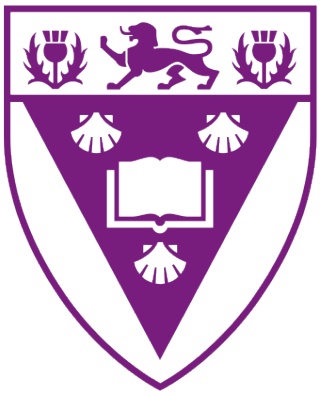
Can thermal metabolic physiology information predict fish behaviour observed on Baited Remote Underwater Video? – case study on fransmadam, *Boopsoidea inornata*



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Thesis submitted in the fulfilment of the requirements for the degree of

Master of Science

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By

Bradley van Heerden

Supervisors: Prof. WM Potts, Prof. A-R Childs, Ms Bontle Mataboge

ABSTRACT

Globally, climate change is placing fish populations under pressure through multiple environmental stressors including ocean warming. Fish may respond to these stressors through physiological acclimation, altering their behaviour or shifting their distributions. However, since the physiology and behaviour of fishes is linked, understanding this relationship is critical for improving our understanding of the likely response of fishes to a rapidly changing climate. Up to now there is limited information on the link between physiological attributes and the wild behaviour of fishes, primarily because of methodological difficulties of observing behaviour in aquatic environments. However, Baited Remote Underwater Videos (BRUVs) allows us to observe fish behaviour in the wild and with the increase in use and the advancement of BRUV systems provides a technique to better understand the wild behaviour of fishes. When this information is combined with appropriate metabolic physiology experiments, it may provide information on the link between physiology and wild behaviour.

This study aimed to improve our understanding of the link between metabolic physiology and the wild behaviour of a linefish species, the fransmadam, *Boopsiodea inornata* by combining thermal metabolic information with wild behaviour observed using BRUVs. A total of 45 live adult and subadult *B. inornata* were collected from an area (Cape St Francis) that is heavily exploited by the hook and line fishery. Fish were transported to the NRF SAIAB Aquatic Ecophysiology Research Platform (AERP) laboratory at the Department of Ichthyology and Fisheries Science (DIFS), Rhodes University, and acclimated for at least two months at 16 ˚C. Standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) of *B. inornata* was quantified using flow-through respirometry techniques at 8 ˚C, 12 ˚C, 16 ˚C, 20 ˚C, and 24 ˚C. The relationship between the metabolic rates and temperature were modelled using a second order polynomial relationship and a population-level aerobic scope curve was developed for the species. Behavioural information was collected from existing stereo-BRUV videos collected by the NRF SAIAB Marine Remote Imagery Platform (MARIP) in Algoa Bay, Cape Recife and Cape St Francis. These videos were available at temperatures between 10 ˚C and 18 ˚C. The videos were analysed using EventMeasure software and the “MaxN” (maximum number of individuals observed within a single frame), “time to arrive” (first time for individual to appear within a single frame once BRUV on seafloor) and “time to feed” (time for first individual to feed on BRUV bait canister within a single frame) was recorded. The relationships between fish behaviour and temperature were modelled using a GAM with the Negative

Binomial family for “MaxN”, and a GLM with Tweedie family for “time to arrive” and “time to feed”.

The SMR of *B. inornata* ranged from 0.58 to 3.86 O_2mg.min^{-1}.kg^{-1} across test temperatures, with increased variability at the higher temperatures. Temperature had no significant effect on the polynomial relationship of SMR (p-value = 0.20, R^2 = 0.58) but was a significant predictor for the linear relationship ($p < 0.01$). MMR ranged from 1.64 O_2mg.min^{-1}.kg^{-1} (SD = ± 0.41) at 8 ˚C to 7.39 O_2mg.min^{-1}.kg^{-1} (SD = ± 1.33) at 20 ˚C across test temperatures with increased variability at the higher temperatures. Temperature had a significant effect on MMR for both linear ($p < 0.01$) and polynomial relationship ($p < 0.01$, R^2 = 0.77). The resultant AS ranged from 0.39 O_2mg.min^{-1}.kg^{-1} (SD = ± 0.47) at 8 ˚C to 4.51 O_2mg.min^{-1}.kg^{-1} (SD = ± 1.00) at 20 ˚C. Temperature had a significant effect on AS for both the linear ($p < 0.01$) and polynomial relationship ($p < 0.01$, R^2 = 0.41). The findings suggest an optimal peak AS at a temperature of 18.5 ˚C, which coincided with a relatively low SMR and a peak in MMR, and declines in metabolic performance below 12 ˚C and above 20 ˚C.

“MaxN” ranged from three to 110 individuals. Highest variability in “MaxN” was observed between 16 ˚C and 18 ˚C. Temperature did not have a significant effect on “MaxN” ($p = 0.22$, R^2 = 0.10). “Time to arrive” ranged from 2.25 minutes (17.5 ˚C) to 38.69 minutes (11.4 ˚C). Temperature ($p < 0.01$) and “MaxN” ($p < 0.01$) both had a negatively significant effect. The interaction effect between “MaxN” and temperature revealed a positive significant effect on “time to arrive” ($p < 0.01$, R^2 = 0.33). “Time to feed” ranged from 3.58 minutes (13.6 ˚C) to 50.92 minutes (11.74 ˚C). Temperature ($p < 0.01$) and “MaxN” ($p < 0.01$) both had a significant effect on “time to feed”. In addition, there was a significant relationship between “time to feed” and the interaction between “MaxN” and temperature ($p < 0.01$, R^2 = 0.71). The findings suggest an increase in “MaxN” and decrease in “time to arrive” and “time to feed” with highest “MaxN”, fastest “time to arrive” and “time to feed” around 17 ˚C, whereafter “MaxN” decreases and “time to arrive” and “time to feed” increases slightly until 18 ˚C.

The peak physiological performance (AS) at 18.5 ˚C closely corresponded to the peak in “MaxN” and fastest “time to arrive” and “time to feed” around 17 ˚C. Similarly, the low AS at 8 ˚C corresponded to the lowest mean “MaxN”, and the highest times for the “time to arrive” and “time to feed”.

The findings of this study indicate that there may be a link between the metabolic physiology and behaviour of fish in the wild at average and cold temperatures and suggests that aerobic scope (AS) may be informative for understanding responses to environmental change in the wild. It also highlights the potential of archived BRUVs for understanding the wild response of fishes to environmental change. However, this study was limited by the availability of BRUVs at warmer temperatures and by a lack of information on the dissolved oxygen concentration in the wild. Therefore, future research should endeavour to collect this information. While this approach is valuable, it represents only one of several methods (including bioenergetic models, growth experiments, and survival analyses) for assessing thermal performance, and which may provide complementary insights into fitness, population persistence, and productivity. Future research should integrate these multiple approaches, alongside physiological and environmental data such as dissolved oxygen availability, to generate robust performance curves that capture both individual and population-level responses to changing thermal environments.

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PREFACE

This thesis consists of a general introduction (Chapter 1), materials and methods (Chapter 2), results (Chapter 3), and discussion (Chapter 4).

Additional outputs completed, or in the process of completion during this thesis:

Conference presentations:

• Department of Ichthyology and Fisheries Science seminars, Rhodes University 2023.

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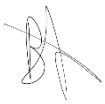
DECLARATION

I, Bradley Garth van Heerden, hereby declare that the work described in this thesis was carried out in the Department of Ichthyology and Fisheries Science, Rhodes University. Under the supervision of Professor Warren Potts, Professor Amber-Robyn Childs and Ms. Bontle Mataboge. The components of this thesis comprise of original work by the author and have not been submitted to any other university.

Signed: 

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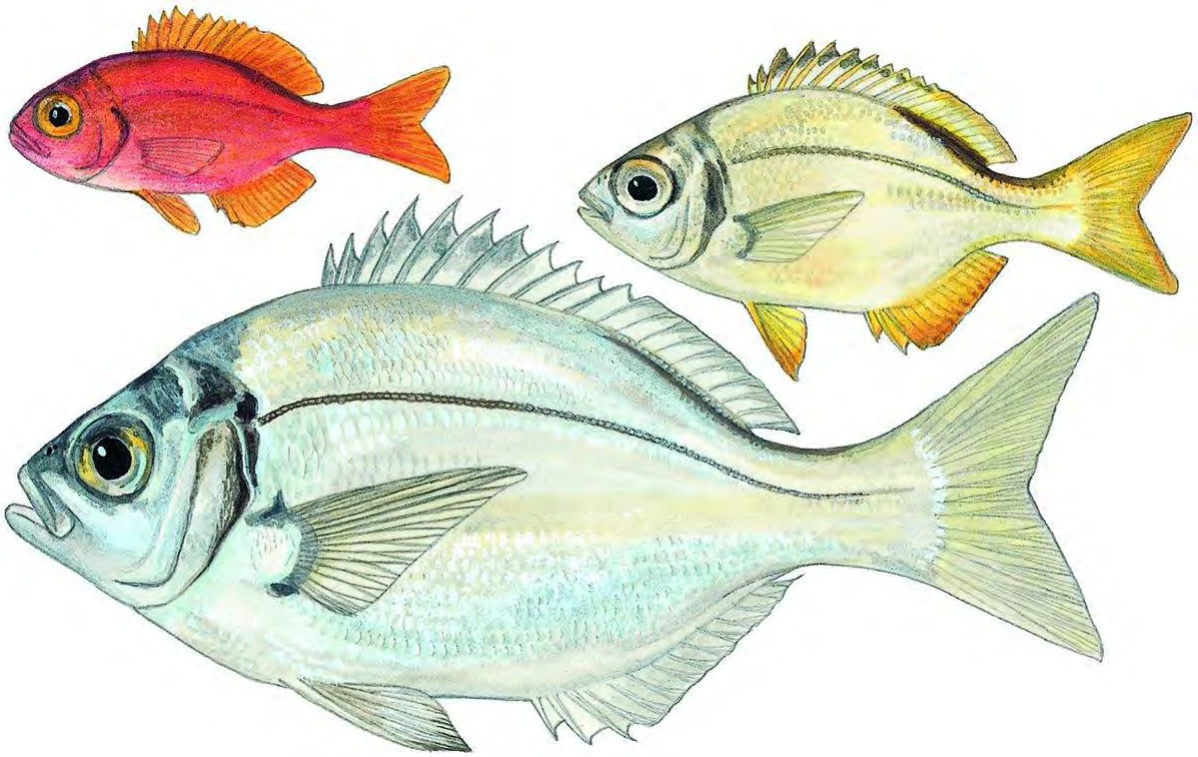
ABBREVIATIONS

AB	Algoa Bay
AERP	Aquatic Ecophysiology Research Laboratory
AS	Aerobic Scope
BRUV(s)	Baited remote underwater Video(s)
CT_{max}	Critical thermal maximum
CT_{min}	Critical thermal minimum
CSF	Cape St Francis
DEB	Dynamic energy budget
DIFS	Department of Ichthyology and Fisheries Science
DO	Dissolved oxygen
ENM(s)	Ecological Niche Model(s)
FL	Fork length
GAM	Generalised additive model
GLM	Generalised linear model
GLS	Generalised least squares
GSI	Gonad Somatic Index
GQ	Gqeberha
MARIP	Marine Remote Imagery Platform
MCS(s)	Marine Cold Spell(s)
MHW(s)	Marine Heat Wave(s)
MTE	Metabolic theory of ecology
MMR	Maximum metabolic rate
MO_2	Mass corrected oxygen consumption rate

Mono-BRUV	Baited Remote Underwater Video (one camera)
OCLTT	Oxygen capacity-limited thermal tolerance
PE	Port Elizabeth
RO_2	Non-mass corrected oxygen consumption rate
SAIAB	South African Institute for Aquatic Biodiversity
SDM(s)	Species Distribution Model(s)
SMR	Standard metabolic rate
SST	Sea surface temperature
Stereo-BRUV	Baited Remote Underwater Video (two cameras)
$T_{opt,AS}$	Optimum temperature, where aerobic scope is maximal
T1st	“Time to arrive” event

CHAPTER 1: GENERAL INTRODUCTION



Depiction of fransmadam, *Boopsoidea inornata*

Human activities dominate the climate and environment in the Anthropocene, driving significant changes in marine ecosystems (Johnson and Layman 2020, Bailey et al. 2022). The activities which drive these changes include the burning of fossil fuels, deforestation, overfishing, and pollution. The former factor, in particular, increases greenhouse gas emissions, which in turn drives global warming and ocean acidification. Anthropogenic climate change has led to several other environmental changes such as rising ocean temperatures, increased environmental variability and widespread deoxygenation (Rouault et al. 2010, Hoegh-Guldberg et al. 2014, Holt and Jorgensen 2015). Of all these, thermal changes are considered to be the major driver of changes in ocean ecosystems (Paaijmans et al. 2013, Pörtner et al. 2014, Deutsch et al. 2015) and most research has focused on the response of organisms to the patterns of long-term change (Alfonso et al. 2021). While the consequences of long-term thermal changes in sea surface temperatures (SSTs) have been well studied, the effects of short-term thermal variability (i.e., marine heatwaves and marine cold spells) remain an understudied area in modern scientific research. Although research is scarce, existing studies indicate that short-term variability can pose more immediate risks to fish populations (primarily resident species) than long-term variability, as they are capable of exceeding physiological tolerance thresholds, driving sudden mass mortality events, and causing rapid ecosystem disruption within short time frames (Potts et al. 2015, Bates et al. 2018, Bates et al. 2019, Duncan et al. 2019a).

When exposed to rapid thermal changes, the first response from fish is usually behavioural (Bailey et al. 2022). This is typical in mobile fish that can seek out optimal thermal conditions by moving. However, for resident species, or mobile species that are unable to locate optimal conditions, individuals must resort to physiological adaptation, such as increasing their oxygen uptake, or entering metabolic depression, to overcome these environmental changes (Donelson et al. 2011, Neubauer and Anderson 2019). However, these physiological modifications may influence other processes, such as growth, reproduction, and activity (Potts et al. 2015). Understanding the metabolic physiology of fishes and how it is influenced by a changing climate is fundamental for predicting the responses of fishes.

Current theories for understanding the metabolic response of fishes to changing thermal conditions include the Metabolic Theory of Ecology (MTE) (Brown et al. 2004), the Dynamic Energy Budget (DEB) (Kooijman 2009) for organisms in general, and the oxygen- and capacity-limited thermal tolerance (OCLTT) (Pörtner and Knust 2007), which was developed in the context of marine fishes. The OCLTT theory is a mechanistic framework that examines

how thermal constraints affect the balance between oxygen supply and demand in organisms, from molecular to whole-organism levels.

It emphasizes the importance of the "total excess aerobic power budget" (aerobic scope), which supports survival functions like locomotion (swimming), reproduction, and growth within an individual's thermal range (Pörtner 2010). This concept is based on the relationship between aerobic supply, aerobic demand, and temperature, which all define an individual's overall aerobic performance (MacMillan 2019). The OCLTT theory explains that the specialization of an individuals' thermal tolerance is based on the observation that the functional capacity of tissues, particularly those involved in oxygen transport, is optimized within a limited temperature range, enabling aerobic scope within that thermal window (Pörtner 2001, Pörtner and Knust 2007, Pörtner 2010, Seebacher and Little 2017).

The OCLTT theory has been extensively used to explain the metabolic responses of fishes to climate change, but it has faced significant criticism (Clark et al. 2013, Gräns et al. 2014, Norin et al. 2014, Jutfelt et al. 2018). Critics highlight its lack of universal applicability, as some species, such as insects and intertidal organisms, exhibit thermal limits that are not linked to oxygen demand. Additionally, the hypothesis is seen to overestimate oxygen limitation, neglecting other important factors like protein stability, membrane fluidity, and enzyme function, which can independently influence thermal limits (Verberk et al. 2016, Jutfelt et al. 2018, Clark et al. 2013, Rezende et al. 2014). A key debate concerns whether the optimal temperature for performance (Topt) aligns with the temperature at which aerobic scope is maximized (ToptAS), as laboratory results often do not match observed fish distributions in natural environments (Clark et al. 2013). Experimental findings have been inconsistent, with some studies showing no connection between oxygen availability and thermal tolerance, particularly in hypoxic conditions. For instance, Lefevre (2016), in a meta-analysis of fish studies using OCLTT, found no consensus on aerobic scope curve shapes or the effects of additional stressors.

A further concern of the OCLTT theory is that measuring oxygen transport capacity accurately is challenging, and there is a great deal of variability across life stages or acclimation periods, which further complicates generalization (Pörtner et al. 2017, Jutfelt et al. 2018). Unsurprisingly, this theory has also been criticized for overgeneralizing across taxa, insufficiently addressing behavioural and ecological factors, and being less relevant in extreme environments where thermal limits often diverge from OCLTT predictions (Clark et al. 2013).

To address these limitations, researchers propose integrating OCLTT with broader models that account for multiple stressors, environmental factors, and species-specific traits, improving our understanding of aerobic performance under climate change (Schulte 2015).

Despite criticism of the OCLTT theory, the measurements of aerobic scope AS, which is defined as an animal's capacity to increase its aerobic metabolic rate above maintenance levels (Fry 1947, Killen et al. 2013), has been used widely to address questions around the response of fishes to climate change (Clarke et al. 2013). Aerobic metabolism can be quantified as the rate of oxygen consumption which can be further summarized into three main rates, standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) (Roche et al. 2013). SMR is the required aerobic energy to maintain survival (Chabot et al. 2016) while MMR is the maximum output of aerobic energy an individual can sustain during an activity (Norin et al. 2014). AS is calculated as the difference between MMR and SMR and reflects the metabolic capacity available for everything beyond maintenance, such as growth, reproduction, foraging, and movement (Clark et al. 2013, Pörtner et al. 2017). These metabolic rates can be observed and recorded through an array of methods such as respirometry.

A respirometer consists of a chamber (depending on shape, usually cylindrical) and a medium (usually water) which surrounds the chamber and has access into the chamber itself. The fish is placed inside the chamber and depending on the type of respirometer (closed (Snyder et al. 2016), open/flow-through (Ward 2018), intermittent-flow (Svenden et al. 2016)) may be placed in a water bath. Intermittent-flow respirometers are the easiest and most accurate method to use as they are a combination of the closed and open types, utilizing their best features while eliminating or reducing the problems of the other two types. These problems come in the form of progressive hypoxia and simultaneous hypercapnia in closed respirometers due to lack of fresh water running through the respirometer, whereas open/flow-through respirometry has equilibrium issues due to continuous flush out of fresh water (Eriksen 2002, Svendsen et al. 2016). Intermittent flow-respirometry eliminates or reduces these problems by interchanging between short periods of closed-chamber oxygen consumption for measurements with regular flush (open) periods to replenish dissolved oxygen within the chamber once measurements periods are completed (Svendsen et al. 2016). This interchange between measurement and flush periods, which is improved and more consistent with automated software, reduces the accumulation of waste products like carbon dioxide within the chamber and improves the accuracy of the data as well as reduces stress of individuals within the chamber (Svendsen et al. 2016).

Because AS provides an indication of the potential energy available for functions beyond survival, such as foraging and swimming, it could be used to predict changes in the wild behaviour of fish at a range of environmental conditions. For example, if the AS of a fish increases, its activity should also increase, which will influence its behaviour. However, despite the potential value of AS in predicting the behavioural response of fishes, few empirical studies (but see Killen et al. 2012, Baktoft et al. 2016) have examined the relationship between metabolic physiology and wild behaviour of fishes (Bailey et al. 2022).

Several methods have been used to describe and monitor the wild behaviour of marine fishes. These include acoustic telemetry (Hellström et al. 2022, Matley et al. 2022), satellite tagging (Patterson and Hartmann 2011), passive integrated transponder tagging (Chrysafi et al. 2021) and conventional dart tagging (Latour 2005, Fonteneau et al. 2015). Although these techniques describe behaviour, they cannot typically provide real-time information, except in the case of acoustic and satellite telemetry tags equipped with behaviour-specific sensors.

This limits the opportunity to assess the behavioural response of fishes to changing environmental conditions. In contrast, visual observations, through underwater visual census such as diving (UVC), remote operated vehicles (ROV), remote underwater video (RUV) and baited remote underwater video (BRUV) provide opportunities to examine fish behaviour under a suite of environmental conditions (Lowry et al. 2012). The advancement of underwater video technology is rapidly increasing, driven by the need for a non-destructive, cost-effective and fishery-independent method to study fish populations in different habitats and depths, while minimising confounding factors such as the influence of the equipment on species behaviour or habitat complexity to produce accurate data (Whitmarsh et al. 2017, Harvey et al. 2021).

Of these techniques, the use of BRUVs has expanded rapidly in marine research (Harvey et al. 2021). A BRUV system is designed as a mono-BRUV (single video camera) or stereo-BRUV (two video cameras) system, recording the area surrounding a bait canister used to attract fish species (Figure 1.1). The bait canister is placed close to the camera, at a distance ranging between 0.5 m and 1.5 m, usually attached to the BRUV system by a metal pole (Willis and Babcock 2000, Heagney et al. 2007). These systems are directly deployed from a boat and sent down via rope to the seafloor (Watson et al. 2005, Cappo et al. 2007, Bassett and Montgomery 2011). These BRUV systems usually have a soak time (time taken to record on the seafloor) between 25 and 60 minutes (Willis and Babcock, Watson et al. 2005, Whitmarsh et al. 2017)

The primary benefit of this method is that it is minimally destructive and non-extractive, yielding a permanent and archivable record ability to record a diverse range of species (including both targeted and non-targeted species) and is a relatively cheap and easy-to-use method. They can be used in more areas compared to other observational methods such as UVC and are often deemed a more suitable choice because of the depth limitations and diver biases of UVC (Colton and Swearer 2010, Lowry et al. 2012). However, there is a wide variability in the set-up, experimental design, and implementation of BRUVs. The advancement and use of BRUV technology within the last two decades have increased immensely and the methods used when deploying BRUVs have progressively increased in variety as well.

Over the past two decades, advancements in BRUVs technology have greatly expanded the scope of studies and their aims. As a result, the methods used in these studies have become more diverse, with several factors varying from study to study, including the number and orientation of cameras (Willis and Babcock 2000, Langlois et al. 2006), soak time (Gladstone et al. 2012, Santana-Garcon et al. 2014), sampled habitats (Scott et al. 2015), deployment depth ranges, and the type, quantity, and preparation method of bait (Harvey et al. 2007, Hannah and Blume 2014). Even though there are established standards for BRUV usage, such as those by Cappo et al. (2007) and (Langlois et al. 2020), with the continuous development of new or modified approaches to this technology and the varying environmental contexts where BRUVs are deployed, variability in methods will always occur. More recently, BRUV data has increasingly been used to get a better understanding of fish behaviour with the bait canister (Figure 1.1(E)) mounted on the system, looking for fish to be attracted to the canister and feed on it, this simulates a “fishing” event where the bait from hook and line is dropped into the ocean and fish feed on it. Using this method may then provide a way to link the AS and behaviour of fishes.

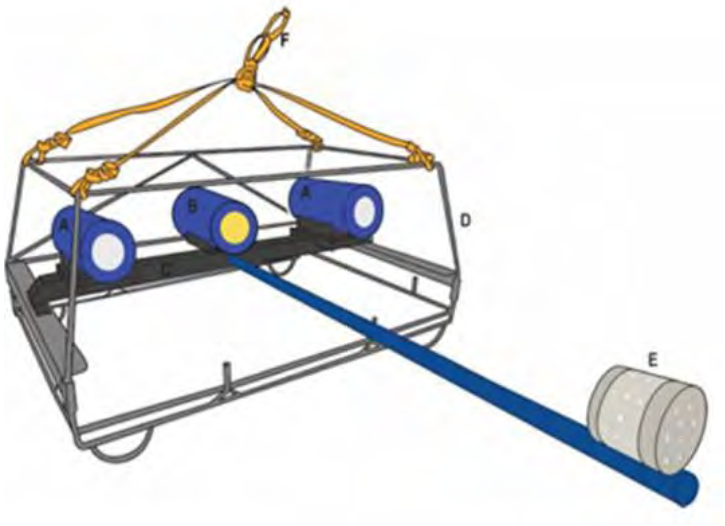


Figure 1.1: Drawing of the baited remote underwater stereo-video system. Underwater housings for HD video cameras (A), underwater housing for blue LED lighting (B), basebar (C), the system's frame (D), bait canister (E) and rope attachment for buoys during deployment and retrieval (F). Drawing by Dr Elodie Heyns.

Whitmarsh et al. (2017), in a review of 161 peer-reviewed studies published between 1950 and 2016, highlighted considerable variation in study design, including soak time, bait type, habitat, and replication. Their review emphasised the importance of reporting methodological details to ensure replicability. While BRUVs have been widely applied to assess MPAs (Bornt et al. 2015, Coleman et al. 2015), species behaviour (Denny et al. 2004), habitat differences (Gomelyuk 2009, Langlois et al. 2012) and methodological comparisons between and within BRUVs (Gladstone et al. 2012, Brooks et al. 2011), relatively few studies have examined how environmental variables influence fish behaviour (Figure 1.2) (Whitmarsh et al. 2017).

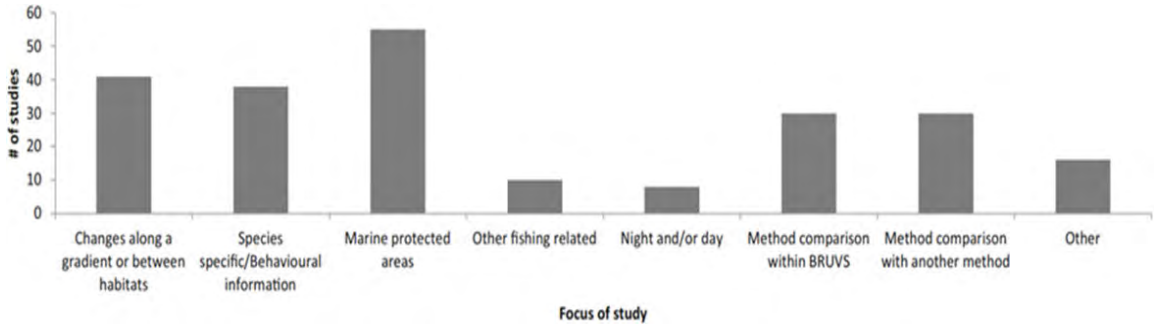


Figure 1.2: The "focus of study" from the 161 studies assessed in the review by Whitmarsh et al. (2017). Studies were counted in more than one column where they covered more than a single focus. The 'Other' category includes those which did not fit in any other category, including artificial versus natural reef assessments and other sorts of impacts.

With a growing desire for a better understanding of changes in behaviour along thermal gradients, BRUVs can serve as an appropriate, cheap, repeatable, and comparable method for assessing the behaviour of fishes in a changing thermal environment (Mataboge 2020).

The South African coastline extends for over 3000 km, and exhibits a diverse array of habitats, including rocky, sandy and mixed shores (Potts et al. 2015). The oceanography of this coastline is influenced by two major currents. The first is the Benguela Current, which is a cold and slow-moving current that moves northward up South Africa's west coast from the Cape point towards southern Angola (Olivar and Shelton 1993, Potts et al. 2015). The second is the warm, fast-moving Agulhas Current that moves southward down the east coast from the KwaZulu-Natal Province to the tip of the Agulhas bank (Lutjeharms 2006, Biastoch et al. 2024). These two currents meet at the Cape Point and make the South African coastline one of the most diverse landscapes. With these two currents being distinctly different, a wide variety of environments are found along the coastline (Bally et al. 1984).

Along the South African coast, short-term variability in oceanic conditions can induce rapid temperature changes, of up to 10 °C, within several hours (Goschen and Schumann 1995). These rapid fluctuations are driven by two mechanisms. The southern Cape coast of South Africa is characterized as having highly variable climatic conditions with extreme cooling and warming events. Marine cold spells (MCS) are driven by upwelling events. These events are driven when warm surface waters are transported offshore and replaced by deep, cold, nutrient-rich waters (Schlegel et al. 2017). In South Africa, this is driven either by the prevailing Southeasterly trade winds or by the strengthening of the Agulhas Current which enhances the Ekman transport along its landward edge (Lutjeharms 2006). The first is a combination of the strengthening of the Agulhas Current, which is increasing the temperature of the coastal waters along the coast, and its irregular shifts (Natal Pulses'), which drive offshore Ekman transport (movement of surface waters away from the coast) and rapid declines in water temperature (Goschen and Schumann 1995). The second mechanism which is independent of the strengthening of the Agulhas Current, is the increase in the intensity and frequency of northeasterly winds in the summer months, which drive upwelling (Duncan et al. 2019a). When marine heat waves (MHW) driven by the strengthening Agulhas Current are followed by intense wind-driven upwelling events, the coastal temperatures can drop extremely rapidly and have negative impacts, including extensive fish mortality, due to cold shock (Allison et al. 2021).

Marine heatwaves are prolonged periods of anomalously warm seawater that can significantly impact marine ecosystems (Pearce et al. 2011). Initially, the characterisation of MHWs was hampered by inconsistent definitions across studies. To address this, Hobday et al. (2016) proposed a widely adopted quantitative framework, defining MHWs as "periods when sea surface temperature exceeds the seasonally varying 90th percentile for at least five consecutive days". Alternative approaches include fixed-threshold definitions (Frölicher et al. 2018) and cumulative heat stress metrics (Eakin et al. 2010). In South African waters, MHWs are commonly associated with intensification of the Agulhas Current, where frontal meanders transport warm tropical water southward and onto the Agulhas Bank, where it may persist for several days (Lutjeharms 2006, Biastoch et al. 2024).

Of the fishes found along the South African southern coast, resident species are likely to be more susceptible to this thermal variability due to their lack of mobility (Potts et al. 2015). Unlike migratory species that are able to shift their distribution to seek optimal thermal refuge, resident species will be exposed to sub-optimal temperatures for longer periods (Donaldson et al. 2008, Van Der Kraak and Pankhurst 1997) and ultimately, even lethal temperatures (Pörtner 2001, Pörtner and Farrell 2008, Allison et al. 2021). Generally, all fishes have a particular range of thermal conditions where their metabolism (aerobic energy production) functions optimally (Neuheimer et al. 2011, Jain et al. 2013). For example, in thermally stable areas (e.g. the tropics) resident species have evolved narrower thermal scopes (Rummer et al. 2014) and can be classified to be stenothermic, while in highly variable environments, such as in temperate upwelling regions, resident species have evolved to be eurythermic (Pörtner et al. 2000, Logan and Buckley 2015, Farrell 2016). In the increasingly variable conditions associated with a changing climate, temperature may drop below or exceed critical thresholds and energy production is limited by low levels of oxygen in their body fluids (Pörtner et al 2000, Logan and Buckley 2015).

The reduced energy available at sub-optimal thermal conditions will influence fish populations in various ways (Holt and Jorgensen 2015, Lindmark et al. 2018). The effects of sub-optimal thermal conditions on life-history traits are strongly dependent on whether the environment is colder or warmer than the optimal thermal range of the species' (Lindmark et al. 2018). In colder environments, populations tend to grow slower, mature later, and live longer, aligning with the temperature-size rule (TSR), which states that lower temperatures during ontogeny lead to slower growth and development but larger adult body sizes (Lindmark et al. 2018). Conversely, in warmer environments, populations grow faster, mature earlier, and have shorter

lifespans, as higher temperatures accelerate metabolic rates, resulting in faster growth and development but smaller adult body sizes (Alfonso et al. 2021). These temperature effects, combined with body size and metabolic scaling, play a crucial role in shaping population regulation, stage structure, and community dynamics (Duncan et al. 2020, Gillooly et al. 2001).

Resident species that are increasingly subjected to suboptimal temperatures, in this case cold, reductions in their metabolic rate exhibit reduced growth rates, increased age-at-maturity, decreased size-at-maturity and decreased age- specific fecundity (Pörtner 2010, Duncan et al. 2019b). Reduced metabolism and energy availability will also have an impact on the reproductive output of a species (Pörtner 2001, Potts et al. 2015, Farrell 2016, Brownscombe et al. 2022). Here, reductions in energy will limit the investment of energy to egg production and to other important reproductive behaviours such as nest building, courtship displays migration to spawn sites and gonad development.

Finally, the reduced energy available will influence the swimming performance, and thus behaviour of fishes (Clark et al. 2013). Reduced burst speeds and movement, associated with declines in fish metabolism (Claireaux et al. 2006), will influence a range of activities, including feeding (Brownscombe et al. 2014), predator avoidance, courtship, shoaling, and these will ultimately have negative impacts on the survival of the population through its impacts on fish growth, survival, and reproduction (Pörtner 2001, Brownscombe et al. 2022).

From a bioenergetic perspective, these constraints can be mechanistically linked to aerobic scope (AS), which defines the energetic capacity available for activities beyond maintenance metabolism (Brownscombe et al. 2022). Under thermal stress, when AS narrows, individuals have less energy to allocate to ecologically relevant behaviours, including foraging (Careau and Garland 2012). Feeding behaviour, in particular, is tightly coupled to AS because successful foraging requires not only basic locomotor performance but also the capacity for predator avoidance, competition, and digestional which all draw from the same limited energy budget (Brownscombe et al. 2014). Thus, reductions in AS under suboptimal thermal conditions may manifest as changes in feeding motivation, efficiency, or timing, ultimately influencing growth trajectories, survival, and reproductive success (Holt and Jorgensen 2015). Ultimately, however, the behavioural, phenological, demographic and distributional responses that determine resilience to climate change are dependent on the physiological responses of ectotherms to their environment (Rijnsdorp et al. 2009, Bozinovic and Pörtner 2015). Therefore, it is vital to augment our understanding of the links between physiological and

behavioural traits in response to environmental change. This understanding is not only key for developing management strategies that support the persistence of genetically diverse and adaptive phenotypes in fish populations, but also for enhancing our understanding of how metabolic physiology data can be used to predict fish responses to a changing climate.

1.1 Aim and objectives

The aim of this thesis is to examine the link between the metabolic physiology and wild behaviour of a marine fish across a thermal gradient to improve our knowledge on the potential utilisation of metabolic physiology information for the prediction of the response of fish to climate change. To do this, the objectives of the thesis were to:

(i) Quantify the metabolic performance of *B. inornata* across a thermal gradient. This was done by conducting metabolic physiology experiments to measure the standard metabolic rate (SMR), maximum metabolic rate (MMR), and aerobic scope (AS) of *B. inornata* across a range of ecological relevant temperatures.

(ii) Quantify the *in-situ* behavioural patterns of *B. inornata* across a thermal gradient. This was done by quantifying the relative abundance (MaxN), time to arrive and time to feed of *B. inornata* in the wild from existing BRUV footage captured across a similar thermal gradient.

(iii) Compare the physiology with *in-situ* behaviour metrics. This was done by overlaying the AS curve and *in-situ* behavioural data.

CHAPTER 2: MATERIALS AND METHODS

Bradley van Heerden (left) and Dr. Cuen Muller (right) transferring *Boopsoidea inornata* from the transport vehicle to housing facility (Image credit: Prof. Amber Childs).

2.1 Study sites

2.1.1 Algoa Bay, Cape Recife and Cape St Francis

The coastal oceanography of the area between Gqeberha (GQ) (Algoa Bay and Cape Recife), formerly known as Port Elizabeth (PE), and Cape St Francis (CSF) (Figure 2.1) is dominated by the warm, south-flowing Agulhas Current, with intermittent shelf-edge and wind-driven upwelling events (mostly in summer) which brings cold, nutrient rich, benthic water to the surface, sometimes up to a few weeks (Pillay et al. 2021).

Water temperatures in this area vary seasonally with temperature ranges between 16 °C and 22°C (Smit et al. 2013, Bouveroux et al. 2018), but generally warmer in summer. However, wind-driven upwellings, which are caused by easterly winds during the summer months (Lubitz et al. 2024) drive an increase in thermal variability, with changes in temperature exceeding 13 °C within a few hours (Schumann et al. 1988).

2.1.2 Cape St Francis

There is limited information on the oceanographic conditions of Cape St Francis. However, Harris (1978) suggested that the main surface currents in Cape St Francis are like Algoa Bay but stronger and more polarized in the eastward and westward directions. This area is also known for its chokka squid fishing as it is one of the main and dominant areas along the Southern coast for this activity (Roberts 2005, Voogt 2014). Mlotshwa (2023), found that the *in-situ* temperatures (15.77m – 27m depth) in this area ranged between 10 °C and 20 °C while the mean was between 15 °C and 16 °C from February to November 2022.

2.1.3 Algoa Bay

Algoa Bay is the easternmost and largest of several log-spiral shaped embayments along the south Cape coast of South Africa (Schumann et al. 1988). The main environment in Algoa Bay is highly dynamic, largely because of the interaction between oceanographic processes, weather systems and local bathymetry and shoreline contours of the region (Schumann et al. 1995). The normal seasonal range of sea surface temperatures (SSTs) in this area range between 16 °C and 22 °C but may decrease to 10 °C during upwelling events (Smit et al. 2013, Bouveroux et al. 2018). Upwelling at Cape Recife have resulted in SST declines of between 11°C and 13 °C within 12 hours (Schumann et al. 1988).

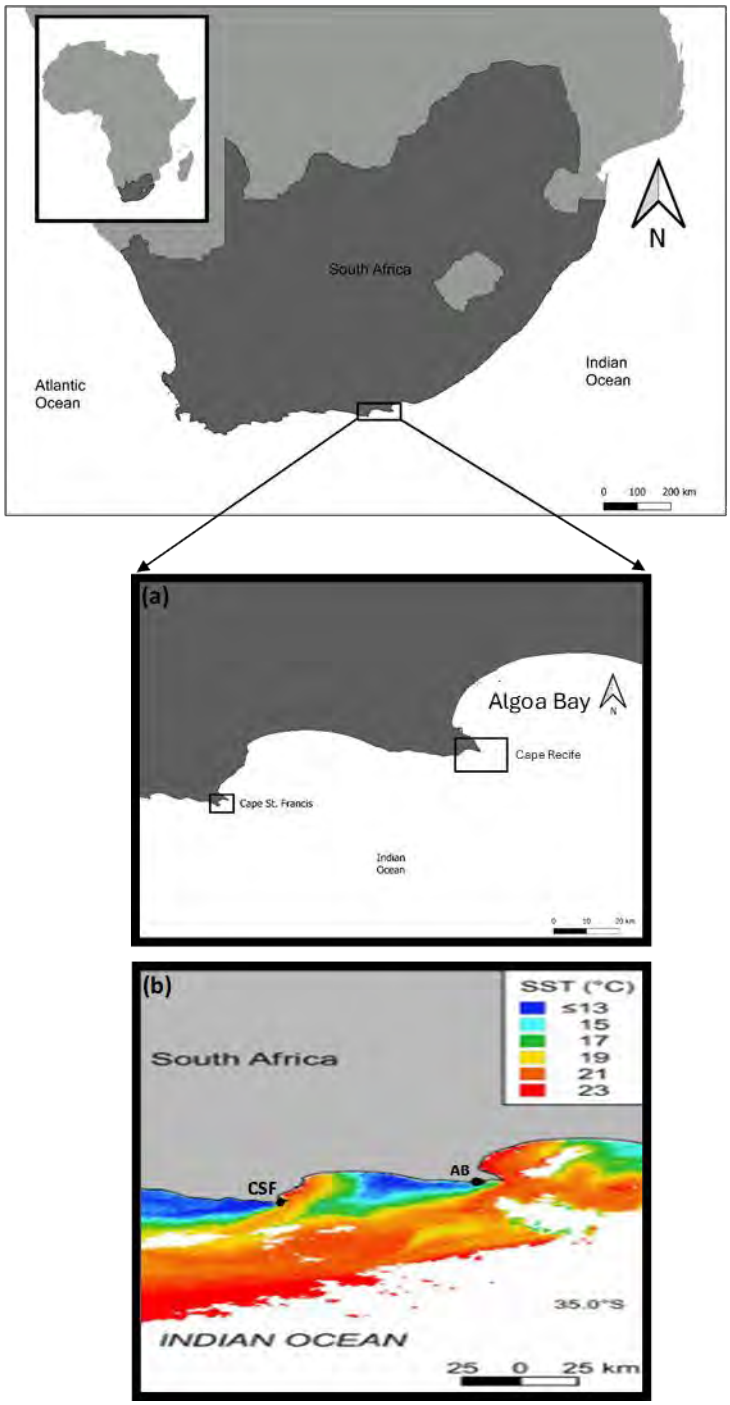


Figure 2.1: Study site contextualisation. **(a)** Location of study sites, Algoa Bay, Cape Recife and Cape St. Francis. **(b)** Upwelling events depicted by MODIS Terra satellite sea surface temperature data taken on 04-03-2010 for Algoa Bay and Cape St Francis. Adapted from Duncan et al. (2019b).

2.2 Study species

The Frans madam, *Boopsoidea inornata*, was selected as a candidate species for this research because it is abundant in exploited areas (Beckley and Buxton 1989), is resident (Attwood and Ensair 2020) and there is already some existing information on the thermal tolerance (Allison et al. 2021) and life history (Attwood and Ensair 2020) of the species.

This species is a small (max. length = 223 FL), long-lived (t_{tmax} = 37 years) endemic, resident sparid with a distribution from the southern KwaZulu-Natal Province to the Cape Point in the Western Cape Province, South Africa (Smith and Heemstra 1991, Attwood and Ensair 2020). With their wide distribution across the South African coastline, they are exposed to a broad range of temperatures, from as low as 10 °C during upwelling events along the southern coast to 25 °C in the KwaZulu-Natal region (Attwood and Ensair 2020, Allison et al. 2021). The species has a broad thermal tolerance of up to 22 °C but are usually found in waters averaging 16 °C (Allison et al. 2021).

They are a small gonochoristic species ($L\infty$= 222.7 mm) with high longevity (tmax= 37) that reach sexual maturity at 178 mm FL for females and 185 mm FL for males (Attwood and Ensair 2020). Females have a low fecundity and spawn throughout the year with the main spawning season starting in August and continuing through spring (Attwood and Ensair 2020). The sex ratio is heavily skewed towards females (1:3.35) but Attwood and Ensair (2020) found that the percentage of males in each population increases as you move eastward up the coast as the male to female sex ratio at the extremes of the range of *B. inornata* are 1:1 (warm end of range) and 1:7 (cold end of the range). They are omnivorous, with a diet dominated by small sand and reef-dwelling prey, with algae and small fish making up a smaller portion of the diet (Trow 1982, Lechanteur and Griffiths 2003). *Boopsoidea inornata* is not targeted by the linefishery and are therefore highly abundant in exploited/overfished areas due to lowered competition for resources (Boehlert 1996). Their stock status is unknown, but they are becoming more important in the fisheries as commercialised species are overharvested (van der Elst 1999, Jayiya et al. 2000, Attwood and Ensair 2020).

2.3 Physiology experiments

2.3.1 Fish collection

A total of 45 *B. inornata* were collected from Cape St Francis in April 2023 using hook and line at depths between 10 and 30 m. After capture, fish were vented using a hypodermic needle (16 gauge) to prevent barotrauma-related mortality (Kerwath et al. 2013) (Figure 2.2a). After venting, the fish were placed into two 250 L PVC tanks (Figure 2.2b) with fresh seawater and transported back to the shore and transferred into a large cylindrical holding tank (with 1 000 L of fresh seawater) on the back of a transport vehicle (Figure 2.2c). Oxygen was bubbled into the tank (rate) and additional aeration was supplied using battery-operated aerators during transportation to the NRF South African Institute of Aquatic Biodiversity's (SAIAB) Aquatic Ecophysiology Research Platform (AERP) laboratory at the Department of Ichthyology and Fisheries Science (DIFS), Rhodes University.

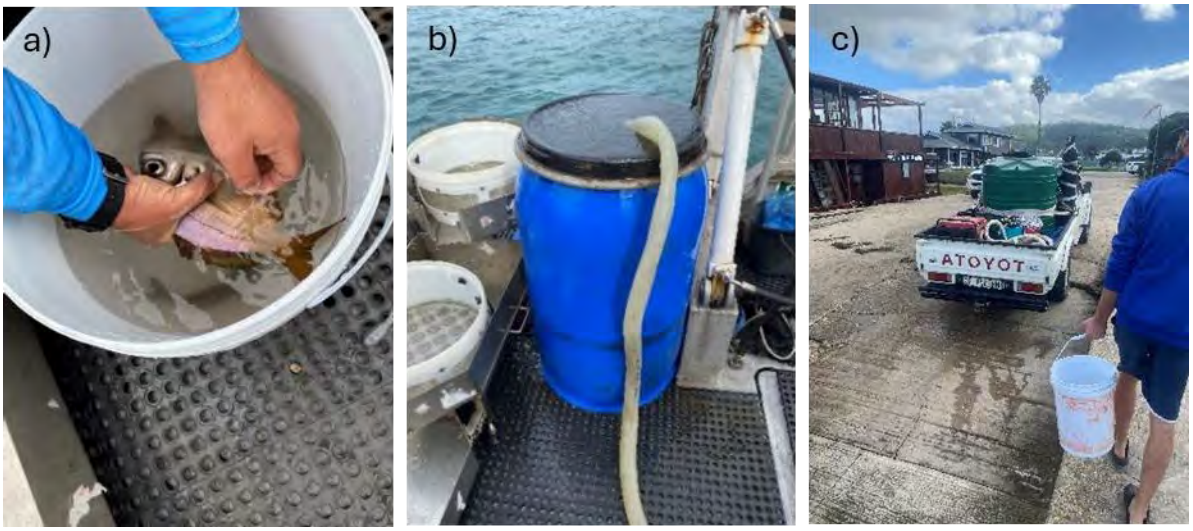


Figure 2.2: a) Venting of *Boopsoidea inornata* after being caught to prevent barotrauma. b) 250L drum used to hold *Boopsoidea inornata* while being transported from the NRF SAIAB RV Observer to the 1000L holding tank on the back of the vehicle. Fresh seawater was continuously supplied using the NRF SAIAB RV Observer bilge pump. c) Toyota Landcruiser with 1000l holding tank filled with fresh seawater for transportation of *Boopsoidea inornata* from Cape St Francis to the NRF SAIAB Aquatic Ecophysiology Research Platform (AERP) laboratory at the Department of Ichthyology and Fisheries Science (DIFS), Rhodes University. A battery-operated aerator and an oxygen cylinder were used to maintain the oxygen concentration in the tank.

2.3.2 Housing system and fish welfare

Once fish were transported back to the AERP, they were transferred to one of two cylindrical holding tanks (5 900 L each) connected to a marine recirculating system with a total volume of 1 400 L (Figure 2.3). The system comprised a protein skimmer (UltraZap, Red Devil DC 5000s pump), a bubble bead filter (BBF-200-COMP, Wilpet Koi Products) for filtration of dirt particles, ultraviolet sterilizers (UVS-30, Wilpet Koi Products) to clear seawater and destroy small pathogens, a fluidised biological filter (750 L slime tank, SuperActiFlo Media) and a sump (750 L slimline). Water temperature was maintained by a heat element (1.5 kW titanium hotrod) connected to temperature controller (STC-1000) and wall-mounted heat pump (AquaHeat) connected to an adjustable temperature controller (STC-1000). Tanks were aerated using an air blower (2.2 kW) located outside the laboratory, to maintain oxygen saturation at 100%.

Fish were acclimated at 16 ˚C for a period of four months before the start of the experiments. Animal ethics was approved prior to the collection and husbandry of the fish (Appendix table 5). The photoperiod was set at 9.5 hours of light and 14.5 hours of dark. Water quality parameters, including pH, dissolved oxygen, ammonia, nitrite and nitrate concentrations were monitored daily. Fish were fed a diet of frozen/thawed squid every two days and feeding rates were controlled (1 – 2 % of fish mass) due to the positive relationship between food availability and standard metabolic rate (Auer et al. 2016).

Figure 2.3: Marine recirculating aquaculture system (RAS) holding tanks, used to house *Boopsoidea inornata* during experiments in the NRF SAIAB Aquatic Ecophysiology Research Platform (AERP) laboratory at the Department of Ichthyology and Fisheries Science (DIFS), Rhodes University.

2.3.3 Experimental set up

Intermittent-flow respirometers were used to measure the oxygen consumption of *B. inornata* following the experimental procedure by Duncan et al. (2019b) (See checklist of 53 essential criteria for the reporting of methods for aquatic intermittent-flow respirometry (Killen et al. 2021) for the experiment in Appendix Table 3). Four cylindrical respirometers (40 cm length and 19 cm diameter) made from thick-walled Perspex were contained in glass water-baths and shielded from each other and from external disturbance by covering the sides of water-baths with black plastic sheets (Figure 2.4a). Each respirometer consisted of a flush pump (saltwater submersible pump) inlet which pumps water into the respirometer chamber after each measurement (closed) period, a recirculation loop made from an oxygen impermeable clear tubbing (Oxygen-impermeable material) and a peristaltic pump (Masterflex HV-07522 with 4 multi-channel F/S pump) (Figure 2.4b) which was connected to FireStingO_2 fibre optic oxygen sensor (FSO_2-4, Pro Science GmbH). The oxygen sensor was used to take measurements of

oxygen concentration from the circulation loop connected to the respirometer chamber. Pro Oxygen Logger Software (Pro Science GmbH) was used to read measurements taken by the FireSting oxygen sensor every second.

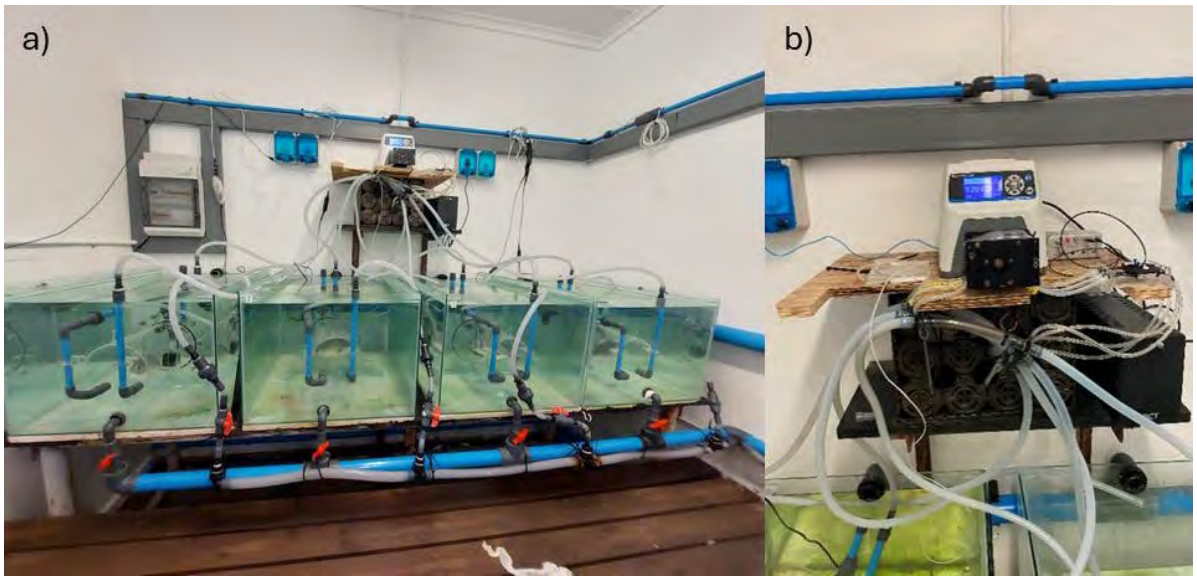


Figure 2.4: a) Experimental set up for respirometry trials. Four identical Intermittent-flow respirometers placed in identical water-baths, shielded from each other with black plastic sheeting to prevent external disturbance. b) The peristaltic pump (Masterflex HV-07522 with 4 multi-channel F/S pump) which was used to pull seawater through capillary tubing at a constant rate, connected to FireStingO_2 fibre optic oxygen sensor (FSO_2-4, Pro Science GmbH), used to measure oxygen concentration from the circulation loop connected to the respirometer chamber.

2.3.4 Experimental procedure

Fish were fasted for 36 hours to reduce postprandial effects before the experiments. After the fasting period, a single fish was placed into each of the four respirometers at 16°C. Once in the respirometer, the temperature was either increased or decreased to one of the test temperatures (8 °C, 12 °C, 16 °C, 20 °C, 24 °C) at a rate of one degree per hour, and the fish were given either six (12, 16 or 20 °C) or 24 (8, 24 °C) hours to acclimate to the new temperature. Fish were held for 6 hours at moderate temperatures (12–20°C), as these temperatures fall within the typical thermal range experienced by *B. inornata* (Allison et al. 2021). At extreme temperatures (8 °C and 24 °C), however, fish were closer to their thermal limits and an extended acclimation period (24 hours) was deemed necessary to allow individuals to stabilise, reducing

the risk of thermal shock and ensuring that subsequent measurements reflected physiological capacity rather than an acute stress response. The one degree temperature change was used as it simulated a typical extreme upwelling or marine heatwave event experienced by these fish in the wild (Duncan et al. 2019b). After acclimation, the dissolved oxygen (DO) concentration within each respirometer was recorded every second over a certain measurement period (5, 10, 15, 20 or 25 minutes), allowing for a > 0.5 mg/L DO decline in each respirometer. Followed by a 10-minute flush period (12 °C, 16 °C and 20 °C) or a 15-minute flush period (8 and 24 °C). Flush periods were adjusted according to temperature to maintain oxygen saturation and water quality within the chambers. Longer flushes at extreme temperatures ensured sufficient replenishment of dissolved oxygen, preventing hypoxia and minimising stress effects so that the results accurately represented metabolic performance. The RO_2 measurements for standard metabolic rate (SMR) were taken between 12am and 5am when this diurnal species is less active, this was done also to ensure that the SMR is not overestimated since the background respiration was measured only after the maximum metabolic rate (MMR) measurements. Following SMR measurements, each fish was removed from respirometers and placed in a tank with fresh seawater. The individual was then chased around the tank with a small net for a standardised set time of 10 minutes or until the individual exhibited signs of extreme exhaustion or stress (i.e. loss of equilibrium) (Figure 2.5b). The fish was then removed from the tank in a net, exposed to air for 30 seconds before being returned to the respirometer. The flush valve was closed just before the fish was returned into the respirometer to stop the flow of new oxygenated water for the MMR measurement phase. The RO_2 measurements begun immediately after the fish were placed into the respirometer, with a flush phase commencing after eight minutes for the next four hours. Following this, individuals were removed from the respirometers and euthanised with 0.4 ml/L clove oil in a 100L bucket, weighed, measured, and placed into freezer bags for later biological assessment. The blank (empty chamber, no fish) respirometers were closed and the RO_2 was measured for one hour after each MMR measurement to account for any background respiration. For the background rate, the rate was measured from the start of background respiration decline for the same time as the measurement period for the trial (5, 10, 15, 20 or 25 minutes) as a single decline.

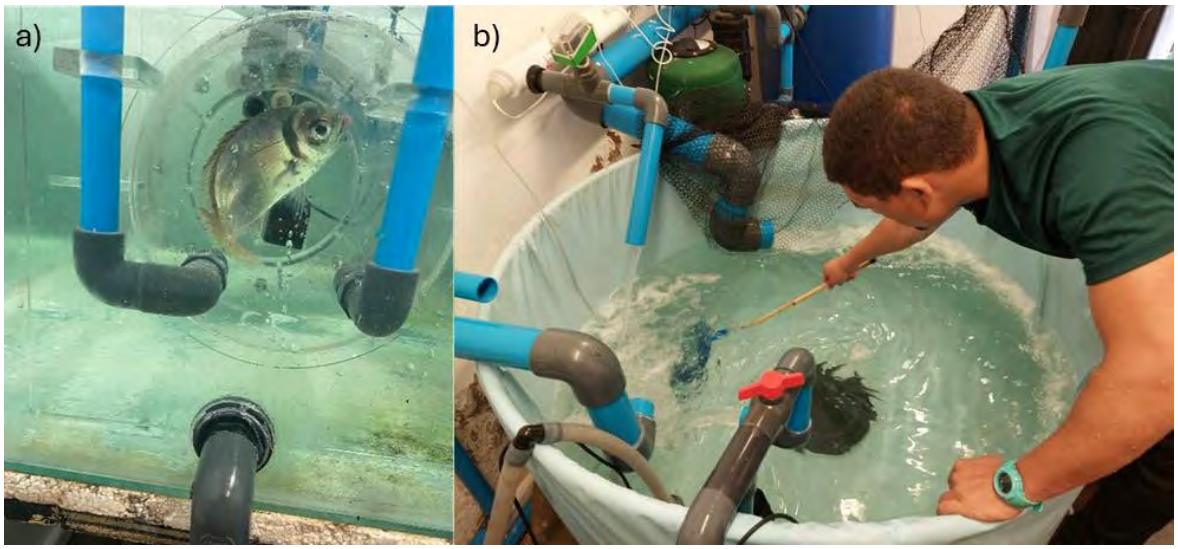


Figure 2.5: a) *Boopsoidea inornata* in an Intermittent-Flow respirometer before acclimation period started. b) Student Bradley van Heerden fin chasing a fish in the experimental sump before being placed back into the respirometer to estimate Maximum Metabolic Rate (MMR).

2.3.5 Data handling and statistical analysis

Data generated throughout the experimental protocol consisted of a series of measurement and flushing periods (Figure 2.6).

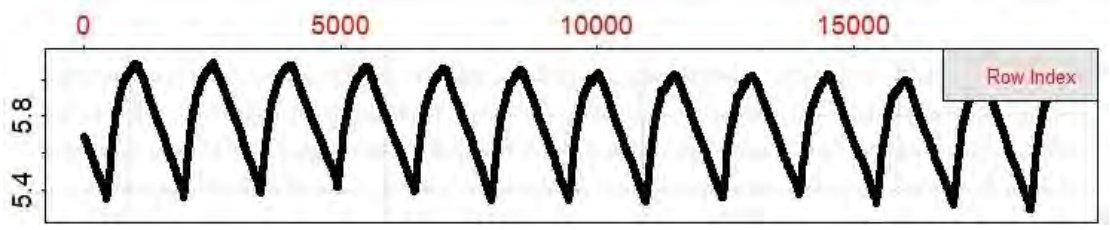


Figure 2.6: Example of an intermittent flow respirometry dataset. Each decline in oxygen concentration (O_2(mg. L^{-1})) represents the measurement period and increases in oxygen concentration represent the flushing period over a time period measured in seconds (sec.) represented above the dataset with the numbers in red and dissolved oxygen (DO) measurement represented in black on the left.

The *respR* package was used to estimate SMR and MMR in RStudio software (Harianto et al. 2019). To ensure data quality, only measurements with a linear decline in oxygen concentration meeting a threshold of $R^2 > 0.9$ were retained. The rate of oxygen consumption ($mg.kg^{-1}.h^{-1}$) for each measurement period (RO2) was calculated using the below equation (Equation 2.1) which was adapted from Svendsen et al. (2016).

$$RO_2 = \left(\left(\frac{V_{re} - M}{W}\right)\left(\frac{\Delta[O_{2a}]}{\Delta t} \times 60\right)\right) - \left(\left(\frac{V_{re} - M}{W}\right)\left(\frac{\Delta[O_{2b}]}{\Delta t} \times 60\right)\left(\frac{V_{re}}{(V_{re} - M)}\right)\right)$$

Where V_{re} is the total volume of the respirometer in litres; M is the mass of the specimen in kg (expressed in litres); W is mass of the specimen in kg; $\frac{\Delta[O_{2a}]}{\Delta t}$ is the slope of linear decrease in oxygen concentration during the measurement period and $\frac{\Delta[O_{2b}]}{\Delta t}$ is the slope of the linear decrease in oxygen concentration when no specimen was in the chamber (background respiration).

Standard metabolic rate (SMR) for each measurement period and test temperature was estimated using the 20th quantile of oxygen consumption data (Chabot et al. 2016). Maximum metabolic rate (MMR) was defined as the highest single rate of oxygen consumption recorded during the post-exhaustive recovery period (Killen et al. 2016), unless there was an erroneous reading (areas where the FireStingO_2 fibre optic oxygen sensor (FSO_2-4, Pro Science GmbH) could not calculate drastic change in oxygen concentration (O_2(mg. L^{-1})) values due to errors caused by faulty probe. If there were erroneous readings, then the closest decline with no erroneous readings was chosen.

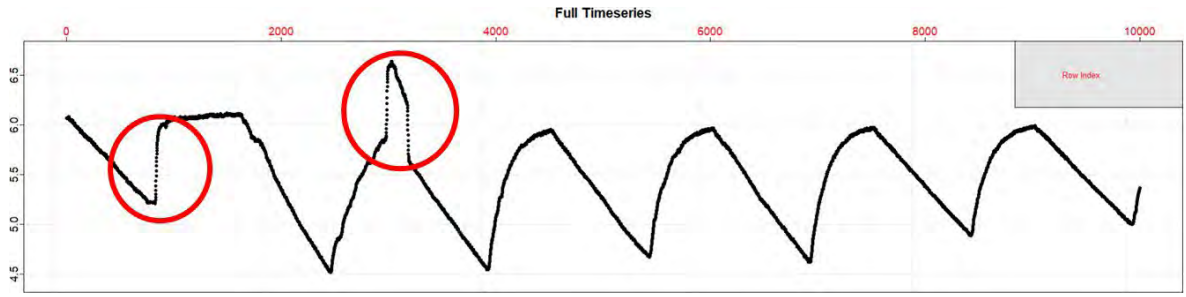


Figure 2.7: Example of an intermittent flow respirometry dataset. The areas circled in red represent areas in the dataset with erroneous readings (areas where the FireStingO_2 fibre optic oxygen sensor (FSO_2-4, Pro Science GmbH) could not calculate drastic change in oxygen concentration (O_2(mg. L^{-1})) values due to errors caused by faulty probe). Each decline in oxygen concentration (O_2(mg. L^{-1})) represents the measurement period and increases in oxygen concentration represent the flushing period over a time period measured in seconds (sec.) represented above the dataset with the numbers in red and dissolved oxygen (DO) measurement represented in black on the left.

Metabolic rates are well approximated when their major influences, temperature, and mass, are accounted for (Gillooly et al. 2001). Typically, metabolic rates scale with mass as a power function and temperature as a function of the Boltzmann factor (Brown et al. 2004). To determine the effect of mass on metabolic rates, data was temperature corrected ($RO_{2(temp\ corrected)}$) following Equation 2.2.

$$RO_{2(temp\ corrected)} = RO_2 \times e^{\frac{-E}{kT}}$$

where E is the average activation energy of ectotherms ~ 0.63 eV (Gillooly et al. 2001) k is the Boltzmann constant 8.617 3303 × 10^{-5} eV.K^{-1} and T is the absolute temperature in kelvin.

The slope of the linear regression between the natural logarithm of $RO_{2(temp\ corrected)}$ and the natural logarithm of mass was used to estimate the allometric exponent (α) of the mass scaling relationship with both SMR and MMR data. RO_2 data was then mass corrected (MO_2) using the mass scaling relationship following Equation 2.3.

$$MO_2 = \frac{RO_2}{M^{\propto}}$$

where MO_2 is mass normalised SMR or MMR, RO_2 is standard or maximum oxygen consumption rate, M is the mass of the organism and α is the allometric mass scaling exponent.

Absolute aerobic scope (AS) was calculated using mass normalised metabolic rates following Equation 2.4.

$$AS = MMR - SMR$$

Where MMR is mass normalised maximum metabolic rate and SMR is mass normalised standard metabolic rate. The microbial respiration was accounted for by using the first decline measurement period of the oxygen decline during background respiration and subtracting the decline from the MMR and SMR data.

Linear models and generalised least squares models, with different data transformations (log or log1p transformed) were tested to find the best fit structure with the lowest AIC score for SMR and MMR data as assumptions were violated, AS data did not violate any assumptions (Appendix Table 1). A linear (Lm) modelling approach was implemented using the *mgcv* package (Pinheiro et al. 2017) in R version 2024.12.0+467. To test the effect of temperature on metabolic rates, mass-corrected metabolic rate data was modelled using a second order polynomial relationship between temperature and metabolic rate (Rawlings et al. 1998).

2.4 Baited Remote Underwater Video experiment

2.4.1 Sampling approach

Behavioural metrics were analysed using existing BRUV data collected by the NRF SAIAB Marine Remote Imagery Platform (MARIP). These were collected in October 2019 (Algoa Bay), January 2020 (Cape St. Francis), February 2020 (Cape Recife, Algoa Bay) and October 2020 (Cape St. Francis). Sampling was restricted to depths of ≤ 30 m and all videos were filmed over 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-BRUV 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. The water temperature (in °C) during the deployment of each sample was also recorded using a HOBO Onset temperature logger, which were attached to each stereo-BRUVs.

2.4.2. Sample selection

BRUV footage were selected for inclusion in the study after confirming that the stereo-BRUVs landed on reef habitat and that at least one *B. inornata* appeared in the field of view during the 60 minutes of deployment. The latter criterion was included as the focus of the study to examine the relationship between water temperature and the behaviour of *B. inornata*. BRUV footage was limited when selecting for temperature ranges, as the water temperature during deployments only ranged from 10 – 18 °C. This was due to water temperatures only going above 20 °C during MHWs, making deployments at those temperatures difficult to plan as it is very challenging to predict when these events will occur. “MaxN” and “time to arrive” had a total of 48 samples each, while “time to feed” had only 24 observations, primarily because this data was not recorded for all videos and the raw videos were not available for reanalysis.

2.4.3. Video analyses

2.4.3.1 Relative abundance and Size

The EventMeasure (Stereo) software version 3.54 (SeaGIS Pty Ltd.) was used to estimate the relative abundance of *B. inornata*. Relative abundance was measured as “MaxN”, which is defined as the maximum number of individuals of a given species identified in a single video frame (Langlois et al. 2020).

2.4.3.2 Behaviour

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

2.4.4. Data handling and statistical analysis

Statistical analyses were conducted in the R environment version 4.1.1 using the RStudio version 2023.12.1+402 interface (RStudio: Integrated Development Environment for R 2023).

Protocols by Zuur et al. (2009) were followed when conducting exploratory data analyses. This was done to understand the nature of the different response and explanatory variables typical of BRUV data (Wood 2011, 2017). This protocol includes checking for collinearity and interactions between covariates, outliers in the data, zero-inflation, normality of the response variables, spatial patterns and the balance of the data. “Time to arrive” and “time to feed” were both measured at the individual level. As multiple individual fish were recorded from a sample this creates dependency in the data. Most studies using stereo-BRUV data have worked with multivariate datasets, meaning there are two or more variables being measured for each observation. In this study, the main task was to identify if temperature, as an isolated variable, influenced *in-situ* behaviour, making it univariate. Therefore, linear regression models were first applied to test the effect of temperature on “MaxN”, “time to arrive” and “time to feed”. The linear regression model did not fit the data well and a more advanced modelling approach was needed to fit the data.

A series of error distributions (families), including poisson, gaussian, gamma, tweedie and negative binomial, were tested and used in the models and the family was chosen based on the type of response variable (count, continuous or binomial) and dispersion parameter (number as close to 1).

For “MaxN”, a generalised additive model (GAM) was fitted using the *mgcv* package (Wood 2011, 2017). As the data were skewed, a Gaussian distribution was not possible and even after transforming the data it did not meet the protocols. To overcome this bias, the model was fitted with the Poisson distribution (family normally used for count data), however tests for overdispersion revealed a high dispersion parameter (16.76), meaning the variance of the observed data exceeded the variance predicted by the model therefore was not suitable (Saxena 2023) (Appendix Table 2 (Model 1)). The Quasi-Poisson distribution is usually used when the standard Poisson distribution is violated due to over-dispersion. This distribution however returned an even greater dispersion parameter value (21.04) than the standard Poisson distribution and was also considered not suitable (Appendix Table 2 (Model 2)). The Tweedie-Poisson distribution yielded a similar dispersion parameter value (16.04) as the Poisson distribution even though Tweedie allows the user to manipulate and overlap different error distributions (Appendix Table 2 (Model 3)). The Tweedie family was fitted using the *mgcv* package as it is designed for GAMs. A negative binomial distribution was then used to account for the overdispersion as it is normally more flexible and resilient than the Poisson distribution (Stoklosa et al. 2022). This reduced the dispersion parameter value to 1.05 (Appendix Table 2

(Model 4)). Tweedie-Poisson and negative binomial distributions are starting to become the "standard default" distribution models as most studies are seen to struggle with overdispersion and this cannot be ignored as overdispersion leads to overestimated and unreliable results (Stoklosa et al. 2022).

Data for "time to arrive" and for "time to feed" response variables were not zero-inflated and as they were continuous, the dispersion parameter was not considered a crucial factor in determining which distribution was used. Continuous data models assume that variability of the response variable is constant and is not manipulated by the mean. Therefore, GLMs were used instead of GAMs to simplify the models.

The "time to arrive" (T1st) data was normally distributed and therefore the Gaussian distribution was tested first (Appendix Table 2 (Model 5)). The Gamma and Tweedie-Gamma were also used but both yielded dispersion values of 0.42, and not suitable for a reliable model (Appendix Table 2 (Model 6 and 7)). "MaxN" was then added as an interaction term with temperature, as it was seen in studies that "MaxN" had a negatively significant effect on behavioural metrics (Currey-Randall et al. 2020). This meant that "MaxN" could influence the relationship between temperature and "time to arrive". A GLM fitted with the Tweedie family and interaction term of temperature and "MaxN" was then used to model "time to arrive". This brought the dispersion parameter up to 0.98 (Appendix Table 2 (Model 8)). This was fitted using the *statmod* package as it is designed for GLMs (Dunn and Smith 2018).

The analyses of the "time to feed" parameter followed the same procedure as "time to arrive" with first the Gaussian distribution returning a 168.98 dispersion parameter (Appendix Table 2 (Model 9)), the Gamma distribution returning a 0.43 value (Appendix Table 2 (Model 10)) and finally Tweedie-Gamma returning a 0.58 value (Appendix Table 2 (Model 11)). A GLM fitted with the Tweedie family and same interaction term between temperature and "MaxN" was used (Appendix Table 2 (Model 12)). This brought the dispersion parameter up to 0.97. The Tweedie family was fitted using the *statmod* package as it is designed for GLMs (Dunn and Smith 2018).

CHAPTER 3: RESULTS

Fransmadam, *Boopsoidea inornata*, viewed on *stereo*-BRUV footage.

3.1. Physiology experiment

3.1.1 Mass-correcting MO_2 data

Variation in non-mass corrected SMR data, which could obscure any clear trend with temperature, was recorded (Figure 3.1a). The natural logarithm of temperature-corrected SMR scaled linearly with the natural logarithm of mass, with a mass scaling exponent estimated as –1; however, the relationship was not significant ($p > 0.05$, $t = –1.08$, $R^2 = 0.03$) (Figure 3.1b and Table 3.1). Given the lack of a significant scaling relationship, SMR was estimated with a mass-specific scaling factor equal to 1. Mass-correcting the SMR reduced the variability among the data but showed conditional heteroscedasticity, as variances increased with temperature (Figure 3.1c).

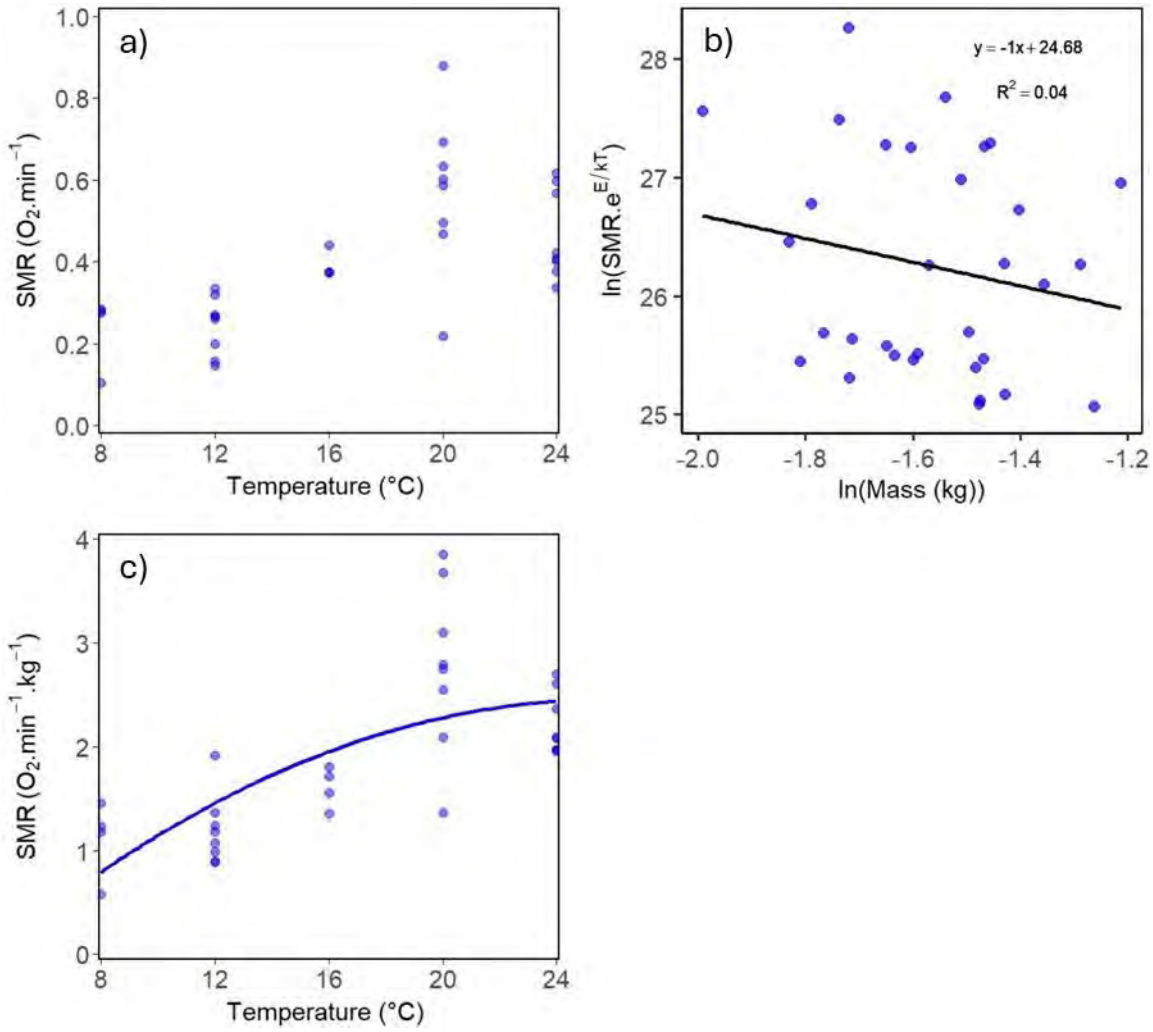


Figure 3.1: Mass-correcting SMR data process representing, a) raw SMR data (SMR ($O_2.min^{-1}$)) per temperature. b) regression of the natural logarithm of temperature-corrected SMR ($ln(SMR.e^{E/kT})$) against the natural logarithm of mass (ln(Mass(kg)). c) mass-corrected SMR data (SMR ($O_2.min^{-1}.kg^{-1}$)) per temperature used for the analysis.

Non-mass-corrected MMR data also showed variability, which again obscured any clear trend with temperature (Figure 3.2a). The natural logarithm of temperature-corrected MMR scaled linearly with the natural logarithm of mass, with a mass scaling exponent estimated as –0.91; however, the relationship was not significant ($p > 0.05$, $t = –1.07$, $R^2 = 0.04$) (Figure 3.2b and Table 3.1). Given the lack of a significant scaling relationship, MMR was estimated with a mass-specific scaling factor equal to 1. Mass-corrected MMR also reduced the variability among the data (Figure 3.2c).

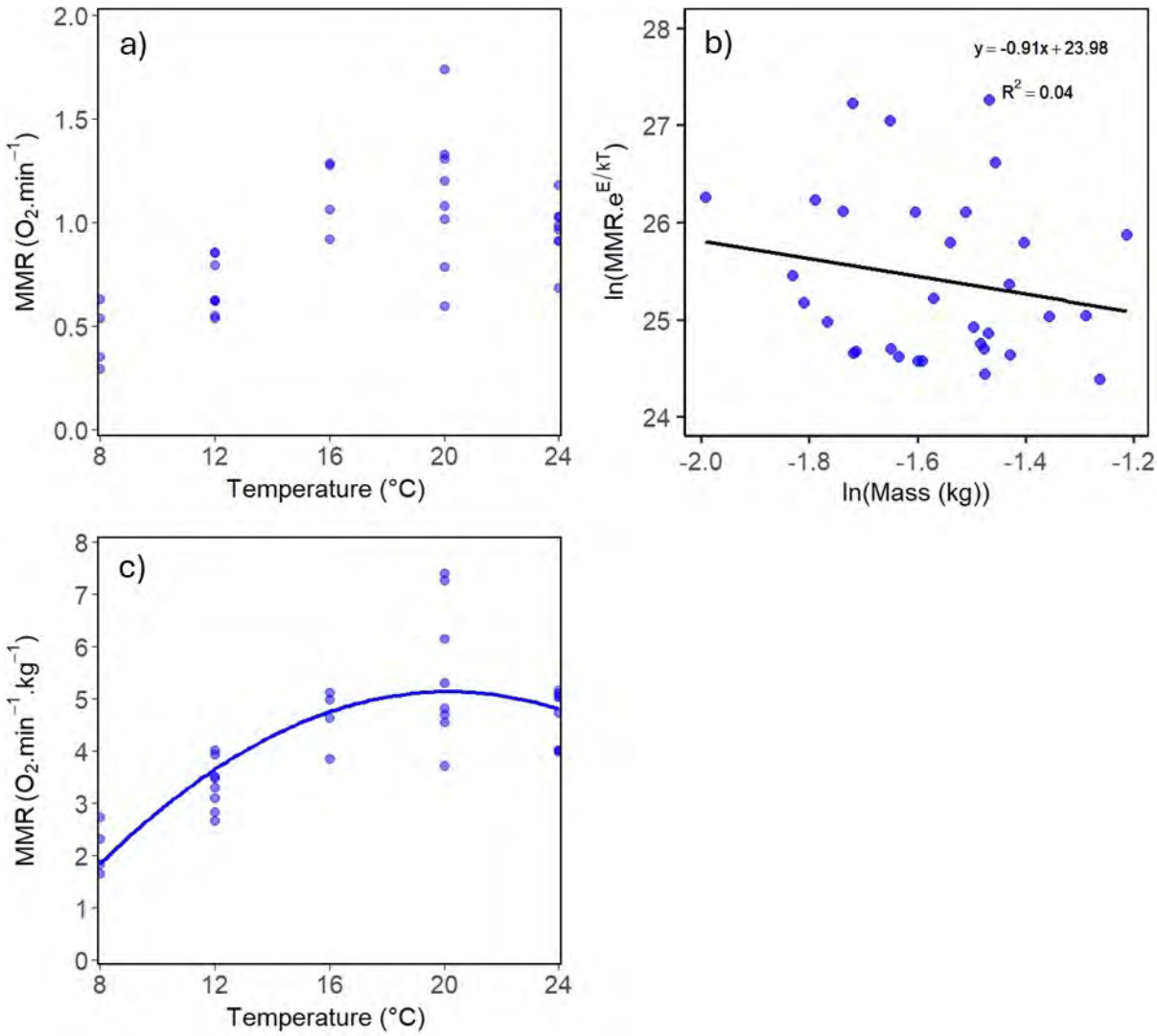


Figure 3.2: Mass-correcting MMR data process showing, a) raw MMR data (SMR (O_2.min^{-1})) per temperature. b) regression of the natural logarithm of temperature-corrected MMR (ln(MMR.eE/kT)) against the natural logarithm of mass (ln(Mass(kg)). c) mass-corrected MMR data (MMR (O_2.min^{-1}.kg^{-1})) per temperature used for the analysis.

Table 3.1: Linear regression model results for the relationship between the natural logarithm of $RO_{2(temp\ corrected)}$ and the natural logarithm of mass (Ln(Mass(kg))) of an exploited population of *Boopsoidea inornata* for standard metabolic rate (SMR) and maximum metabolic rate (MMR). Significant p values appear in bold.

Ln(SMR.$e^{E/kT}$)				
Predictors	*Estimates*	*SE*	*t value*	*p*
(Intercept)	24.68	1.46	16.90	**<0.01**
Ln(Mass)	-1.00	0.93	-1.08	0.29
Observations		32		
R^2 / R^2 adjusted		0.038 / 0.005		
Deviance		25.398		
Ln(MMR.$e^{E/kT}$)				
Predictors	*Estimates*	*SE*	*t value*	*p*
(Intercept)	23.98	1.35	17.77	**<0.01**
Ln(Mass)	-0.91	0.86	-1.07	0.30
Observations		32		
R^2 / R^2 adjusted		0.037 / 0.004		
Deviance		21.681		

3.1.2 Effect of temperature on Standard Metabolic Rate (SMR), Maximum Metabolic Rates (MMR) and Aerobic Scope (AS)

Mass-corrected SMR of *B. inornata* ranged from 0.58 to 1.45 at 8 ℃, 0.89 to 1.91 at 12 ℃, 1.36 to 1.81 at 16 ℃, 1.36 to 3.86 at 20 ℃ and 1.96 to 2.70 O_2 $mg.min^{-1}.kg^{-1}$ at 24 ℃ (Figure 3.1c). The relationship between temperature and mass-corrected SMR assumed an increasing trajectory with temperature with a plateau near 24 ℃ (Figure 3.3). Variability in SMR was lowest at the temperatures 16℃ (SD = ± 0.20) and 24℃ (SD = ± 0.30) and highest at 20℃ (SD = ± 0.81) (Table 3.3, Table 3.4). The log -transformed model was selected as it scored the lowest AIC (52.82) (Appendix Table 1). The linear relationship between temperature and SMR was significant (p-value < 0.01, t = 6.19) while the polynomial relationship was not significant (p-value = 0.20, t = -1.33, R^2 = 0.58).

The mass-corrected MMR of *B. inornata* ranged from 1.65 to 2.74 at 8 ℃, 2.66 to 4.01 at 12 ℃, 3.84 to 5.12 at 16 ℃, 3.72 to 7.39 at 20 ℃ and 3.99 to 5.16 O_2 $mg.min^{-1}.kg^{-1}$ at 24 ℃. The relationship between temperature and MMR assumed a bell-shaped curve (Figure 3.2) with a peak at 19.9 ℃. The lowest variability around the mean was observed at 12 ℃ (SD = ± 0.48), while the highest variability in MMR was observed at 20 ℃ (SD = ± 1.32) (Table 3.2 and Table 3.3). The log-transformed model was selected as it scored the lowest AIC (72.31) (Appendix Table 1). Both the linear (p < 0.01, t = 8.22) and polynomial (p-value < 0.01, t = -5.16, R^2 = 0.77) relationship between temperature and MMR was significant (Table 3.3 and Figure 3.3).

Table 3.2: Mean ($\bar{x}$), standard error (SE) and standard deviation (SD) for standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) at 8 ℃, 12 ℃, 16℃, 20 ℃ and 24 ℃.

	SMR			MMR			AS		
Temp (℃)	Mean	SE (±)	SD (±)	Mean	SE (±)	SD (±)	Mean	SE (±)	SD (±)
8	1.112	0.187	0.374	2.135	0.246	0.491	1.023	0.233	0.466
12	1.194	0.118	0.335	3.355	0.270	0.483	2.161	0.195	0.551
16	1.608	0.098	0.197	4.647	0.285	0.570	3.039	0.249	0.497
20	2.775	0.286	0.810	5.482	0.469	1.327	2.709	0.355	1.003
24	2.219	0.106	0.299	4.634	0.189	0.533	2.415	0.238	0.673

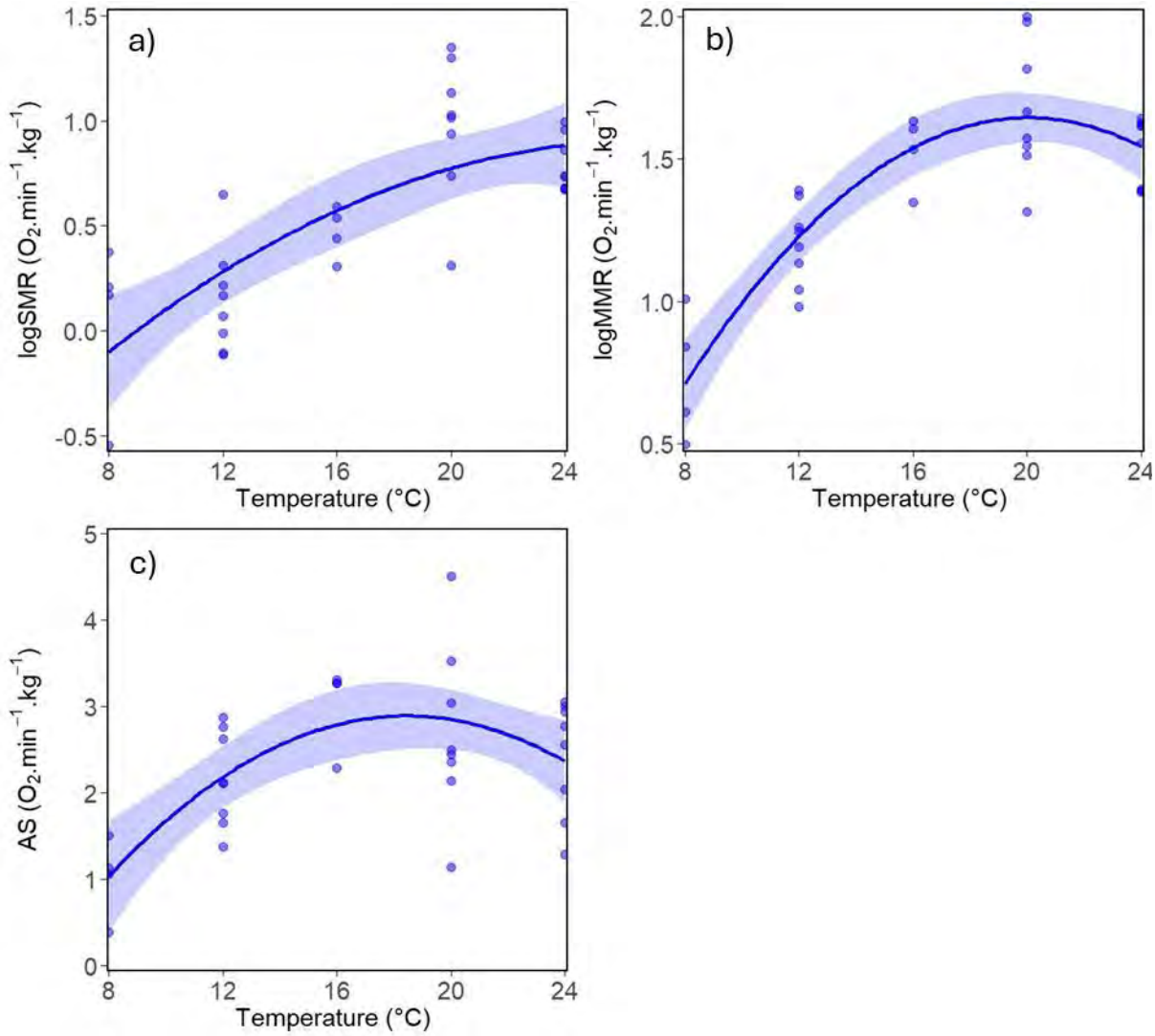


Figure 3.3: Second order polynomial regressions (with shaded regions representing 95% confidence intervals) of the relationship between a) standard metabolic rate (SMR) (log-transformed) b) maximum metabolic rate (MMR) (log-transformed) c) aerobic scope (AS) and temperature of an exploited population of *Boopsoidea inornata.*

Aerobic scope of *B. inornata* ranged from 0.39 to 1.51 at 8 ℃, 1.38 to 2.87 at 12 ℃, 2.29 to 3.31 at 16 ℃, 1.14 to 4.51 at 20 ℃ and 1.29 to 3.05 O_2 mg.min^{-1}.kg^{-1} at 24 ℃. The relationship between temperature and AS assumed as bell-shaped curve (Figure 3.3c) with a peak at 18.5 ℃. The lowest variability around the mean was observed at 8 ℃ (SD = ± 0.47) and the highest (SD = ± 1.00) at 20 ℃ (Figure 3.3c and Table 3.3). Both the linear relationship ($p < 0.01$, $t = 2.94$) and second order polynomial relationship ($p < 0.01$, $t = -3.39$) between temperature and AS were significant ($R^2 = 0.41$).

Table 3.3: Second order polynomial regression model output modelling the effect of temperature on the log-transformed standard metabolic rate (log(SMR)), log-transformed maximum metabolic rate (log(MMR)) and resultant aerobic scope (AS) of an exploited population of *Boopsoidea inornata*. Significant p values appear in bold.

Log(SMR)				
Predictors	*Estimates*	*SE*	*t value*	*p*
(Intercept)	0.54	0.05	10.34	**<0.01**
Temperature	1.84	0.30	6.19	**<0.01**
Temperature^2	-0.39	0.30	-1.33	0.20
Observations	32			
R^2 / R^2 adjusted	0.580 / 0.552			
Deviance	2.564			
AIC	52.816			

Log(MMR)				
Predictors	*Estimates*	*SE*	*t value*	*p*
(Intercept)	1.38	0.03	45.07	**<0.01**
Temperature	1.43	0.17	8.22	**<0.01**
Temperature^2	-0.90	0.17	-5.16	**<0.01**
Observations	32			
R^2 / R^2 adjusted	0.765 / 0.748			
Deviance	0.876			
AIC	72.306			

AS				
Predictors	*Estimates*	*SE*	*t value*	*p*
(Intercept)	2.33	0.12	18.85	**<0.01**

Temperature	2.06	0.70	2.94	**<0.01**
Temperature^2	-2.37	0.70	-3.39	**<0.01**
Observations	32			
R^2 / R^2 adjusted	0.410 / 0.369			
Deviance	14.165			
AIC	72.733			

3.2 BRUV experiment

3.2.1 MaxN

"MaxN" ranged between three (17.6 °C) and 110 (16.7 °C) individuals. "MaxN" appeared to increase with temperature and peak at around 16 °C after which it declined (Figure 3.4). The highest variability in "MaxN" appeared to be between 16 and 18°C (Figure 3.4). Results from the GAM indicated that temperature did not have a significant effect on "MaxN" ($p = 0.218$), with 10.2% of the variance explained by the model (Table 3.4). Observed "MaxN" values tended to be higher at the temperatures where a high AS (solid grey line on secondary axis; Figure 3.4) was observed, with the highest variability observed near the peak of the AS performance.

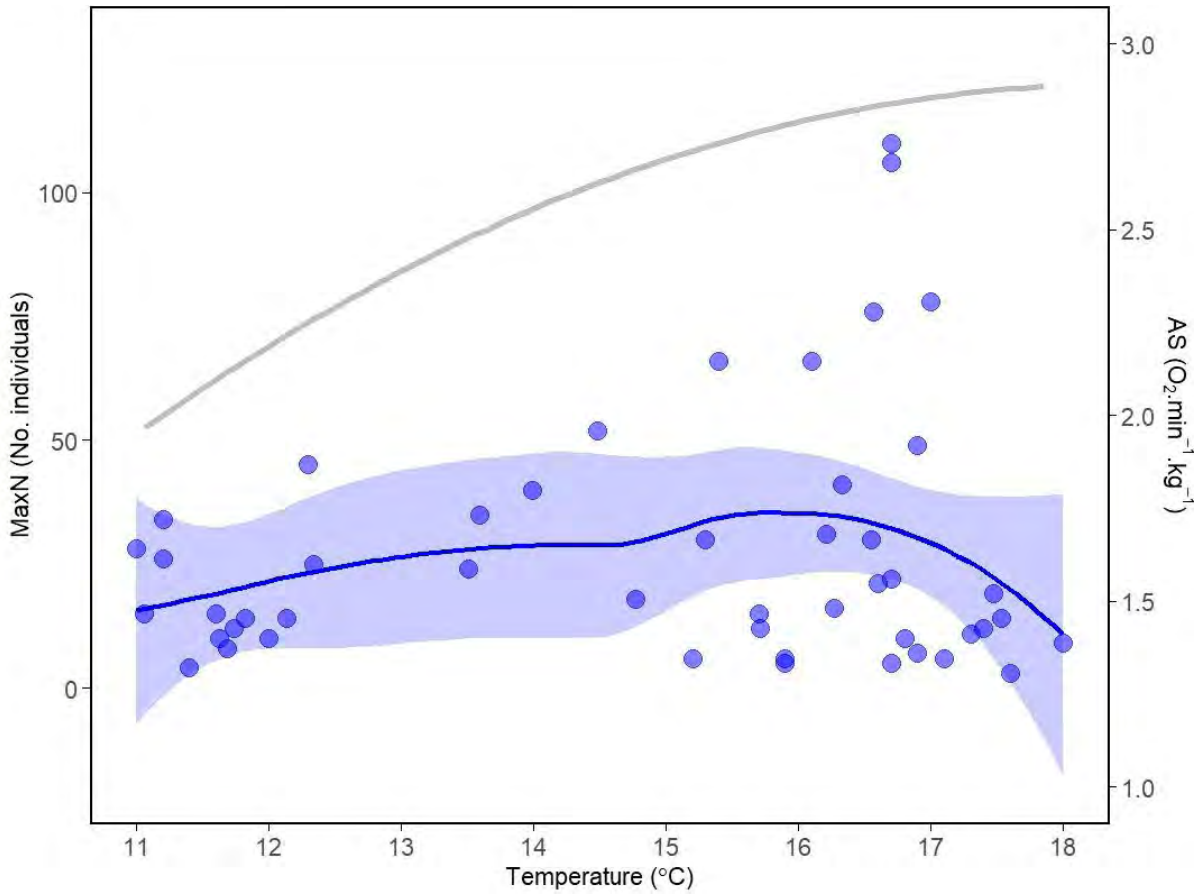


Figure 3.4: Results from the generalised additive model showing the relationship between temperature and "MaxN" for an exploited population of *Boopsoidea inornata.* Shaded area around the trend line represents the approximate 95% confidence interval. Solid grey line indicates aerobic scope (AS) on secondary y axis.

3.2.2 Time to arrive (T1st)

"Time to arrive" ranged between 2.25 (17.7 °C) and 38.69 (11.4 °C) minutes. "Time to arrive" appeared to decrease with an increase in temperature and was lowest around 16 °C, after which it increased slightly as temperature increased (Figure 3.5). Highest variability was found around 11 °C and lowest variability between 16 °C and 17 °C. The GLM explained 32.67% of the observed variability (Table 3.4). Both temperature ($p < 0.01$, $t = -2.78$) and "MaxN" ($p < 0.01$, $t = -2.98$) had a significant negative effect on "time to arrive" (Table 3.4). The interaction term between "MaxN" and temperature (combined effect of "MaxN" and temperature on "time to arrive") also revealed a significant effect on "time to arrive" ($p < 0.01$, $t = 2.74$). The highest "time to arrive" corresponded with the lowest AS (solid grey line on secondary axis: Figure 3.5), while the lowest "time to arrive" and lowest variability in "time to arrive" was observed near the peak of AS performance curve.

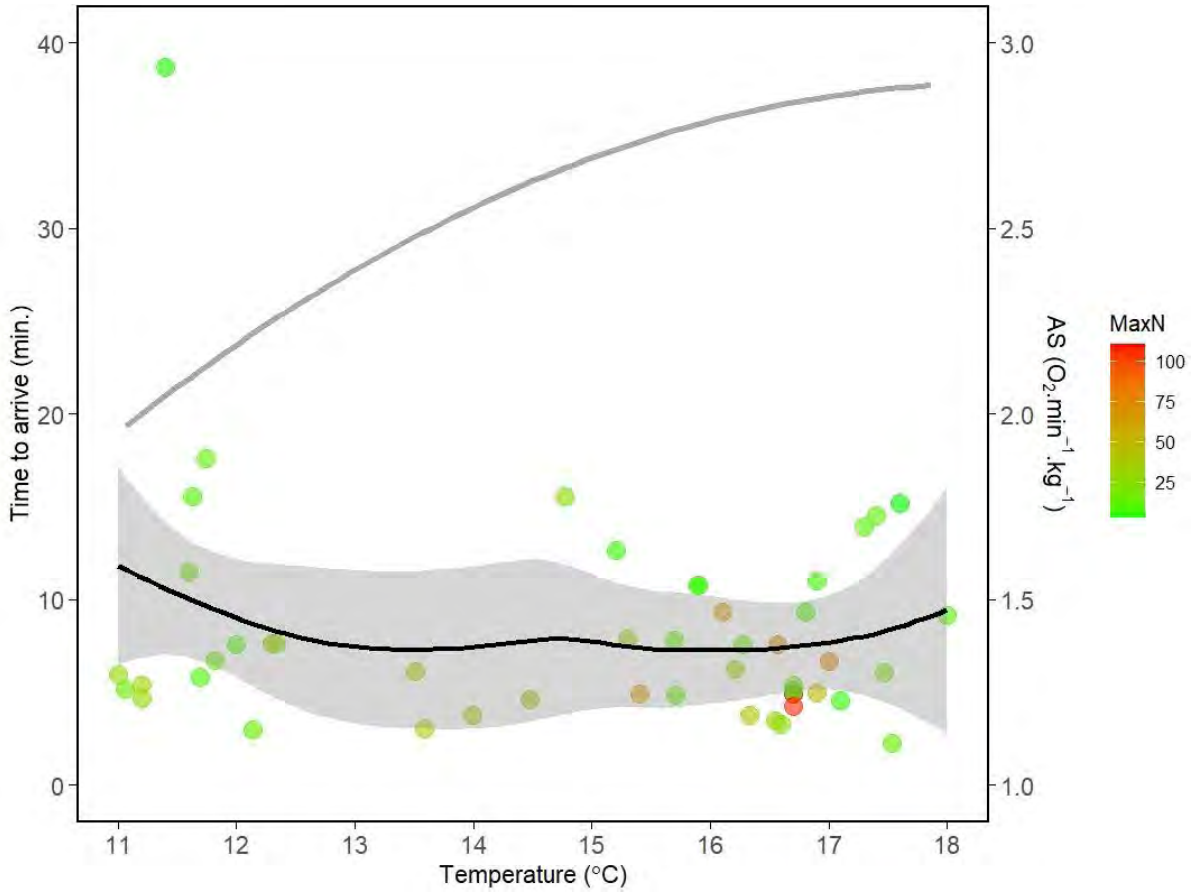


Figure 3.5: Results from the generalised additive model showing the relationship between "time to arrive" (T1st) and "MaxN" for an exploited population of *Boopsoidea inornata.* Shaded area around the trend line represents the 95% confidence interval. "MaxN" count is

represented by coloured dots, green for low range of individuals, orange for mid-range and red for high range. Solid grey line indicates aerobic scope (AS) on secondary y axis.

3.2.3 Time to feed

The “time to feed” data was limited to a total of 24 observations, primarily because this data was not recorded for all videos and the raw videos were not available for reanalyses. Despite the limited data, trends in “time to feed” and temperature were still observed. The “time to feed” ranged from 3.58 at 13.60 ℃ to 50.92 at 11.70 ℃, respectively. Generally, there was a decrease in “time to feed” with increasing temperature (Figure 3.6). Highest variability in “time to feed” was observed between 11 and 12 °C and lowest variability between 16 and 17 ℃.

The GLM model explained 70.84% of the observed variability (Table 3.4). Temperature ($p < 0.01$, $t = -3.77$) and “MaxN” ($p < 0.01$, $t = -4.45$) both had a significant effect on “time to feed” (Table 3.4). In addition, the interaction effect between “MaxN” and temperature (combined effect of “MaxN” and temperature on “time to feed”) revealed a significant effect on “time to feed” ($p < 0.01$, $t = 4.04$). “Time to feed” was the longest when AS (solid grey line on secondary axis: Figure 3.6) was low. The lowest variability in “time to feed” was observed near the peak of the AS performance curve.

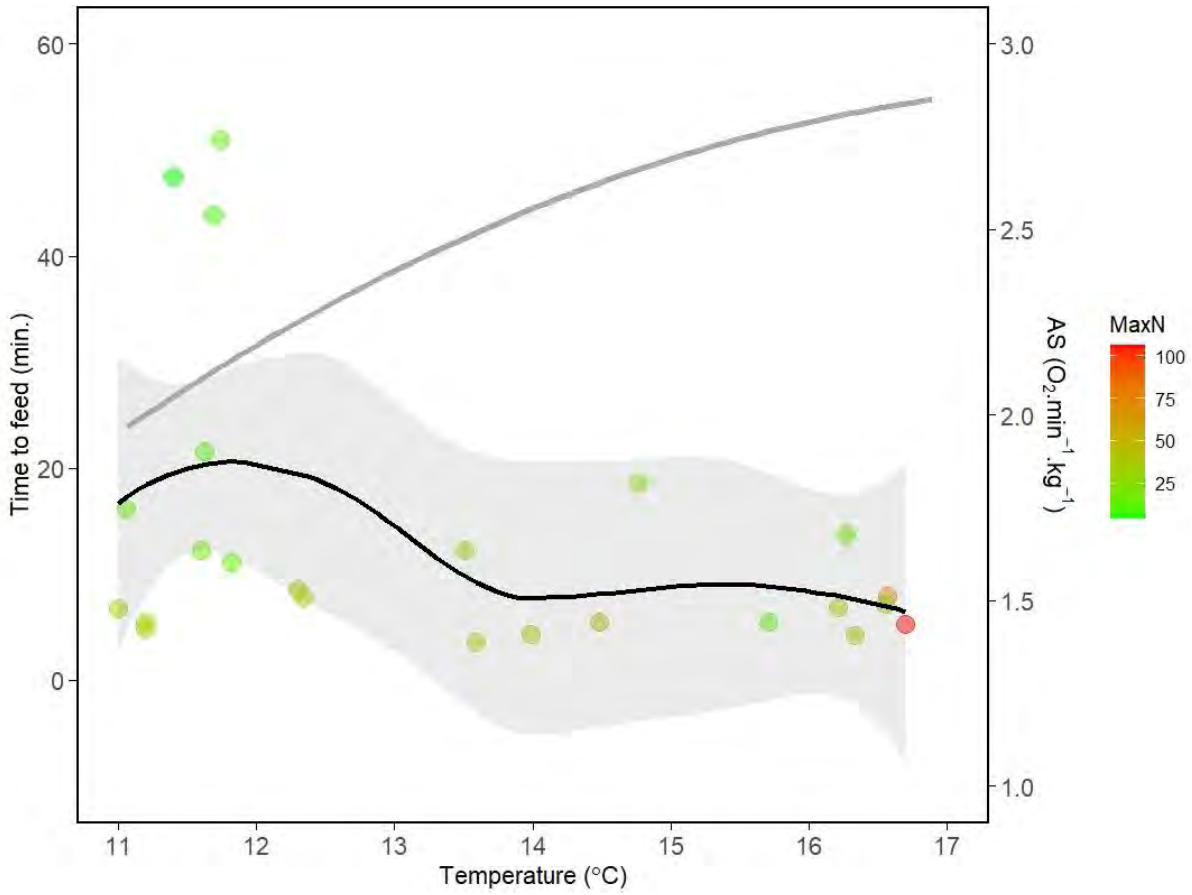


Figure 3.6: Results from the generalised additive model showing the relationship between "time to feed" and "MaxN" for an exploited population of *Boopsoidea inornata*. Shaded area around the trend line represents the 95% confidence interval. "MaxN" count is represented by coloured dots, green for low range of individuals, orange for mid-range and red for high range. Solid grey line indicates aerobic scope (AS) on secondary y axis.

Table 3.4: Generalised additive model (GAM) results for the relationship between temperature and the "MaxN" and generalised linear model (loess method) outputs for the relationship between temperature (with "MaxN" as an interaction term) on "time to feed" and "time to arrive" of an exploited population of *Boopsoidea inornata*. Significant p values appear in bold.

MaxN				
Predictors	*Estimates*	*SE*	*t value*	*p*
(Intercept)	7.87	1.18	6.66	**<0.01**
Smooth terms	*Edf*	Ref.df	Chi.sq	*p*
s(temperature)	2.09	2.60	3.35	0.22
Dispersion parameter	1.05			
R^2 / R^2 adjusted	0.04			
(T1st) Time to arrive				
Predictors	*Estimates*	*SE*	*t value*	*p*
(Intercept)	4.66	3.19	5.68	**<0.01**
Temperature	-0.15	0.05	-2.78	**<0.01**
MaxN	-0.12	0.03	-2.98	**<0.01**
Temperature:MaxN	0.01	0.002	2.74	**<0.01**
Dispersion parameter	0.93			
Null deviance	59.23 on 47 degrees of freedom			
Residual deviance	39.89 on 44 degrees of freedom			
Time to feed				
Predictors	*Estimates*	*SE*	*t value*	*p*
(Intercept)	7.87	1.18	6.66	**<0.01**

Temperature	-0.33	0.09	2.94	**<0.01**
MaxN	-0.20	0.05	-3.39	**<0.01**
Temperature:MaxN	0.01	0.002	4.04	**<0.01**
Dispersion parameter	0.97			
Null deviance	60.90 on 23 degrees of freedom			
Residual deviance	17.01 on 20 degrees of freedom			

CHAPTER 4: DISCUSSION

Fransmadam, *Boopsoidea inornata*, in an intermittent flow respirometry chamber.

The findings of this study suggest that there is a link between the metabolic physiology and the wild behaviour of *B. inornata*. The reduced AS, which represents the potential energy available for activity (Figure 3.3), at the lower temperatures (8-12 °C) was reflected in the wild behaviour, with an increase in the "time to arrive" and "time to feed" observed at temperatures below 12 °C. While there may have been similar physiological responses at the warmer temperature (> 20 °C), where the AS declined (Figure 3.3), there were no videos captured above 20 °C due to temperatures along the south coast rarely exceeding 20 °C (see *in-situ* data in Allison et al. 2021). While temperatures above 20°C mainly occur during marine heat waves, these events are becoming more frequent along the South African coastline (Schlegel et al. 2017) and future studies should investigate this link. Previous research assessing the thermal tolerance of *B. inornata* highlighted the vulnerability of this species to cold rather than warm temperatures (Allison et al. 2021), and the results of this study further illustrate how this susceptibility translates into reduced activity in the wild. These results not only highlight the potential impact of increased climate change-induced upwelling events on the activity of this species, but also the suitability of AS for predicting responses of fish in the wild and the role that BRUV footage can play in assessing the impacts of climate change at both an individual and population level.

Although the conclusions drawn here are primarily relevant to responses under cold extremes, this study is among the few to link aerobic physiology and wild behaviour in fishes directly (Bailey et al. 2022). Previous debates around AS have questioned its validity in predicting wild behaviour (Clarke et al. 2013, Brownscombe et al. 2014, Farrell 2016, Alfonso et al. 2021, Brownscombe et al. 2022). While this study provides preliminary support for AS as an informative metric, it is critical to acknowledge that aerobic performance interacts with a suite of other physiological, behavioural, and ecological factors that influence fish responses in the wild.

Specifically, bioenergetics provides a conceptual framework to interpret these interactions. AS represents the energy available above baseline metabolic maintenance (standard metabolic rate, SMR) for activity, growth, reproduction, and survival (Brownscombe et al. 2022). However, the translation of aerobic capacity into observed behaviour is modulated by factors including individual variation in metabolic phenotypes, life-history trade-offs, ecological pressures, and environmental variability (Schulte 2015). Individual fish differ in metabolic and behavioural traits, such that some may be bold and highly active, while others remain cautious under identical conditions (Bailey et al. 2025). Life-history trade-offs, including energy allocation to reproduction, somatic growth, and maintenance, further shape behavioural outputs (Holt and

Jorgensen 2015). Environmental factors, such as predator presence, prey availability, oxygen availability, and habitat complexity, modulate the expression of behaviours despite underlying physiological capacity (Fry 1971, Mckenzie and Claireaux 2010, Killen 2013,). Thus, while AS provides insight into the potential for activity, its predictive utility must be considered within the broader context of these interacting bioenergetic and ecological factors.

Based on the findings of this study, it is expected that the increased frequency and intensity of upwelling events (Schlegel et al. 2017, Duncan et al 2019a, Lubitz et al. 2024) and with that, marine cold spells (MCS) (Lubitz et al. 2024), will result in a decrease in the aerobic performance of this species, which will result in reduced activity (represented by the "MaxN" and "first to appear" estimates) and feeding (represented by "time to first feed"). From a population perspective, increases in unfavourable thermal conditions (cooler temperatures), associated declines in aerobic performance and reduced wild activity and feeding will most likely result in changes in their life history characteristics. A recent paper by Attwood and Ensair (2020) focused on the life history and trade-offs of *B. inornata* and compared them to three other seabream species trade-offs and life history traits. They found that a wide range of options are available to seabreams and show how disparate life histories can be equally adaptive under identical conditions. They also showed how a variety of life-history traits, such as migration, sex-ratio, reproductive strategy and somatic growth form interact to define a life-history. The findings of Allison et al. (2021) and this study, indicate it is likely that the increase in intensity and frequency of upwelling events may result in a reduction in the metabolism and growth rate of *B. inornata.* This may then have consequences for this species in the future as Attwood and Ensair (2020) found trade-offs in life history for the four species, especially *B. inornata* between semelparity and iteroparity, age-at-maturity and maximum size, annual fecundity and longevity, length of spawning season and parental care, and length of spawning season and migration.

Attwood and Ensair (2020) found that females with spent gonads and males were in worse condition during the spawning season (summer months) than in the pre-spawning season (winter months). While the poor condition of the females was attributed to the energy that was dedicated to gonad development, they suggested that the poor condition of the males could be attributed to the energy investment associated with their courtship battles (Attwood and Ensair 2020). With a finite energy budget and a predicted increase in upwelling in the summer months, it is likely that the energy available for gonad development and courtship will be increasingly reduced, likely resulting in poorer condition, and reduced reproductive output in this species.

In the study it was also stated that sex determination could be temperature dependent, with the percentage of males increasing in the populations as you move further eastward up the coast towards Kwa-Zulu Natal (Attwood and Ensair 2020). Although metabolic rates were not distinguished between males and females in the study, could it be temperature dependent or possibly that females have more aerobic energy and broader thermal curve than the males and that is why the percentage of males decreases as you move into colder waters as the males are not able to adapt to the cold temperatures? With all the trade-offs *B. inornata* are seen to use to survive and having used all their energy during spawning and leading to the summer months, November – February, this could leave adult *B. inornata*, especially the males, vulnerable to an intense upwelling event.

Despite the likely negative changes for the population of *B. inornata*, environmental stressors (such as increasing frequent MCS) that amplify individual differences in behaviour or physiology can increase phenotypic variation, creating more opportunities for natural selection to occur. For example, in food-limited environments, individuals with higher metabolic rates would tend to lose more body mass due to increased energy usage, potentially making them bolder and more susceptible to predation. This may drive correlated selection for specific personality traits or behavioural syndromes, shaped by how energy and oxygen demands influence responses to stressors (Careau and Garland 2012, Réale et al. 2010, Sutter et al. 2012). Therefore, while whole population aerobic scope (AS) estimates may provide insight into why certain populations persist in specific environments (Gannon et al. 2014) and how ecological and anthropogenic factors shape the behaviour and fitness of populations in the face of a changing climate (Clark et al. 2013), understanding the physiological attributes of individuals in the population is critical to understand its adaptive potential.

The findings of this study provided preliminary evidence and rudimentary insight to suggest that AS could be used as a metric for predicting responses of fish to changing thermal conditions in the wild and also provided new physiological information on *B. inornata*. The findings suggest a peak in aerobic performance (AS) at a temperature of 18.5 °C, which coincided with a relatively low SMR and a peak in MMR, and declines in performance below 12 °C and above 20 °C (Figures 3.1abc). The declines in AS at these cold and warm temperatures were primarily attributed to the reduced MMR at the low temperatures and to an increase in the SMR and decline in MMR at the higher temperatures (Figures 3.1, 3.2). Fry (1971) showed that, depending on the fish species, the curve for AS can take a variety of shapes (Farrell et al. 2008, Eliason and Farrell 2016). However, a bell-shaped curve (Pörtner and

Farrell 2008) is common and the simplest to model and conceptualize. In the case of this species and another closely related species in this region (red roman, *Chrysoblephus laticeps*, Duncan et al. 2019b, Nabani 2023, Bailey 2023), the AS performance assumed a typical bell-shaped curve, which suggests that this pattern is well-suited for the thermal profile in this region. In addition, the broad nature of the thermal performance curve for *B. inornata* (Figure 3.3) is typical for a eurythermal species that has to perform in a wide range of thermal conditions (Pörtner 2000).

The findings of this study also corroborate previous work on the relationship between temperature and the thermal physiology of *B. inornata* (Allison et al. 2021). In their work on the thermal endpoints of this species, Allison et al. (2021) suggested that lower cold sea surface temperatures during upwelling events may be more detrimental to the species than higher sea surface temperatures (> 24 °C). This is because the colder temperatures during MCS reach the lower thermal breakpoint (based on respiration rate) of the species (9 °C), while the temperatures during MHWs were well below the upper thermal breakpoint (25 °C) of the species (Allison et al. 2021). At *in-situ* temperatures reaching the lower thermal break point (9 °C) and below, individuals are theorised to have an increase in oxygen demand as Pörtner et al. (2000) stated that mitrochondrial proliferation occurs at these low temperatures. The mitochondrial proliferation allows the increase in aerobic capacity to meet energy demands for survival at low temperatures (Pörtner et al. 2000). This increase in aerobic capacity is, however, detrimental to the species as it showcases tell signs of cellular processes becoming unstable and out of balance (Pörtner et al. 2000). Certainly, the results from the present study (Figure 3.1c) suggest that *B. inornata* will have limited aerobic capacity for performance at these low temperatures, when compared with the higher temperatures (> 24 °C).

Allison et al. (2021) found that the critical lower thermal limit for *B. inornata* was 7.8 °C, hence the low observed AS at 8 °C is as expected, theoretically, since AS should approximate zero as the fish nears their critical limit ($CT_{min/max}$), when a fish is forced into an anaerobic and time-limited lifestyle (Pörtner 2001, Pörtner and Farrell 2008). The AS at 24 °C was also much higher than the AS at 8 °C. This is not unexpected because the CT_{max} for the species was 30.1 °C and upper thermal breakpoint (from measures of changes in the respiration rate) was at 25 °C. This finding suggests that the full thermal performance curve for this species was not modelled at the warmest temperatures. The upper T_{pej} (area where metabolic rate deviates as temperature deviates from optimal temperature) at higher temperatures after optimal peak aerobic temperature of 18.5 °C starts to decline at a slower rate than the T_{pej} at lower

temperatures before 18.5 °C for this population. This provides additional evidence of the eurythermal nature of this species. In stenothermal fish, with a sharply peaked AS curve, T_{pej} and T_{opt} may be identical, as AS declines immediately when the temperature deviates from the optimal. In contrast, eurythermal species can sustain peak AS across a broader thermal range, referred to as their optimal thermal window (Pörtner 2000, Farrell 2016).

The pattern of the AS curve in this study aligned with the observed changes in aggression of *B. inornata* with increasing temperature observed by Allison et al. 2021) (Figure 4.1). A study by Bailey et al. (2022) reviewing the current knowledge on the links between metabolic physiology and behaviour also found the same evidence that aggression is increased with an increase of SMR. The increase in aggression follows the same curve trend as the SMR curve in this study from 10 – 24 °C, with a rapid incline until plateauing at 24 °C (Figure 4.1). The highest rates of aggression were seen between 18 °C and 20 °C, coinciding with the peak of AS in this study.

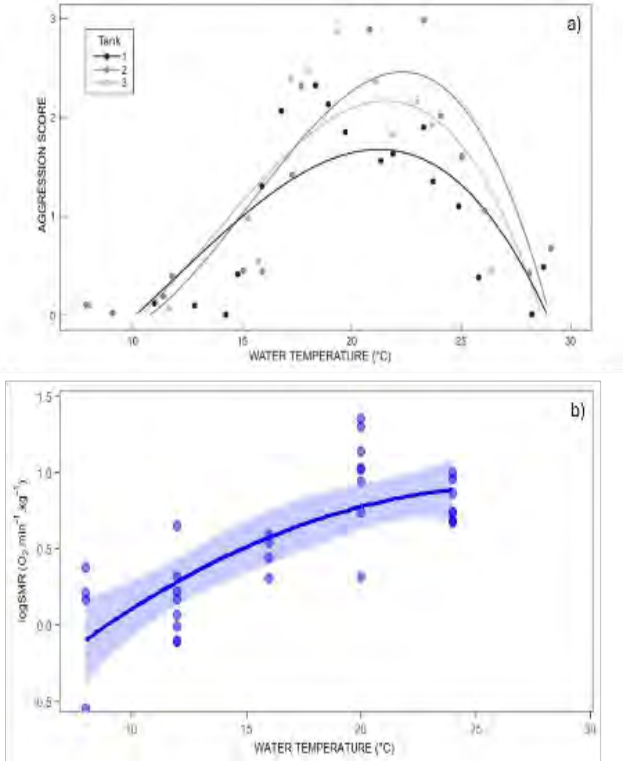


Figure 4.1: a) Levels of aggression by *Boopsoidea inornata* in response to temperature change and recorded by tank. Scores denote increasing rates of aggression categorised from 0 (none) to 3 (high) (Allison et al. 2021) b) Second order polynomial regression (with shaded regions representing 95% confidence intervals) of the relationship between standard metabolic rate (SMR) and temperature of *Boopsoidea inornata.*

The likely reductions in aerobic performance of *B. inornata* in a future climate may drive changes in their distribution. Distributional shifts can be predicted using ecological niche models (ENMs) and species distribution models (SDMs). ENMs and SDMs are commonly used in theoretical and applied studies in ecology and biogeography (Peterson et al. 2015). These models can be used to predict impacts of future climate change on species' distributions of which the most common model that uses physiological information to build the model is mechanistic models (Pearson and Dawson 2003, Kearney and Porter 2009). ENMs estimate fundamental niches of species and are applied when the aim is to know the potential distribution, as in the case of invasive species or projections in space and time. On the other hand, SDMs attempt to estimate objects in geographic space, referring to actual distributions of species (Peterson and Soberón 2012, Soberón et al. 2017).

Physiology can be useful for the development of SDMs for a species as it informs the bounds of the model for environmental variables. However, with the high thermal variability and variable environmental changes predicted across the biogeographic regions along the South African coastline, it will be necessary to extend the physiological information collected for the species to the cool temperate and subtropical areas. This will be necessary as the fish in each biogeographical area have different thermal histories and may therefore be locally adapted to their environment (Dowd et al. 2015). This is a common phenomenon, as many species with broad distributional ranges that extend (across biogeographic boundaries) will likely be locally adapted to their resident conditions (Melo-Merino 2020).

BRUVs have been used to answer a wide variety of questions in the wild. One of the main reasons is to assess the effects of MPAs, while other reasons are to assess fish assemblages and behaviours related to BRUVs. Other methods also include the effects BRUVs have on fish species themselves compared to other methods such as RUVs and ROVs (Gladstone et al. 2012, Brooks et al. 2011). Many of the studies conducted with BRUVs are to assess the effectiveness of sample design and variables and for most people it is said that BRUVs are still in the development phase with more methods and designs needed to improve their effectiveness in the wild (Whitmarsh et al. 2017, see Figure 1.2, Chapter 1). However, there are few studies that have used BRUV data to understand the wild behaviour of fishes (Whitmarsh et al. 2017, Mataboge 2021) and the potential for understanding impacts of climate change. Although it is acknowledged that the typical behaviour is impacted by the presence of the camera and bait, this study has shown that some metrics may be useful in understanding how temperature may influence behaviour (for example feeding behaviour).

In this study, the “MaxN” metric provided an estimate of relative abundance. In this case it is the relative abundance of “active fish” as they were the individuals that were attracted and went to the bait canister first. Essentially, in this context, this metric measures the proportion of the total population in the area that are active and therefore would be relatively well predicted by a population level physiological study. With “MaxN” decreasing at the lower temperatures, it follows the same decrease as AS and can be interpreted as most of the population at these lower temperatures do not have the aerobic capacity for activity and feeding. It is possible that the individuals that are observed in these videos are only those that have the aerobic capacity for activity. In contrast to the “MaxN” data, the “time to first arrival” and “time to first feeding” are not population metrics as it only takes one individual to undertake the action in a video. Therefore, there is a mismatch between the population physiology information and the individual behavioural information. There is evidence demonstrating that variability in behaviour and physiological traits is high within fish populations (Duncan et al. 2019b, Bailey et al. 2022, Nabani 2023). To account for the confounding factor of individual variability, “MaxN” was used as an interaction term. This would to some degree mitigate the effect of the behavioural metrics being measured at the individual level and not population level in the BRUV footage.

To further reduce the potential bias of comparing population physiology with the behaviour of an individual, future work should examine the variability in physiological phenotypes in populations (i.e. use a repeated measures approach) by estimating the AS curve of individuals to understand the diversity of physiological phenotypes within a population (Bailey 2023). This information can then be used to better interpret the videos of wild behaviour. Future research should look at the possibility of using conventional tagging (with colour coded tags) and BRUVs together on resident species. This will allow one to track individual fish on a BRUV video and may be useful to bridge the gap between population level and individual level metrics. For example, “MaxN” does not consider individuals that have left the frame of view and come back into view in BRUVs and a way to track individuals even outside the field of view and being able to compute that a fish has left the view and come back in could improve knowledge on individual variability in the wild.

Despite the caveats of the study, it has demonstrated that libraries of BRUV videos may be extremely useful for understanding the wild behaviour of fishes in relation to temperature. Future research in this area should include projects that specifically monitor the real time temperatures in the study sites and deploy BRUVs during marine heat waves and cold spells.

Future research should also look to include the effect that multiple stressors and their interactions have on the physiology and behaviour of fish species. For example, Duncan et al. (2020) looked at the predictability of modern physiological models and found that when temperature and oxygen availability are set to conditions seen in the wild, the aerobic/thermal curve changes, which in turn means that distribution patterns change as well. The study highlights the important role of oxygen availability in setting the thermal preference and limits of aquatic species. The full range of temperatures for laboratory metabolic rate and *in-situ* behaviour data should be explored to get a better understanding of the behaviour and physiology at temperatures > 20 °C. As stated earlier, we were only limited to temperatures below 18 °C and due to this challenge, we were unable to assess the link between the AS of the species with the *in-situ* behaviour as *B. inornata* thermal breakpoint (25 °C) and CTmax (30 °C) were above the temperatures recorded in the BRUVs. Therefore, while the laboratory AS estimates appeared to align with behaviour at cold temperatures, the wild behaviour of fish at warm temperatures should be investigated.

Since South Africa's oxygen and temperature dynamics are predicted to become even more variable in the future, it is important that studies assessing focal species' climate resilience consider both these environmental variables. Another important parameter to consider in future studies is to try to obtain a full representation of the diversity in the physiology and behaviour of fish populations by looking at other possible fish collection methods that do not have bias towards a certain group within the population as the hook and line method may have a bias towards active/bold fish (Klefoth et al. 2017, Alos et al. 2012). The rocky reef habitats where this species resides are difficult to sample using active gears, while passive gears, such as traps selectively catch active fish. However, despite the potential bias of passive hook and line methods, Bailey (2023), using behavioural assays found a high degree of phenotypic diversity in behaviours (individuals ranging from shy to bold phenotypes) within a sampled population of reef fish *Chrysoblephus laticeps* caught using rod and line. One potential strategy to overcome some of the gear bias could be to identify a certain percentage of fish caught first as mainly high performers and the following same percentage as low performers and identify if there is a marked difference between the two or more groups.

Another avenue for future work should be to look at the swimming speed of individual fish in the videos. This is potentially possible, but also vitally important as exercise is deemed to have significant impact on individuals, contributing to their biological fitness in diverse ways (Cooke 2004, Heuer et al. 2021). However, there is limited understanding of how

environmental and ecological factors place constraints on the physiological capacity for exercise in wild fish, especially activities that enhance fitness. (McKenzie and Claireaux 2010, Killen 2013, Farrell 2016).

In conclusion, this study has contributed to our limited knowledge on the link between the physiology and wild behaviour of South African linefish. It provides some evidence to suggest that the AS curve can be used to predict the wild behaviour of fishes at cooler temperatures, which provides support for the OCLTT hypothesis (Pörtner et al. 2010). The findings also provide evidence to suggest that stereo-BRUV work can be used to understand the likely response of fishes to thermal change. This means that BRUVs could be used as a potential source to understand the performance of fish across an environmental gradient in the wild. When captured, this performance information has huge potential to better predict the likely responses of fish populations to the impacts of climate change. However, the full range of temperatures, experienced in the wild, need to be included to understand how temperature affects fish at both high and low extremes. While this approach is valuable, it represents only one of several methods (including bioenergetic models, growth experiments, and survival analyses) for assessing thermal performance, which may provide complementary insights into fitness, population persistence, and productivity. Future research should integrate these multiple approaches, alongside physiological and environmental data such as dissolved oxygen availability, to generate robust performance curves that capture both individual and population-level responses to changing thermal environments.

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APPENDIX

Appendix Table 1: Structure of models applied to investigate *Boopsoidea inornata* SMR and MMR. For each response variable, with model and transformation, the model with the lowest AIC value was selected in bold.

Response variable	Model	Transformation	Best fit structure	AIC
SMR	Linear (Lm)	None	lm(MO2 ~ poly(Temp, 2), phys_data)	62.583
	Linear (Lm)	Log	lm(log(MO2) ~ poly(Temp, 2), phys_data)	**52.816**
	Linear (Lm)	Log1p	lm(log1p(MO2) ~ poly(Temp, 2), phys_data)	54.350
	General least squares (GLS)	None	gls(MO2 ~ poly(Temp, 2), weights = varPower(form = ~ Temp), data = phys_data)	61.737
	General least squares (GLS)	Log	gls(log(MO2) ~ poly(Temp, 2), weights = varPower(form = ~ Temp), data = phys_data)	59.969
	General least squares (GLS)	Log1p	gls(log1p(MO2) ~ poly(Temp, 2), weights = varPower(form = ~ Temp), data = phys_data)	60.508
MMR	Linear (Lm)	None	lm(MMO2 ~ poly(Temp, 2), phys_data)	83.691
	Linear (Lm)	Log	lm(log(MMO2) ~ poly(Temp, 2), phys_data)	**72.306**
	Linear (Lm)	Log1p	lm(log1p(MMO2) ~ poly(Temp, 2), phys_data)	73.385
	General least squares (GLS)	None	gls(MMO2 ~ poly(Temp, 2), weights = varPower(form = ~ Temp), data = phys_data)	81.842
	General least squares (GLS)	Log	gls(log(MMO2) ~ poly(Temp, 2), weights = varPower(form = ~ Temp), data = phys_data)	79.532
	General least squares (GLS)	Log1p	gls(log1p(MMO2) ~ poly(Temp, 2), weights = varPower(form = ~ Temp), data = phys_data)	79.387

Appendix Table 2: Structure of models applied to investigate *Boopsoidea inornata* "MaxN", "time to arrive" and "time to feed". For each response variable and error distribution, the model with the dispersion parameter closest to 1 was selected.

Response variable	Model	Error distribution	Best fit structure	Dispersion parameter
MaxN	1	Poisson	gam(y ~ s(x), family = poisson(link = "log")	16.76
	2	Quasi-Poisson	gam(y ~ s(x), family = quasipoisson())	21.04
	3	Tweedie-Poisson	gam(y~x, tweedie(var.power = 1.01, link.power = 0))	16.04
	4	**Negative Binomial**	gam(y ~ s(x, bs = "cr"), family = negbin(theta = 1.5), method = "REML")	**1.05**
T1st (Time to arrive)	5	Gaussian	gam(y ~ s(x), family = gaussian(link = "log")	34.60
	6	Gamma	glm(y ~ x, family = Gamma(link = "log"))	0.42
	7	Tweedie-Gamma	glm(y~x, family = tweedie(var.power = 2, link.power = 0))	0.42
	8	**Tweedie**	glm(formula = y ~ x * x1, family = tweedie(var.power = 1.4, link.power = 0.3))	**0.98**
Time to feed	9	Gaussian	gam(y ~ s(x), family = gaussian(link = "log")	168.98
	10	Gamma	glm(y ~ x, family = Gamma(link = "log"))	0.43
	11	Tweedie-Gamma	glm(y~x, family = tweedie(var.power = 2, link.power = 0))	0.58
	12	**Tweedie**	glm(y ~ x*x1, family = tweedie(var.power = 1.5, link.power = 0))	**0.97**

Appendix Table 3: Checklist of 53 essential criteria for the reporting of methods for aquatic intermittent-flow respirometry (Killen et al. 2021).

Number	Criterion and Category	Response
	EQUIPMENT, MATERIALS, AND SETUP	
1	Body mass of animals at time of respirometry	Measured immediately after respirometry
2	Volume of empty respirometers	13.046 L
3	How chamber mixing was achieved	Internally connected pumps (880L/h 15w 1.2m AC SOBO water pump) mixed water within respirometers to minimise water stratification
4	Ratio of net respirometer volume (plus any associated tubing in mixing circuit) to animal body mass	40:1 Based off the 13L tank to average 300g individual
5	Material of tubing used in any mixing circuit	Oxygen-impermeable clear thick-wall hose
6	Volume of tubing in any mixing circuit	Mean: 0.65 L SD: 0.09 L
7	Confirm volume of tubing in any mixing circuit was included in calculations of oxygen uptake	Confirmed
8	Material of respirometer (e.g. glass, acrylic, etc.)	Thick-wall Perspex
9	Type of oxygen probe and data recording	Optical oxygen sensor (OXFTC, Pyro Science GmbH). FireStingO2 fibre

		optic oxygen meter (FSO2-4, Pyro Science GmbH) with bare optical fibres (SPFIB-BARE, Pyro Science GmbH. Recorded using Pyro Oxygen Logger Software (Pyro Science GmbH)
10	Sampling frequency of water dissolved oxygen	1 second
11	Describe placement of oxygen probe (in mixing circuit or directly in chamber)	In mixing circuit, where the peristaltic pump drew water from and fed through flow-through cells with an optical oxygen sensor
12	Flow rate during flushing and recirculation, or confirm that chamber returned to normoxia during flushing	Chamber returned to normoxia during flushing
13	Timing of flush/closed cycles	Closed/measurement cycle: 5, 10, 15 or 20 minutes which ever obtained a 0.8 mg/L or greater O2 saturation decline in three or more of the fish Open/Flush period: 10-minute flush period at 12°C, 16°C and 20°C or a 15-minute flush period at 8°C and 24°C).
14	Wait (delay) time excluded from closed measurement cycles	1 minute

15	Frequency and method of probe calibration (for both 0 and 100% calibrations)	Before each trial. Point calibration in saturated water
16	State whether software temperature compensation was used during recording of water oxygen concentration	Used the FireStingO2 temperature probe and software to adjust O2 measurements. No other temperature compensation
MEASUREMENT CONDITIONS		
17	Temperature during respirometry	8, 12, 16, 20 or 24 ̊C depending on the treatment.
18	How temperature was controlled	Using a heat pump (AQUAHEAT SF020P)
19	Photoperiod during respirometry	14hr day (lights on) 10hr night (lights off) Cool florescent lighting
20	If (and how) ambient water bath was cleaned and aerated during measurement of oxygen uptake (e.g. filtration, periodic or continuous water changes)	Complete replacement of water within the experimental system (water bath and chambers) and use of bleach to clean tanks and tubing was conducted prior to trials.
21	Total volume of ambient water bath and any associated reservoirs	2240 L

22	Minimum water oxygen dissolved oxygen reached during closed phases	3.5 mg/l at 24 ̊C (41% saturation). In general, measurements never went below 80% saturation unless the animal was stressed (typically at the beginning of the trial or during MMR protocol)
23	State whether chambers were visually shielded from external	Confirmed
24	How many animals were measured during a given respirometry trial (i.e. how many animals were in the same water bath)	4 (1 per bath) in a connected system
25	If multiple animals were measured simultaneously, state whether they were able to see each other during measurements	Not able to see each other
26	Duration of animal fasting before placement in respirometer	36 hours
27	Duration of all trials combined (number of days to measure all animals in the study)	04/08/2023-11/09/2023
28	Acclimation time to the laboratory (or time since capture for field studies) before respirometry measurements	Wild captured 4 months
BACKGROUND RESPIRATION		
29	State whether background microbial respiration was measured and accounted for, and if so, method used (e.g. parallel	Measured and accounted for. Measurements taken for all chambers while empty

	measures with empty respirometry chamber, measurements before and after for all chambers while empty, both)	
30	State if background respiration was measured at beginning and/or end, state how many slopes and for what duration	End of trial 2-hour blank with closed chambers (one continuous slope)
31	State how changes in background respiration were modelled over time (e.g. linear, exponential, parallel measures)	linear We used the blank from each tank to assume background respiration for each individual tank
32	Level of background respiration (e.g. as a percentage of SMR)	<1%
33	Method and frequency of system cleaning (e.g. system bleached between each trial, UV lamp)	The system was completely flushed, bleached and replaced with fresh seawater between trials
STANDARD OR ROUTINE METABOLIC RATE		
34	Acclimation time after transfer to chamber, or alternatively, time to reach beginning of metabolic rate measurements after introduction to chamber	six (12, 16 or 20°C) or 24 (8, 24°C) hours
35	Time period, within a trial, over which oxygen uptake was measured (e.g. number of hours)	22 hours
36	Value taken as SMR/RMR (e.g. quantile, mean of lowest 10 percent, mean of all values)	The SMR was estimated as the quantile assigned to the

		bottom 20 % of the RO2 data, as the coefficient of variation between readings was above the suggested 5.4 % threshold, following the guidelines of Chabot et al. (2016)
37	Total number of slopes measured and used to derive metabolic rate (e.g. how much data were used to calculate quantiles)	We required a minimum of 15 measurements above our R2
38	Whether any time periods were removed from calculations of SMR/RMR (e.g. data during acclimation, periods of high activity [e.g. daytime])	Daytime, only data between 8pm and 5am were taken when species is least active.
39	r2 threshold for slopes used for SMR/RMR (or mean)	0.9
40	Proportion of data removed due to being outliers below r-squared threshold	We tested 45 healthy specimens, 45 produced > 25 SMR measurements above the r2 Threshold were included in the analysis. Of those 45 fish, RO_2 measurement exclusion was 0%
MAXIMUM METABOLIC RATE		
41	When MMR was measured in relation to SMR (i.e. before or after)	After

42	Method used (e.g. critical swimming speed respirometry, swim to exhaustion in swim tunnel, or chase to exhaustion)	Chasing and tail grabbing (10 minutes) and exposed to air (30 seconds)
43	Value taken as MMR (e.g. the highest rate of oxygen uptake value after transfer, average of highest values)	Estimated from the single steepest decline in oxygen concentration during 3 hours of intermittent-flow respirometry after the chasing protocol
44	If MMR measured post-exhaustion, length of activity challenge or chase (e.g. 2 min, until exhaustion, etc.)	10 minutes of chasing and tail grabbing
45	If MMR measured post-exhaustion, state whether further air-exposure was added after exercise	30 seconds of air exposure
46	If MMR measured post-exhaustion, time until transfer to chamber after exhaustion or time to start of oxygen uptake recording	<20 seconds
47	Duration of slopes used to calculate MMR (e.g. 1 min, 5 min, etc.)	8 minutes
48	Slope estimation method for MMR (e.g. rolling regression, sequential discrete time frames)	Linear regression
49	How absolute aerobic scope and/or factorial aerobic scope is calculated (i.e. using raw SMR and MMR, allometrically mass-	Allometrically mass-adjusted SMR and MMR

	adjusted SMR and MMR, or allometrically mass-adjusting aerobic scope itself)	
DATA HANDLING AND STATISTICS		
50	Sample size	n = 45 Pretrial: 8 ̊C (*B. inornata* n = 4) 16 ̊C (*B. inornata* n = 4) Trials: 8 ̊C (*B. inornata* n = 4) 12 ̊C (*B. inornata* n = 8) 16 ̊C (*B. inornata* n = 4) 20 ̊C (*B. inornata* n = 8) 24 ̊C (*B. inornata* n = 8)
51	How oxygen uptake rates were calculated (software or script, equation, units, etc.)	Software
52	Confirm that volume (mass) of animal was subtracted from respirometer volume when calculating oxygen uptake rates	Confirmed
53	State whether analyses accounted for variation in body mass and describe any allometric mass-corrections or adjustments	To estimate the mass-scaling exponent for the metabolic rate of *B. inornata* species, the data were first temperature-corrected by dividing metabolic rate data by the Arrhenius

function. The slope of the linear regression between the natural logarithm of RO2 (temperature corrected) and the natural logarithm of mass was taken as the allometric exponent (α) of the mass scaling relationship for either SMR or MMR data. RO2 data was then mass corrected (MO2) using the mass scaling relationship

Appendix Table 4: Raw data of the Standard metabolic rate (SMR), maximum metabolic rate (MMR) and aerobic scope (AS) (O_2 $mg.min^{-1}.kg^{-1}$) indices with treatment temperature, fish identification code (FishID) and fish mass (kg) for ***Boopsoidea inornata***.

Temperature	FISH ID	Mass	MO2	MMO2	AS
8	F8.1B	0.2304	1.231473	2.7393173	1.507844
8	F8.2B	0.2331	1.184547	2.3145916	1.130045
8	F8.3B	0.192	1.453136	1.8409885	0.387852
8	F8.4B	0.1791	0.580114	1.6448431	1.064729
12	F12.1	0.2458	1.363447	3.4751664	2.11172
12	F12.2	0.2143	1.240773	4.0079216	2.767148
12	F12.3	0.2975	0.901119	2.6631008	1.761982
12	F12.4	0.2207	1.18019	2.8313829	1.651193
12	F12.1B	0.201	0.987368	3.1051144	2.117746
12	F12.2B	0.1364	1.069713	3.9396239	2.869911
12	F12.3B	0.1671	1.913587	3.293091	1.379504
12	F12.4B	0.176	0.892841	3.5228011	2.62996
16	F16.1B	0.2079	1.807275	5.1193025	3.312028
16	F16.2B	0.2393	1.555318	3.8489912	2.293674
16	F16.3B	0.2577	1.711652	4.986787	3.275135
16	F16.4B	0.2755	1.357424	4.6316334	3.27421
20	F20.1	0.2829	3.105049	6.1477554	3.042706
20	F20.2	0.1603	1.363941	3.7224279	2.358487
20	F20.3	0.1801	2.75235	7.2603554	4.508006
20	F20.4	0.1793	3.856706	7.3891355	3.532429
20	F20.1B	0.1635	3.673247	4.8129052	1.139658
20	F20.2B	0.2267	2.796445	5.2914204	2.494976
20	F20.3B	0.2303	2.548393	4.6938949	2.145502
20	F20.4B	0.2238	2.093691	4.5408311	2.44714
24	F24.1	0.2019	2.092274	5.0919812	2.999707
24	F24.2	0.1708	1.973547	4.011079	2.037532
24	F24.3	0.2398	2.366623	4.0219091	1.655286
24	F24.4	0.1923	1.956491	4.7330671	2.776576
24	F24.1B	0.2282	2.698937	3.9886827	1.289745

24	F24.2B	0.2287	2.607016	5.1611019	2.554086
24	F24.3B	0.2038	1.970549	5.026737	3.056188
24	F24.4B	0.1951	2.086177	5.0335192	2.947342

Appendix Table 5: Ethical clearance letters for 2022-2023, reference: 2022-5456-7052, and 2023-2024, refercence 2023-5456-8123.

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Rhodes University Animal Research Ethics Committee
PO Box 94, Makhanda, 6140, South Africa
t: +27 (0) 46 603 7727
f: +27 (0) 46 603 8822
e: s.manqele@ru.ac.za
NHREC Registration number: AREC-251114-018

https://www.ru.ac.za/researchgateway/ethics/

30 August 2022

Mr Bradley VAN HEERDEN

Email: g18v3473@campus.ru.ac.za

Review Reference: 2022-5456-7052

Dear Mr Bradley VAN HEERDEN

Re: Animal ethics application: The metabolic physiology and behaviour of fransmadam fish.

Principal Investigator: Prof. Warren Potts

Collaborators: Mr Bradley van Heerden, Dr Brendon Cole

This letter confirms that the above research proposal has been reviewed and **APPROVED** by the Rhodes University Animal Research Ethics Committee (RU-AREC). Your Approval number is 2022-5456-7052.

Approval has been granted for one year from the date of this letter. **An annual progress report** will be required in order to renew approval for an additional period of one year.

Please ensure that the RU-AREC committee is notified should any substantive change(s) be made, for whatever reason, during the research process. This includes changes in investigators. Please also ensure that a brief report is submitted to the ethics committee on the completion of the research. The purpose of this report is to indicate whether the research was conducted successfully, if any aspects could not be completed, or if any problems arose that the RU-AREC should be aware of. If a thesis or dissertation arising from this research is submitted to the library's electronic theses and dissertations (ETD) repository, please notify the committee of the date of submission and/or any reference or cataloging number allocated.

Sincerely

Dr. Roman Tandlich

Chair: Rhodes University Animal Research Ethics Committee, RU-AREC

cc: Ethics Coordinator

RHODES UNIVERSITY
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Rhodes University Animal Research Ethics Committee
PO Box 94, Makhanda, 6140, South Africa
t: +27 (0) 46 603 7727
f: +27 (0) 46 603 8822
e: s.manqele@ru.ac.za
NHREC Registration number: AREC-251114-018

https://www.ru.ac.za/researchgateway/ethics/

1 November2023

Mr Bradley VAN HEERDEN

Email: g18v3473@campus.ru.ac.za

Review Reference: 2023-5456-8123

Dear Mr Bradley VAN HEERDEN

Re: Animal ethics application: The metabolic physiology and behaviour of fransmadam fish.

Principal Investigator: Professor Warren Potts

Collaborators: Professor Amber-Robyn Childs

This letter confirms that the above Annual Report has been reviewed and **APPROVED** by the Rhodes University Animal Research Ethics Committee (RU-AREC). Your Approval number is: 2023-5456-8123**. The approval is conditional on the following conditions:**

You are requested to submit bimonthly reports about the progression of the project. Any unexpected events must be reported to RUAREC as a matter of urgency.

Approval has been granted for one year from the date of this letter. **An annual progress report** will be required in order to renew approval for an additional period of one year. Ethics approval for a project can be renewed twice for a project (i.e. the maximum number of years that a project can receive ethics approval for is 3 years). Thereafter, the project will need to undergo a full application should you require ethics clearance for longer than 3 years.

Sincerely

Dr. Roman Tandlich

Chair: Rhodes University Animal Research Ethics Committee, RU-AREC

cc: Ethics Coordinator