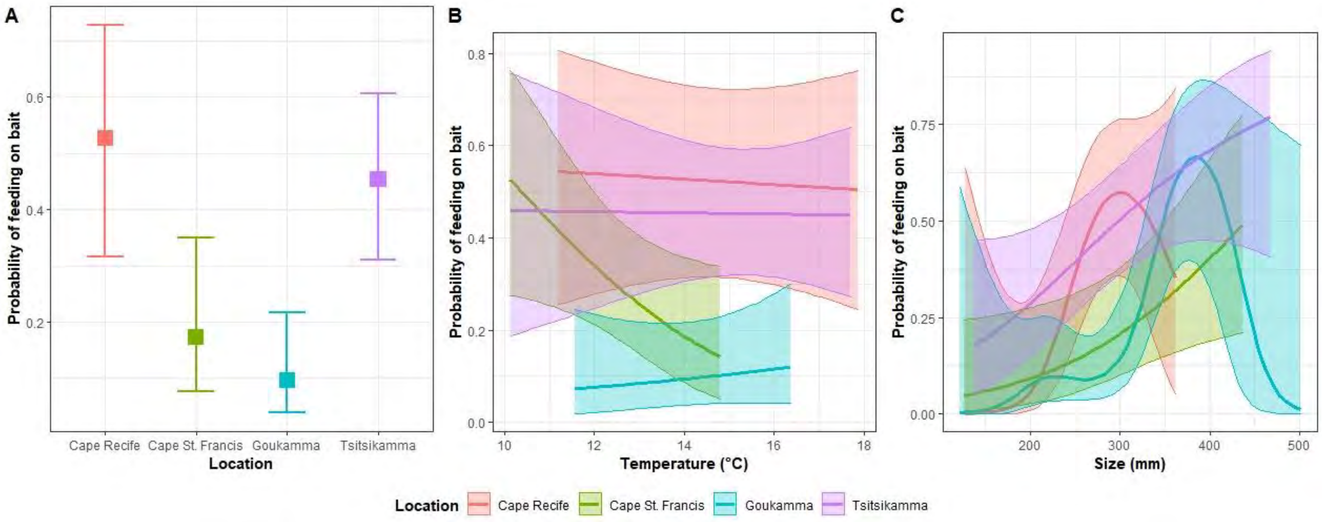

Figure 4.13: Predicted results from the generalised additive mixed model (Table 4.5: Model 8) showing (A) the effect of location on the probability of feeding, holding all other covariates constant, (B) the effect of temperature on the probability of feeding, holding all other covariates constant and (C) the effect of size on the probability of feeding, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

4.3.6 CHASING

The best-fit model investigating the effect of management on the probability of chasing explained 12.0% of the observed variability. Management did not have a significant effect on the probability of chasing (Wald's test, *p* = 0.248; Figure 4.14A), with the mean probability of chasing from the raw data being 0.22 ± 0.42 in MPAs and 0.15 ± 0.36 in exploited areas. Similarly, temperature did not have a significant effect on the probability of chasing (Wald's test, *p* = 0.368; Figure 4.14B). However, the effect of size on the probability of chasing was significant (Wald's test, *p* <0.001). The model selection process excluded the interaction effect between management and size indicating that the effect of size was consistent between the management zones. The probability of chasing on increased with increasing size until about 400 mm FL, beyond which the probability of chasing sharply decreased (Figure 4.14C). The random effects of sample and location were not significant (Table 4.14).

Table 4.14: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of the probability of *Chrysoblephus laticeps* chasing other fish at the management scale (Table 4.5: Model 9). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Management	1	1.337	0.248	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Size	3.870	20.383	<0.001	***
Visibility	1.000	2.313	0.128	ns
Location	4.49×10^{-06}	0.000	0.679	ns
Sample	2.16×10^{-04}	0.000	0.852	ns
Temperature	1.000	0.809	0.368	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

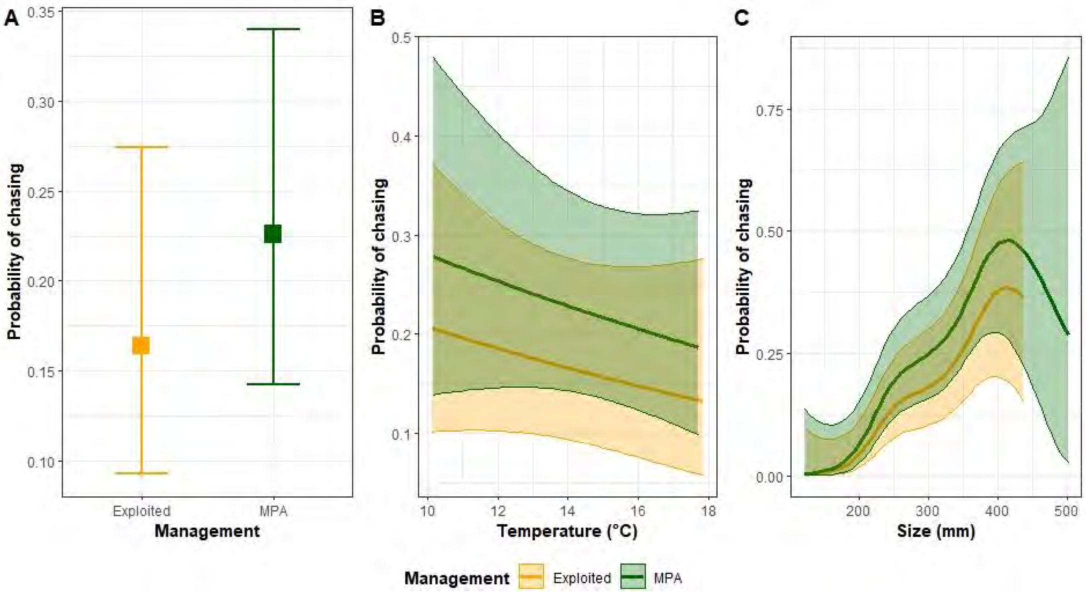

Figure 4.14: Predicted results from the generalised additive mixed model (Table 4.5: Model 9) showing (A) the effect of management on the probability of chasing, holding all other covariates constant (B) the effect of temperature on the probability of chasing, holding all other covariates constant and (C) the effect of size on the probability of chasing, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval

The best-fit model investigating the effect of location on the probability of chasing explained 14.5% of the observed variability and the effect of location was not significant (Wald's test, *p* =

0.441; Figure 4.15A). The mean probability of feeding from the raw data was 0.20 ± 0.40 in Tsitsikamma, 0.25 ± 0.43 in Goukamma, 0.16 ± 0.37 in Cape Recife and 0.15 ± 0.36 in Cape St. Francis. Temperature did not have a significant effect on the probability of chasing, regardless of location (Table 4.15; Figure 4.15B). Alternatively, the effect of size on the probability of chasing was significant at Goukamma (*p* = 0.029) and Tsitsikamma (*p* = <0.001) with larger individuals being more likely to display the behaviour (Figure 4.15C). The random effect of sample was not significant (Table 4.15).

Table 4.15: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of the probability of chasing at the location scale (Table 4.5: Model 10). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Location	3	2.694	0.441	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
MaxN	1.730	2.007	0.394	ns
Size: Location-Cape Recife	1.910	1.072	0.526	ns
Size: Location-Cape St. Francis	1.350	2.392	0.168	ns
Size: Location-Goukamma	1.400	5.594	0.029	*
Size: Location-Tsitsikamma	1.000	10.980	<0.001	***
Sample	5.24×10^{-04}	0.000	0.725	ns
Temperature: Location-Cape Recife	1.000	1.725	0.189	ns
Temperature: Location-Cape St. Francis	2.140	1.698	0.524	ns
Temperature: Location-Goukamma	1.000	0.022	0.881	ns
Temperature: Location-Tsitsikamma	1.000	0.354	0.552	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

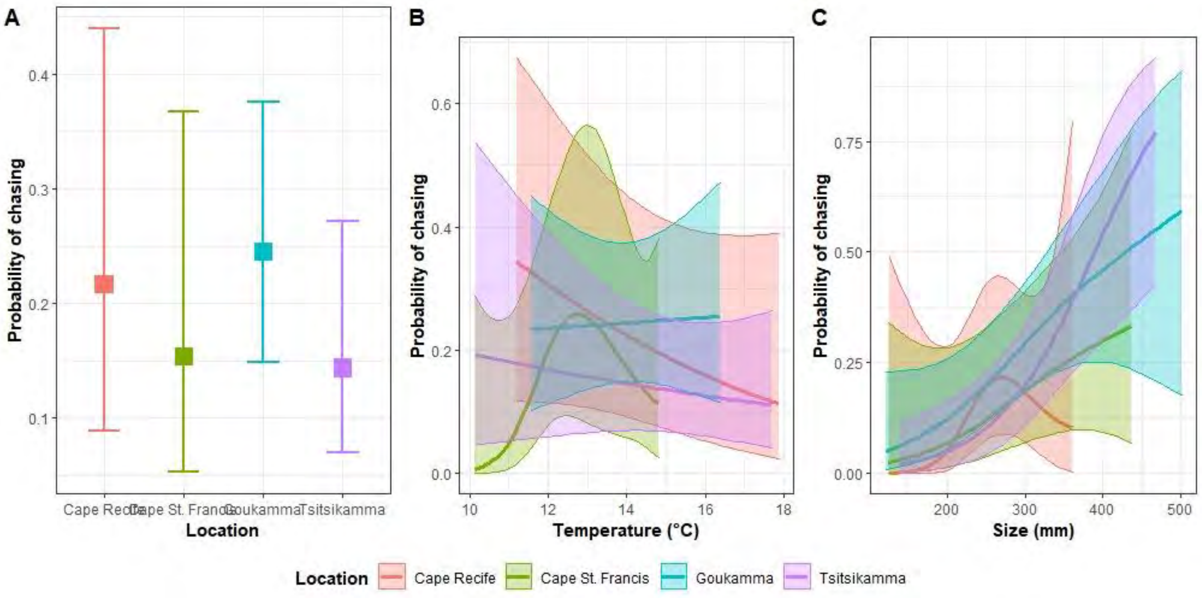

Figure 4.15: Predicted results from the generalised additive mixed model (Table 4.5: Model 10) showing (A) the effect of management on the probability of chasing, holding all other covariates constant (B) the effect of temperature on the probability of chasing, holding all other covariates constant and (C) the effect of size on the probability of chasing, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

4.3.7 FLEEING

The best-fit model for the effect of management on the probability of fleeing explained 11.6% of the observed variability. Management did not have a significant effect on the probability of fleeing (Wald's test, *p* = 0.672; Figure 4.16A), with the mean probability of fleeing from the raw data being 0.21 ± 0.41 in MPAs and 0.26 ± 0.44 in exploited areas. The probability of fleeing was not influenced by temperature, regardless of management (Table 4.16; Figure 4.16B). Furthermore, the Wald's test did find any covariate to have a significant effect on the probability of fleeing, including the random effects of sample and location (Table 4.16).

Table 4.16: Results of the Wald's test for the best-fit generalised additive mixed model investigating determinants of the probability of *Chrysoblephus laticeps* fleeing from aggressors (both conspecifics and heterospecifics) at the management scale (Table 4.5: Model 11). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Management	1	0.179	0.672	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Depth	1.000	2.108	0.147	ns
MaxN	2.890	5.710	0.195	ns
Size: Management-Exploited	4.480	7.106	0.159	ns
Size: Management-MPA	1.000	0.792	0.374	ns
Location	$4.02\text{x}10^{-06}$	0.000	0.811	ns
Sample	$1.03\text{x}10^{-03}$	0.001	0.539	ns
Temperature: Management-Exploited	1.000	1.113	0.291	ns
Temperature: Management-MPA	3.917	8.230	0.089	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

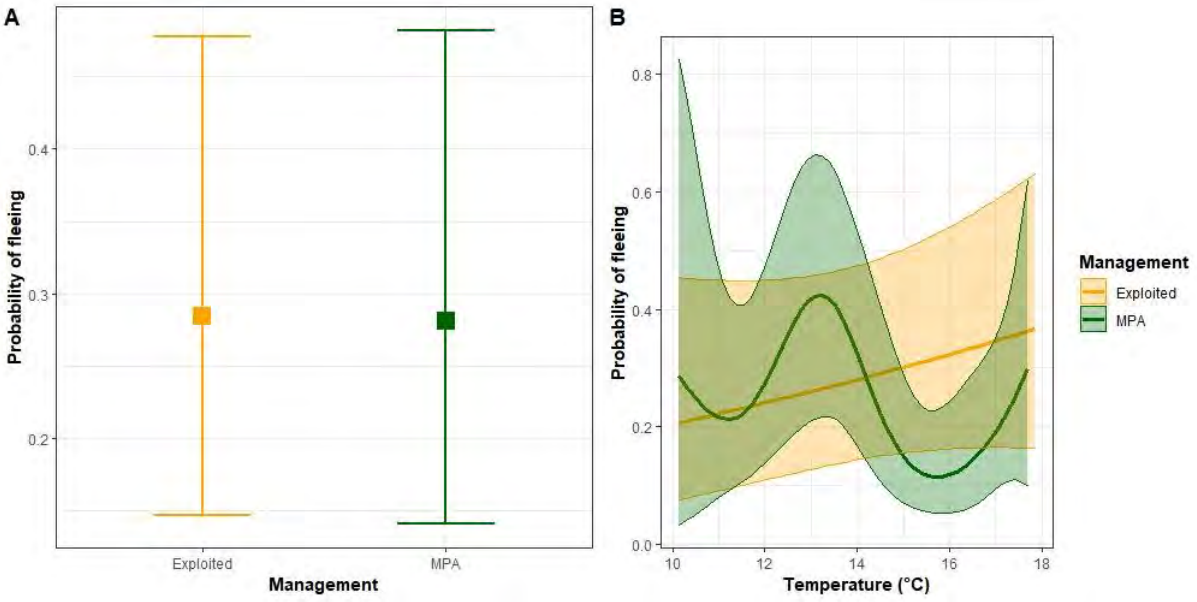

Figure 4.16: Predicted results from the generalised additive mixed model (Table 4.5: Model 11) showing (A) the effect of management on the probability of fleeing, holding all other covariates constant and (B) the effect of temperature on the probability of fleeing, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval

The best-fit model investigating the effect of location on the probability of fleeing explained 23.4% of the observed variability. Location did not have a significant effect on the probability of fleeing (Wald's test, *p* = 0.412; Figure 4.17A). The mean probability of fleeing from the raw data being 0.21 ± 0.41 in Tsitsikamma, 0.22 ± 0.41 in Goukamma, 0.27 ± 0.45 in Cape Recife and 0.24 ± 0.43 in Cape St. Francis. The probability of *C. laticeps* displaying fleeing behaviour was not influenced by temperature (Table 4.17; Figure 4.17B). In contrast, MaxN of *C. laticeps* had a significant effect on the probability of an individual displaying fleeing behaviour (*p* = 0.011). Generally, as MaxN increased so did the probability of fleeing (Figure 4.17C). The random effects of sample and location were not significant (Table 4.17).

Table 4.17: Results of the Wald's test from the best-fit generalised additive mixed model investigating the determinants of the probability of Chrysoblephus laticeps fleeing from aggressors (both conspecifics and heterospecifics) at the location scale (Table 4.5: Model 12). df = Degrees of freedom; edf = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Location	3	2.869	0.412	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
MaxN	1.000	6.461	0.011	*
Size: Location-Cape Recife	2.169	5.288	0.173	ns
Size: Location-Cape St. Francis	8.063	12.697	0.155	ns
Size: Location-Goukamma	1.000	0.79	0.374	ns
Size: Location-Tsitsikamma	1.000	0.061	0.805	ns
Visibility	1.000	0.053	0.818	ns
Sample	0.002	0.002	0.470	ns
Temperature: Location-Cape Recife	1.000	0.474	0.491	ns
Temperature: Location-Cape St. Francis	6.922	7.734	0.353	ns
Temperature: Location-Goukamma	2.103	10.271	0.056	ns
Temperature: Location-Tsitsikamma	1.000	0.000	0.992	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

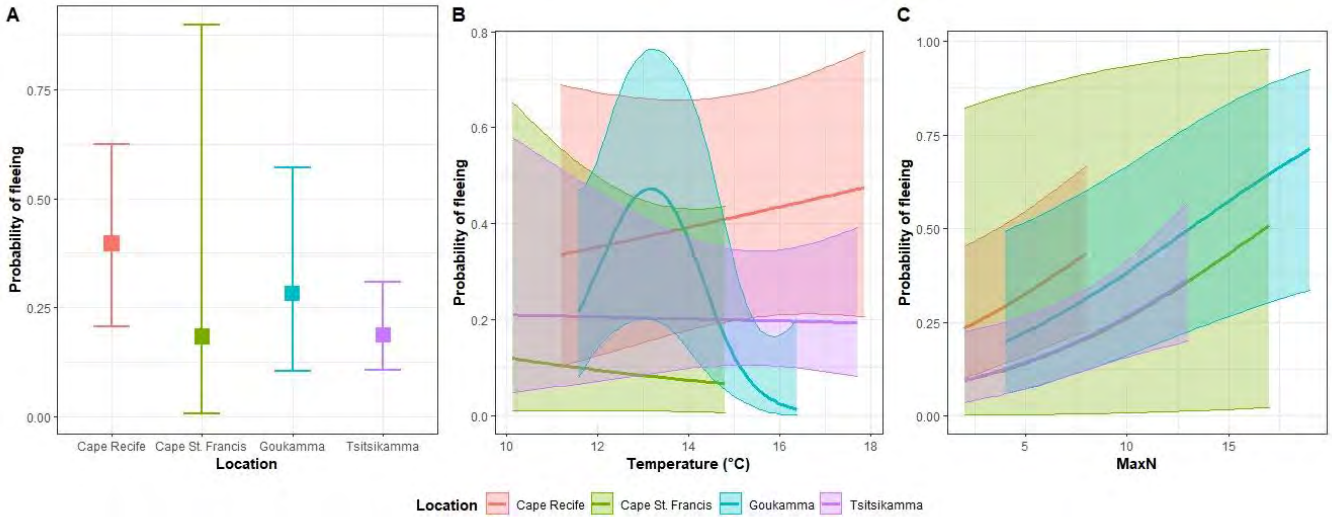

Figure 4.17: Predicted results from the generalised additive mixed model (Table 4.5: Model 12) showing (A) the effect of location on the probability of fleeing, holding all other covariates constant (B) the effect of temperature on the probability of fleeing, holding all other covariates constant and (C) the effect of relative abundance (MaxN) on the probability of fleeing, holding all other covariates constant Error bars and the shaded area around each trend line represent the approximate 95% confidence interval

4.3.8 FEEDING RATE

The best-fit model investigating the effect of management on the feeding rate explained 14.1% of the observed variability. Management did not have a significant effect on the feeding rate (Wald's test, p = 0.373; Figure 4.18A), with the mean feeding rate from the raw data being 4.77 ± 4.74 bites/s in MPAs and 4.66 ± 3.35 bites/s in exploited areas. Similarly, temperature did not have a significant effect on the on the feeding rate (Wald's test, p = 0.060; Figure 4.18B). The random effect of sample was not significant (Table 4.18).

Table 4.18: Results of the Wald's test from the best-fit generalised additive mixed model investigating determinants of *Chrysoblephus laticeps* feeding rate at the management scale (Table 4.5: Model 13). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Management	1	0.802	0.373	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Visibility	1.740	2.099	0.187	ns
Water column	1.420	4.806	0.011	*
Location	0.897	0.844	0.155	ns
Sample	5.39x10^{-04}	0.000	0.582	ns
Temperature	1.000	3.63	0.060	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

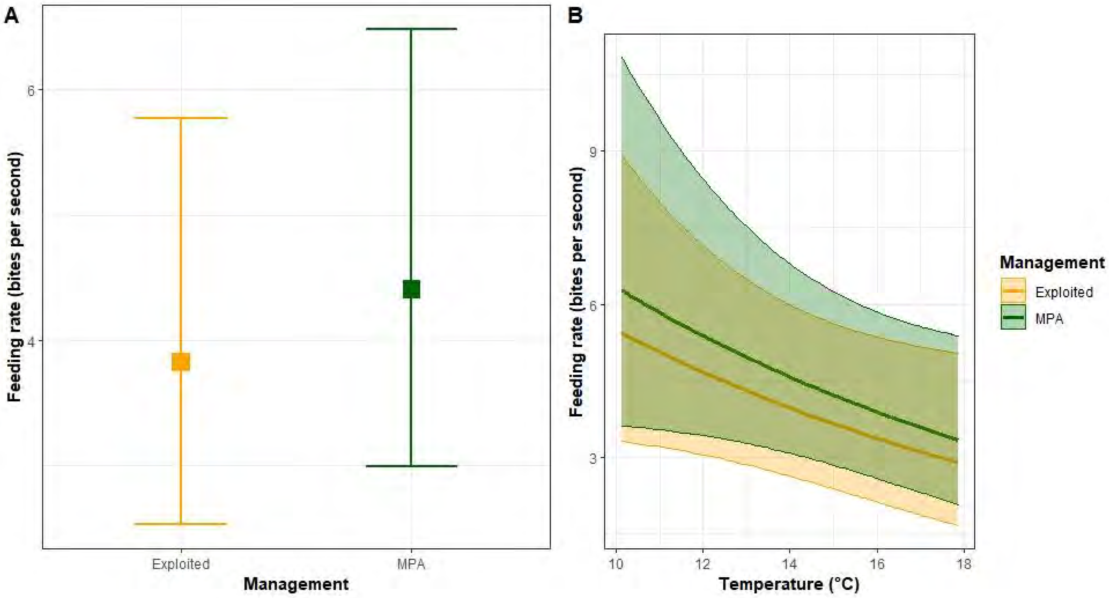

Figure 4.18: Predicted results from the generalised additive mixed model (Table 4.5: Model 13) showing (A) the effect of management on feeding rate, holding all other covariates constant and (B) the effect of temperature on feeding rate, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

The mean feeding rate was 5.31 ± 5.65 bites/s in Tsitsikamma, 3.97 ± 2.88 bites/s in Goukamma, 4.49 ± 3.20 bites/s in Cape Recife and 4.80 ± 3.56 bites/s in Cape St. Francis. The best-fit model for the effect of location on the feeding rate explained 23.8% of the observed variability. Location did not have a significant effect on the feeding rate (Wald's test, *p* = 0.101; Figure 4.19A). Temperature did have a significant effect on the feeding rate at Tsitsikamma (Wald's test, *p* = 0.025), with feeding rate decreasing with increasing temperature (Figure 4.19B). In addition, MaxN had a significant effect on the on the feeding rate (Wald's test, *p* = 0.029). Here, feeding rate was lowest at intermediate *C. laticeps* MaxN (Figure 4.19C). The random effects of sample and location were not significant (Table 4.19).

Table 4.19: Results of the Wald's test from the best-fit generalised additive mixed model investigating determinants of *Chrysoblephus laticeps* feeding rate at the location scale (Table 4.5: Model 14). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Location	3	2.146	0.101	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
MaxN	2.490	3.172	0.029	*
Water column	1.000	12.910	<0.001	***
Sample	1.27×10^{-04}	0.000	0.741	ns
Temperature: Location-Cape Recife	1.000	0.006	0.939	ns
Temperature: Location-Cape St. Francis	1.970	0.823	0.282	ns
Temperature: Location-Goukamma	1.000	1.246	0.268	ns
Temperature: Location-Tsitsikamma	1.000	5.200	0.025	*

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

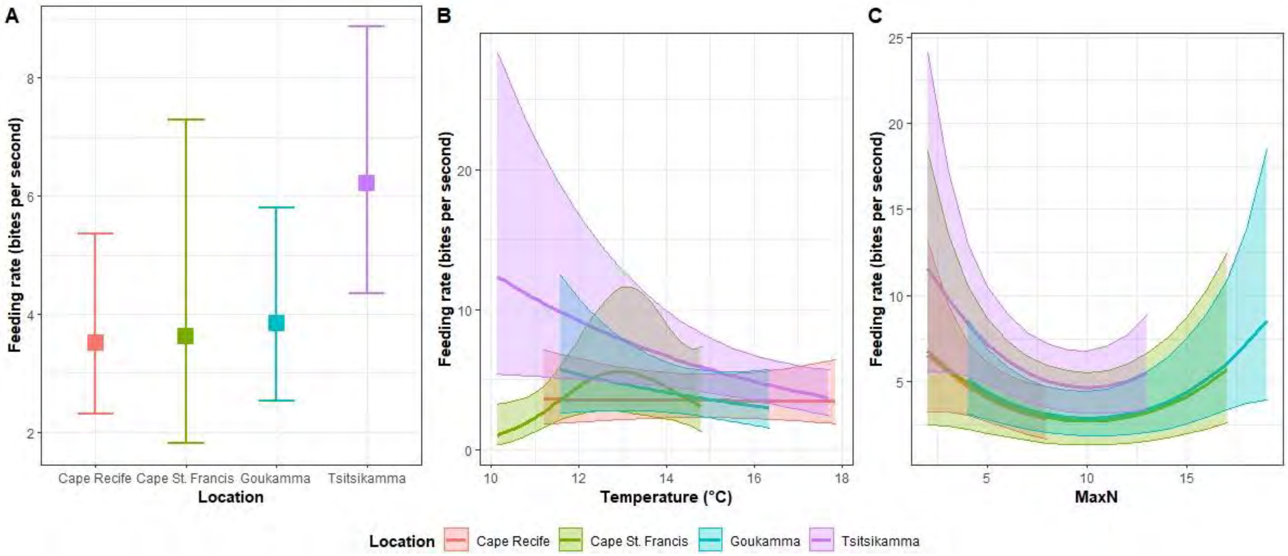

Figure 4.19: Predicted results from the generalised additive mixed model (Table 4.5: Model 14) showing (A) the effect of location on the feeding rate, holding all other covariates constant (B) the effect of temperature on the feeding rate, holding all other covariates constant and (C) the effect of MaxN on the feeding rate, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval

4.3.9 TIME SPENT IN THE FIELD OF VIEW

The best-fit model investigating the effect of management on the time spent in the field of view explained 52.4% of the observed variability. Management did not have a significant effect on the time spent in the field of view ($p = 0.716$; Figure 4.20A), with the mean time spent in the field of view from the raw data being 52.9 ± 109.3 s in MPAs and 49.8 ± 81.8 s in exploited areas. While temperature did not have a significant effect (Wald's test, $p = 0.593$; Figure 4.20B), *C. laticeps* size significantly influenced the time spent in the field of view (Wald's test, p <0.001), and this appeared to be consistent between the management levels (interaction excluded from best-fit model, Table 4.20). The time spent in the field of view increased with increasing size until about 400 mm FL, beyond which the time spent in the field of view sharply decreased (Figure 4.20C). A positive and significant relationship was found between depth and time spent in the field of view (Wald's test, $p = 0.024$). With the random effects, sample but not location was found to significantly influence time spent in the field of view (Table 4.20).

Table 4.20: Results of the Wald's test from the best-fit generalised additive mixed model investigating determinants of time spent in the field of view by *Chrysoblephus laticeps* at the management scale (Table 4.5: Model 15). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Management	1	0.133	0.716	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Depth	1.000	5.141	0.024	*
MaxN	1.000	2.574	0.110	ns
Size	4.828	13.952	<0.001	***
Water column	1.000	3.035	0.083	ns
Location	3.819×10^{-04}	0.000	0. 623	ns
Sample	50.310	1.677	<0.001	***
Temperature	1.001	0.288	0.593	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

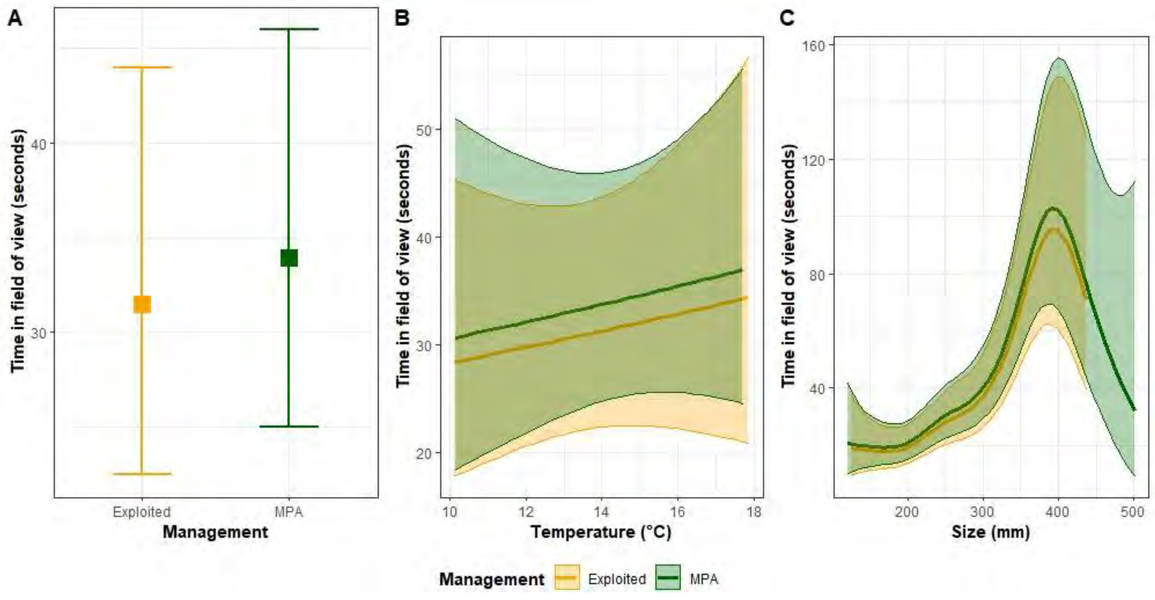

Figure 4.20: Predicted results from the generalised additive mixed model (Table 4.5: Model 15) showing (A) the effect of management on time spent in the field of view, holding all other covariates constant, (B) the effect of temperature on time spent in the field of view, holding all other covariates constant and (C) the effect of size on time spent in the field of view, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

The best-fit model investigating the effect of location on the time spent in the field of view explained 55.6% of the observed variability. The Wald's test found that location did not have a significant effect on the time spent in the field of view (*p* = 0.503; Figure 4.21A), with the mean time in the field of view from the raw data being 51.0 ± 60.3 s in Tsitsikamma, 54.3 ± 136.9 s in Goukamma, 60.7 ± 109.0 s in Cape Recife and 42.2 ± 55.6 s in Cape St. Francis. Similarly, time spent in the field of view was not influenced by temperature at any of the locations (Wald's test, Table 4.21; Figure 4.21B). Individual size did have a significant effect on the time spent in the field of view at all locations (Table 4.21; Figure 4.21B). Generally, the time spent in the field of view increased with increasing size (Figure 4.21C). However, at Goukamma the time spent in the field of view only increased with increasing size until about 400 mm FL, beyond which it decreased sharply (Figure 4.21C). The random effect of sample was significant (Table 4.21).

Table 4.21: Results of the Wald's test from the best-fit generalised additive mixed model investigating determinants of time spent in the field of view by *Chrysoblephus laticeps* at the location scale (Table 4.5: Model 16). *df* = Degrees of freedom; *edf* = estimated degrees of freedom; Chi.sq = Chi square value.

Parametric terms	***df***	**Chi.sq**	***p-value***	
Location	3	0.786	0.503	ns
Smooth terms	***edf***	**Chi.sq**	***p***	
Size: Location-Cape Recife	3.190	2.816	0.021	*
Size: Location-Cape St. Francis	1.000	11.260	<0.001	***
Size: Location-Goukamma	4.970	11.217	<0.001	***
Size: Location-Tsitsikamma	1.000	13.559	<0.001	***
Water column	1.000	1.175	0.279	ns
Sample	48.400	1.637	<0.001	***
Temperature: Location-Cape Recife	1.000	0.024	0.880	ns
Temperature: Location-Cape St. Francis	1.000	1.506	0.221	ns
Temperature: Location-Goukamma	1.000	2.206	0.139	ns
Temperature: Location-Tsitsikamma	1.238	0.072	0.807	ns

Significance codes: *** < 0.001; ** < 0.01; * < 0.05; ns = not significant

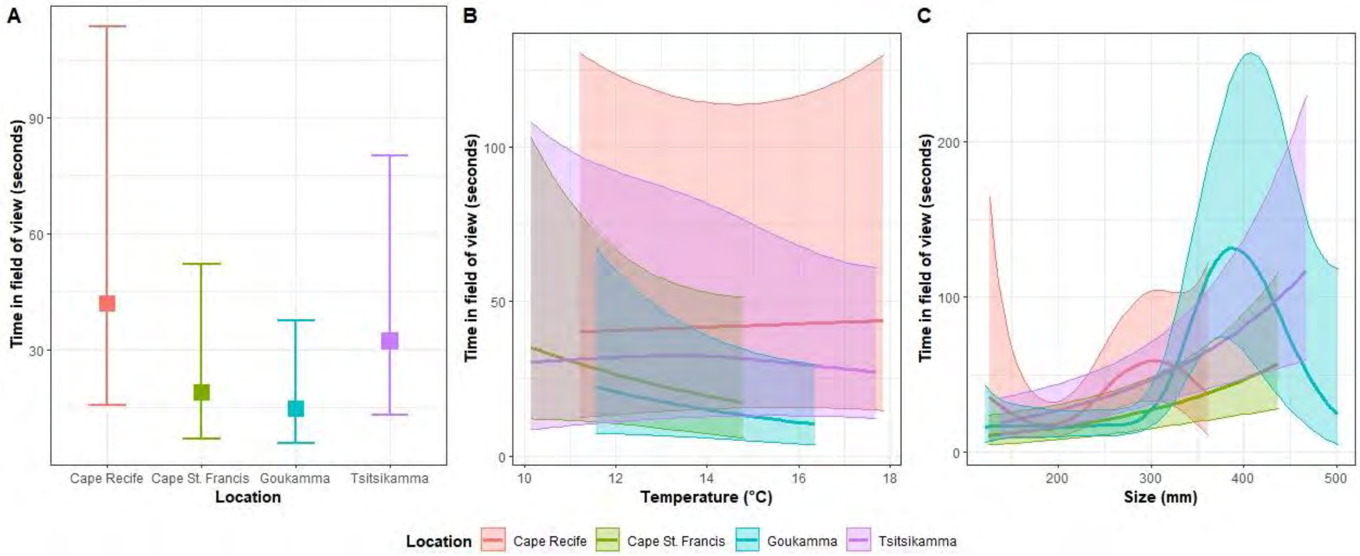

Figure 4.21: Predicted results from the generalised additive mixed model (Table 4.5: Model 16). showing (A) the effect of location on time spent in the field of view, holding all other covariates constant, (B) the effect of temperature on time spent in the field of view, holding all other covariates constant and (C) the effect of size on time spent in the field of view, holding all other covariates constant. Error bars and the shaded area around each trend line represent the approximate 95% confidence interval.

4.4 DISCUSSION

This chapter aimed to determine how temperature changes, particularly at low temperatures, affected the population structure, activity and behaviour of *Chrysoblephus laticeps* and whether the effects were consistent between established MPAs and areas open to fishing. No evidence was found to suggest evidence that *C. laticeps* from MPAs had higher activity levels at low temperatures, compared to *C. laticeps* from exploited areas. Generally, the effect of temperature on all measured behaviours was consistent between management zones. There was, however, considerable variation in the effect of temperature on behaviour when looking at the scale of location. Patterns in behaviour were not consistent between the MPAs or between the exploited zones, thus providing no conclusive evidence to support the original hypothesis. The exception was MaxN, which increased significantly with increasing temperature in the exploited areas, but not in the protected areas. Strong evidence was found to suggest that temperature, size and the presence of conspecifics (MaxN) most influence the behaviour of *C. laticeps*.

The findings of this study suggest that management was not a reliable predictor of behaviour and grouping the data by management level could result in the loss of location-specific detail. However, for the behaviours time to arrive, time to feed, feed on bait and chasing the model describing the effect of management had a lower AIC score (indicating better model fit) than the model describing the effect of location. Alternatively, for MaxN and the behaviours fleeing, feeding rate and time in the field of view the inverse was true. Thus, consistency in the results from within the protected and within the exploited locations was unpredictable and dependant on the response variable and behaviour. This highlights that caution needs to be applied when interpreting results from a limited number of replicates and that this research may have benefited from the inclusion of more protected and exploited locations. Additionally, the MPAs lied to the west of the exploited sites so future studies should include MPAs that lie on both the east and west of the exploited sites.

Temperature had a significant effect on MaxN and the time to arrive. At the exploited sites, MaxN increased with increasing temperature. The effect of temperature on MaxN was less significant within the MPAs. The time taken to arrive was longer at lower temperatures, regardless of management. As the metabolic rate of *C. laticeps* increases with increasing temperature (Duncan et al. 2019), individuals would be able to pursue the bait more readily at higher temperatures. The low abundance of *C. laticeps* at cold temperatures (below 12°C), particularly in the exploited sites, might have artificially strengthened the perceived relationship between temperature and time to arrive. However, the prediction plots used mean values of abundance to predict the effect of temperature on time to arrive and the pattern was still very strong. Further, the feeding rate at Tsitsikamma MPA was significantly higher than at Cape St. Francis at low (below 11.5 °C) temperatures (Figure 4.19B). This suggests that low temperatures may constrain the metabolic rates of exploited *C. laticeps* populations more than protected populations (Skeeles 2019), resulting in them limiting their activity to conserve energy until suitable temperature conditions arise. The inability to detect a significant effect of temperature on the individual-level behaviours may be a result of individual-level variability in behaviour obscuring its effects. It was not possible to obtain samples from warmer waters (above 18 °C) and thus, not possible to determine how management or location influence the behaviour *C. laticeps* at their upper temperature limits. Given that Duncan et al. (2019) found that differences in aerobic scope between protected and exploited populations were most pronounced at high temperatures (20-24 °C), it is possible that differences in behaviour between these populations would also be more apparent at higher temperatures.

Generally, size had a positive relationship with the behavioural metrics measured, with larger individuals more likely to feed on the bait, chase other fish and spend more time in the field of view. This is likely due to larger individuals feeding more to meet their higher energetic demands and keeping competitors away from the bait (e.g. Gerlotto & Fréon 1992, Webster 2004, Xu et al. 2007, Briones et al. 2012). Previous stereo-BRUVs studies by De Vos (2012) and Sanguinetti (2013) have noted the antagonistic behaviour of *C. laticeps* around the bait. Other stereo-BRUVs studies of reef fish have also found large individuals to be more aggressive, chasing both conspecifics and heterospecifics away from the bait (Ebner et al. 2009, Finucci et al. 2019). Notably, size only had a significant effect of the probability of chasing in the MPAs. A similar BRUVs study also found that agonistic behaviours in snapper *Pagrus auratus* (Sparidae) were significantly higher in MPAs compared to adjacent exploited sites (Dunlop et al. 2015). These results may be reflect fisheries-induced evolution; the passive fishing techniques used in the exploited areas may have removed bold and dominant individuals or these individuals may have learned to be more cautious to avoid capture (Colefax et al. 2016, Arlinghaus et al. 2017). This is particularly true when comparing the pattern from the MPAs with Cape St. Francis where similar sized *C. laticeps* were recorded. Rhoades et al. (2019) found that reef fish from older MPAs (established in 1917 and 1973) fed more readily than similarly sized conspecifics from newer MPAs (established in 2007), suggesting that it may take multiple generations to recover bold phenotypes in fished populations. As both Tsitsikamma MPA and Goukamma MPA are well-established MPAs, having prohibited fishing for more than 30 years, sufficient time may have passed to recover bold and dominant phenotypes in their *C. laticeps* populations. At Goukamma MPA, very large individuals (>400 mm FL) were markedly less likely to feed on the bait and spent less time in the field of view compared to smaller individuals. However, as there were very few (four) individuals of this size class at Goukamma MPA, so it is likely that too few individuals were sampled to reliably predict the behavioural patterns of larger fish in this MPA.

The relative abundance (MaxN) of *C. laticeps* was not significantly higher inside the MPAs compared to the exploited sites. This result is contrary to the findings of several studies, where the abundance of *C. laticeps* was significantly higher within MPAs compared to exploited sites (Buxton 1987, 1989, Buxton & Smale 1989, Burger 1990, Lechanteur 1999, Smith 2005, Götz 2005, Bennett 2007, Götz et al. 2008b, 2009, Sanguinetti 2013, Roberson et al. 2015). Location had some effect on abundance, with MaxN at Cape Recife lower than at Goukamma MPA and Cape St. Francis and MaxN at Cape St. Francis was significantly higher than at Tsitsikamma MPA (Figure 4.7A). The above finding was from the model predictions based on mean water temperature over all samples. Here, it is important to note that samples warmer than 15 °C were not collected from Cape St. Francis and this might have influenced the observed patterns. In comparison to size, however, abundance isn't always a good indicator to use as it is quite variable, particularly at a local-scale (Götz et al. 2008a). The size of *C. laticeps* did not vary significantly across management zones, however, *C. laticeps* from Cape Recife were smaller compared to those from the three other locations. Cape St. Francis had higher abundance and larger-sized *C. laticeps* compared to Cape Recife. While commercial fishing at Cape Recife and Cape St. Francis occurs at similar intensities (as Figure 4.2 illustrates), it might be that recreational anglers are exhorting a greater pressure on the inshore reefs at Cape Recife than at Cape St. Francis, explaining the differences between the two areas. Recreational fishing can also be highly extractive as well as remove large and bold individuals (Cooke & Cowx 2006, Seytre et al. 2013, Alós et al. 2014, 2016).

The abundance of conspecifics significantly influenced the time to arrive, time to feed, the probability of fleeing and feeding rates. The time to arrive and time to feed shortened with increasing number of conspecifics in the area while the probability of fleeing and feeding rate increased with an increasing number of conspecifics. If *C. laticeps* are randomly distributed within an area, then the time to arrive will shorten as abundance increases. The other behaviours were independent of time to arrive and are likely a result of increasing competition as the abundance of conspecifics increased (Finucci et al. 2019, Lester et al. 2021). Higher fish densities, particularly higher densities of conspecifics, drive competition and in stereo-BRUVs surveys these manifest as increased displays of aggression or increased rates of feeding (Dunlop et al. 2015, Juhel et al. 2019, Finucci et al. 2019, Lester et al. 2021).

As in the pilot study, spawning was not observed in any sample. Perhaps spawning behaviour cannot be detected using stereo-BRUVs as the individuals seen in the field of view appear due to their attraction to the bait (Harvey et al. 2007, Bernard & Götz 2012). Thus, the individuals seen would prioritise feeding, defending the bait or avoiding aggressors as opposed to spawning. The samples collected during the spawning season (October-January) may have also fallen outside of optimal spawning temperatures. The spawning season of *C. laticeps* (October-January) is strongly correlated with peaks in mean monthly sea temperatures of 16-19 °C and gonadal regression begins as temperatures fall. Most of the samples (73%) collected during the spawning season had water temperatures below 16 °C. Additionally, as the spawning season coincides with the upwelling the season (Buxton 1990, Goschen & Schumann 2011), a large amount (40%) of the samples collected during the spawning season had very low (below 12 °C) water temperatures. Following an upwelling event during the spawning season in Tsitsikamma MPA that resulted in 9 °C water temperature, female *C. laticeps* caught from these waters produced few opaque eggs and when dissected the ovaries appeared to have regressed to the developing stage (Davis 1996). A week later the water temperature at the same location was 19 °C and the ovaries of the female *C. laticeps* caught this time were in the active stage and the fish could be stripped as part of a larval study (Davis 1996). Thus, the temperatures at which samples were collected for this study likely limited the potential to observe spawning behaviour. In future, if spawning is to be investigated a much more specific study should be designed to observe and quantify the behaviour.

The random effect of sample was only significant in the models investigating the time spent in the field of view. This means that some sample-specific parameters, which have not been measured, are responsible for the patterns seen in the time spent in the field of view. For the most part, behaviour of *C. laticeps* was independent of sample and behaviour could be explained by other variables such as size, temperature and location.

Overall, the results of this study provide support to the findings of the physiological studies of *C. laticeps,* wherein protected fish demonstrated greater metabolic performance than exploited populations at thermal extremes (Duncan et al. 2019, Skeeles 2019). It is possible that the measurements used by these studies were more sensitive to detecting differences between the sites. Though, notably these two studies only compared *C. laticeps* from Tsitsikamma MPA and Cape Recife whereas this study included two additional study sites. Perhaps the differences in metabolic rates observed by Duncan et al. (2019) and Skeeles (2019) would not persist with the inclusion of additional protected and exploited study sites. Furthermore, these two studies employed passive fishing techniques to collect their *C. laticeps,* which would have selected for the most active or fit individuals at each location. As a result of fisheries selection, the individuals caught in the protected area may have been more fit compared to the individuals caught in the exploited area. In comparison, stereo-BRUVs may record a more representative portion of the *C. laticeps* assemblage as the individuals observed did not have to be caught.

The high variability in behavioural responses across protection level may be a result of high metabolic and behavioural phenotypic diversity among individuals. Environmental stressors, such as temperature fluctuations, can amplify behavioural and physiological differences between individuals (Killen et al. 2013). Biro et al. (2010) investigated the effect of small (3 °C or less) within-day temperature variations on the behaviour of juvenile damselfish (*Pomacentrus moluccensis* and *Pomacentrus bankanensis*). Activity levels and boldness increased with increasing temperature for most individuals (Biro et al. 2010). However, in some individuals the levels of activity or boldness remained similar regardless of temperature increases (Biro et al. 2010). Further, the observed changes in an individual's levels of activity and boldness were not correlated, i.e. an individual that increased its activity levels with increasing temperatures could display no change in its boldness with increasing temperatures and vice versa (Biro et al. 2010). With regards to *C. laticeps*, Duncan et al. (2019) found that protected populations had significantly higher aerobic scope phenotypic diversity and a greater proportion of high performance aerobic scope phenotypes. However, the results of this study suggest that these differences in aerobic scope may not necessarily translate to differences in behaviour that are detectable by stereo-BRUVs. This highlights that the relationship between physiology and behaviour is more complex than initially thought and requires further investigation.

It is also possible is that the individuals observed in the exploited areas are offspring of *C. laticeps* from MPAs. Although adult *C. laticeps* are highly resident, they are broadcast spawners, with pelagic larvae, thus making it possible for the larvae of *C. laticeps* from protected populations to be dispersed into exploited areas (Buxton 1990, Davis 1996, Griffiths & Wilke 2002, Kerwath et al. 2007a). Studies investigating larval dispersal out of Tsitsikamma MPA during the spawning season of sparids suggest that larvae can be dispersed 42-583 km alongshore and up to 90 km offshore (Tilney et al. 1996, Brouwer et al. 2003). Consequently, due to spillover and larval recruitment from the MPAs, the *C. laticeps* from the exploited areas may have the same genetic predispositions to physiological stress as the individuals in the MPAs (Kerwath et al. 2007b, Teske et al. 2010, Wright et al. 2015, Lombard et al. 2019). Hence, behavioural differences between protected and exploited fish were not detected by this study.

4.5 CONCLUSIONS

Temperature has a significant effect on the behaviour of *C. laticeps,* whereas protection level was not a reliable predictor of behaviour. Abundance and size did not vary by protection level, however, abundance (MaxN) and size were lower at Cape Recife compared to the three other locations. Temperature had a positive relationship with relative abundance (MaxN). Temperature had an inverse relationship with the time to arrive and feeding on bait at Cape St. Francis and the feeding rate at Tsitsikamma: as temperature increased these behaviours decreased. Size was one of the most important determinants of behaviour and generally had a positive relationship with the probability of feeding on bait, probability of chasing and the time spent in the field of view. The time to arrive and time to feed were longer when *C. laticeps* abundance was low and shortened with increasing *C. laticeps* abundance. As the abundance of conspecifics increased, so did the probability of fleeing.

Overall, his chapter did not find *C. laticeps* from MPAs were more active than *C. laticeps* from exploited areas, particularly at lower temperatures. The inability to detect significant behavioural changes across protection level may be a result of (1) high behavioural phenotypic diversity among *C. laticeps* individuals, (2) spillover and larval recruitment from MPAs to exploited sites, resulting in genetic mixing between these two populations and/or (3) the sampling methods used, with stereo-BRUVs sampling across greater behavioural phenotypic diversity.

In the context of ongoing climate change, the results of this chapter suggest that an increase in upwelling in the Agulhas Ecoregion may impact fish behaviour similarly across management zones. Although, further research should look into patterns of abundance (MaxN) at different temperatures across more MPAs and exploited sites. Further, it was not possible to determine behavioural patterns in warmer temperatures to compare to the findings of Duncan et al. (2019), which suggest that protected *C. laticeps* would be better able to cope with long-term ocean warming.

5 SYNTHESIS

5.1 THESIS PURPOSE

The aim of this thesis was to improve our understanding of how exploitation will influence the behaviour of fishes in a rapidly changing climate. Using baited remote underwater video systems (stereo-BRUVs), the natural behaviour of exploited and unexploited populations of *Chrysoblephus laticeps* (red roman) in a thermally variable environment were compared. The thesis aim was formulated as sea temperatures in the Agulhas Ecoregion have become more variable in summer months due to an increase in seasonal upwelling, driven by an increase in upwelling-favourable (easterly) winds and a stronger Agulhas current as part of ongoing global climate change (Rouault et al. 2010, Malan et al. 2018, 2019, IPCC 2019, Jury 2020). Upwelling causes rapid and large decreases in water temperature and this has a negative impact on the aerobic performance and survivability of fish (Hanekom et al. 1989, van der Walt et al. 2021). However, recent studies found that protected *C. laticeps* populations were able to achieve higher metabolic rates than exploited populations at very low temperatures (Skeeles 2019). Thus, suggesting that protected *C. laticeps* populations may be more resilient to the physiological stresses brought on by upwelling if they are able to maintain their activity levels despite changing temperatures. This study provided the opportunity to investigate whether both temperature and exploitation affected the behaviour of *C. laticeps*. Behaviour can be altered by fishing practices and is closely linked with metabolism as behaviours have associated metabolic costs (Clark et al. 2013, Killen et al. 2013, Metcalfe et al. 2016).

5.2 BEHAVIOURAL STUDIES OF *C. LATICEPS*

A systematic review was conducted to collate all research on the study species and to determine whether stereo-BRUVs could be used to study the behaviour of *C. laticeps* (Chapter 2). The systematic review revealed that although *C. laticeps* had been extensively studied, aspects of its behaviour were still unknown. What was known about its behaviour was limited to a few observations made during diving surveys (Penrith 1972a, Buxton 1987), in laboratory settings (Buxton 1990, Davis 1996) or in stereo-BRUVs samples (De Vos 2012, Sanguinetti 2013), with no studies dedicated to investigating *C. laticeps* behaviour. As behaviours observed in a laboratory settings may not reflect natural behaviour, any study of behaviour should be conducted *in situ.* The second part of the review assessed studies that had used RUVs to investigate fish behaviour. Many studies had in fact employed RUVs to study a variety of behaviours in many taxa. From these studies, a list of behaviours that could be measured in *C. laticeps* were created.

5.3 UPWELLING SEASON VS. SPAWNING SEASON

Summer is the spawning season of *C. laticeps,* coinciding with the months that have the highest thermal variability (Buxton 1990, Goschen & Schumann 2011). This presented challenges for the sampling programme and study design as the behaviour of *C. laticeps* could vary seasonally. Thus, a pilot study was conducted to determine if there were seasonal differences in *C. laticeps* behaviour. Additionally, the pilot study aimed to find appropriate metrics to describe *C. laticeps* behaviour as well as test the suitability of the software BORIS (Friard & Gamba 2016) for quantifying these behavioural metrics.

The pilot study found that season did not have a significant effect on *C. laticeps* behaviour. Instead, temperature and size most influenced their behaviour. Generally, individuals were more active at higher temperatures and size had a positive relationship with most behaviours (aggressive feeding, chasing, time in field of view). This was attributed to metabolic constraints placed on the fish at low temperatures, larger individuals feeding more aggressively to meet their higher energetic demands and the territorial nature of large males (Penrith 1972a, Buxton & Garratt 1990, Xu et al. 2007). The results of the pilot study enabled sampling to occur across seasons as well as the inclusion of historical stereo-BRUVs datasets in the main study.

5.4 THE EFFECT OF MANAGEMENT ON POPULATION PARAMETERS AND BEHAVIOUR

The main study measured relative abundance (MaxN), size and behaviour of *C. laticeps* in two marine protected areas (MPAs), namely Tsitsikamma MPA and Goukamma MPA and at two exploited sites, namely Cape Recife (Port Elizabeth) and Cape St. Francis (Figure 4.2). Size, MaxN and behaviour did not vary by protection level. This was due to highly variability in behavioural responses within the two MPAs and two exploited sites. Consequently, location was a better predictor of MaxN, size and behaviour. Notably, Cape Recife had significantly lower MaxN and smaller-sized fish compared to the other locations, which had similar results of these metrics. The lack of significant behavioural differences between the MPAs and exploited areas could be due to high behavioural phenotypic diversity in the population or spillover from the MPAs to the exploited sites, resulting in all four populations having the same genetic predisposition to physiological stressors (Tilney et al. 1996, Brouwer et al. 2003, Kerwath et al. 2007b, Teske et al. 2010). Spillover from MPAs to exploited areas is one of key benefits and justifications of MPAs; protected a breeding stock allows fish species to recover whilst also improving recruitment in adjacent fished areas (Kerwath et al. 2008, Lombard et al. 2019). Additionally, the sampling method of stereo-BRUVs may have sampled greater behavioural phenotypic diversity compared to the methods used by Duncan et al. (2019) and Skeeles (2019) which may have sampled narrower diversity as result of using passive gears to collect their *C. laticeps*.

5.5 THE EFFECT OF TEMPERATURE ON POPULATION PARAMETERS AND BEHAVIOUR

Temperature had a positive relationship with MaxN in the exploited areas, but not the protected areas. In terms of behaviour, both the time to arrive and time to feed shortened with increasing temperatures, regardless of management. Overall, the main study did not find that protected *C. laticeps* performed better than their exploited counter parts at cold temperatures. The only exception was feeding rate at Tsitsikamma MPA that was significantly higher than at Cape St. Francis at 10.15-11.30 °C (Figure 4.19).

5.6 THE EFFECT OF SIZE AND CONSPECIFICS ON POPULATION PARAMETERS AND BEHAVIOUR

Size was one of the most important predictors of behaviour. Models that excluded size as an explanatory variable had very poor fit and explained very little variability in the data, thus size had to be included in all models for the individual-level data. Generally, size had a positive relationship with behaviour. Notably, size had a significant, positive relationship with the probability of chasing in the MPAs only. This may be attributed to learnt behaviour or fisheries induced evolution selecting for timid and less dominant individuals in the exploited areas, as these individuals are more likely to be avoid capture (Colefax et al. 2016, Arlinghaus et al. 2017, Rhoades et al. 2019). The absence of large size classes of *C. laticeps* at Cape Recife should be cause for concern as our study indicates that larger individuals are more active. Although there were no significant differences in *C. laticeps* behaviour between Cape Recife and the other locations in this study, the continued extraction of large individuals could eventually lead to a significant loss of bold and dominant phenotypes at Cape Recife.

When abundances of *C. laticeps* were high, the time to arrive and time to feed was shorter. This was attributed to more individuals being likely to encounter the bait when abundances are high. High abundances of conspecifics appeared to increase competition among *C. laticeps* individuals, which manifested as increasing feeding rate and probability of fleeing as the abundance of conspecifics increased.

5.7 LIMITATIONS OF THE STUDY

Limitations of this study were the inability to sample at temperatures higher than 15 °C at Cape St. Francis and higher than 18 °C at all locations. This was mainly due to the COVID-19 pandemic limiting field work. It is particularly important to know whether the results seen at Cape St. Francis are consistent across a wider temperature range or if the behaviour of *C. laticeps* changes at higher temperatures. Duncan et al. (2019) found that the differences in the metabolic scope of protected and exploited *C. laticeps* populations were most significant between the temperatures 20-24 °C. Similarly, the temperatures at which Skeeles (2019) observed significantly lower metabolic rates in exploited *C. laticeps* populations compared to protected populations (8-8.5 °C and 20.5-22 °C) were outside of the temperature range sampled by this study.

Given that behaviour varied between the two MPAs and the two exploited sites, future studies should also include more study sites. Future studies should also sample across a wider temperature range and include additional species in the analyses. Another limitation was the inability to measure all individuals observed at MaxN. Only individuals that could be measured were included in the analysis and a large amount of behavioural data (about half) was discarded. The finding of this study would be strengthened if more size data could be extracted from the samples collected. Another limitation of this study was high zero inflation in some of the behaviours and the count data was converted to absence/presence data for the purposes of modelling. This may have contributed towards behaviours appearing more similar as, for example, both five and 10 bites of the bait would be recorded as present (1) when converting count data to presence/absence data. A larger sample size, zero inflated models or hurdle models might address this limitation. Furthermore, if future studies could assess the behavioural responses of fish at both thermal extremes (cold and hot), it would help discern whether cooling or warming is more of a threat to fish populations and enact appropriate management measures.

5.8 CONCLUSIONS AND RECOMMENDATIONS

The effects of temperature, size and the abundance of conspecifics on behaviour of *C. laticeps* were generally consistent across protection level and location. Although, the absence of large size classes of *C. laticeps* at Cape Recife may be cause for concern as large and male individuals are typically more active, bold and dominant. If the removal of large individuals persists over time, it may result in shy and less active *C. laticeps* at Cape Recife, which could negatively impact the fitness of the population. Overall, this thesis has contributed to understanding the interactions between temperature and protection in the context of ongoing climate change.

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7 APPENDICES

APPENDIX 1

Table 7.1 Date of collection, geographical coordinates, depth and associated water temperature of samples used in the pilot study.

Sample code	Date (dd/mm/yyyy)	Y	X	Depth (m)	Temperature (°C)
13-02_TNP_040	10/02/2013	-34.02868	23.91819	17.0	16.89
13-02_TNP_041	10/02/2013	-34.03166	23.94062	19.0	14.41
13-09_TNP_001	07/09/2013	-34.0317	23.940642	16.0	17.20
13-09_TNP_004	07/09/2013	-34.0311	23.93011	25.0	17.10
13-09_TNP_006	07/09/2013	-34.02863	23.93167	16.0	17.40
13-09_TNP_010	07/09/2013	-34.02726	23.91342	16.0	17.40
13-09_TNP_011	08/09/2013	-34.0287	23.91809	18.0	17.60
13-09_TNP_014	08/09/2013	-34.02164	23.94067	20.0	17.50
13-09_TNP_016	08/09/2013	-34.02725	23.91352	14.0	17.60
13-09_TNP_021	10/09/2013	-34.03025	23.93897	18.0	17.60
13-09_TNP_023	11/09/2013	-38.08277	23.92248	19.0	17.40
13-09_TNP_027	11/09/2013	-34.02706	23.91795	14.0	17.40
13-09_TNP_031	11/09/2013	-34.02869	23.91807	18.0	17.60
13-09_TNP_034	11/09/2013	-34.03177	23.94063	18.0	17.60
13-09_TNP_041	12/09/2013	-34.02865	23.93596	15.0	17.40
14-02_TNP_010	20/02/2014	-34.02733	23.9275	17.0	17.54
14-02_TNP_012	20/02/2014	-34.02878	23.917	17.3	14.24
14-02_TNP_014	20/02/2014	-34.02718	23.92256	16.0	15.17
14-02_TNP_015	20/02/2014	-34.02865	23.90785	19.1	14.32
14-02_TNP_016	21/02/2014	-34.02857	23.91671	18.0	17.91
14-02_TNP_018	21/02/2014	-34.02854	23.92278	18.0	16.22
14-02_TNP_019	21/02/2014	-34.031	23.94909	19.0	18.39
14-07_TNP_008	17/07/2014	-34.02819	23.91176	19.0	17.00
14-07_TNP_009	17/07/2014	-34.021028	23.90899	16.0	17.20
14-07_TNP_011	22/07/2014	-34.02902	23.93563	16.0	17.00
14-07_TNP_030	23/07/2014	-34.03222	23.94993	21.0	17.00
14-07_TNP_061	28/07/2014	-34.03075	23.93845	22.0	16.70
14-07_TNP_064	29/07/2014	-34.03279	23.952	22.0	16.70

APPENDIX 2

Table 7.2 Location, date of collection, geographical coordinates, depth and associated water temperature of samples used in the main study.

Sample code	Location	Date (dd/mm/yyyy)	Y	X	Depth (m)	Temperature (°C)
13-02_TNP_012	Tsitsikamma	07/02/2013	-34.02888	23.91077	23.0	10.15
13-02_TNP_040	Tsitsikamma	10/02/2013	-34.02868	23.91819	17.0	16.89
13-02_TNP_055	Tsitsikamma	11/02/2013	-34.02878	23.91838	17.0	13.25
13-02_TNP_056	Tsitsikamma	11/02/2013	-34.03173	23.94060	19.0	11.95
13-09_TNP_001	Tsitsikamma	07/09/2013	-34.0317	23.940642	16.0	17.20
13-09_TNP_004	Tsitsikamma	07/09/2013	-34.0311	23.93011	17.0	17.40
13-09_TNP_006	Tsitsikamma	07/09/2013	-34.02863	23.93167	16.0	17.40
13-09_TNP_011	Tsitsikamma	08/09/2013	-34.0287	23.91809	20.0	17.70
13-09_TNP_021	Tsitsikamma	10/09/2013	-34.03025	23.93897	18.0	17.60
13-09_TNP_041	Tsitsikamma	12/09/2013	-34.02865	23.93596	17.0	17.50
14-02_TNP_010	Tsitsikamma	20/02/2014	-34.027330	23.927500	17.0	17.65
14-02_TNP_012	Tsitsikamma	20/02/2014	-34.028780	23.917000	17.3	14.32
14-02_TNP_014	Tsitsikamma	20/02/2014	-34.027180	23.922560	16.0	15.14
14-02_TNP_015	Tsitsikamma	20/02/2014	-34.028650	23.907850	19.1	14.26
14-02_TNP_018	Tsitsikamma	21/02/2014	-34.028540	23.922780	18.0	16.34
14-07_TNP_008	Tsitsikamma	17/07/2014	-34.028190	23.911760	19.0	17.00
14-07_TNP_009	Tsitsikamma	17/07/2014	-34.021028	23.908990	16.0	17.20
14-07_TNP_011	Tsitsikamma	22/07/2014	-34.029020	23.935630	16.0	17.00
14-07_TNP_030	Tsitsikamma	23/07/2014	-34.032220	23.949930	21.0	17.00
14-07_TNP_061	Tsitsikamma	28/07/2014	-34.030750	23.938450	22.0	16.70
14-07_TNP_064	Tsitsikamma	29/07/2014	-34.032790	23.952000	22.0	16.70
19-06_TNP_001	Tsitsikamma	31/05/2019	-34.03738	23.95748	21.9	10.16
19-06_TNP_005	Tsitsikamma	31/05/2019	-34.03521	23.96030	15.1	13.73
19-06_TNP_018	Tsitsikamma	01/06/2019	-34.03078	23.94962	17.4	10.63
19-06_TNP_030	Tsitsikamma	01/06/2019	-34.03020	23.92811	24.7	10.58
19-06_TNP_057	Tsitsikamma	04/06/2019	-34.03299	23.95479	17.3	14.91
19-06_TNP_058	Tsitsikamma	04/06/2019	-34.03054	23.93841	21.1	14.13
19-06_TNP_060	Tsitsikamma	04/06/2019	-34.02811	23.91698	16.5	15.59
19-06_TNP_062	Tsitsikamma	04/06/2019	-34.03278	23.95212	23.3	13.45
19-06_TNP_063	Tsitsikamma	04/06/2019	-34.07281	23.93565	15.2	15.46
19-06_TNP_064	Tsitsikamma	04/06/2019	-34.03049	23.93317	16.7	15.33
19-06_TNP_066	Tsitsikamma	04/06/2019	-34.03019	23.93049	23.3	11.54
19-06_GK_001	Goukamma	19/06/2019	-34.09957	22.98127	20.4	15.37
19-06_GK_002	Goukamma	19/06/2019	-34.09696	22.97539	18.3	15.41
19-06_GK_005	Goukamma	19/06/2019	-34.09709	22.97008	24.1	15.49

19-06_GK_007	Goukamma	19/06/2019	-34.09157	22.95880	17.6	15.44
19-06_GK_010	Goukamma	19/06/2019	-34.09164	22.94742	24.7	15.54
19-06_GK_011	Goukamma	19/06/2019	-34.08875	22.94806	22.4	15.45
19-06_GK_013	Goukamma	19/06/2019	-34.09176	22.94260	15.4	15.41
19-06_GK_014	Goukamma	19/06/2019	-34.09146	22.94555	15.4	15.58
19-06_GK_018	Goukamma	19/06/2019	-34.07530	22.90489	24.0	15.41
19-06_GK_019	Goukamma	19/06/2019	-34.09289	22.95746	19.4	15.55
20-01_Upwelling_030	Goukamma	24/01/2020	-34.09839	22.98083	19.3	11.63
20-01_Upwelling_031	Goukamma	24/01/2020	-34.09688	22.97505	16.8	11.69
20-01_Upwelling_034	Goukamma	24/01/2020	-34.09640	22.97000	24.4	11.57
20-01_Upwelling_036	Goukamma	24/01/2020	-34.08904	22.94879	22.6	11.81
20-01_Upwelling_037	Goukamma	24/01/2020	-34.09178	22.94583	19.5	11.82
20-01_Upwelling_038	Goukamma	24/01/2020	-34.07993	22.92112	23.6	11.74
20-01_Upwelling_047	Goukamma	25/01/2020	-34.08088	22.92148	16.3	15.98
20-01_Upwelling_051	Goukamma	25/01/2020	-34.09149	22.94601	23.6	14.66
20-01_Upwelling_055	Goukamma	25/01/2020	-34.09608	22.97800	16.7	14.12
20-01_Upwelling_056	Goukamma	25/01/2020	-34.09618	22.96860	24.4	12.99
20-01_Upwelling_057	Goukamma	25/01/2020	-34.09466	22.96775	15.7	16.36
15-04_AB_004	Cape Recife	13/04/2015	-34.04916	25.70348	24.0	11.20
15-04_AB_012	Cape Recife	13/04/2015	-34.04368	25.71985	24.0	11.20
19-10_Upwell_001	Cape Recife	19/10/2019	-34.04210	25.70702	15.7	17.77
19-10_Upwell_002	Cape Recife	19/10/2019	-34.04444	25.70765	17.7	17.72
19-10_Upwell_003	Cape Recife	19/10/2019	-34.04572	25.71032	21.5	17.69
19-10_Upwell_007	Cape Recife	19/10/2019	-34.04309	25.71868	22.1	17.71
19-10_Upwell_008	Cape Recife	19/10/2019	-34.04011	25.71851	17.5	17.74
19-10_Upwell_010	Cape Recife	19/10/2019	-34.03733	25.71891	15.7	17.77
19-10_Upwell_011	Cape Recife	19/10/2019	-34.03976	25.71250	21.2	17.76
19-10_Upwell_013	Cape Recife	19/10/2019	-34.03499	25.71804	17.8	17.80
19-10_Upwell_014	Cape Recife	19/10/2019	-34.03226	25.71649	16.6	17.86
19-10_Upwell_015	Cape Recife	19/10/2019	-34.04202	25.71273	22.2	17.47
19-10_Upwell_016	Cape Recife	19/10/2019	-34.03391	25.71106	24.8	17.72
20-01_Upwelling_058	Cape Recife	04/02/2020	-34.04297	25.70679	15.3	14.70
20-01_Upwelling_059	Cape Recife	04/02/2020	-34.04495	25.70827	20.0	13.70
20-01_Upwelling_060	Cape Recife	04/02/2020	-34.04611	25.71020	24.0	12.70
20-01_Upwelling_061	Cape Recife	04/02/2020	-34.04520	25.71237	21.9	12.88
20-01_Upwelling_064	Cape Recife	04/02/2020	-34.04336	25.71838	21.2	14.24
20-01_Upwelling_065	Cape Recife	04/02/2020	-34.04053	25.71846	19.1	14.41
20-01_Upwelling_066	Cape Recife	04/02/2020	-34.04016	25.72284	21.7	13.02
20-01_Upwelling_067	Cape Recife	04/02/2020	-34.04003	25.72395	23.7	12.79
20-01_Upwelling_068	Cape Recife	04/02/2020	-34.04324	25.72055	22.0	13.04
20-01_Upwelling_001	Cape St Francis	15/01/2020	-34.20737	24.74321	20.9	11.23
20-01_Upwelling_004	Cape St Francis	15/01/2020	-34.20624	24.73319	22.8	11.57
20-01_Upwelling_007	Cape St Francis	15/01/2020	-34.20427	24.74359	19.2	11.20

20-01_Upwelling_010	Cape St Francis	15/01/2020	-34.20253	24.73118	15.9	11.85
20-01_Upwelling_011	Cape St Francis	15/01/2020	-34.20079	24.72448	18.3	12.25
20-01_Upwelling_014	Cape St Francis	15/01/2020	-34.19980	24.73635	17.6	11.32
20-01_Upwelling_016	Cape St Francis	15/01/2020	-34.20053	24.72639	15.0	12.29
20-01_Upwelling_020	Cape St Francis	15/01/2020	-34.20817	24.80632	21.5	10.61
20-01_Upwelling_021	Cape St Francis	15/01/2020	-34.20996	24.80832	23.6	10.13
20-01_Upwelling_029	Cape St Francis	15/01/2020	-34.21532	24.82403	22.6	10.64
20-10_Upwelling_001	Cape St Francis	07/10/2020	-34.20245	24.72063	20.1	11.06
20-10_Upwelling_002	Cape St Francis	07/10/2020	-34.20368	24.72317	22.6	11.52
20-10_Upwelling_003	Cape St Francis	07/10/2020	-34.20079	24.72448	17.2	14.80
20-10_Upwelling_004	Cape St Francis	07/10/2020	-34.20053	24.72639	16.6	13.51
20-10_Upwelling_005	Cape St Francis	07/10/2020	-34.20314	24.72720	20.6	11.80
20-10_Upwelling_006	Cape St Francis	07/10/2020	-34.20002	24.73009	15.5	14.79
20-10_Upwelling_007	Cape St Francis	07/10/2020	-34.20514	24.72998	24.1	11.30
20-10_Upwelling_008	Cape St Francis	07/10/2020	-34.20253	24.73118	15.1	14.48
20-10_Upwelling_010	Cape St Francis	07/10/2020	-34.19980	24.73635	17.8	14.28
20-10_Upwelling_011	Cape St Francis	07/10/2020	-34.20624	24.73319	17.1	12.14
20-10_Upwelling_012	Cape St Francis	07/10/2020	-34.20483	24.73639	15.6	13.59
20-10_Upwelling_013	Cape St Francis	07/10/2020	-34.20612	24.73983	19.0	12.34
20-10_Upwelling_014	Cape St Francis	07/10/2020	-34.20312	24.73831	15.0	13.99