

37	Table of Contents	
38	Abstract	4
39	Acknowledgements	8
40		
41	Chapter 1: What do we know, and where do we need to go to understand the links between fish	
42	behaviour and physiology in the Anthropocene?	9
43	Introduction.....	9
44	Methods	13
45	Results.....	14
46	Discussion	22
47	Aims of thesis.....	3
48		
49	Chapter 2: Study area and study species	33
50	Climate change along the South African coast.....	33
51	Study area.....	34
52	Sampling locality.....	37
53	<i>Chrysoblephus laticeps</i> as a model species.....	38
54		
55	Chapter 3: The importance of individual variation in physiological phenotype to predict the	
56	resilience of fished populations in the Anthropocene	41
57	Introduction.....	41
58	Methods	44
59	Results.....	51
60	Discussion	61
61	Appendix A.....	66
62		
63	Chapter 4: Plastic behavioural responses to cope with thermal variability are determined by	
64	both bold personality and a broad aerobic scope in a temperate fish species	70
65	Introduction.....	71
66	Methods	73
67	Results.....	81
68	Discussion	94
69	Appendix B	98
70		
71		
72		

73	Chapter 5: Social dominance across thermally variable conditions is predicted by high	
74	metabolic performance.....	100
75	Introduction.....	100
76	Methods	104
77	Results.....	110
78	Discussion	116
79	Appendix C	122
80		
81	Chapter 6: Management of phenotypic diversity and promoting the climate resilience of fish	
82	stocks.....	129
83	Main findings	129
84	Relevance to fisheries policy.....	131
85	Limitations to the study	137
86	Future research priorities	140
87	Conclusion	146
88		
89	Reference list	146
90		
91		
92		
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Abstract

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Thermal variability in the marine environment is likely to have a considerable effect on fishes as it impacts physiological performance and vital (i.e. metabolism, foraging and swimming style) and non-vital (i.e. reproductive fitness) energetic processes. When fish are subjected to thermal stress, they may primarily respond by changing their behaviour. Species that have broad phenotypic behavioural plasticity (i.e. defined as the ability to adjust behavioural activity in presiding environmental conditions in order to remain within their optimal thermal range) may have a competitive advantage. Fish behavioural plasticity may take many forms. Some species may seek out thermal refugia by changing their phenology or distribution, while others alter the timing of their seasonal and spawning migrations in response to a changing environment. Although fishes can use behavioural changes to cope with climate change impacts, there does appear to be variability in the behavioural responses within species. However, if alterations in behaviour are insufficient to ensure that the individual remains within their optimal thermal range, physiological acclimation (i.e. defined as the process in which an organism adjusts to prevailing conditions by broadening their thermal performance curve so that their performance is maximized in the new thermal environment) may be required. Therefore, there is a critical link between the behaviour and thermal physiology of fishes, particularly in a world where they are facing increasing thermal stress.

Fishing-induced mortality is aggravated by marine environmental stressors by reducing the genetic potential for adaptation and selecting for particular phenotypes. For example, fishing-induced selection on those individuals with broad aerobic scope, or bold fish deemed to have high fitness potential and increased behavioural plasticity. Although understanding the impact of climate variability and exploitation on the link between behavioural plasticity and aerobic scope phenotypes is critical to predict the survival of angling species, the causal link between physiological phenotypes and behavioural phenotypes is not known.

The purpose of this study is to evaluate the impact of climate variability on the link between behavioural plasticity and aerobic scope phenotypes of an important linefish species, *Chrysoblephus laticeps*. This study is the first to examine how hierarchical behavioural plasticity varies with aerobic scope under changing temperatures, in a fished population.

140 To address the susceptibility of exploited species to temperature variability, intermittent-flow
141 respirometry was used to quantify and compare changes in metabolic rate under different
142 temperatures (10 °C, 16 °C and 21 °C) mimicking thermal variations experienced in the home
143 range of the species (Chapter 3). The absolute aerobic scope (AS) for each individual was then
144 calculated by subtracting mass corrected SMR from mass corrected MMR. A total performance
145 score was developed to represent aerobic performance across the range of test temperatures.
146 These scores were used to classify individuals according to the percentile method as high
147 performers (i.e. the >75 % percentile with a total score above 9.75, rounded off as 10),
148 intermediate performers (25 – 75 % percentile), and low performers (i.e. the <25 % percentile
149 with a total score below 5.25, rounded off as 5). High and low performance aerobic phenotypes
150 were related to behavioural syndromes (bold vs timid) of individuals through a series of
151 hierarchical behavioural tests (Chapter 4). Chapter 5 examined which combinations of aerobic
152 scope and behavioural phenotypes are likely to be selected for, based on competitive ability
153 and adaptive potential, in a climate variability scenario. Here, individuals of various phenotype
154 combinations (i.e. bold high performer, timid high performer, bold low performer, timid low
155 performer) were paired according to size in competitive dual feeding contests.

156

157 The results of this Chapter 3 identified heterogeneity in physiological performance phenotypes
158 amongst individuals of the exploited Noordhoek *Chrysoblephus laticeps* population.
159 Temperature influenced SMR, MMR and AS. There was significant variation in the aerobic
160 performance of high, intermediate, and low performers at higher temperatures. However,
161 differences in performance were not significant at low temperatures, where several
162 intermediate performers maintained high performance. These results indicate that individuals
163 with a broad aerobic scope (i.e. high AS values across a range of temperatures) are likely to be
164 the most resilient to short-term thermal variability caused by the marine heat waves and
165 upwelling events present in temperate coastal environments. Since the shape of thermal
166 performance curves differs between individuals and reflects the range at which individuals can
167 function above specified performance thresholds, individual thermal performance must be
168 measured repeatedly in the same individual over a thermal gradient. An understanding of
169 physiological phenotype diversity and variation of phenotypes amongst individuals is critical
170 to understand the impacts of thermal variability on fished populations.

171

172 For Chapter 4, behavioural tests included assessing aggressive interactions (i.e. mirror test),
173 boldness (i.e. novel object test) and activity level in isolated individuals to classify individual

174 behavioural phenotype along a continuum (i.e. ranging from bold to timid). To determine
175 different physiological responses amongst behavioural phenotypes, the plasticity of individual
176 behavioural responses under temperature variability was assessed. Behavioural phenotypes
177 were linked to metabolic performance using Principal Component Analyses (i.e. PCA) and
178 cluster analyses. The separation of bold and timid phenotypes (by composite score) became
179 more apparent when metabolic performance was assigned to each individual and resulted in
180 three distinct clusters (i.e. bold individuals with high aerobic performance; timid individuals
181 of primarily intermediate aerobic performance; and bold individuals with intermediate
182 performance). Individuals with both a high aerobic performance phenotype and bold
183 behavioural phenotype had the most plastic behavioural response to thermal variability. The
184 maintenance of bold personality traits (i.e. aggression, exploratory activity, risk behaviour) at
185 a range of temperatures was dependent on the aerobic performance of the individual. This
186 suggests that metabolism may be an important driver of animal personality. Indeed, the
187 inability of individuals with low aerobic performance to maintain bold personality traits at a
188 range of temperatures suggests that behavioural plasticity was constrained by aerobic scope. In
189 this study, bold, high aerobic performers had the capacity to sustain bold personality traits
190 across variable temperatures, and as a result, had the ability to maintain their behavioural traits
191 in a thermally variable environment when compared with all other combinations of
192 physiological and behavioural phenotypes.

193

194 Chapter 5 assessed how social competition for resources in a climate change scenario (i.e.
195 across thermally variable temperatures mimicking upwelling and heat wave events) is
196 influenced by individual physiological and behavioural phenotype in *C. laticeps*, and whether
197 this will drive the restructuring of hierarchical dominance ranks by phenotype under thermal
198 variability. To do this, high performers, intermediate performers and low performers (identified
199 in Chapter 3 and 4), were subjected to sized-matched duels across a thermal gradient. For all
200 behavioural experiments, fish feeding, aggression and activity were classified via a weighted
201 scoring system (where higher scores are equivalent to bolder or dominant behaviour) and
202 assessed via principal component analyses. This study found that both physiological phenotype
203 and behavioural phenotype are important in determining dominance in *C. laticeps*, with bold
204 intermediate performers having the highest probability of winning dual contests closely
205 followed by bold high performers at normal and warming temperatures. Both bold and timid
206 low performers lost duels as temperatures increased, and as such, physiological phenotype may
207 ultimately be more important than behavioural phenotype in determining dominance and

208 competitive access to food resources as temperatures increase. There was less variation in the
209 expression of physiological phenotypes between all individuals at cold temperatures, however,
210 low performers were comparatively more dominant and just as likely to win duels. These
211 findings not only provide insight into the role of physiology and behaviour in the social
212 structure of fishes, but also emphasize the importance of maintaining phenotype diversity in
213 rapidly changing climates.

214 In summary, individuals with a broad aerobic scope were identified as the physiologically
215 fittest individuals with the greatest resilience to thermal variability. Individuals with a broad
216 aerobic scope had the energetic capacity for adaptive behavioural plasticity to changing
217 temperatures. Individual variation in physiological and behavioural phenotype did determine
218 competitive access to food resources in a climate variability scenario. Social dominance was
219 predicted by aerobic scope, where bold high and intermediate performers occupied upper
220 dominance ranks across thermal contexts. Hence, physiological and behavioural traits are
221 crucial to predict the survival of fished populations to thermal variability. The scientific
222 community has the capacity to inform fisheries policy using data collected on the coupled
223 effects of exploitation and climate stressors on fish metabolic physiology and behaviour. This
224 emphasises the importance of spatial protection, such as Marine Protected Areas, of the fittest
225 individuals with the aerobic capacity to respond to climate variability through behavioural
226 plasticity. For the sustainable management of fished stocks, the offspring of these protected
227 individuals can move into nearby fished areas and preserve the phenotypic diversity needed for
228 social groups to respond to climate change.

229

230 **Key words:** marine; fisheries management; climate adaptation; Climate change; Over-fishing;
231 Phenotypic plasticity; Metabolic shifts; Stress response

232

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240

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271 Chapter 1

272 What do we know, and where do we need to go to understand the 273 links between fish behaviour and physiology in the 274 Anthropocene?

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277 physiology in fishes in the Anthropocene. *Reviews in Fish Biology and Fisheries*.
278 <https://doi.org/10.1007/s11160-022-09701-2>).

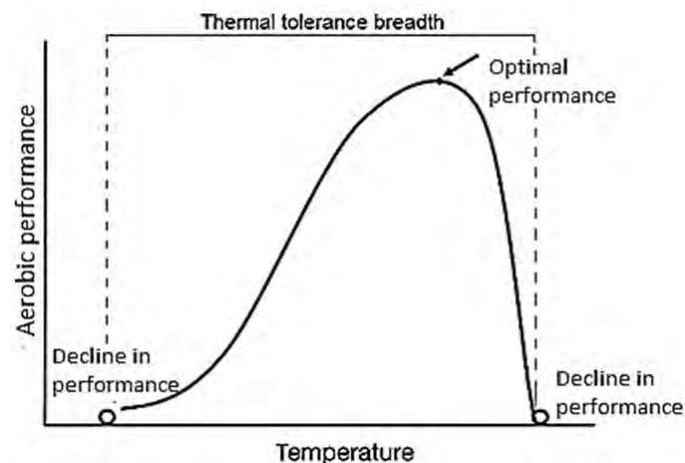
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281 1.1 Introduction

282 The Anthropocene is defined as the current geological Epoch where human activities dominate
283 the climate and environment (Crutzer and Stoermer 2000). Fish populations in this Epoch are
284 subjected to the coupled threats of human-induced climate change and exploitation (Cooke et
285 al. 2019). Anthropogenic climate change is driving substantial changes in the marine
286 environment, including increased ocean temperatures (Rhein et. 2013; Holt and Jorgensen
287 2015), localized environmental variability (Rouault et al. 2010), ocean acidification (Collins et
288 al. 2013) and deoxygenation (Hoegh-Guldberg et al. 2014). Generally, fishes first respond to
289 environmental changes by adjusting their behaviour. For example, in the case of altered thermal
290 conditions, Claireaux et al. (1995) found that Atlantic cod (*Gadus morhua*) exhibited
291 thermoregulatory behaviour by avoiding the altered thermal conditions and shifting their
292 vertical position to the original thermal conditions within an experimentally stratified water
293 column, with no perceptible changes to their heart rate. However, if behavioural adjustments
294 are not successful or possible, fishes have to respond to environmental changes by modifying
295 their physiological processes, such as rates of oxygen uptake (Clarke and Johnston 2002), or
296 acid base regulation in the case of ocean acidification (Cattano et al. 2018). These physiological
297 adjustments, in turn, influence their vital metabolic processes, such as foraging efficiency and
298 swimming style (Brownscombe et al. 2014; Johansen et al. 2014; Chabot et al. 2016) and the
299 energy available for reproductive fitness (Pankhurst and Munday 2011). The capacity for
300 physiological plasticity and acclimatization of fish populations in response to environmental
301 shifts will therefore partly determine their resilience to climate change (Wong and Candolin
302 2015; Donelson et al. 2019; Neubauer and Anderson 2019).

303

304 The environmental conditions (i.e. temperature or pH) that ectothermic organisms, such as
305 fishes, can tolerate are typically represented by a bell-shaped performance curve where
306 physiological performance rises to an optimum and then declines as conditions exceed tolerable
307 levels (Huey and Stevenson 1979). This mechanism applies to the effects of both altered
308 thermal conditions and ocean acidification, but as temperature can have a greater impact on the
309 physiological performance of ectotherms (Holt and Jorgensen 2015; Cattano et al. 2018;
310 Laubenstein et al. 2018; Laubenstein et al. 2019), we provide an example of a thermal
311 performance curve to portray this mechanism (e.g., Figure 1.1). This performance curve is
312 often described by examining temperature (or pH) sensitive physiological process such as
313 aerobic metabolic scope (the potential to increase the rate of oxygen uptake, defined as the
314 difference between standard and maximum metabolic rates; Portner and Knust 2007). If
315 temperatures (or pH) move outside of the optimal range, physiological performance is
316 compromised. If fishes cannot respond by primarily shifting their distribution to more
317 favourable conditions, fishes may acclimatize to prevailing conditions by broadening their
318 thermal performance curves, or genetic adaptation (over several generations) so that their
319 performance curves are maximized in the new thermal environment (Donelson et al. 2012;
320 Munday 2014; Chown et al. 2010; Donelson et al. 2019; Neubauer and Anderson 2019).
321 However, since climatic changes can occur rapidly, genetic adaptation may not always be
322 possible, as it may be a relatively slow process, particularly in organisms with long generation
323 times (Somero 2010). Should behavioural adjustments not be possible, physiological
324 acclimatization is thus important in inferring climate resilience in species with slow rates of
325 genetic adaptation (Donelson et al. 2012; Munday 2014).



326

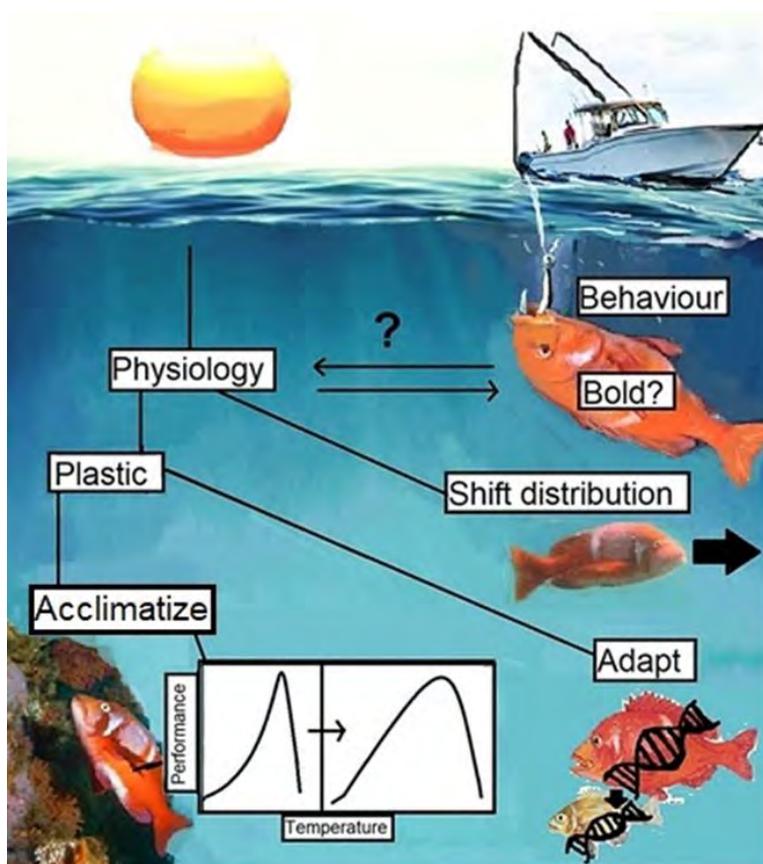
327 **Figure 1.1 Conceptual diagram of an animal thermal performance response curve (adapted from**
328 **Schrödinger 1944).**

329 **Aerobic performance rises to an optimum and then declines as conditions exceed tolerable levels.**

330
331 To compound the challenges posed by a changing climate, exploitation influences fish
332 populations around the planet by altering their demographic (Planque et al. 2010), life history
333 (Olsen et al. 2004) and physiological (Hessenauer et al. 2015; Duncan et al. 2019)
334 characteristics. When combined, climate change and exploitation may interact in their impacts
335 (Planque et al. 2010; Clark et al. 2017; Vedor et al. 2021). For example, climate warming can
336 select for a decrease in body size as the gill surface area of large fish cannot maintain the
337 elevated oxygen demand required by their three-dimensional bodies under climate warming
338 (Pauly and Cheung 2018). This is termed the gill oxygen limitation theory and is tied to fishing
339 pressure, which can similarly select for a decrease in body size and earlier size at maturity
340 (Olsen et al. 2004). Fishing pressure may select for certain phenotypes and reduce the genetic
341 potential for adaptation; a process termed fishing-induced evolution (Marty et al. 2015).

342
343 Fishing pressure may reduce behavioural diversity by selecting against certain behaviour types
344 (i.e., bold fish that are highly aggressive and actively respond to stressors, as opposed to timid
345 inactive fish that passively respond to stressors) and this may have implications for how
346 exploited populations respond to environmental change by reducing the potential for
347 acclimation and adaptation (Wong and Candolin 2015; Arlinghaus et al. 2017; Beever et al.
348 2017; Biro et al. 2018; Vedor et al. 2021). There is some empirical information for this. Alos
349 et al. (2012) and Koeck et al. (2019) found that bold, active fish with a larger home range and
350 greater dispersal ability are more likely to encounter and take the risk of biting fishing gear
351 (Alos et al. 2012; Koeck et al. 2019). This kind of behavioural selection by a fishery has been
352 shown to reduce the diversity of behavioural phenotypes in largemouth bass *Micropterus*
353 *salmoides* (Cooke et al. 2007), and thus populations that are exploited by hook and line fisheries
354 may have a greater proportion of timid phenotypes (Arlinghaus et al. 2017). Short-term
355 phenotypic behavioural changes are often a first response to environmental stressors as fishes
356 seek to maintain performance (Wong and Candolin 2015). Indeed, behavioural plasticity has
357 allowed many taxa to cope with changing environmental signals by altering their phenology
358 (e.g., timing of seasonal or spawning migrations; Sims et al. 2004; Sousa et al. 2016) or
359 distribution (e.g., James et al. 2008; Rijnsdorp et al. 2009; Brander 2010; Freitas et al. 2015;
360 Wong and Candolin 2015; Beever et al. 2017). By selecting for a greater proportion of timid
361 behavioural phenotypes in fished populations (Cooke et al. 2017), fishing pressure may reduce
362 the proportion of bold exploratory phenotypes that have the potential to colonize new habitats
363 and recover from climate stressors (Biro et al. 2018).

364
 365 The selection of particular phenotypes has implications for the way in which fishes respond to
 366 a changing climate as their behavioural and aerobic metabolic trait groups appear to be
 367 mechanistically linked. For example, bold personality traits have been shown to covary with
 368 aerobic scope (Seebacher et al. 2013; Killen et al. 2014; Rupia et al. 2016). Fisheries selection
 369 on behavioural traits could therefore affect the distribution of metabolic physiological traits
 370 within a population. Indeed, Duncan et al. (2019) provided evidence that a fished population
 371 of red roman, *Chrysoblephus laticeps*, had fewer high aerobic scope phenotypes relative to a
 372 protected population and attributed this to fisheries selection. It is therefore critical to develop
 373 an improved understanding of the proximate link between physiological and behavioural trait
 374 groups of fish populations to anthropogenic impacts, such as climate change and exploitation,
 375 in order to develop adaptive plans that will contribute to conserving the potential of their
 376 adaptive responses (Figure 1.2).



377
 378 **Figure 1.2: Outline of review**

379 **Fish can respond to altered environmental conditions by primarily shifting their distribution to**
 380 **more favourable conditions, or acclimatize to prevailing conditions by broadening their thermal**
 381 **performance curves, or genetic adaptation (over several generations) so that their performance**
 382 **curves are maximized in the new thermal environment.**

383
384 The aim of this meta-analysis is to review the evidence for links between behaviour and aerobic
385 metabolic physiology in freshwater and marine fishes, and relate these to information on the
386 impacts of exploitation and climate change on marine fish populations. This information will
387 be used to identify gaps in our knowledge on fisheries-induced evolution on metabolic and
388 behavioural traits, and recommend avenues for future research. To do this, the manuscript has
389 been divided into three sections. The first section will review the current literature on the links
390 between heritable physiological and behavioural phenotypes in freshwater and marine fishes.
391 The second section will relate these findings to the effects of climate change and exploitation
392 in the Anthropocene. The last section will focus on future research priorities regarding the
393 importance of adaptive links between behaviour and metabolic physiology in the exploited fish
394 populations of the Anthropocene.

395

396 **1.2 Methods**

397 Our aim was to identify peer-reviewed studies for links between behaviour and metabolic
398 physiology in fishes, to ultimately relate this to fisheries-induced evolution on metabolic and
399 behavioural traits. We targeted studies that directly measured whole-animal metabolic rate in
400 relation to behavioural traits, as this constitutes a major research gap in terms of fisheries-
401 induced evolution on metabolic and behavioural traits. We conducted a meta-analysis on the
402 mean effect sizes of published research since 1970 until April 2021 using a Boolean string in
403 Google Scholar with the following search terms: ('fish' OR 'teleost') AND ('metabolic rate'
404 OR 'oxygen uptake' OR 'oxygen consumption' OR 'aerobic scope' OR 'MO₂') AND
405 ('behaviour' OR 'animal personality' OR 'boldness' OR 'aggression' OR 'social dominance'
406 OR 'exploration' OR 'stress recovery'), where the first 80 search pages were reviewed for
407 appropriate papers along with their reference lists (Haddaway et al. 2015).

408

409 We included studies that either correlated whole-animal metabolic and behavioural trait groups
410 (i.e. bold or timid), or identified a causal relationship between these trait groups through
411 experimental manipulation (i.e. either through introduction to a novel environment or object,
412 or by manipulating abiotic or biotic variables and measuring the effect on the relationship
413 between metabolic and behavioural traits). We focussed on studies done on both adult and
414 juvenile fishes. Studies that were excluded based on title alone were those that were conducted
415 on terrestrial animals or non-fish species, or studies that were unrelated, unavailable or not

416 peer-reviewed (e.g., research theses). Given the abundance of research addressing fisheries-
417 induced evolution on demographic (Planque et al. 2010) and life history traits (Olsen et al.
418 2004), the focus of this literature review did not extend to other physiological aspects such as
419 growth and digestive physiology, or locomotion and movement. We did not include indirect
420 estimates of metabolic rates (e.g., using biotelemetry) of mobile fishes in their natural habitats,
421 as these estimates need to be calibrated to MO_2 equivalents to maximize their usefulness
422 (Eliason and Farrell 2016). However, we do discuss the usefulness of biotelemetry as a future
423 research avenue (i.e. Skeeles et al. 2020). Furthermore, we did not review the abundance of
424 endocrinological studies on the link between stress physiology and behaviour (there are an
425 abundance of such studies in the field of ecotoxicology and they do not constitute a major
426 research gap; Sih et al. 2004, Aubin-Horth et al. 2012), but we do discuss behavioural stress
427 coping styles in the context of Anthropogenic stressors. Additional relevant references that
428 were referred to in the papers of interest were also included in the literature search.

429

430 We extracted the following information from each paper for the meta-analysis: (1) the mean
431 effect size of the measurement of whole animal metabolic rate, (2) the measurement of
432 behavioural trait, (3) species, (4) life-history stage, (5) biogeographic zone and (6) the change
433 in the mean effect size of phenotypic traits following exposure to biotic (eg. stocking density,
434 predation pressure, angling pressure) or abiotic (e.g., temperature, salinity, CO_2 , hypoxia)
435 environmental stressors. We tested for a significant difference in the relationship between
436 metabolic rate and behaviour type by comparing the mean effect sizes of reviewed papers using
437 the R packages ‘meta’ and ‘metamean’ (Balduzzi et al. 2019). We tested whether this
438 relationship varied by life-history stage, biogeographic zone and stressor using the ‘metafor’
439 package. We identified the studies that quantified links between physiology and behaviour in
440 relation to stressors, identified gaps in our knowledge and then described future research
441 priorities for understanding how fisheries may select for linked metabolic and behavioural trait
442 groups in fished populations of the Anthropocene.

443

444 **1.3 Results from the meta-analysis**

445 Of these 53 manuscripts, the majority (57%) focused on freshwater fishes, followed by
446 anadromous fishes (28%) and tropical reef fishes (7 %). Studies that measured whole-animal
447 metabolic rate in relation to behavioural traits were divided between adult (53 %) and juvenile

448 fishes (47%). Sixty-eight percent of studies examined how linked physiological and
 449 behavioural traits were impacted by abiotic stressors, following by biotic stressors (21%) and
 450 fishing (11%). The meta-analysis revealed significant metabolic differences between bold and
 451 timid behavioural types ($df = 49$, $p < 0.001$) across all reviewed manuscripts, regardless of
 452 biogeographic zone or fish family ($df = 49$, $p > 0,05$; Table 1.1).

453

454 **Table 1.1: The relationship between metabolic and behavioural traits as a function of life-**
 455 **history, biogeographic zone, fishery species and stressor**

Effect	Estimate	SE	Z-value	P-value
Intercept	28.859	1.572	0.1835	0.854
Behavioural metric	0.0105	0.008	1.605	0.001
Biogeographic zone	-13.047	11.321	-1.926	0.069
Fishery species	-2.720	7.397	-0.037	0.971
Life history	0.0000	9.1605	-0.000	0.001
Continent	1.414	14.218	-0.010	0.992
Abiotic stressor	13.529	5.883	0.230	0.007
Biotic	-14.3760	11.386	-0.1263	0.470
Angling	21.1498	6.839	0,3093	0.040
Aic	112.19			
Residual heterogeneity	40.25 % ($df = 49$)			

456

457 Studies from our meta-analysis found that individuals with a high standard metabolic rate
 458 (SMR; the rate at which an animal oxidizes metabolic substrates to produce the energy required
 459 to maintain homeostasis in a post absorptive, inactive state; McNab 2002; Metcalfe et al. 2016)
 460 had a suite of bold behavioural traits, including aggression, dominance and competitive
 461 foraging behaviour (Figure 1.3a and 1.4). Indeed, we found that behavioural traits of
 462 aggression, boldness and activity were positively correlated with each other ($df = 49$, $p <$
 463 0.001). Links between standard metabolic rate and aggression have been established in several
 464 juvenile salmonid species (Metcalfe 1995; Pucket and Dill 1985; Cutts et al. 1998, 1999;
 465 Yamamoto et al. 1998; Cutts et al. 2001; McCarthy 2001; Lathi et al. 2002; Sloat and Reeves
 466 2014), adult and juvenile spinyhead and roughhead blennies (*Acanthemblemaria spinosa* and
 467 *A. aspera*; Clark 1992), adult mangrove killifish (*Kryptolebias marmoratus*; Li et al. 2020) and

468 adult cichlids (Grantner and Taborsky 1998; Ros et al. 2006; Dijkstra et al. 2013, Dijkstra et al.
469 2016; Figure 1.3a). However, both Seppanen et al. (2009) and Vaz-Serrano et al. (2011) found
470 no correlation between standard metabolic rate and aggression in juvenile Atlantic salmon,
471 *Salmo salar*. Whereas, Forstner and Wieser (1990) found no difference in SMR between bold
472 and timid juvenile common roach, *Rutilus rutilus*. Of the above-mentioned studies comparing
473 SMR to aggressive behaviour, six studies focussed on adults and twelve on juveniles.

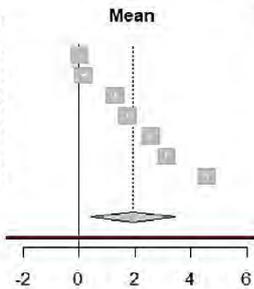
474

475 The comparability of metabolism and behaviour between adult and juvenile fishes may be
476 limited, as the behaviour of adults is most likely determined by different behavioural costs and
477 benefits when compared with juveniles (Biro et al. 2005). Indeed, our meta-analysis revealed
478 significant differences in the behavioural responses of adults compared to those of juveniles
479 across all metabolic measures ($df = 49$, $p = 0.001$; Table 1.1). However, the proportions of
480 reviewed papers conducted on adults and juveniles differed in the measure of metabolic trait,
481 preventing further post-hoc analysis of behavioural differences between adults and juveniles
482 within metabolic measurement groups (i.e. SMR, MMR or AS). The observed differences may
483 be attributed to the difference in thermal performance curves across life history stages (Portner
484 and Peck 2010). Furthermore, some of these studies (e.g., McCarthy 2001; Croft et al. 2004)
485 have examined aggressive social interactions using paired dual competitions (i.e. where size-
486 matched individuals compete for food), which are a reasonable experimental proxy for what
487 likely occurs between juvenile territorial stream dwelling fishes, such as juvenile coho salmon
488 (*Oncorhynchus kisutch*). However, SMR may relate differently to the behaviour of adult
489 fishes. For example, paired dual competitions most likely do not accurately represent the
490 aggressive interactions naturally occurring amongst members of fishes that have groups with
491 established dominance hierarchies, and thus the behaviour often associated with adult fishes
492 (Careau et al. 2008). Hence, the territorial behaviour in juvenile fishes may not represent the
493 behaviour that occurs in the established dominance hierarchies of adult social groups. While
494 studies linking SMR to aggression have focussed on juvenile fishes, several studies focussing
495 on adult fishes have linked SMR to predator avoidance and exploratory behaviour (Ruxton et
496 al. 2000, Dwyer et al. 2014, Holt and Jorgensen 2015, Behrens et al. 2019).

497

SMR and Activity

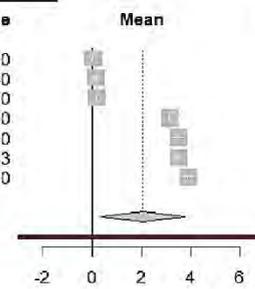
Author	Total	SE	P-value
Crocker & Cech 1997	24	0.02	0.0100
Killen et al. 2018	44	0.15	0.2040
Forstner & Wieser 1990	15	1.30	0.0080
Dwyer et al. 1994	16	1.73	0.0580
Dwyer et al. 2014	16	2.56	0.0730
Claireaux et al. 1994	5	3.12	0.0500
Norin et al. 2016	60	4.56	0.1300



MRAW	95%-CI	Weight
0.02	[0.02; 0.03]	14.3%
0.15	[0.09; 0.21]	14.3%
1.30	[1.30; 1.30]	14.3%
1.73	[1.70; 1.76]	14.3%
2.56	[2.52; 2.60]	14.3%
3.12	[3.08; 3.16]	14.3%
4.56	[4.53; 4.59]	14.3%
1.92	[0.41; 3.43]	100.0%

Abiotic stressor

SE	P-value	Mean	MRAW	95%-CI
0.01	0.0100		0.01	[0.01; 0.01]
0.13	0.2040		0.13	[0.07; 0.19]
0.16	0.0070		0.16	[0.16; 0.17]
3.12	0.0500		3.12	[3.08; 3.16]
3.48	0.4800		3.48	[3.24; 3.72]
3.48	0.1933		3.48	[3.43; 3.53]
3.88	0.4800		3.88	[3.64; 4.12]
2.04	[0.35; 3.72]		2.04	[2.97; 7.05]

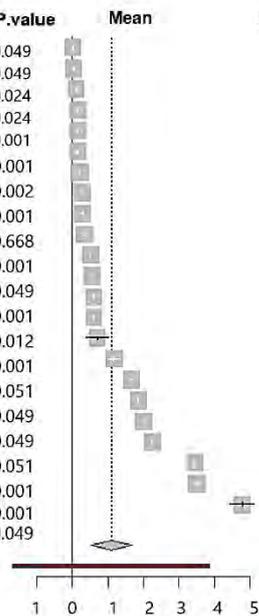


Random effects model
Prediction interval
Heterogeneity: $t^2 = 2.660$, $p = 0.016$

$p = 0.029$

SMR and Aggression

Study	Total	Mean	SD	P-value
Cutts et al. 1999	53	0.01	0.0080	0.049
Cutts et al. 1998	70	0.04	0.2000	0.049
Clark 1992	49	0.10	0.1000	0.024
Clark 1992	49	0.15	0.1000	0.024
Li et al. 2020	30	0.15	0.0190	0.001
Clark 1992	49	0.15	0.1000	0.001
Dijkstra et al. 2016	34	0.20	0.1000	0.001
Metcalfe 1995	70	0.27	0.0200	0.002
Yamamoto et al. 1997	15	0.28	0.0900	0.001
Killen et al. 2018	44	0.35	0.0600	0.668
McCarthy 2001	55	0.52	0.0100	0.001
Pucket & Dill 1984	60	0.55	0.0200	0.049
Alton et al. 2013	13	0.60	0.4000	0.001
Sloat & Reeves 2014	50	0.60	0.0700	0.012
Ros et al. 2016	24	0.70	0.8100	0.001
Dijkstra et al. 2013	34	1.17	0.5000	0.051
Vaz Serrano 2011	11	1.65	0.0130	0.051
Dorfman 2005	30	1.86	0.0070	0.049
Lathi et al. 2002	200	2.00	0.0600	0.049
Seppanen et al. 2009	1500	2.25	0.1000	0.051
Finstad et al. 2007	184	3.45	0.2000	0.001
Reid et al. 2012	24	3.50	0.2000	0.001
Cutts et al. 2001	40	4.78	1.1000	0.049

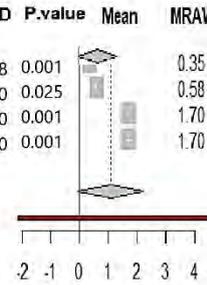


MRAW	95%-CI	Weight
0.01	[0.01; 0.01]	4.4%
0.04	[0.01; 0.09]	4.4%
0.10	[0.07; 0.13]	4.4%
0.15	[0.12; 0.18]	4.4%
0.15	[0.14; 0.16]	4.4%
0.15	[0.12; 0.18]	4.4%
0.20	[0.17; 0.23]	4.4%
0.27	[0.27; 0.27]	4.4%
0.28	[0.23; 0.33]	4.4%
0.35	[0.33; 0.37]	4.4%
0.52	[0.51; 0.52]	4.4%
0.55	[0.54; 0.56]	4.4%
0.60	[0.38; 0.82]	4.3%
0.60	[0.58; 0.62]	4.4%
0.70	[0.38; 1.02]	4.3%
1.17	[1.00; 1.34]	4.3%
1.65	[1.64; 1.66]	4.4%
1.86	[1.86; 1.86]	4.4%
2.00	[1.99; 2.01]	4.4%
2.25	[2.24; 2.26]	4.4%
3.45	[3.42; 3.48]	4.4%
3.50	[3.42; 3.58]	4.4%
4.78	[4.44; 5.12]	4.3%
1.05	[0.53; 1.67]	100.0%

Random effects model
Prediction interval
Heterogeneity: $t^2 = 1.704$, $p = 0.05$

Biotic stressor

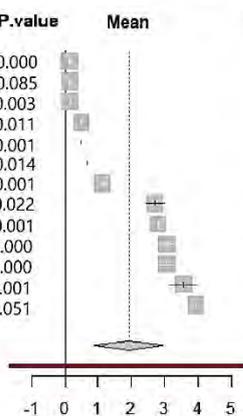
Study	Mean	SD	P-value	Mean	MRAW	95%-CI	Weight
Killen et al. 2018	0.35	0.278	0.001		0.35	[0.27; 0.43]	25.0%
Metcalfe 1995	0.58	0.020	0.025		0.58	[0.58; 0.58]	25.0%
Reid et al. 2012	1.70	0.050	0.001		1.70	[1.68; 1.72]	25.0%
Sloat & Reeves 2014	1.70	0.030	0.001		1.70	[1.62; 1.78]	25.0%



1.32 [-0.06; 2.23] 100.0%
[-2.37; 4.54]
 $p = 0.008$

SMR and Boldness

Study	Total	Mean	SD	P-value
Herrera et al. 2014	23	0.14	0.1000	0.000
Hansen et al. 2020	24	0.16	0.0100	0.085
Urbina et al. 2011	36	0.16	0.0100	0.003
Petersen & Petersen 1990	13	0.50	0.0100	0.011
Krause et al. 2000	21	0.50	0.0000	0.001
Behrens et al. 2019	9	0.68	0.0000	0.014
Killen et al. 2011	39	1.14	0.3000	0.001
Fischer 2000	12	2.71	0.5000	0.022
Ruxton et al. 2000	20	2.80	0.0500	0.001
Tan et al. 2020	63	3.07	0.9000	0.000
Tan et al. 2020	63	3.07	0.9000	0.000
Fischer 2000	12	3.57	0.7500	0.001
Killen et al. 2012	23	3.94	0.0100	0.051

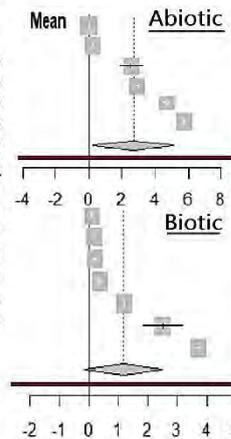


MRAW	95%-CI	Weight
0.14	[0.10; 0.18]	9.1%
0.16	[0.15; 0.16]	9.1%
0.16	[0.15; 0.16]	9.1%
0.50	[0.49; 0.51]	9.1%
0.50		0.0%
0.68		0.0%
1.14	[1.04; 1.23]	9.1%
2.71	[2.43; 2.99]	9.0%
2.80	[2.78; 2.82]	9.1%
3.07	[2.84; 3.29]	9.1%
3.07	[2.84; 3.29]	9.1%
3.57	[3.14; 3.99]	8.9%
3.94	[3.94; 3.94]	9.1%
1.93	[0.91; 2.94]	100.0%

Random effects model
Prediction interval
Heterogeneity: $t^2 = 2.277$, $p = 0.090$

Stressor

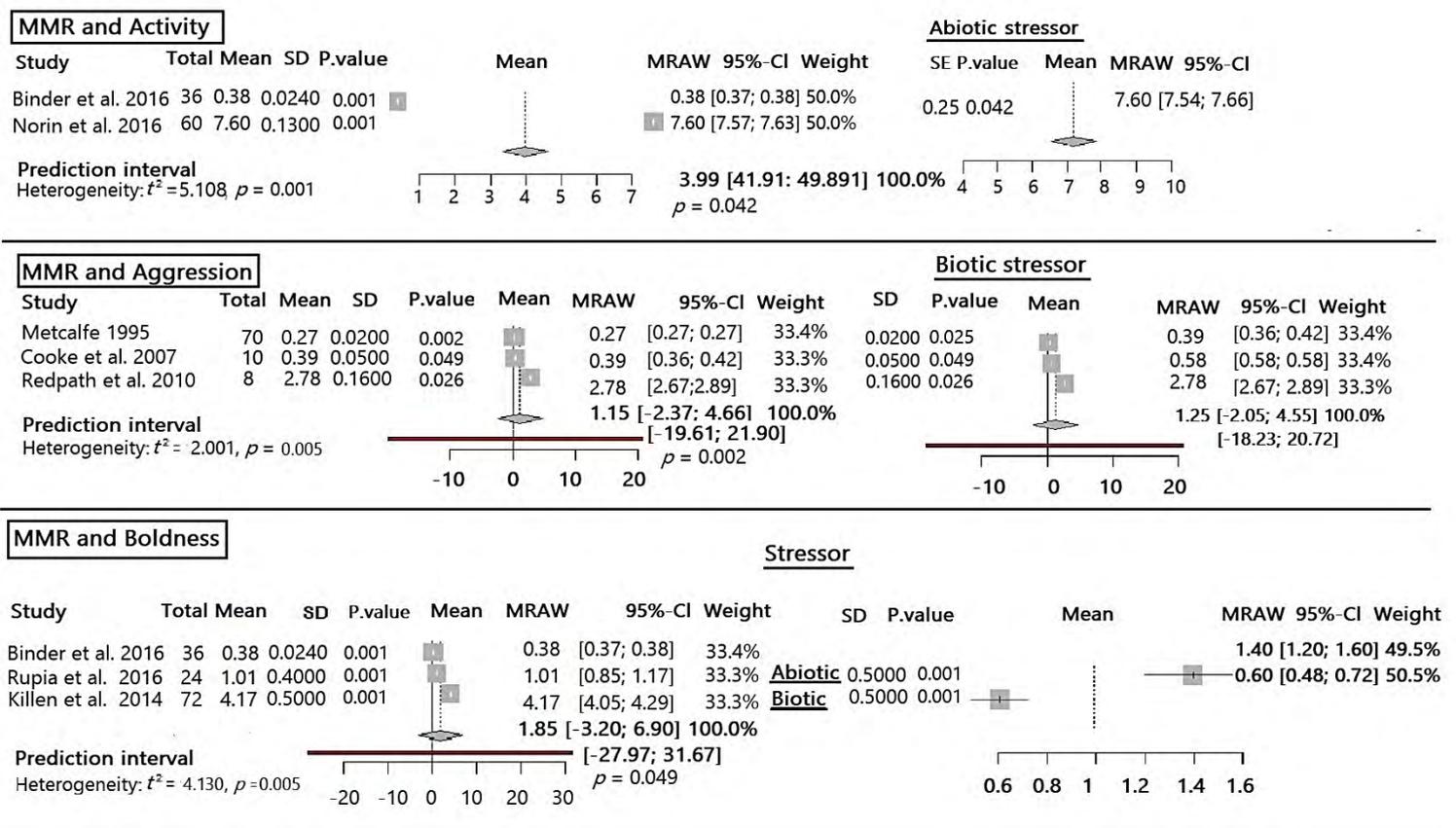
Mean	SD	P-value	MRAW	95%-CI	Weight
0.01	0.0100	0.001	0.01	[0.00; 0.01]	16.7%
0.23	0.23	0.016	0.23	[0.23; 0.24]	16.7%
2.55	1.85	0.001	2.55	[1.85; 3.25]	16.3%
2.94	2.83	0.008	2.94	[2.83; 3.04]	16.7%
4.72	4.55	0.797	4.72	[4.55; 4.89]	16.7%
5.74	5.74	0.007	5.74	[5.74; 5.75]	16.7%
2.70	[0.27; 5.13]		2.70	[4.26; 9.66]	100.0%
0.10	0.10	0.001	0.10	[0.10; 0.10]	14.4%
0.17	0.14	0.02	0.17	[0.14; 0.19]	14.4%
0.21	0.16	0.131	0.21	[0.16; 0.27]	14.4%
0.37	0.27	0.032	0.37	[0.27; 0.46]	14.4%
1.20	1.18	0.022	1.20	[1.18; 1.22]	14.4%
2.50	1.81	0.001	2.50	[1.81; 3.20]	13.6%
3.73	3.60	0.032	3.73	[3.60; 3.86]	14.4%
1.17	[-0.14; 2.48]		1.17	[-2.70; 5.05]	100.0%



$p = 0.089$

499 **Figure 1.3(a):** Meta-analysis of studies using physiology (SMR) to predict behavioural performance
 500 parameters. The stressor analysis examines the effect of the stressor on each of these traits and not
 501 necessarily the link between the traits. The meta-analysis included key papers with proxies for certain
 502 metrics (i.e. weight loss for minimum energy requirements; Ruxton et al. 2000).

503 Several studies have linked SMR to aggression, predator avoidance and foraging behaviour,
 504 but few have examined the influence of maximum metabolic rate (MMR; the rate at which an
 505 animal oxidizes metabolic substrates to produce the energy required to maintain homeostasis
 506 in a state of maximum locomotor activity; Portner et al. 2007) on individual behaviour despite
 507 the general recognition that aggressive behaviour in fishes is related to the capacity for intense
 508 exercise (i.e. Jonas et al. 2010; Killen et al. 2014; Binder et al. 2016, Rupia et al. 2016; Figure
 509 1.3b). We found significant differences in the maximum metabolic rate in bold and timid
 510 behavioural types ($df= 5, p < 0.005$), however studies on this topic were sparse (Figure 1.3b).
 511

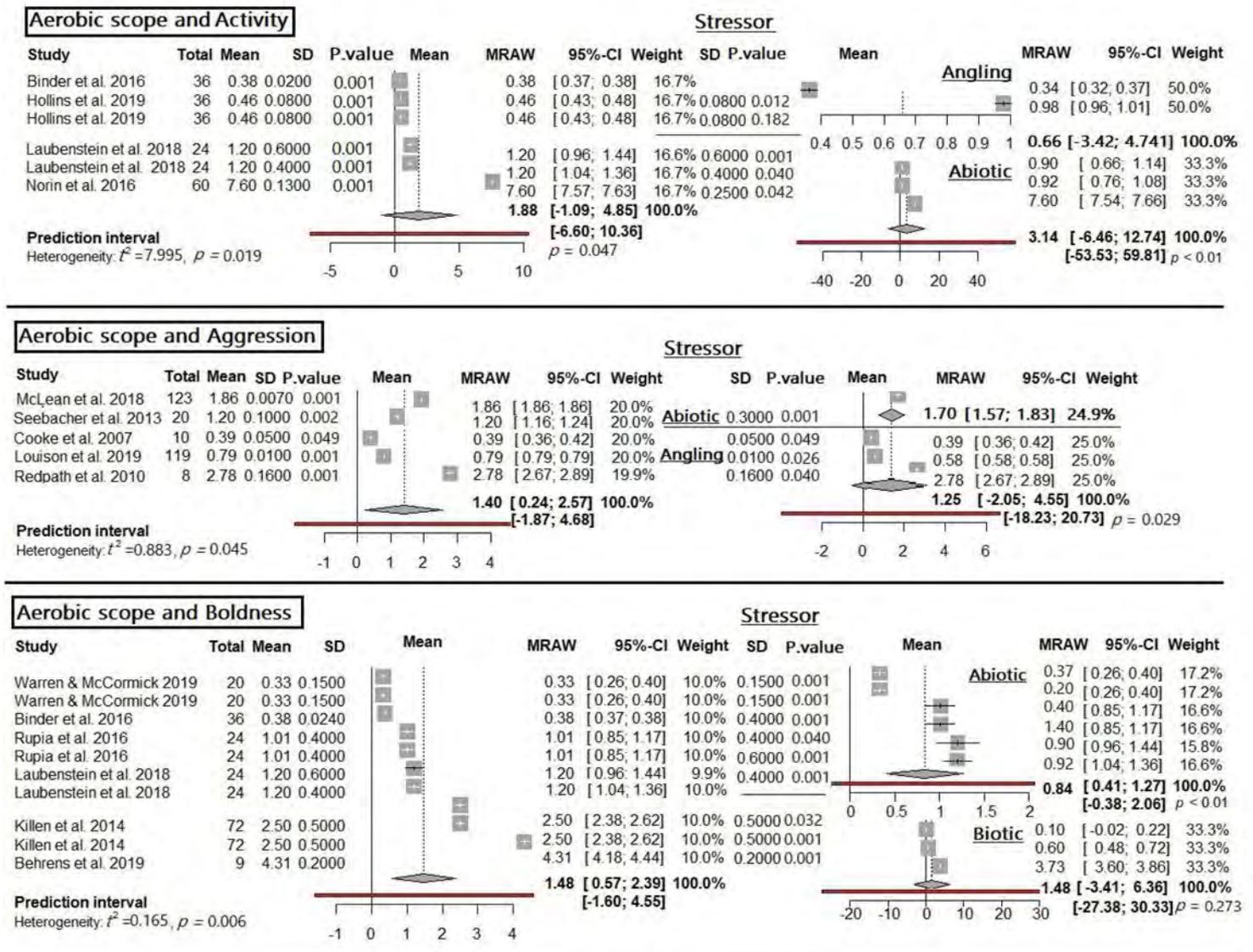


512 **Figure 1.3 (b): Meta-analysis of studies using physiology (MMR) to predict behavioural**
 513 **performance parameters. The stressor analysis examines the effect of the stressor on each of**
 514 **these traits and not necessarily the link between the traits.**

515

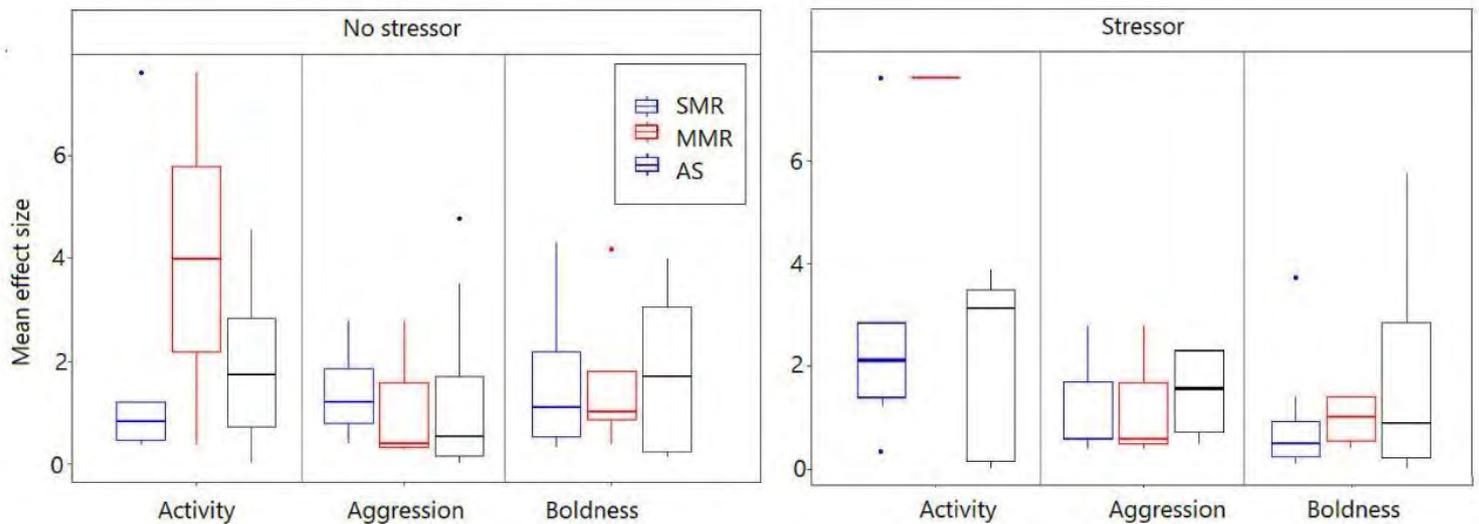
516 Similarly, there has been little focus on the influence of aerobic scope (the potential to increase
 517 the rate of oxygen uptake defined as the difference between SMR and MMR; Halsey et al.
 518 2018) on individual behaviour (bold vs timid; as classified through a series of multi-trait
 519 behavioural tests), despite the positive relationship between aerobic scope and feeding and

520 aggression (Biro et al. 2010; Seebacher et al. 2013; Auer et al. 2014; Killen et al. 2014; Rupia
 521 et al. 2016; McLean et al. 2018. See Figure 1.3c). However, dominance has been positively
 522 related to aerobic scope, with indirect links to SMR. Our meta-analysis showed that bold fish
 523 had a significantly higher aerobic scope ($df = 9, p < 0.006$; Figure 1.3c), attributed to a high
 524 SMR and significantly higher MMR ($df = 2, p < 0.005$; Figure 1.3b), relative to timid fish.
 525



526 **Figure 1.3(c): Meta-analysis of studies using physiology (Aerobic scope) to predict behavioural**
 527 **performance parameters. The stressor analysis which examines the effect of the stressor on each**
 528 **of these traits and not necessarily the link between the traits (i.e. Warren and McCormick**
 529 **2019). The meta-analysis included key papers with proxies for certain metrics (i.e. swimming**
 530 **performance for aerobic scope; Louison et al. 2019).**
 531

532 The upper aerobic scope, or MMR, of personality types may differ based on biogeographic
533 zone. Although we found no significant differences in the metabolic rates of bold and timid
534 fish amongst biogeographic zones ($df = 49$; $p = 0.06$; Table 1.1), we could not statistically
535 compare the links between metabolic physiology and behaviour in tropical versus temperate
536 fishes due to the limited studies available on temperate fishes ($n = 3$). However, these reviewed
537 studies suggest that there may be differences in the steepness of aerobic scope curves in fishes
538 from temperate and tropical biogeographic zones. For example, tropical Ambon damselfish
539 (*Pomacentrus amboinensis*) individuals with a broad aerobic scope (i.e. a greater difference
540 between MMR and SMR) had a competitive dominance over their conspecifics (Killen et al.
541 2014; Warren and McCormick 2019). The mechanism behind these links are unclear as this
542 coral reef fish did not reach MMR following aggressive encounters (Killen et al. 2014). This
543 is unlike the temperate freshwater eastern mosquito fish (*Gambusia holbrooki*) where MMR
544 can be reached through aggressive behaviour, potentially occupying the whole aerobic scope
545 (Seebacher et al 2013). It appears that fishes from relatively stable tropical regions may
546 maximize performance (maintaining high rates of activity and seldom reach MMR; Killen et
547 al. 2014) at extreme temperatures through a steeper aerobic scope slope (Clark et al. 2017;
548 Neubauer and Anderson 2019), relative to temperate fishes. However, much of the research
549 assessing links between aerobic scope and behaviour has focussed on coral reef fishes (e.g.,
550 Biro et al. 2010; Seebacher et al. 2013; Killen et al. 2014). Up until 2020, there was little
551 information on linked metabolic physiological and behavioural traits in temperate fishes and
552 temperate coastal reef fishes in particular. Temperate fishes are likely to require a broader
553 aerobic performance window to tolerate a greater range of thermal variability (Neubauer and
554 Anderson 2019). It is imperative to compare metabolic and behavioural data on numerous fish
555 species from various biogeographic zones, where fishes may experience differences in the
556 extent of external stressors on metabolic and behavioural traits (Figure 1.4).



558 **Figure 1.4: The relationship between metabolic and behavioural traits, with and without**
 559 **stressors.**

560

561

562 The meta-analysis showed that abiotic, biotic and angling stressors impact the relationship
 563 between metabolism and behaviour differently. Biotic stressors did not significantly affect the
 564 relationship between physiological and behavioural traits in fishes overall ($df = 10$, $p = 0.47$;
 565 Table 1.1), but aggression during competitive interactions was linked to a significantly higher
 566 SMR ($df = 22$, $p = 0.008$; Figure 1.3a) and MMR ($df = 2$, $p = 0.002$; Figure 1.3b). Abiotic
 567 stressors had a significant influence on linked physiological and behavioural traits ($df = 33$, p -
 568 val = 0.007; Table 1.1). For example, bold individuals showed a significant increase in
 569 metabolic rate with environmental stress (i.e. temperature, salinity, hypoxia; $df = 33$, p -val
 570 < 0.001 ; Table 1.1), while metabolic rate decreased in timid individuals (p -val < 0.001). Overall,
 571 the use of metabolic physiology to predict behavioural performance parameters has only been
 572 applied to 21 fish families. Such information is important as the selective removal of bold
 573 individuals through angling ($df = 6$, p -val = 0.04, Table 1.1; e.g., Suski and Philipp 2004, Alos
 574 et al. 2012) could therefore affect the distribution of metabolic physiological traits within a
 575 population.

576

577

578

579 **1.4 Discussing the link between physiological and behavioural phenotypes**

580

581 It was evident from the reviewed literature that the causal links between animal behavioural
582 traits (bold vs timid) and metabolic physiology are poorly understood. However, internal
583 physiological mechanisms appear to underpin behavioural responses (as indicated by several
584 seminal studies by von Holst 1936, Hassenstein and Reichardt 1956, Tinbergen 1963). For
585 example, electrophysiological impulses from the central nervous system (CNS) control the
586 direct expression of activity, behavioural co-ordination (i.e. impulses from statoliths control
587 behavioural equilibrium in fishes; Von Holst and Mittelstaedt 1950) and rhythmic locomotor
588 patterns of movement; all of which constitute the classification of animal personality (Von
589 Holst 1936, Hassenstein 1956). Modern research has shown that physiological traits, such as
590 energy metabolism, may be key drivers of animal personalities, which, in turn, drives
591 intraspecific variability in stress responses and activity (Schjolden et al. 2005; Careau et al.
592 2008; Biro and Stamps 2010). Furthermore, there are studies that link mitochondrial function
593 to whole-animal metabolic rate. For example, Norin and Malte (2012) found that intraspecific
594 variation in both SMR and (to a lesser extent) MMR in brown trout were positively correlated
595 with the activity of two key aerobic mitochondrial enzymes (cytochrome C oxidase and citrate
596 synthase). This was suggested to have an impact on aerobic performance, activity and stress
597 recovery. Differences in energetic demands imposed by the metabolic rate of an individual may
598 promote aggressive activity that may assist in the acquisition of resources (i.e. food or mates;
599 Cutts et al. 2001); although aggressive activity is itself energetically costly. Heritable energetic
600 and behaviour traits have been shown to covary predictably; and this is most likely because
601 energetic demands can constrain behaviour (Careau et al. 2008; Killen et al. 2014).

602 Individuals differ in the expression of energetic and behavioural traits and this is thought to be
603 partially controlled by the genotype (Coleman and Wilson 1998; Thomas et al. 2001;
604 Scantlebury et al. 2007; Chown et al. 2010, Zou et al. 2021). Several authors have suggested
605 that environmental heterogeneity can act to increase variability in physiological (i.e. high or
606 low performance) and behavioural (bold vs timid) traits (Bolnick et al. 2003; Parmesan 2006;
607 Careau et al. 2008; Williams 2008; Chown et al. 2010; Metcalfe et al. 2016). Variation in
608 minimum metabolic rates (SMR or RMR) differs amongst populations, but this variation is 20-
609 fold greater between individuals within a population (Meagher and Connor 2001; Thomas et
610 al. 2001; Mathias et al. 2006; Scantlebury et al. 2007; Careau et al. 2008). Furthermore, there
611 is also a high degree of variability in behavioural traits, whereas there tends to be less variability

612 in mechanistic physiological traits; however both physiological and behavioural traits fall
613 along a continuum of variation (Sih et al.2004, Meagher and Connor 2001; Thomas et al. 2001;
614 Mathias et al. 2006; Scantlebury et al. 2007; Careau et al. 2008). Although variation in
615 behaviour and metabolic traits has been established, studies aiming to understand the link
616 between the two are still scarce, particularly as to how fisheries may select for coupled
617 behavioural and metabolic trait groups.

618

619 One of the reasons for the lack of understanding of the link between fish behaviour and
620 metabolic physiology may be the considerable behavioural variability within populations
621 (Neubauer and Anderson 2019). Physiologists often interpreted individuals with unusual
622 behaviour as outliers and excluded them from respirometry trials (e.g., hyperactivity or restless
623 behaviour; as suggested by Metcalfe et al. 2016). This practice has reduced our understanding
624 of the mechanisms linking fish metabolic physiology and behaviour and has reduced our
625 quantification of individual variability in the responses to stressors, which may be linked to
626 personality (or otherwise termed behavioural syndrome – an intrinsic, repeatable individual
627 attribute; Sih et al. 2004; Reale et al. 2007; Careau et al. 2008; Metcalfe et al. 2016; Neubauer
628 and Anderson 2019).

629

630 Another potential reason for our lack of understanding of the link between fish behaviour and
631 metabolic physiology is that animal personality influences both daily energy expenditure and
632 biological fitness, which may explain why these two latter measures are weakly correlated to
633 metabolic rate without accounting for animal personality (Careau et al. 2008). Very recently,
634 researchers have begun to qualify animal personality (bold *vs* timid, i.e. bold with coupled
635 traits of aggression, high exploratory activity and a low stress response; *vs* timid and passive
636 with a high stress response) and its relationship with energetics and metabolism. Despite the
637 lack of directed research, it has been proposed that behaviours such as aggression and
638 exploration are energetically costly and are expected to be correlated with individual variation
639 in metabolic phenotype (Careau et al. 2008; Killen et al. 2011; Killen et al. 2012; Rupia et al.
640 2016; Biro et al. 2018; Neubauer and Anderson 2019). A greater understanding of the links
641 between animal behaviour and metabolic physiology is thus needed to understand the
642 evolutionary importance of individual variation in metabolism as a means for adaptation to
643 climate and exploitation stressors.

644

645 Environmental variation can separate individuals into low and high performance phenotypes.
646 For example, Neubauer and Anderson (2019) showed that high performers in relatively stable
647 environments (e.g., the tropics or polar regions) are most likely to maximize performance at
648 extreme stressors through a steep aerobic scope (e.g., a narrow range between SMR and MMR,
649 but a higher peak in maximum performance at relevant temperatures; Chown et al. 2010;
650 Neubauer and Anderson 2019). However, in heterogeneous temperate environments, high
651 performers may have a broader aerobic performance window (low SMR and high MMR;
652 Portner et al. 2007; Portner et al. 2008; Clark et al 2013). High performers in temperate
653 environments have broader tolerance ranges and are able to quickly recover from external
654 stressors through their low metabolic costs and ability to sustain activity across changing
655 conditions (Auer et al. 2015; Holt and Jorgensen 2015; Norin et al. 2015; Metcalfe et al. 2016;
656 McLean et al. 2018; Pörtner et al. 2018). In contrast, low performance individuals may
657 experience extended periods of physiological stress, which may have lethal and sub-lethal
658 consequences, such as reducing the energy available for reproductive fitness (Portner and
659 Knust 2007). High performance metabolic phenotypes (HPMP) have also been linked to a
660 number of fitness measures, including greater stress recovery (e.g., to a parasite load),
661 competitive ability or social rank (which influence mate choice), and activity (e.g., exploratory
662 behaviour, migratory ability and habitat selection; McNab 2002; Careau et al. 2008) (See Table
663 1.1). Environmental heterogeneity may favour high performance phenotypes with a greater
664 energetic capacity for stress tolerance, adaptive behaviour and high fitness potential (McNab
665 2002; Careau et al. 2008; Pörtner et al. 2018; Neubauer and Anderson 2019).

666

667 In terms of mechanisms, research on fishes suggests that the correlation between energy
668 metabolism and animal personality may be attributed to the shared hormonal control via the
669 hypothalamic-pituitary (HPI) axis, which is responsible for regulating both metabolism and
670 stress responses (Archard et al. 2012; Aubin-Horth et al. 2012). Along this axis, the
671 pleiotrophic effect of glucocorticoid receptors may explain the inverse link between cortisol
672 and exploratory activity. For example, in threespine sticklebacks (*Gasterosteus aculeatus*),
673 bolder, exploratory individuals (this suite of behaviours is termed proactive at the population
674 level; Sih et al. 2004) exhibited low HPI hormonal stress responses and high sympathetic
675 activity (Aubin-Horth et al. 2012). Based on this finding, it is possible that bolder individuals
676 in a population are more likely to rapidly recover from a stressor.

677

678 From an evolutionary perspective, the role that genetics plays in determining the characteristics
679 of this suite of physiological and behavioural phenotypic traits in relation to the HPI axis is
680 important, given that selection for a high metabolic rate may promote selection for exploration
681 and aggression (Tinbergen 1963; Barrett et al. 2013; Careau et al. 2008; Archard et al. 2012).
682 This may have consequences for fish populations as individuals exhibiting bold behaviour and
683 high levels of activity may provide the potential to colonize new habitats and recover from
684 climate stressors (Careau et al. 2008; Archard et al. 2012).

685

686 **1.4.1 The relevance of the links between metabolic physiology and behaviour in the** 687 **Anthropocene**

688 Understanding physiological tolerance and behaviour is important in predicting the response
689 of fishes to human impacts including environmental toxicity (Scott and Sloman 2004), climate
690 change (Killen et al. 2014) and overexploitation (Duncan et al. 2019). Behaviour and
691 physiology also determine the adaptive response to ecological stressors, such as those
692 encountered in novel environments (Romero et al. 2009; Tudorache et al. 2013) or via
693 predation (Bell and Sih 2007; Metcalfe et al. 2016). Individuals with high performance
694 phenotypes and a broad aerobic scope may have a greater energetic capacity to tolerate a
695 broader range of stressors and facilitate rapid recovery. In a study on zebrafish *Danio rerio*,
696 the dominant individuals had lower cortisol levels in novel environments (Tudorache et al.
697 2013). Martins et al. (2011) found that *Oreochromis niloticus* with lower cortisol levels
698 recovered faster when exposed to novel objects when compared to their subordinates.
699 Similarly, dominant or aggressive individuals had greater oxidative stress recovery responses
700 when exposed to heavy metal toxicity (Scott and Sloman 2004; Almeida et al. 2009), as well
701 as faster recovery following intensive exercise, rapidly resuming normal foraging and anti-
702 predation behaviour (Killen et al. 2014). Fishes with high performance metabolic phenotypes
703 may also have a greater thermal tolerance capacity (Pörtner et al. 2018; Duncan et al. 2019).
704 Thus, although high performance metabolic phenotypes may have a competitive advantage in
705 a changing climate, it is likely that they may, as a consequence of their behavioural attributes,
706 be more susceptible to exploitation (Suski and Philipp 2004; Cooke et al. 2007; Clark et al.
707 2017; Huntingford et al. 2010; Redpath et al. 2010; Duncan et al. 2019; Louison et al. 2019).
708 In the first subsection to follow, we discuss the impact of environmental change on fished

709 populations of the Anthropocene. Secondly, we discuss how exploitation may exacerbate the
710 effects of environmental stressors on fished populations.

711

712 *1.4.1.1 The impact of Anthropogenic environmental change*

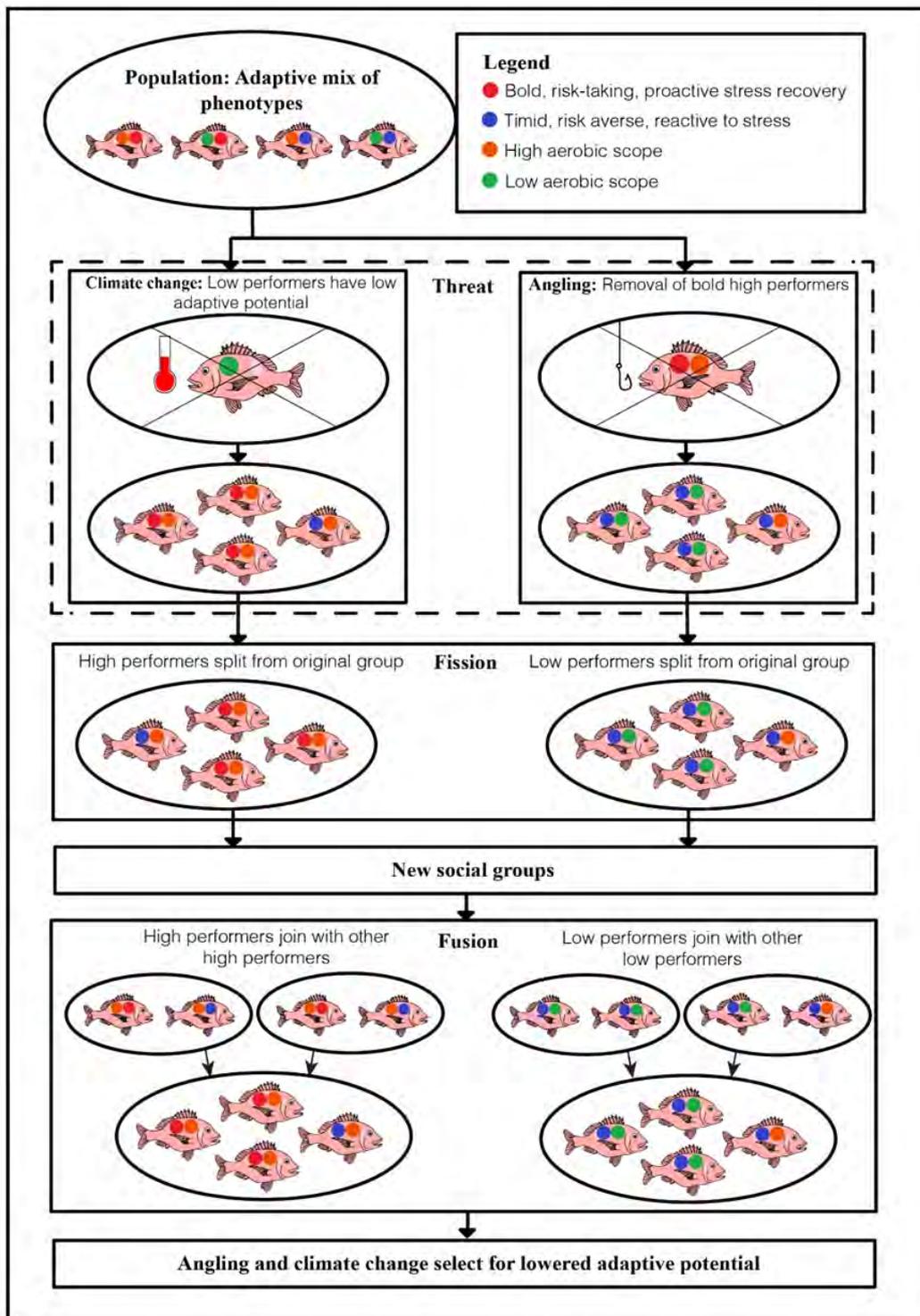
713

714 To assess the responses of fishes to impacts associated with the Anthropocene, it is necessary
715 to understand the impact of various stressors on a range of physiological and behavioural
716 phenotypes (Bell and Sih 2007). Environmental stressors have received the main focus in the
717 literature as they may mediate the relationship between behaviour and metabolic physiology
718 Killen et al. (2013) suggested that the relationship between behaviour and metabolic
719 physiology may be accentuated under moderate stressors or masked under severe stressors.
720 This review revealed that there was a significant positive relationship between SMR and
721 territorial behaviour in populations subjected to biotic stressors (21% of reviewed studies
722 examined such stressors; the effects of stressors on SMR are visible in Figure 1.4), such as high
723 conspecific density (Cockrem 2007; Reid 2012). Other biotic stressors, such as food shortages
724 or high rates of predation, have been found to influence the metabolic rate and risk-taking
725 behaviours associated with foraging (Ruxton et al. 2000; Killen et al. 2011). In contrast,
726 stressors such as hypoxia (Killen et al. 2012), or toxicants (i.e. heavy metals or chemical
727 pollutants) have been observed to mask aggressive behaviour (Kolok et al. 2002). Dominance
728 and activity have been correlated with the maximal metabolic rate (MMR) of fishes in
729 thermally variable conditions (Killen et al. 2014). However, the relationship between
730 behavioural exploratory activity and MMR decreases at extreme temperatures where even bold
731 and active individuals may not express these traits (Chappel et al. 2004; Killen et al. 2013).
732 Killen et al. (2011, 2012) examined changes to both behaviour and metabolic physiology under
733 the same stressor and then measured these changes under different severities of the stressor
734 (Killen et al. 2013). They found that juvenile European bass *Dicentrarchus labrax* with a high
735 metabolic rate increased risk-taking behaviour as food became scarce or as hypoxic conditions
736 intensified. It appears that environmental change may increase the diversity of aerobic scope
737 and behavioural phenotypes expressed, on which natural selection can act (Killen et al. 2013;
738 see Figure 1.5).

739

740

741



742

743 **Figure 1.5: The fission or fusion of social groups is expected in the Anthropocene as climate**
 744 **change and angling have coupled effects on the selection for metabolic and behavioural traits.**
 745 **Fission or fusion of social groups is expected to be common under environmental change as**
 746 **metabolic costs are altered, excluding individuals without the aerobic capacity for behavioural**
 747 **change. However, fisheries may act to remove the fittest individuals with metabolic and**
 748 **behavioural traits needed for climate resilience. (This figure was produced in collaboration with**
 749 **graphic artist, Carys C. Bailey).**

750 To date, research assessing the relationship between fish behaviour and aerobic scope in the
751 context of environmental change is limited. This is concerning given its relevance in the context
752 of climate change and increasing levels of exploitation. For example, high performance
753 individuals with the energetic capacity, likely provided by a broad aerobic scope, may have
754 greater tolerance to stressors and potential for adaptive behaviour (Biro et al. 2018; Pörtner et
755 al. 2018) yet appear to be more vulnerable to capture. Differences in the aerobic scope
756 responses to environmental change by different behavioural types has not been tested apart
757 from a study by Rupia et al. (2016), who found that fish with bold and timid behavioural
758 phenotypes exhibited different metabolic responses across a salinity gradient. Thus, the
759 relationship between fish behaviour and aerobic scope remains a considerable research gap.
760 However, according to the plastic floors and concrete ceilings hypothesis, basal energy
761 requirements (SMR) are thermally plastic, while maximum capacities (MMR) are less flexible
762 (Sandblom et al. 2016). Hence, if we can understand how a stressor affects SMR or MMR, or
763 both, then we can understand the effect of a stressor on aerobic scope and behavioural
764 plasticity.

765

766 Individual behavioural plasticity has been researched and it appears that it is likely determined
767 by the intraindividual variation in behaviour over time (Careau et al. 2008; Biro et al. 2018).
768 There is no research linking individual behavioural plasticity to aerobic scope in fishes,
769 however, Biro et al. (2018), using a rodent dataset, found that individuals with a greater aerobic
770 scope had broader behavioural plasticity (i.e. the ability to adjust behaviour and sustain activity
771 across a range of stressors). With this in mind, the response of individuals to climate stressors,
772 such as thermal variability, will be difficult to predict without an understanding of the
773 behavioural plasticity of the individual and this should be tested in both constant and changing
774 energetic conditions (Metcalf et al. 2012; Biro et al. 2018; Pörtner et al. 2018).

775

776 The energetic consequence and adaptive value of individual behaviour will determine whether
777 these behavioural traits will be selected for at the population level (Killen et al. 2013).
778 Tinbergen (1963) proposed that metabolic physiology is an important proximate mechanism
779 constraining the evolution of adaptive behaviour. Aerobic metabolic physiology has been
780 found to determine the extent of locomotor performance, and it is likely that high performance
781 individuals have the locomotor capacity for behavioural adaptation (Barrett et al. 2013;
782 Seebacher and Krause 2017). These individuals can maintain high swimming speeds and
783 respond rapidly to escape threatening stimuli, while maintaining these high rates of

784 performance across broad environmental tolerance ranges (Killen et al. 2017). Generalists, with
785 the aerobic capacity to adjust behaviour, are most likely to be selected for under environmental
786 heterogeneity (Parmesan 2006; Biro et al. 2018; Pörtner et al. 2018). These high performance
787 individuals will typically dominate leading shoal positions with the greatest access to resources
788 (i.e. food or mates). Furthermore, their broad aerobic capacity may facilitate adaptive dispersal
789 or migratory behaviours (Warnock and Rasmussen 2014; Seebacher and Krause 2017; Pörtner
790 et al. 2018).

791

792 The maintenance of individuals with broader aerobic capacity will allow fish populations to
793 adjust their behaviour and will determine the adaptive potential of a population (Seebacher and
794 Krause 2017; Pörtner et al. 2018). Should individuals within a population lack the aerobic
795 capacity to alter behaviour (i.e. maintain high rates of performance across broad tolerance
796 ranges), environmental change may cause fission amongst population members (i.e. the
797 separation of social groups; Killen et al. 2017; Seebacher and Krause 2017) (Figure 1.5). For
798 example, in shoaling species, it is likely that individuals with similar aerobic phenotypes will
799 shoal together, enabling members to remain within the shoal by maintaining similar swimming
800 speeds and sharing similar metabolic costs within the environment (Nadler et al. 2016, Killen
801 et al. 2017; Seebacher and Krause 2017). Fission or fusion (i.e. regrouping to form new social
802 groups) of social groups is expected to be common under environmental change as metabolic
803 costs are altered, excluding individuals without the aerobic capacity for behavioural change
804 (Killen et al. 2017; Seebacher and Krause 2017) (See Figure 1.5). Understanding the link
805 between metabolic physiology and behavioural plasticity is crucial given that these are likely
806 the most important adaptive responses to climate variability (Pörtner et al. 2018), and that both
807 behavioural and metabolic phenotypes are under selection by fisheries (see Figure 1.5).

808

809 ***1.4.2.2 The impact of exploitation***

810

811 Fishing-induced mortality is thought to aggravate the impact of marine environmental stressors
812 on targeted species (Harley et al. 2006; Hsieh et al. 2008; Vedor et al. 2021) by selecting for
813 particular phenotypes (e.g., smaller body size and earlier maturity, a process named fisheries-
814 induced evolution; Marty et al. 2015) and reducing the genetic potential for adaptation.
815 Fisheries research has focussed on the selection for morphological and life history traits, but
816 there is a need to study the selective nature of fisheries on behavioural and metabolic

817 physiological traits (Uusi-Heikkilä et al. 2008), which determine the responses of fished
818 populations to environmental stressors.

819

820 Vulnerability to fishing has been found to covary with heritable metabolic (Hessenauer et al.
821 2015; Clark et al. 2017; Duncan et al. 2019) and behavioural traits (Suski and Philipp 2004).
822 Duncan et al. (2019) provide the first evidence linking exploitation with thermal metabolic
823 effects. In this study, red roman, *Chrysoblephus laticeps*, that were captured from a wild
824 exploited population exhibited a reduction in physiological performance (i.e. reduced aerobic
825 scope, which was measured using respirometry) and tolerance to temperature variability, in
826 comparison to a wild protected population. Furthermore, the exploited population had lower
827 metabolic phenotype diversity relative to the protected population. This was attributed to the
828 increased likelihood of the capture of the physiologically fittest fish by the commercial and
829 recreational hook and line fishery. Indeed, fish with bold personalities may have a greater
830 reproductive output and migratory potential (see section above), and are known to be more
831 susceptible to passive fishing gears (i.e. stationary gear where capture is dependent on the
832 movement of fishes towards the gear), and in particular, hook and line (Figure 1.4) (Biro and
833 Post 2008; Careau et al. 2008; Alos et al. 2012; Sutter et al. 2012). For example, Alos et al.
834 (2012) suggested that bold, active fish may be more susceptible to capture in gillnets. This
835 study used *in situ* fish behaviour from telemetry data and created an individual-based model to
836 simulate the trajectory of fish as they encounter fishers within their home range. They found
837 that bold fish with high activity phenotypes (attributed to a high metabolic rate) and larger
838 home ranges are more likely to encounter and be captured by angling gear; which is in
839 agreement with several other studies (Suski and Philipp 2004; Cooke et al. 2007; Huntingford
840 et al. 2010; Redpath et al. 2010, Wilson et al. 2015, Satterfield and Johnson 2020). The removal
841 of these bold aggressive individuals, which are considered to be more effective in protecting
842 their nests and young, is likely to reduce overall population fitness (Suski and Philipp 2004;
843 Cooke et al. 2007). Based on the available research, it appears that passive gears may influence
844 metabolic traits by either direct selection of high-performance metabolic phenotypes or indirect
845 selection of particular metabolic phenotypes most often associated with bold behaviour (Koeck
846 et al. 2019). However, fisheries selection on physiological and behavioural traits may differ
847 depending on fishing gear and environmental conditions (Hollins et al. 2020).

848

849 Although passive gears have been demonstrated to influence the metabolism and behaviour of
850 fishes, the impact of active gears (i.e. gear where capture is determined by chasing the target)

851 on fishes has only recently become apparent. Hollins et al. (2019) found that active trawling
852 gear may select for a decrease in shoal cohesion in the common minnow *Phoxinus phoxinus*
853 by removing slower swimmers with a lower aerobic capacity and lower spontaneous activity.
854 This may have consequences for faster swimmers, which are only less vulnerable to trawling
855 when in shoals with familiar conspecifics. Hence, a reduction in shoal cohesion may ultimately
856 change phenotypic selection by the fishery by increasing the vulnerability of high-performance
857 phenotypes to trawling. Furthermore, a reduction in shoal cohesion may reduce the efficiency
858 of active gears that rely on tight shoaling. Thus, it appears that, regardless of whether fish are
859 targeted in active or passive fisheries, exploitation may reduce the phenotypic variability of
860 fish populations, either by changing shoal cohesion or by removing bold individuals with a
861 high aerobic capacity (Hollins et al. 2020, McLean et al. 2020).

862 While the selection pressures of catch-and-kill fisheries (i.e. whereby fish are harvested for
863 local consumption or commercial use) will not be the same as those that practice catch-and-
864 release fishing (C&R; fish are captured for sport and then returned to the aquatic environment),
865 an understanding of how C&R influences fish behaviour and metabolic physiology is
866 fundamental. Several studies have examined the relationship between C&R and the metabolic
867 physiology and behaviour of fishes (Cook et al. 2007; Danylchuk et al. 2007; Arlinghaus et al.
868 2009; Gale et al. 2013; McLean et al 2020). Cooke et al. (2007) found that fish with bold and
869 active behaviour are more likely to be captured, but the sub-lethal effects following release can
870 be substantial and these may considerably alter behaviour and metabolic physiology (in the
871 short-term). For example, the intense exercise and prolonged air exposure following an angling
872 event can result in high metabolic costs (Cooke et al. 2007; Danylchuk et al. 2007; Arlinghaus
873 et al. 2009; McLean et al. 2020). Recovery may also be delayed in fishes released into waters
874 outside of their thermal optima (Cooke et al. 2005; Gale et al. 2013). These coupled metabolic
875 costs can induce reflex impairment, increasing susceptibility to post release predation, or
876 ultimately cause metabolic collapse (Cooke et al. 2007; Arlinghaus et al. 2009; Gale et al.
877 2013). The sub-lethal effects of catch-and-release fishing can induce mortalities that are
878 comparable to catch-and-kill fisheries when coupled with marine environmental change
879 (Arlinghaus et al. 2009; Gale et al. 2013).

880
881 Fishing pressure has been recognised to exacerbate the vulnerability of fish populations to
882 temperature and pH changes in the marine environment, by reducing genetic acclimation
883 potential (Marty et al. 2015) and phenotype diversity (Harley et al. 2006; Pimentel et al. 2016).

884 Exploitation by angling may reduce the phenotypic diversity of populations by removing bold
885 individuals (Alos et al. 2012), with the aerobic capacity for behavioural change or the potential
886 to shift their metabolic scope (Killen et al. 2017; Seebacher and Krause 2017; Pörtner et al.
887 2018). Hence fishing pressure is likely to select for populations with reduced adaptive capacity
888 to climate stressors and reduced potential for dispersal. Fishes may not persist into the future
889 if they are unable to adapt, particularly if there is limited scope for the expansion of their
890 tolerance ranges or behavioural adaptation (Lewin et al. 2006).

891

892 **1.5 Aims of this thesis**

893 The broad aims of this thesis are to evaluate the link between aerobic scope phenotypes and
894 behavioural plasticity in determining resilience to thermal variability, in the near-threatened
895 linefish species, *Chrysoblephus laticeps*.

896 This aim is addressed in the following chapters:

- 897 • Chapter 1 examines published literature for evidence of the links between behaviour and
898 aerobic metabolic physiology in freshwater and marine fishes using a meta-analysis, and
899 relates this information to the impacts of exploitation and climate change on marine fish
900 populations. The content of this chapter has been published in Reviews in Fish Biology and
901 Fisheries.
- 902 • Chapter 2 discusses the study site and study species (*Chrysoblephus laticeps*).
- 903 • Chapter 3 addresses the susceptibility of exploited species to temperature variability by
904 using respirometry to quantify and compare changes in energy expenditure under
905 temperatures mimicking variations experienced in the home range of the species, and as a
906 result of upwelling or downwelling events.
- 907 • In Chapter 4, high and low performance aerobic phenotypes (characterised in Chapter 3)
908 are related to behavioural syndromes (bold vs timid) of individuals through multi-trait
909 personality tests. To determine different physiological responses amongst behaviour types,
910 the plasticity of behavioural responses under temperature variability is assessed.
- 911 • Chapter 5 examines which combinations of aerobic scope and behavioural phenotypes are
912 likely to be selected for, based on competitive ability and adaptive potential, in a climate
913 variability scenario. To do this, a scenario of food resource competition likely under
914 thermal variability was created. Here, individuals of various phenotype combinations (i.e.

915 bold high performer, timid high performer, bold low performer, timid low performer) were
916 paired according to size in competitive dual feeding contests.

- 917 • Chapter 6 synthesises all data chapters and discusses how a behavioural and physiological
918 based-management approach can be incorporated into current South African policy and
919 management frameworks. The chapter ends off with directions for future research.

920 **Chapter 2**

921

922 **Study area and study species**

923

924 **2.1 Study area**

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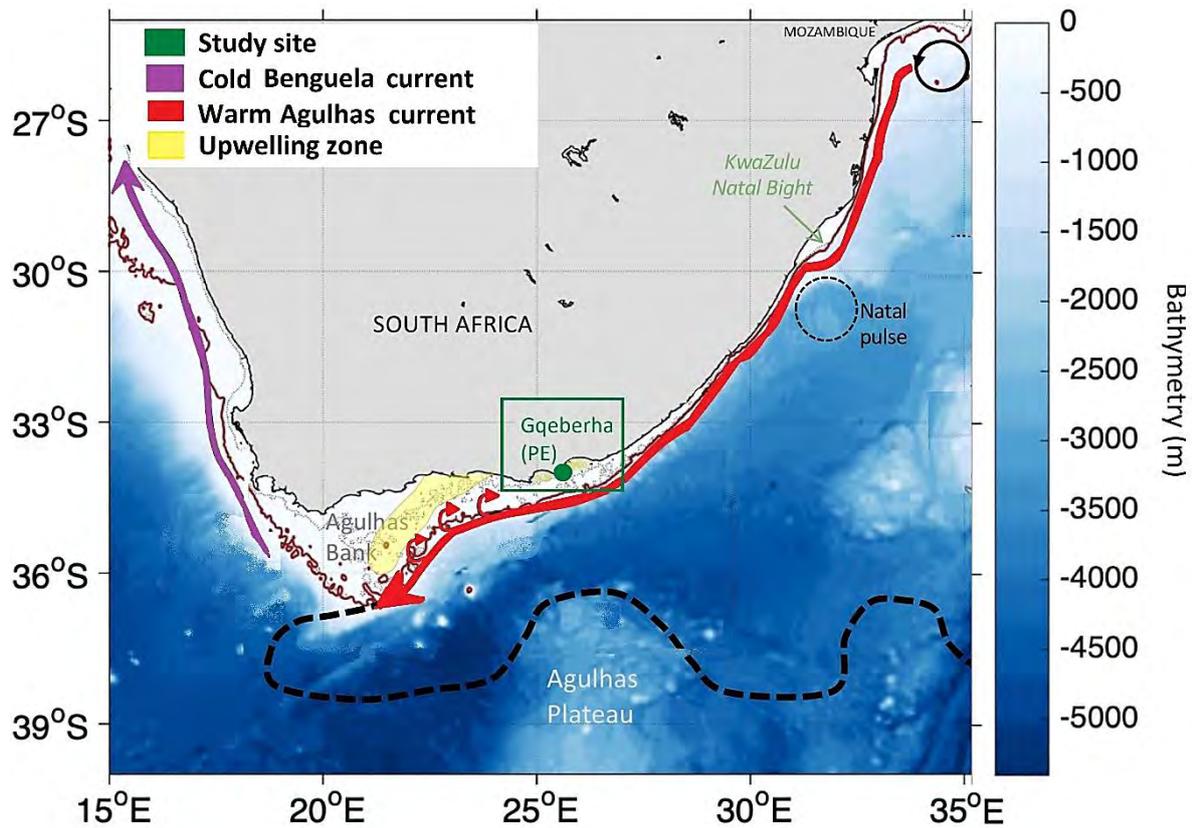
926 **2.1.1 Climate change along the South African coast**

927

928

929 The 3000 km coast of South Africa has four distinct biogeographic zones, a tropical transition
930 zone, a subtropical zone, a warm-temperate zone and a cool-temperate zone (Schlegel and Smit
931 2016). The oceanography of different regions of South Africa's coastline drives the variability
932 in local thermal regimes (James et al. 2013; Potts et al. 2015; Whitfield et al. 2016; Schlegel et
933 al. 2017) (Figure 2.1). The west coast of South Africa is dominated by the cold Benguela
934 Current, while the south and east coasts are dominated by the Agulhas Current (i.e. a western
935 boundary current bringing warmer waters from the Western Indian Ocean; Schlegel et al.
936 2017). The west coast's wide continental shelf broadens further into the Agulhas bank between
937 Cape Town and Gqeberha, before narrowing near east London (except for the Natal Bight, a
938 projection of the continental shelf) (Potts et al. 2015; Schlegel et al. 2017).

939 The warm-temperate south coast of South Africa is a region experiencing increasing thermal
940 variability, and has a larger annual thermal range relative to the cold-temperate west coast and
941 the sub-tropical east coast. The upper end of this thermal variability is attributed to both the
942 strengthening and the warming of Agulhas current on the Agulhas Bank (i.e. which is an area
943 of the continental shelf that widens at the southern tip of the continent; Jackson et al. 2012). In
944 contrast, the lower end of this thermal variability is attributed to the occurrence of cold
945 upwelling zones, some of which are wind-driven, in near shore areas along prominent coastal
946 cape headlands (Schlegel et al., 2017). As such, marine heat waves and cold spells are likely
947 to have the most intensive biological impact on the south coast (Duncan et al. 2019). Indeed,
948 marine heatwaves and marine cold spell events within this warm temperate region are
949 increasing in duration and intensity, relative to those experienced along the cold west coast and
950 sub-tropical east coast (Schlegel et al., 2017).



951

952 **Figure 2.1: The two major currents along South Africa’s coast. The warm Agulhas current moves**
 953 **South-Westwards along the East coast. The cold Benguela current moves Northwards along the**
 954 **West coast.**

955

956 Anthropogenic global change has driven substantial changes in the marine environment,
 957 including increased sea surface temperatures (Rhein et al. 2013; Holt and Jorgensen 2015),
 958 ocean acidification (Collins et al. 2013), hypoxia (Hoegh-Guldbery et al. 2014) and increased
 959 thermal variability. Mean sea surface temperatures have increased by 2 °C since the start of the
 960 century (IPPC 2014). Increases in sea surface temperatures (SST) from remotely sensed data
 961 of up to 0.7 °C have been recorded per decade since the 1980s on the east coast of South Africa
 962 (particularly in the Agulhas Current). In contrast, localized areas of inshore cooling have been
 963 measured along the west and south coasts of South Africa (up to -0.5 °C per decade) during
 964 some parts of the year (Rouault et al. 2009, 2010).

965 Long-term climate change may drive short-term changes in local thermal regimes, particularly
 966 around coastal upwelling zones, for example upwelling is increasing in intensity along the
 967 temperate south coast of South Africa (Duncan et al. 2018). By adversely altering thermal
 968 regimes, global climate change is anticipated to have both broad and localized effects on

969 ecological communities (Bates et al. 2019). Biodiversity is more likely to respond to localized
970 shifts in ocean climate given that these introduce a greater aspect of unpredictability to thermal
971 regimes (Bates et al. 2018; Bates et al. 2019; Duncan et al. 2019). Hence, it is important to
972 understand the effect of localized thermal variability along the coast of South Africa that is
973 ecologically relevant to South Africa's linefish species.

974 The strengthening of the Agulhas current since the 1980's, attributed to the strengthening of
975 trade winds, has likely intensified dynamic upwelling. An increase in upwelling favourable
976 easterly winds has also been linked to seasonal cooling (of up to -0.5 °C per decade) close
977 inshore along South Africa's west and south coasts (Roualt et al. 2009, 2010). (Figure 2.1).
978 Along the south coast, easterly winds (which are more prevalent in summer than winter) along
979 prominent coastal headlands result in surface Ekman transport offshore, which can cause
980 upwelling. Upwelling can cause the temperatures of nearshore areas to rapidly drop as low as
981 12 °C (Goschen and Schumann 1995; Schumann et al. 1995).

982 Research by Schlegal et al. (2017) shows that anomalously warm marine heat waves and cold
983 spells occur at least once annually along South Africa's coast and can persist for five or more
984 days. Marine heat waves occur with the warming of offshore sea surface waters, where the
985 summer thermocline permits sharp changes in water (Schlegal et al. 2017). Light winds, or the
986 presence of a clockwise cyclonic eddy on the Agulhas bank, may drive a small meander of the
987 warm Agulhus Current towards the coast, resulting in a heatwave in coastal waters (while the
988 tailing end of a cyclonic circulation can cause cold upwelling; Schlegal et al. 2017). Onshore
989 Ekman transport can cause the downwelling of warm surface waters, which can result in
990 abnormally high sea temperatures in deeper waters (± 19 m) for one to two days off the coast
991 of South Africa (Schumann 1999).

992

993 Marine heat waves can cause sub-lethal effects in coastal species such as permanent oxidative
994 damage of cardiac tissue (Pichaud et al. 2020), or damage to heat shock proteins at several
995 degrees below lethal temperatures (Iwama et al. 1998). This is concerning as heat waves are
996 expected to occur more frequently off the coast of South Africa with global mean increases in
997 sea surface temperature (Schlegal et al. 2017). Furthermore, it is predicted that ENSO (i.e. El
998 Niño–Southern Oscillation) will increase in strength and drive associated sea temperature
999 variability trends (Bates et al. 2019), including easterly wind-driven cold upwelling events
1000 (Duncan et al. 2018). The increase in thermal variability in South Africa's coastal zone can act

1001 as a barrier to dispersal for migratory species, or limit the optimal thermal condition of resident
1002 fishes (James et al. 2013; Potts et al. 2015; Whitfield et al. 2016).

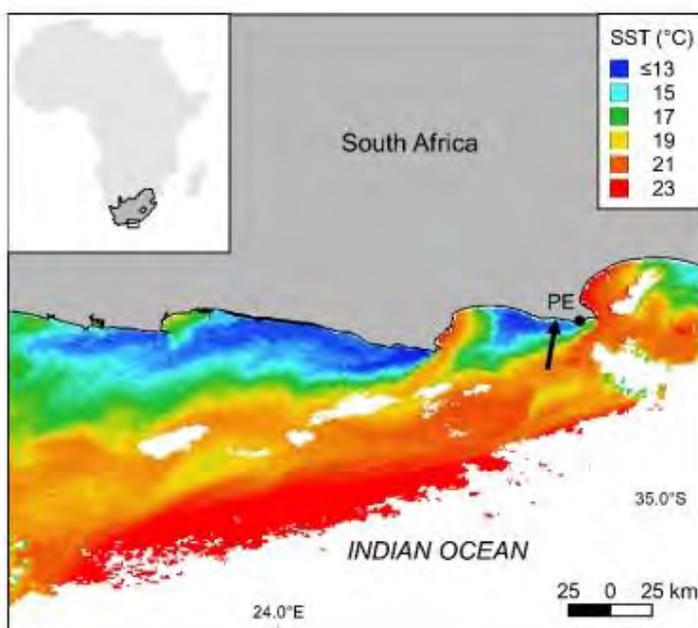
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1004 **2.1.2 Sampling locality**

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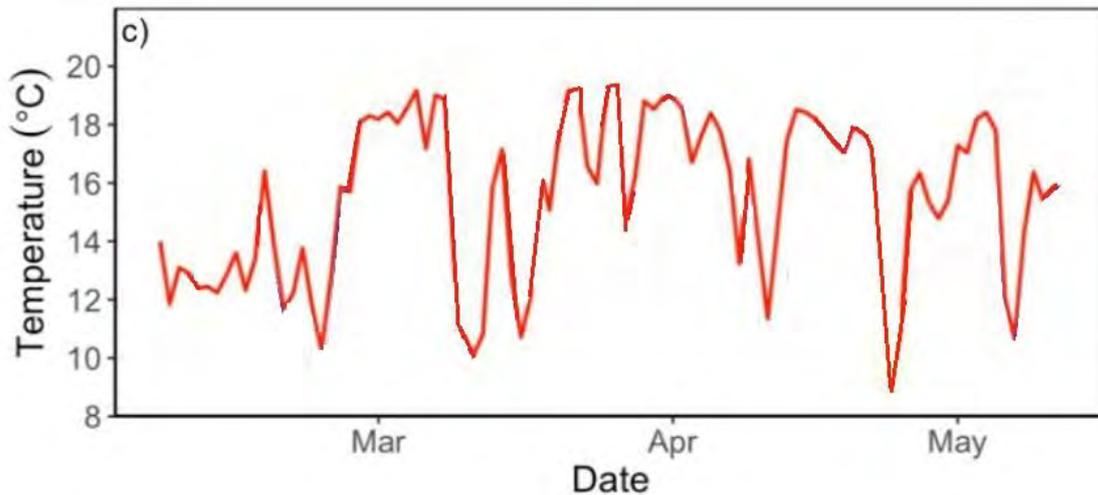
1006 The area offshore of Noordhoek Ski-boat Club (33°58'S 25°38'E; See Figure 2.1 and 2.2) in
1007 Algoa Bay, just outside of Gqeberha metropolitan (previously Port Elizabeth, PE), was the
1008 sampling locality of this study. Algoa Bay has an average Summer minimum sea surface
1009 temperature (SST) of 17.8 °C and an average summer maximum of 23.5 °C. The region has an
1010 average winter minimum SST of 14.6 C and average winter maximum SST of 19.9 °C.
1011 Noordhoek extends along an exposed Cape headland and falls within a dynamic upwelling
1012 region (Figure 2.2). This region experiences localized sea temperature variability owing to
1013 wind-driven upwelling along these prominent coastal headlands (Schumann et al. 2005). Here,
1014 the summer thermocline (reaching an average annual summer maximum of of 23.5 °C in Algoa
1015 Bay at 5 m depths; Smit et al. 2013; Figure 2.2) permits sharp changes in temperature when
1016 followed by an upwelling event (see Figure 2.3 in Duncan et al. 2018). For example, an
1017 upwelling event can cause low temperatures of 11 °C in the Gqeberha region for a one to four-
1018 day period (Goshen and Schumann 1995, Schumann et al. 1995; Schumann 1999; Schumann
1019 et al. 2005; Duncan 2018) (See the annual thermal regime for Algoa Bay in Figure 2.3.).
1020 Duncan et al. (2018) found that these these extreme cold events cause a cold-shock induced
1021 transition to anaerobic metabolism in red roman.

1022



1023
1024

1025 **Figure 2.2: Map of the sampling area of Algoa Bay in Gqeberha (previously Port Elizabeth;**
1026 **PE), South Africa. Colours are MODIS Terra satellite sea surface temperatures depicting an**
1027 **upwelling event on 04-03-2010 taken from Smit et al. (2013). Black arrow indicates the study**
1028 **sampling site west of PE.**

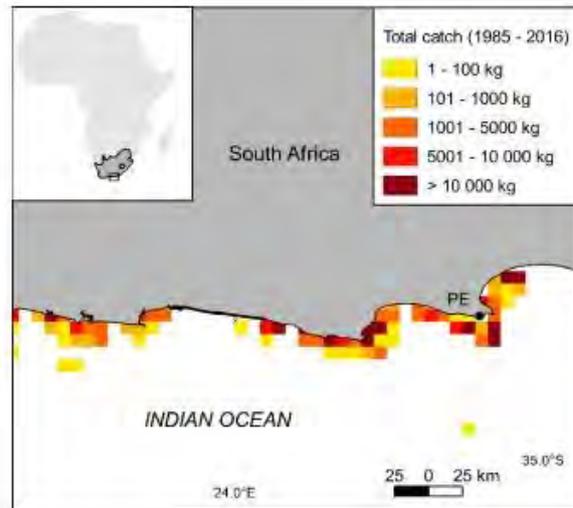


1029 **Figure 2.2: Average daily sea temperature data collected from underwater temperature**
1030 **recorders (14 m) at Noordhoek, Algoa Bay in 2018 (from Skeeles 2019).**

1032
1033

1034 **2.2 *Chrysoblephus laticeps* as a model species to assess how behavioural and** 1035 **physiological traits influence resilience to thermal variability**

1036 The roman seabream *Chrysoblephus laticeps* (Valenciennes, 1830) is endemic to southern
1037 Africa, occurring from False Bay to the Kei River, with a core distribution throughout the
1038 Western and Eastern Cape in South Africa (Smith and Heemstra 1991; Götz and Kerwath 2013)
1039 (Figure 2.3) *Chrysoblephus laticeps* is heavily exploited in the commercial and in the
1040 recreational fishing sectors (Götz and Kerwath 2013). Catch estimates of between 10 000–100
1041 000 kg have been reported from locations to the west of Algoa Bay between the years 1985–
1042 2000 (Kerwath et al. 2013) (Duncan et al. 2018) (Figure 2.3).



1043

1044 **Figure 2.3: Spatial distribution of total commercial *C. laticeps* catch from 1985 to present day.**
 1045 **Data was obtained from the national marine linefish system (NMLS) at DAFF (Duncan 2018).**

1046

1047 This slow growing Sparid species is particularly vulnerable to selective exploitation owing to
 1048 its life-history traits. *Chrysoblephus laticeps* reaches 50 % maturity as a female between 2.5 to
 1049 4.3 years (167 to 190 mm fork length; Buxton 1987, 1990) and undergoes a sex change between
 1050 8 to 10.3 years (between 275 to 350 mm fork length; Buxton 1993), living to a maximum age
 1051 of 19 years (Götz et al. 2008). These fish form social dominance hierarchies, in which dominant
 1052 males will defend their territories during the breeding season (Buxton 1987) and engage in
 1053 aggressive behaviour during foraging or spawning (spawning occurs in the summer months
 1054 between October to January; Buxton 1990, Kerwath et al. 2007). These social behavioural
 1055 traits, exploitation and hardiness in captivity (Kerwath et al. 2007, Duncan et al. 2019) make
 1056 this a model species to address research questions on how physiological and behavioural traits
 1057 influence resilience to thermal variability.

1058 This highly resident species (i.e. home range between 1000 – 3000 m²; Kerwath 2007) is ideal
 1059 for spatial protection, which can assist in recruiting nearby fished areas given the genetic
 1060 connectivity of the species throughout South Africa (Teske et al. 2010). The sampling locality
 1061 of Noordhoek in Algoa Bay lies towards the centre of this distribution. However, *C. laticeps*
 1062 may already reside in areas close to the lower limit of their tolerance range, where the species
 1063 has been shown to enter cold shock as temperatures drop to 8 °C (See Figure 2.1 and 2.2.)
 1064 (Duncan et al. 2019). Additionally, the average annual summer maximum temperature of 23.5
 1065 °C at 5 m depths in Algoa Bay (Duncan et al. 2019) is close to maximum cardiac breakpoint
 1066 temperatures for the species (i.e. 23.92 °C and 25.19 °C; Skeeles et al. 2020). Living in a

1067 climate hotspot on South Africa's South coast, exploited *C. laticeps* stocks may have a limited
1068 scope for the rapid expansion of their tolerance range or physiological adaptation under fishing
1069 pressures (Duncan et al. 2019). Duncan et al (2019) was the first study to link exploitation with
1070 reduced physiological performance where he found that an exploited population of *C. laticeps*
1071 had reduced physiological tolerance to thermal variability, relative to a protected population,
1072 and attributed this to the capture of the physiologically fittest fish by the fishery. Overall, *C.*
1073 *laticeps*' behavioural traits, commercial exploitation and distribution range make it a model
1074 species to address the research questions of this thesis.

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1078 **Chapter 3**

1079

1080 **The importance of individual variability in physiological**
1081 **phenotype to predict the resilience of fish populations to**
1082 **Anthropogenic climate change**

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1104 **A *Chrysolephus laticeps* specimen inside a respirometer, used to measure oxygen consumption**

1105

1106 **3.1. Introduction**

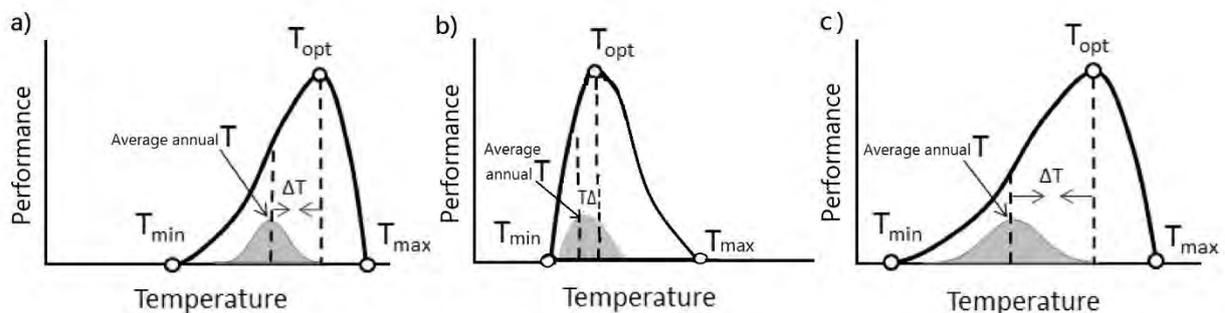
1107 Living in the Anthropocene, fish populations experience the coupled threats of climate change
1108 and exploitation. These threats can act simultaneously to lower the resilience of fished
1109 populations to marine environmental stressors (Cooke et al. 2019). Global increases in mean
1110 sea surface temperatures have altered wind regimes (Rhein et. 2013), driving short-term shifts
1111 in local ocean weather (Bates et al. 2018; Bates et al. 2019). The consequences for fishes in the
1112 ocean is driven by their physiological responses to unpredictable shifts in local thermal
1113 regimes. Fish may alter their tolerance range by shifting their physiological performance curves
1114 (either by broadening their tolerance to a range of stressors, or by maximizing their
1115 performance at extreme stressors; Portner and Knust 2007; Chown et al. 2010), or alter their
1116 behaviour to seek out refugia from external stressors (Wong and Candolin 2015).

1117 As fish are ectotherms and their body temperatures track ambient thermal conditions
1118 (Rijnsdorp et al. 2009; Pauly 2010) the consequences of reduced physiological performance in
1119 fishes are dependent on their tolerance to extreme fluctuations in local thermal regimes (Bates
1120 et al. 2019). Temperature determines the rate at which fish will oxidize substrates to produce
1121 energy, impacting both vital metabolic processes (such as foraging and swimming style;
1122 Brownscombe et al. 2014; Johansen et al. 2014) and the energy remaining for reproductive
1123 fitness (Pankhurst and Munday 2011). As physiological performance is dependent on
1124 temperature, thermal tolerance determines population demographics and range boundaries
1125 (Rijnsdorp et al. 2009). Extreme changes to local thermal regimes will have consequences for
1126 fish that are unable to seek out thermal refugia or for resident species with small home ranges
1127 (Wong and Candolin 2015; Beever et al. 2017). Thermal variability can elevate energetic costs
1128 and reduce physiological performance in resident fishes with limited thermal tolerance (Portner
1129 and Knust 2007; Clark et al. 2013; Bates et al. 2019).

1130 Aerobic scope (AS) is one of the more suitable and useful metrics to assess the influence of
1131 temperature, amongst other environmental factors, on the metabolic performance of ectotherms
1132 (Pörtner and Knust 2007; Pörtner et al. 2018). As a measure of energetic capacity, aerobic
1133 scope is defined as the difference between standard metabolic rate (SMR; the rate at which an
1134 animal oxidizes metabolic substrates to produce the energy required to maintain homeostasis
1135 in a post absorptive, inactive state; McNab 2002; Metcalfe et al. 2016) and maximal metabolic
1136 rate (MMR; maximal locomotor activity; Portner et al. 2007). Metabolic rates are typically
1137 determined for a species as the population mean; however, there can be a two to three-fold

1138 variation between individuals in the expression of these partially heritable metabolic traits (i.e.
1139 metabolic phenotypes; Metcalfe et al. 2016; Taboun 2020; Long et al. 2021).

1140 Environmental variation can separate individuals into low and high performance phenotypes
1141 (Neubauer and Anderson 2019). High performers in relatively stable environments (eg. the
1142 tropics or polar regions) are most likely to maximize performance at extreme temperatures
1143 through a steep aerobic scope curve (eg. a narrow range between SMR and MMR, but a higher
1144 peak in maximum performance at extreme temperatures; Chown et al. 2010, Neubauer and
1145 Anderson 2019) (Figure 3.1 a, b). However, in heterogeneous environments (such as temperate
1146 regions), high performers require a broader aerobic performance window (low SMR and high
1147 MMR; Portner et al. 2007; Portner 2008; Clark et al 2013) (Figure 3.1c). These individuals
1148 have broader tolerance ranges and are able to quickly recover from external stressors as they
1149 have low metabolic costs and the ability to sustain activity across changing conditions (Auer
1150 et al. 2015; Holt and Jorgensen 2015; Norin et al. 2015; Metcalfe et al. 2016; McLean et al.
1151 2018; Pörtner et al. 2018). In contrast, low performance individuals may experience extended
1152 periods of physiological stress, which may have lethal and sub-lethal consequences, such as
1153 reducing the energy available for reproductive fitness (Portner and Knust 2007).



1154
1155 **Figure 3.1: Thermal performance curves of a hypothetical temperate species (a), a tropical species (b) and**
1156 **a polar species (c). T_{min} and T_{max} are the minimum and maximum temperature within which species can**
1157 **perform. T_{opt} is the optimal temperature for performance. The temperature that the species is exposed to**
1158 **during the year is depicted as the grey curve beneath the thermal performance curve. Here, the average**
1159 **annual temperature is indicated. ΔT is the distance between the average annual temperature and the**
1160 **optimal temperature for performance (T_{opt}). Temperate species have a broad thermal performance range.**
1161 **Tropical and polar species are temperature specialists because they have narrower thermal performance**
1162 **curves. Tropical species specialize at high temperatures, whereas polar species specialize at cold**
1163 **temperatures (adapted from Johansson et al. 2020).**
1164

1165 The selection of high performance metabolic phenotypes (HPMPs) can lead to genetic
1166 adaption, but this may be a relatively slow process in organisms with long generation times,
1167 such as many resident fishes (Somero 2010). These organisms can use other mechanisms, such
1168 as acclimation and transgenerational acclimation (Munday 2014, Donelson et al. 2012), to

1169 adapt to external environmental changes through shifts in thermal performance curves
1170 (Donelson et al. 2012; Munday 2014; Donelson et al. 2019). However, short-term phenotypic
1171 behavioural changes are more likely to precede physiological adaptation. Temperate HPMPs
1172 may have the energetic capacity provided by a broad aerobic scope curve to make use of
1173 behavioural plasticity (Biro et al. 2018), which has allowed many taxa to adapt to climate
1174 change by changing their phenology or distribution (Wong and Candolin 2015; Beever et al.
1175 2017; Biro et al. 2018). Hence, the metabolic phenotype of individuals will likely determine if
1176 they can tolerate or behaviourally respond to extreme thermal variability (Ward et al. 2016;
1177 Bates et al. 2019).

1178

1179 An understanding of how thermal variability influences the physiological performance of
1180 individuals is critical to understand the effects of climate change and ensure the persistence of
1181 fished populations in the Anthropocene (Ward et al. 2016). Fishing-induced mortality is
1182 thought to aggravate marine environmental stressors by limiting genetic potential and selecting
1183 for particular phenotypes, such as a smaller body size and earlier maturity (Harley et al. 2006),
1184 a timidity syndrome (Alos et al. 2012) and reduced physiological performance (Duncan et al.
1185 2019). Duncan et al. (2019) provided the first population-level evidence that the removal of
1186 high-performance aerobic phenotypes through fishing may increase the vulnerability of fished
1187 resident fish populations to climate variability. However, to understand the likely response of
1188 a population to thermal change, it is necessary to assess the aerobic performance of individuals
1189 within a population. This can be done by repeatedly measuring the aerobic performance of the
1190 same individual across a thermal gradient (Killen et al. 2021). This information can be used to
1191 classify individual metabolic phenotypes (high vs low performance phenotypes) and will
1192 provide us with an understanding of how resilient the population may be to change.

1193 The aim of this chapter is to assess the metabolic performance of individuals from an exploited
1194 population of *Chrysoblephus laticeps* in order to examine the phenotypic variability within the
1195 population and categorise individuals by their aerobic performance. The information from this
1196 will assist in the prediction of the physiological vulnerability of exploited populations of this
1197 species to the extreme and increasing thermal variability experienced in coastal environments.
1198 To do this, aerobic scope phenotypes were quantified in individuals by using respirometry to
1199 compare changes in energy expenditure at ecologically relevant temperatures, mimicking
1200 variability experienced in the home range of the species as a result of upwelling and marine
1201 heat wave (MHW) events.

1202 **3.2 Methods**

1203 **3.2.1 Fish capture from study site:**

1204 To measure individual aerobic scope performance under thermal variability, 44 *Chrysolephus*
1205 *laticeps* individuals were captured from Noordhoek (33°58'S 25°38'E) in Algoa Bay, Gqeberha
1206 (see Figure 2.1) in November of 2019 and April and June of 2021. Noordhoek extends along
1207 an exposed Cape headland and falls within a dynamic upwelling region. This region
1208 experiences localized sea temperature variability owing to intensified wind-driven upwelling
1209 along these prominent coastal headlands (Buxton 1993; Goshen and Schumann 1995;
1210 Schumann et al. 1995; Rouault et al. 2009, 2010).

1211
1212 Hook and line methods were used to catch fish off a ski-boat from water depths between 12 m
1213 and 25 m. Captured specimens were immediately vented with a hypodermic needle and
1214 transferred to a 1000 L tank containing fresh seawater. On shore, fish were moved to a circular
1215 holding tank (1000 L), which was supplied with fresh seawater at a rate of 225 L/min via a
1216 submersible pump. Following a five-hour holding time, all specimens in the 1000 L tank
1217 received a continuous supply of pure oxygen for transport to the laboratory aquaculture
1218 facilities in the NRF-SAIAB Aquatic Ecophysiology Research Platform at the Department of
1219 Ichthyology and Fisheries Science, Rhodes University.

1220 1221 **3.2.2 Fish husbandry:**

1222 Fish were placed into two 5900 L cylindrical holding tanks and maintained for a two week
1223 acclimation period at a constant temperatures of 16 °C (controlled through a 1.5 kW titanium
1224 hot rod submerged heating element, wall-mounted air conditioner and STC-1000 temperature
1225 controllers) and a light cycle of 9.5 L : 14.5 D. Holding tanks were connected to a filtration
1226 system made up of a 750 L slimline sump, protein skimmer (UltraZap with submerged Jebao
1227 DCP5000 pump), bubble bead filter (BBF-200-COMP, Wilpet Koi Products), fluidised bed
1228 biological filter (750 L slimline tank with SuperActiFlo Media) and UV steriliser (UV 55 W,
1229 UltraZap Pro UVS-55). A pool pump (Speck Porpoise 0.75 kW) was used to recirculate water
1230 through the system. Air was supplied to the holding tanks and bed filter via a 2.2 k W blower
1231 outside the holding room. The O₂, pH, ammonia, nitrite and salinity levels were measured daily.
1232 Fish were individually fed a maintenance diet of squid (*Loligo reynaudii*) every second day.
1233 Fish were tagged using colour combinations of Visible Elastomer Implant (VIE) tags via

1234 intramuscular injection below the dorsal fin (Northwest Marine Technology, USA) for the
1235 purpose of individual identification (Figure 3.2).

1236



1237
1238 **Figure 3.2: Visible Elastomer Implant (VIE) tagging of *Chrysolephus laticeps* specimens for**
1239 **individual identification**

1240

1241 **3.2.3 Physiological measurements:**

1242 Physiology experiments were conducted in the experimental room which housed a 2100 L
1243 cylindrical tank connected to a filtration system comprised of a protein skimmer, bubble bead
1244 filter (BBF-100 COMP), fluidised bed filter and UV sterilizer (UV 55 W, UltraZap Pro UVS-
1245 55). Oxygen was maintained at 100 % saturation in the cylindrical tank and fluidized bed filter
1246 via air supply from a 2.2 kW blower. Water was pumped from the cylindrical tank into four
1247 glass tanks containing respirometers (Figure 3.3).

1248 The respirometry chambers (29.72 litres; 45 cm in length with a 29 cm internal diameter; Figure
1249 3.4 a) were small enough to measure oxygen consumption by individual fish within a limited
1250 time span, but of sufficient size to prevent rapid oxygen depletion. Respirometers were made
1251 from thick-walled Perspex and had a g:ml ratio between 20 and 70 based on fish size, to
1252 comfortably house the specimen while limiting movement within the chamber (Figure 3.4 b).
1253 Openings with silicon O-ring seals were bolted closed. An internal pump (880 L/h 15W SOBO
1254 pump) mounted onto the rear of the respirometer, along with an oxygen-impermeable PVC
1255 recirculation loop, was used to continuously mix water within the chambers to distribute
1256 oxygen and prevent stratification. Water from the recirculation loop was pumped via a
1257 peristaltic pump (Ismatek IPC-N-24 precision cassette pump with 24 multi-channel pump
1258 head) through a cell with an optical oxygen sensor (OXFTC, Pyro Science GmbH), from which
1259 oxygen concentrations ($\text{mg}\cdot\text{l}^{-1}$) were taken by a Firesting oxygen reader (FSO2-4, Pyro Science
1260 GmbH; and bare optical fibres SPFIB-BARE, Pyro Science GmbH). Pyro Oxygen Logger

1261 Software (Pyro science GmbH) was used to record oxygen concentrations. One-way check
1262 valves on the flush pump and overflow lines prevented oxygen leaks. Following the closed
1263 measurement period, the flow of fresh oxygenated seawater into each of the four respirators
1264 was controlled by a flush pump (Bubble Magus DC 10000s guaranteeing a minimum four-fold
1265 flush volume ratio; controlled with a digital timer Eliro VODDTS), eliminating waste products
1266 (Figure 3.4).

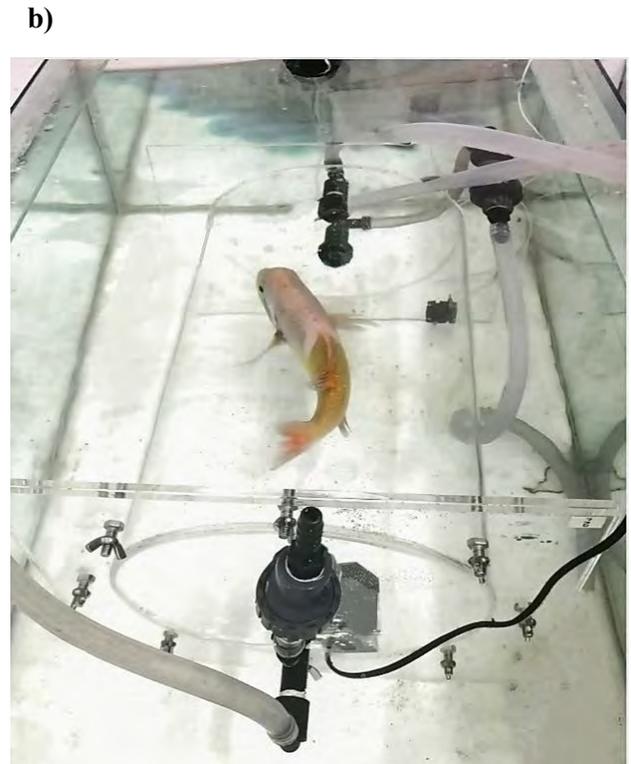
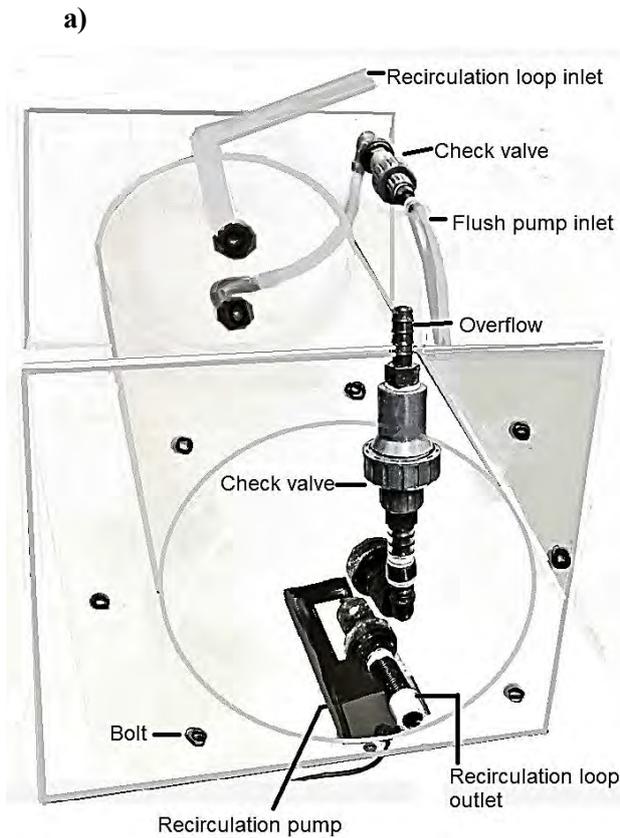
1267 Intermittent-flow respirometers (designed by Duncan et al. 2019) were used, as per the protocol
1268 of Clark et al. (2013) and Svendsen et al. (2016), to determine the oxygen consumption rate of
1269 the 44 *C. laticeps* individuals. Fish were fasted for 36 hours prior to respirometry measurements
1270 to evacuate their guts and decrease post-feeding increments in metabolic rate (Cutts et al. 2001,
1271 Clark et al. 2013). The oxygen consumption (O_2 per minute) of each individual was measured
1272 at a low (10 °C), acclimation (16 °C) and high (24 °C) temperatures. However, upon observing
1273 sub-lethal effects (including loss of equilibrium, disease and delayed mortalities) in the first 16
1274 individuals after being exposed to the high temperature, it was decided to decrease the high
1275 temperature treatment to 21 °C to ensure that the remaining 28 individuals were not
1276 compromised for the remainder of these and the subsequent (see Chapter 4 and 5) experiments.
1277 Each individual fish retained the same numerical ID throughout all Chapters in this body of research.
1278



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1280

1281 **Figure 3.3: Tanks housing respirometers used to measure oxygen consumption (respirometers**
1282 **are pictured during a flush cycle)**

1283



1285

1286 **Figure 3.4: A respirometer (a) containing a *Chrysolephus laticeps* specimen (b)**

1287

1288 To measure standard metabolic rate (SMR), each individual was placed into each of the four
1289 respirometers for a 12-hour acclimation period maintained at 16 °C. Following this,
1290 temperature was either maintained at 16° C or increased or decreased by one degree every hour
1291 using an Aquaheat SF2020P heatpump, to mimic intense upwelling and marine heat wave
1292 events, until the test temperatures of 10, 21 or 24 °C were reached (half of sampled population
1293 was first exposed to 10 °C, while the other half was first exposed to 21 °C to control for
1294 experimental temperature effects). Once the temperature had stabilised, oxygen consumption
1295 was recorded every five minutes, with flushing every 15 minutes for 24 hours. A 24-hour period
1296 was considered necessary for the measurement of SMR as it accounted for circadian rhythm
1297 changes in metabolic rate (Clark et al. 2013; Chabot et al. 2016). To account for an increase in
1298 metabolic rate at high test temperatures (21 or 24 °C), measurement periods were adjusted to
1299 three-minutes, followed by seventeen-minute flush periods.

1300 For maximum metabolic measurements (MMR), individuals were subsequently transferred to
1301 the 2100 L cylindrical tank where they were chased for 10 minutes until exhausted (or
1302 unresponsive to touching of the caudal fin; Clark et al. 2013). This was followed by 30 seconds

1303 of air exposure to ensure that the fish was completely exhausted and likely to reach the
 1304 maximum O₂ consumption rate during the recovery period (Clark et al. 2013). Individuals were
 1305 then returned to respective respirometers for several hours (± 5 hours), until oxygen use
 1306 stabilized near SMR measurement levels (Clark et al. 2013). After the termination of the
 1307 experiment, the oxygen concentration in empty respirometers was measured for three hours to
 1308 record background respiration rates (as per Duncan et al. 2019).

1309 Measurement and flushing periods during respirometry experiments were created into a dataset
 1310 of several independent rates of oxygen consumption (*RO*₂) for each individual (with a quality
 1311 threshold of R² > 0.9 to filter linear oxygen declines within measurement periods; Duncan
 1312 2019). The rate of oxygen consumption (mg.kg⁻¹.h⁻¹) for each measurement period (where the
 1313 first minute of measurement were excluded) was calculated using Svendsen et al.'s (2016)
 1314 equation (3.1):

1315

$$1316 \quad RO_2 = \left(\left(\frac{V_{re}-M}{W} \right) \left(\frac{\Delta[O_{2a}]}{\Delta t} \times 60 \right) \right) - \left(\left(\frac{V_{re}-M}{W} \right) \left(\frac{\Delta[O_{2b}]}{\Delta t} \times 60 \right) \left(\frac{V_{re}}{V_{re}-M} \right) \right)$$

1317 where V_{re} = total volume of respirometer in Litres, M = mass of individual in kg expressed in
 1318 L, W = mass of individual in kg, $\frac{\Delta[O_{2a}]}{\Delta t}$ = slope of linear decrease in O₂ concentration within
 1319 measurement period, $\frac{\Delta[O_{2b}]}{\Delta t}$ = Slope of linear decrease in O₂ concentration in respirometer
 1320 without specimen.

1321

1322 The SMR was calculated from the quantile of the lowest 20 % of the *RO*₂ data for each test
 1323 temperature (Chabot et al. 2016). Maximum metabolic rate, which increased after exhaustive
 1324 exercise until O₂ consumption rates reached a plateau, was recorded as the single highest *RO*₂
 1325 measurement. Prior to accounting for allometric mass effects, the SMR and MMR *RO*₂ data
 1326 were corrected for temperature as a function of the Boltzmann factor (Brown et al. 2004; using
 1327 the average activation energy of ectotherms; Gillooly et al. 2001). Rates of oxygen
 1328 consumption were temperature corrected (*RO*_{2(temp corrected)}) using the Equation (3.2):

$$1329 \quad RO_{2(temp\ corrected)} = RO_2 \times e^{\frac{-E}{kT}}$$

1330 where E = average activation energy of ectotherms (0.63 eV; Gillooly et al. 2001), k =
 1331 Boltzmann constant 8.617 333 × 10⁻⁵ eV.K⁻¹, T = absolute temperature in kelvin.

1332

1333 The allometric exponent (α) of mass scaling effects was then estimated through the slope of
1334 the linear regression between the natural logarithm of $RO_{2(\text{temp corrected})}$ and the natural logarithm
1335 of mass. The allometric exponent (α) of mass scaling effects was used to correct the data using
1336 the equation (3.3):

$$1337 \quad MO_2 = \frac{RO_2}{M^\alpha}$$

1338 where MO_2 = Mass corrected SMR or MMR and RO_2 = Oxygen consumption rate for SMR or
1339 MMR. M = Mass of individual and α = allometric exponent of mass scaling.

1340

1341 The absolute aerobic scope (AS) for each individual was then calculated by subtracting mass
1342 corrected SMR from mass corrected MMR as using the equation (3.4):

$$1343 \quad AS = MMR - SMR$$

1344

1345

1346 **3.2.4 Classification of aerobic performance phenotypes:**

1347 A total performance score was developed to represent aerobic performance across the range of
1348 test temperatures (Table 3.1) (according to the percentile method as per Rousselet et al. 2017).
1349 This score was calculated for each temperature from the lower (25 %), mid (50 %) and upper
1350 (75 %) percentiles of the aerobic scope range available for the species (Duncan et al. 2019).
1351 For each temperature, each individual received a rank score based on the percentile that
1352 included its aerobic scope. Rank scores (ranging from three to 12) were totalled for all
1353 temperatures, where an individual could receive an absolute minimum score of three (i.e. a
1354 score of one for each temperature) and maximum score of 12 (i.e. a score of four for each
1355 temperature). These scores were used to classify individuals according to the percentile method
1356 as high performers (i.e. the >75 % percentile with a total score above 9.75, rounded off as 10),
1357 intermediate performers (25 – 75 % percentile), and low performers (i.e. the <25 % percentile
1358 with a total score below 5.25, rounded off as 5). Hence, an individual that received a score of
1359 five and below was classified as a low performer, whereas an individual that received a score
1360 of 10 and above was classified as a high performer. An individual that was classified as a high
1361 performer exhibited a broad tolerance to a thermally variable environment. An individual that
1362 was classified as a low performer may have performed moderately well at optimal
1363 temperatures, but may be limited by aerobic performance in a thermally variable environment.

1364 3.2.5 Statistics

1365

1366 A linear mixed effects (*lme*) modelling approach was implemented using the *lme4* package
1367 (Bates et al. 2015) in R version 3.3.3 (R Core Team 2017) to account for data homoscedasticity
1368 (model assumptions were also checked using diagnostic plots) and repeated measures (i.e. each
1369 individual was measured repeatedly at each test temperature (Bolker et al. 2009; Zuur 2009;
1370 Harrison et al. 2018). The effect of temperature on metabolic rate was tested by modelling a
1371 second order polynomial relationship between metabolic data and temperature, with a random
1372 effects structure weighted by fish ID and temperature, to take into account the variation of each
1373 individual. (Note, there was no significant differences in the order of individuals tested first at
1374 10 °C and those tested first at 21 °C or 24 °C, and therefore all fish were pooled for individual
1375 analyses). To account for the varying relationship between metabolic rate and temperature of
1376 each individual, temperature was included as a random slope in the random effects structure
1377 with individual as the random intercept (i.e. temp|ID; Harrison et al. 2018). Aerobic
1378 performance group (i.e. as a factor for high performers, intermediate performers and low
1379 performers) was added as a fixed effect. Sex, batch and weight class (see Table A1 in Appendix
1380 A) were not significant in predicting individual metabolic data in the initial model ($p > 0.05$, t
1381 = 1.434, $df = 77$) and these variables were then excluded from further model analyses (i.e. data
1382 was pooled between the sexes, batches and weight classes). The model output was assessed
1383 using the ‘Dredge’ function with libraries ‘mvtnorm’ and ‘MuMIn’ from the ‘CRAN’ package
1384 (R Core Team 2017).

1385

1386

1387

1388 **Table 3.1: Classification of aerobic performance phenotypes**

1389

	Low performer: <25 % percentile (O₂.min⁻¹. kg⁻¹)	Intermediate performer: <50 % percentile (O₂.min⁻¹. kg⁻¹)	Intermediate performer: >50 % percentile (O₂.min⁻¹. kg⁻¹)	High performer > 75 % percentile (O₂.min⁻¹. kg⁻¹)
Point per temperature treatment	1 point	2 points	3 points	4points
16 °C	<1.75	<2.6	>2.6	>3.45
10 °C	<2.59	<3.68	<3.68	>4.77
21 °C	<3.35	<4.2	>4.2	>5.05
Total rank scores (between 3 and 12) based on the percentile cut-off, where ≤ 5 = low performer and ≥ 10 = high performer)	<u>Total score <3 - 5:</u> Low performer Low performance across all temperatures (i.e. total score of 3). OR intermediate aerobic performance ONLY at optimal temperature (i.e. score of 3 at optimal temperature, and then LP scores of 1 at each of the other two temperatures, resulting in a total score of 5).	<u>Total score 6 - 9:</u> Intermediate performer High aerobic performance at optimal temperature and/ or high OR low temperature	<u>Score >10 - 12:</u> High performer High aerobic performance at optimal, low AND high temperature	

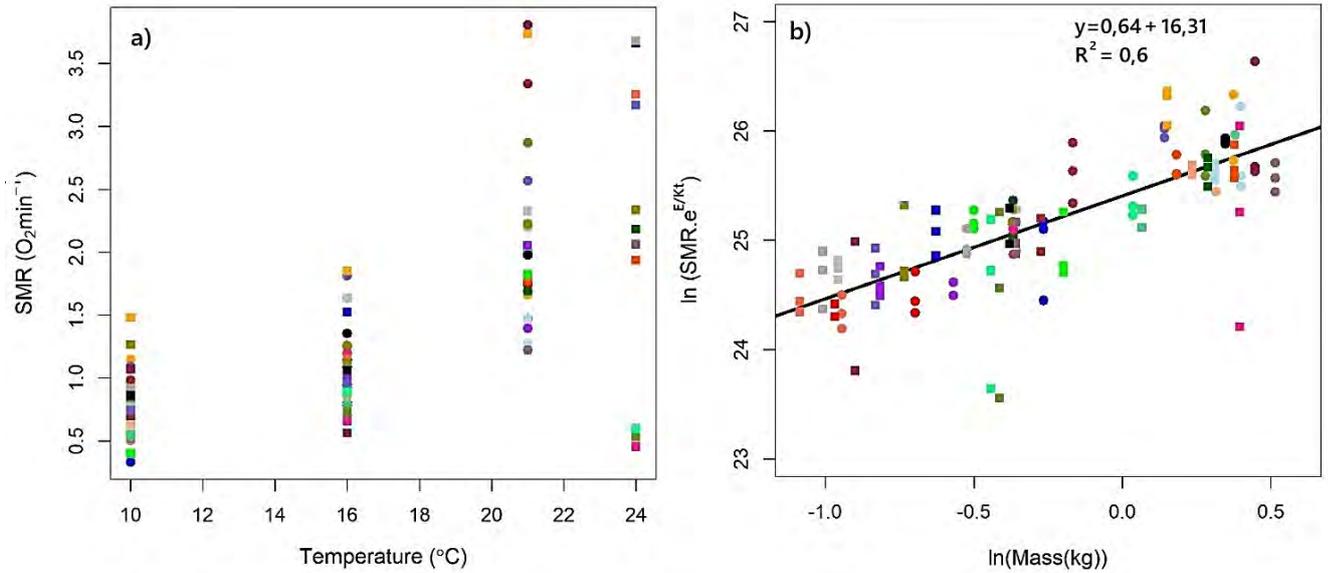
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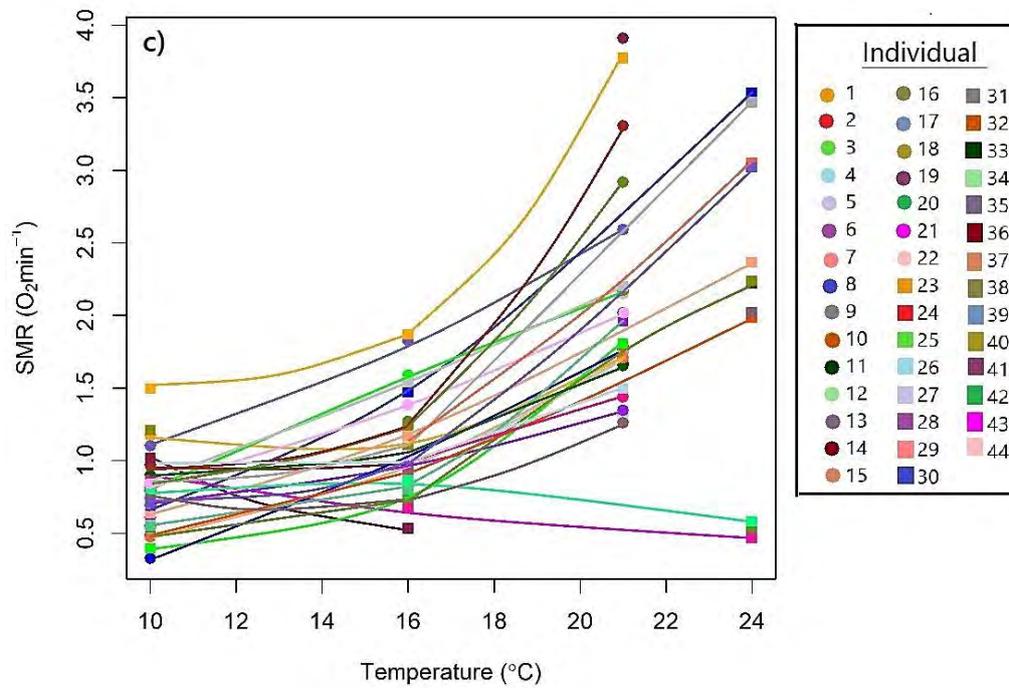
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1393 **3.3 Results**1394 **3.3.1 Mass correcting MO2 data**

1395 Raw SMR data (Figure 3.5a) were mass-corrected using a linear mass scaling exponent of 0.64
 1396 (Figure 3.5b), estimated from the natural logarithm of temperature-corrected SMR and the
 1397 natural logarithm of mass. Mass corrected SMR as a function of temperature is depicted in
 1398 Figure 3.5c.



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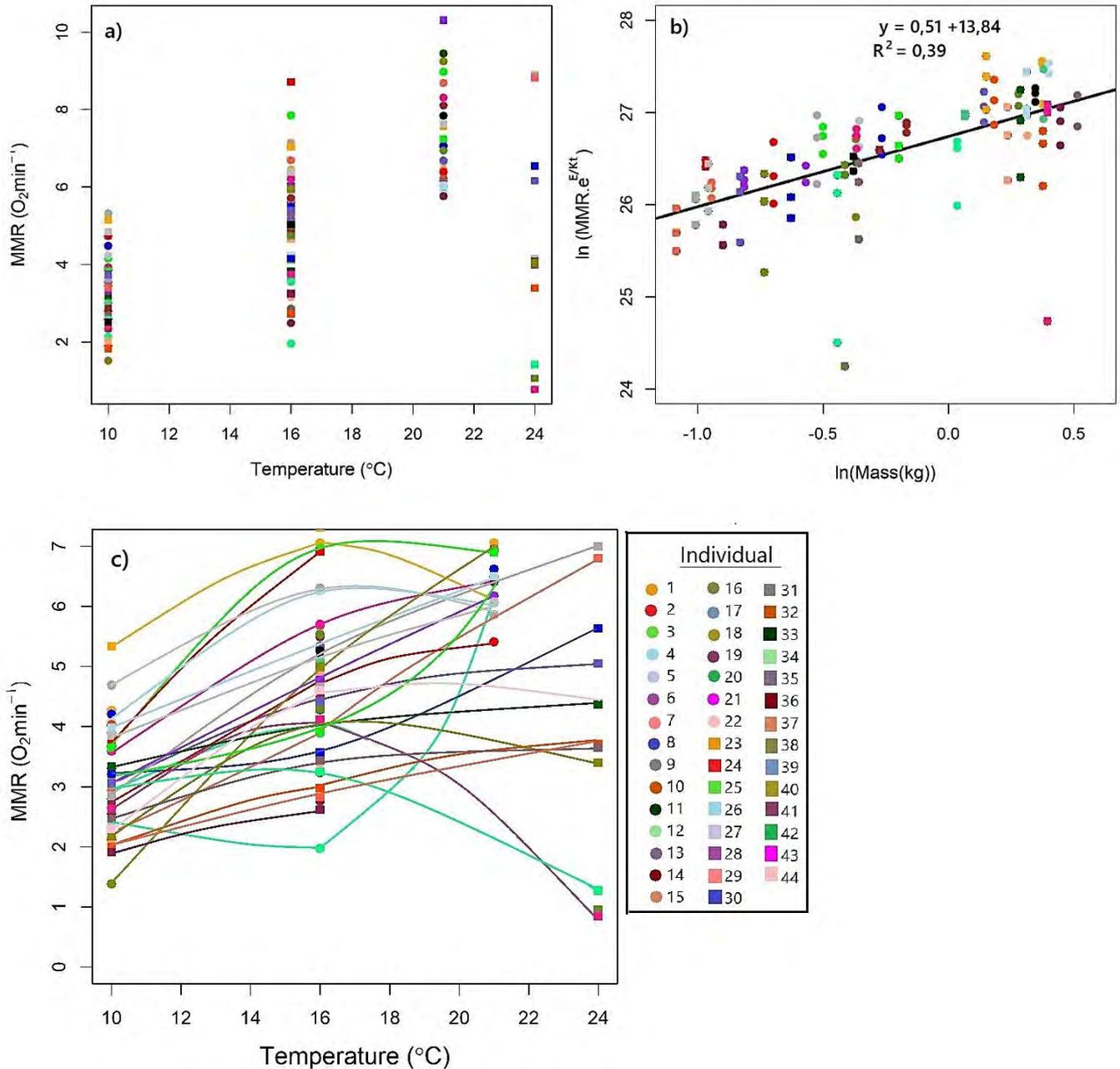
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Figure 3.5: SMR data for an exploited population of *Chrysoblephus laticeps* at temperatures of 10 °C, 16 °C, 21 °C and 24 °C. Raw SMR ($O_2 \cdot \text{min}^{-1}$) data (a) was mass-corrected using the linear mass scaling exponent of SMR data, which was determined from the natural logarithm of temperature-corrected SMR data ($\ln(\text{SMR} \cdot e^{E/kT})$) plotted against the natural logarithm of mass ($\ln(\text{Mass}(\text{kg}))$) (b). Figure 2.5 (c) portrays mass-corrected SMR data, which was used in the analyses.

1410 Raw MMR data (Figure 3.6a) was mass corrected with an allometric mass scaling exponent of
 1411 0.51 (Figure 3.6b). Mass corrected MMR as a function of temperature is depicted in Figure
 1412 3.6c.



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Figure 3.6: Maximum metabolic rate (MMR) data for an exploited population of *Chrysolephus laticeps* at temperatures of 10 $^{\circ}\text{C}$, 16 $^{\circ}\text{C}$, 21 $^{\circ}\text{C}$ and 24 $^{\circ}\text{C}$. Raw MMR ($O_2 \cdot \text{min}^{-1}$) data (a) was mass corrected using the linear mass scaling exponent of MMR data, which was determined from the natural logarithm of temperature-corrected MMR data ($\ln(\text{MMR} \cdot e^{E/Kt})$) plotted against the natural logarithm of mass ($\ln(\text{Mass(kg)})$) (b). Figure 2.6 (c) portrays mass-corrected MMR data, which was used in the analyses.

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3.3.2 Effect of temperature on Standard Metabolic and Maximum Metabolic Rates (SMR and MMR)

Mass corrected SMR ranged from 0.465 to 3.748 O₂.min⁻¹ kg⁻¹ amongst individuals across the various temperatures (Figure 3.5c). SMR ranged between 0.840 to 1.146 O₂.min⁻¹ kg⁻¹ at 10 °C, between 0.533 to 1.841 O₂.min⁻¹ kg⁻¹ at 16 °C, between 1.207 to 3.748 O₂.min⁻¹ kg⁻¹ at 21 °C, and between 0.465 to 3.532 O₂.min⁻¹ kg⁻¹ at 24 °C (Table A2 in Appendix A, Figure 3.5c). Mass corrected MMR ranged from 0.846 to 6.993 O₂.min⁻¹ kg⁻¹ amongst individuals across temperatures (Figure 3.6c). MMR ranged between 1.330 to 5.420 O₂.min⁻¹ kg⁻¹ at 10 °C, between 3.782 to 7.426 O₂.min⁻¹ kg⁻¹ at 16 °C, between 5.611 to 6.918 O₂.min⁻¹ kg⁻¹ at 21 °C, and between 0.846 to 6.993 O₂.min⁻¹ kg⁻¹ at 24 °C (Table A2 in Appendix A; Figure 3.6c).

Mass corrected SMR generally increased with temperature and this effect was found to be significant (p -value = 0.004, t = 2.958, df = 77; Table 3.3; Figure 3.7a). The relationship between SMR and temperature was similar across high performers, intermediate performers and low performers (p > 0.05, t = 0.922, df = 77; Table 3.3). Variation in SMR data was significant at 16 °C (p -value = 0.001, t = 8.135, df = 77), as well as high test temperatures of 21 °C and 24 °C (p -value = 0.005, t = -2.852, df = 77) (Figure 3.5c, 3.7a; Table 3.3). However, variation in SMR was not significant at cold temperatures of 10 °C (p > 0.05, t = 7.144, df = 77).

In contrast, the relationship between MMR and temperature was significant across all test temperatures (p -value < 0.001, t = 4.963, df = 77, Table: 3.4, Figure 3.7b), and individual variation increased with temperature (Figure 3.6c). Maximum metabolic rate significantly differed by phenotypic group (i.e. high performers, intermediate performers, and low performers; p < 0.001; t = 6.404; df = 77; Table 3.4).

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Table 3.3 Linear mixed effects model results for variation in standard metabolic rate (SMR) data amongst *Chrysolephus laticeps* individuals at temperatures of 10 °C, 16 °C, 21 °C and 24 °C. Differences in mass-corrected metabolic rate data between individuals were tested by modelling a second order polynomial relationship between metabolic data and temperature, with a random effects structure weighted by fish ID and temperature. Bold *p-values* depict significant variation in SMR data.

Random effect	SD			
Individual	0.249			
Temperature	0.301			
<hr/>				
Residual	0.517			
<hr/>				
Fixed effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	1.075	0.530	2.026	0.046
Temperature	-0.098	0.070	-1.399	0.166
Temperature ²	0.006	0.002	2.958	0.004
Performance group	0.078	0.085	0.922	0.361
Low performer	1.066	0.537	1.967	0.053
Intermediate performer	0.038	0.137	0.279	0.782
High performer	0.164	0.173	0.950	0.348
<hr/>				
AIC	224.70			
Residual SE	0.4721 (<i>df</i> = 77)			

1462
 1463

1464

1465 **Table 3.4: Linear mixed effects model results for variation in maximum metabolic rate (MMR)**
 1466 **data amongst *Chrysoblephus laticeps* individuals at temperatures of 10 °C, 16 °C, 21 °C and 24 °C.**
 1467 **Differences in mass-corrected metabolic rate data between individuals were tested by modelling**
 1468 **a second order polynomial relationship between metabolic data and temperature, with a random**
 1469 **effects structure weighted by fish ID and temperature. Bold *p-values* depict significant variation**
 1470 **in MMR data.**

1471

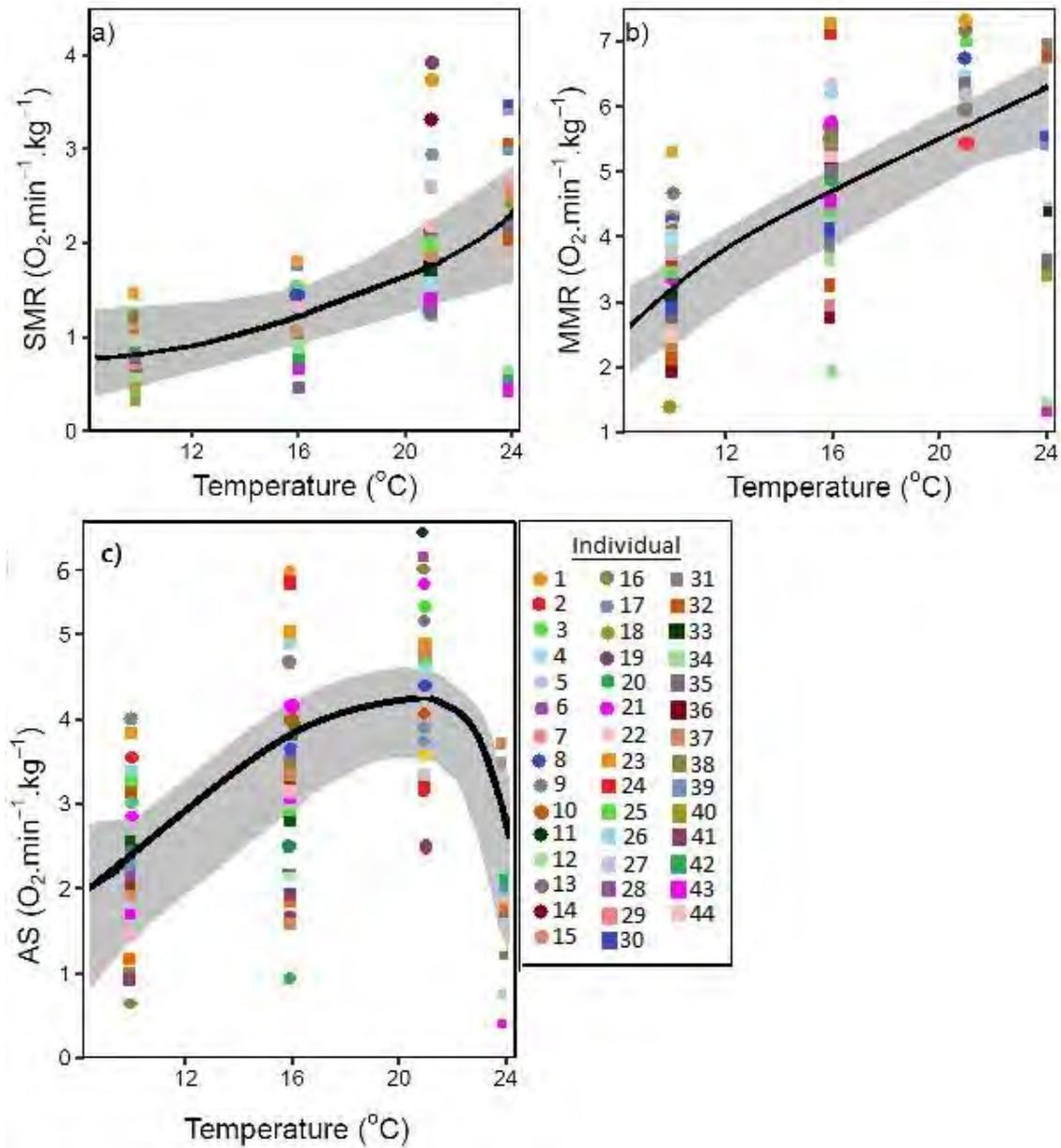
Random effect	SD			
Individual	0.335			
Temperature	1.123			
<hr/>				
Residual	1.123			
	1.188			
<hr/>				
Fixed effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	-5.019	1.328	-3.779	0.007
Temperature	0.881	0.177	4.963	<0.001
Temperature ²	0.021	0.005	4.060	<0.001
Performance group	1.138	0.178	6.404	<0.001
Low performers	0.915	0.174	5.244	<0.001
Intermediate performers	1.645	0.287	4.060	<0.001
High performers	2.272	0.361	6.290	<0.001
<hr/>				
AIC	425			
Residual SE	1.190 (<i>df</i> = 77)			

1472

1473

1474

1475 As a general trend, both SMR and MMR increased with increases in temperature. The model
1476 results indicated that the rate of change in SMR increased with temperature (Table 3.3; Figure
1477 3.7a), but the rate of change in MMR decreased with temperature (Table 3.4; Figure 3.7b).



1478

1479

1480 **Figure 3.7: Linear mixed effects model fits for *Chrysolephus laticeps* standard metabolic rate data (a), maximum metabolic rate data (b) and absolute aerobic scope (c) across test temperatures**
1481 **(10 °C, 16 °C, 21 °C and 24 °C) with shaded areas representing a 95 % confidence interval.**

1482

1483

1484 **3.3.3 Aerobic Scope (AS)**

1485

1486 Aerobic scope ranged from 0.381 to 5.904 O₂.min⁻¹ kg⁻¹ amongst individuals (Figure 3.7c).

1487 Aerobic scope ranged between 0.563 to 3.969 O₂.min⁻¹ kg⁻¹ at 10 °C, between 2.907 to 5.864

1488 O₂.min⁻¹ kg⁻¹ at 16 °C, between 0.990 to 5.904 O₂.min⁻¹ kg⁻¹ at 21 °C, and between 0.381 to

1489 3.746 O₂.min⁻¹ kg⁻¹ at 24 °C (Table A2 in Appendix A; Figure 3.7c).

1490

1491 Aerobic scope increased with temperature and this effect was found to be significant (*p*-value

1492 =0.000, *t* = 6.538, *df* = 77; Table 3.5, Figure 3.7c). Aerobic scope curves varied amongst

1493 individuals (Figure 3.7c). Variation in aerobic scope was significant at control temperatures of

1494 16 °C (*p*-value = > 0,001, *t* = 1.315, *df* = 77) and upper test temperatures of 21 °C and 24 °C

1495 (*p*-value = 0.001, *t* = 2.277, *df* = 75) (Figure 3.7c).

1496

1497 **Table 3.5 Linear mixed effects model results for variation in aerobic scope (AS) data amongst**
 1498 ***Chrysoblephus laticeps* individuals at temperatures of 10 °C, 16 °C, 21 °C and 24 °C. Differences**
 1499 **in mass-corrected metabolic rate data between individuals were tested by modelling a second**
 1500 **order polynomial relationship between metabolic data and temperature, with a random effects**
 1501 **structure weighted by fish ID and temperature. Bold *p*-values depict significant variation in AS**
 1502 **data.**
 1503

Random effect	SD			
Individual	0.000			
Temperature	1.181			
<hr/>				
Residual	1.004			
Fixed effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	-6.240	1.112	-5.609	<0.001
Temperature	0.979	0.150	6.538	<0.001
Temperature ²	0.029	0.004	6.470	<0.001
Performance group	1.060	0.137	7.736	<0.001
Low performer	1.041	0.146	7.105	<0.001
Intermediate performer	1.127	0.220	5.124	<0.001
High performer	2.111	0.276	7.648	<0.001
<hr/>				
AIC	356			
Residual SE	0.859 (<i>df</i> = 77)			

1504

1505 3.3.4. Classifying performance phenotypes

1506

1507 Eight individuals were grouped as high performers, 24 individuals were grouped as
1508 intermediate performers, and 12 individuals were grouped as low performers (Figure 3.8 and
1509 3.9). The performance phenotype classification for each individual with SMR, MMR and AS
1510 at each test temperature is given in Table A2 of Appendix A. SMR across all test temperatures
1511 ranged between 0.530 to 3.809 O₂.min⁻¹ kg⁻¹ in low performers (1.021 ± 0.83 ; mean \pm SD),
1512 SMR ranged between 0.400 to 3.680 O₂.min⁻¹ kg⁻¹ (1.297 ± 0.76 ; mean \pm SD) in intermediate
1513 performers, and SMR ranged between 0.331 to 3.738 O₂.min⁻¹ kg⁻¹ (1.347 ± 0.66 ; mean \pm SD)
1514 in high performers (Appendix A and Figure 3.8). MMR across all test temperatures ranged
1515 between 1.058 to 6.540 O₂.min⁻¹ kg⁻¹ in low performers (3.441 ± 1.33 ; mean \pm SD), MMR of
1516 intermediate performers ranged between 0.770 to 6.990 O₂.min⁻¹ kg⁻¹ (5.093 ± 2.11 ; mean \pm
1517 SD), and MMR of high performers ranged between 3.692 to 7.303 O₂.min⁻¹ kg⁻¹ (5.891 ± 1.49 ;
1518 mean \pm SD) (Appendix A and Figure 3.8).

1519

1520 Aerobic scope across all test temperatures ranged between 0.441 to 3.919 O₂.min⁻¹ kg⁻¹ in low
1521 performers (2.239 ± 0.95 ; mean \pm SD), AS ranged between 0.381 to 5.904 O₂.min⁻¹ kg⁻¹ (3.796
1522 ± 1.68 ; mean \pm SD) in intermediate performers, and AS ranged between 2.738 to 5.822 O₂.min⁻¹
1523 kg⁻¹ in high performers (4.544 ± 1.17 ; mean \pm SD) (Figure 3.8).

1524

1525 Aerobic scope significantly differed by performance phenotype ($p < 0.000$; $t = 7.736$; $df = 77$;
1526 Table 3.5). High performers exhibited the highest aerobic scope across the full range of
1527 temperature treatments. In contrast, low performers were limited by low aerobic performance
1528 in a thermally variable environment (Figure 3.9). In particular, the variation in the aerobic
1529 performance of high, intermediate, and low performers was most significant at the high
1530 temperature treatments of 21 °C and 24 °C ($p < 0.05$; Table 3.5; Figure 3.8 and 3.9).

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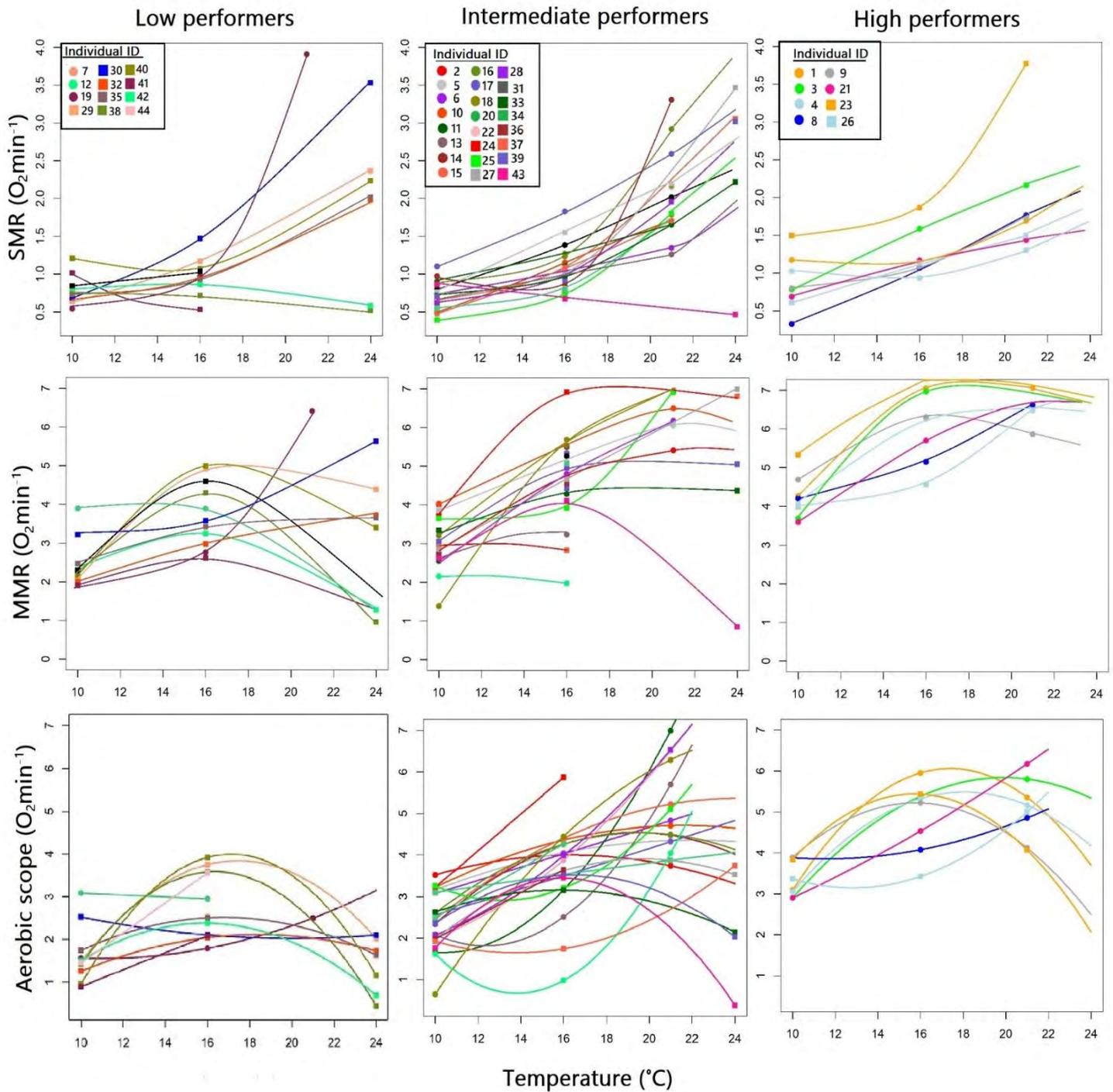
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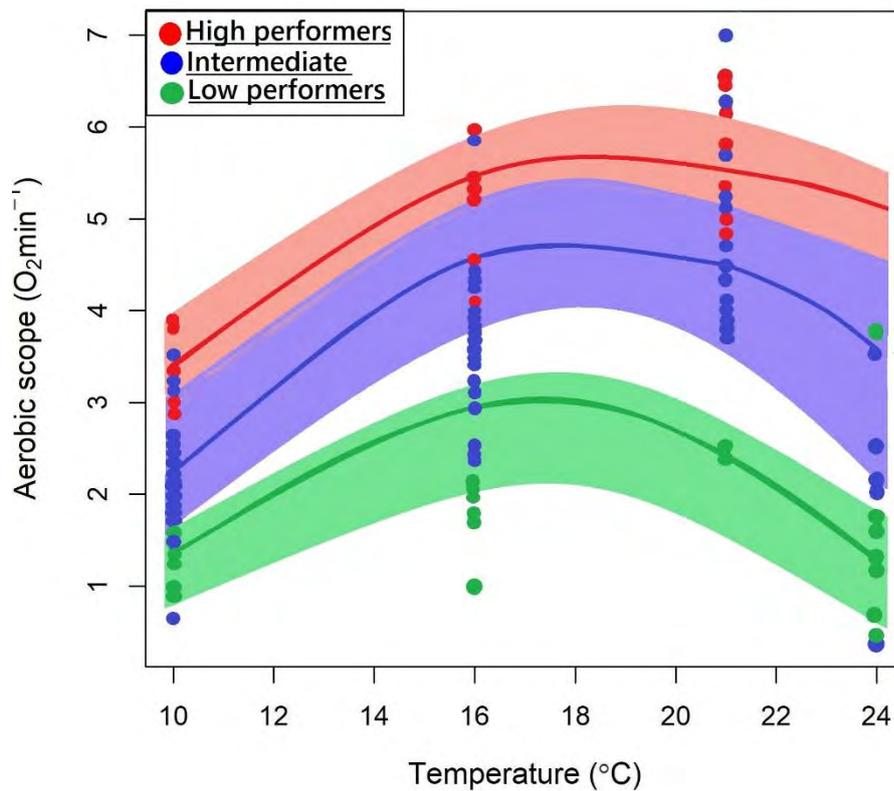
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1540 **Figure 3.8: The change in standard metabolic rate, maximum metabolic rate and aerobic scope**
 1541 **curves for high performers (>75 % percentile), intermediate performers (25 – 75 % percentile),**
 1542 **and low performers (<25 %) of an exploited *Chrysoblephus laticeps* population across a**
 1543 **temperature gradient (10 °C, 16 °C, 21 °C and 24 °C). An individual that was classified as a high**
 1544 **performer exhibited a broad tolerance to a thermally variable environment. An individual that**
 1545 **was classified as a low performer may have performed well at optimal temperatures, but may be**
 1546 **limited by aerobic performance in a thermally variable environment.**
 1547



1548

1549 **Figure 3.9: Overall aerobic scope curves for high, intermediate and low performers for an**
 1550 **exploited *Chrysoblephus laticeps* population across a temperature gradient (10 °C, 16 °C, 21 °C**
 1551 **and 24 °C) with shaded areas representing a 95 % confidence interval. High performers exhibited**
 1552 **a broad tolerance to a thermally variable environment. Low performers may have performed**
 1553 **well at optimal temperatures, but may be limited by aerobic performance in a thermally variable**
 1554 **environment.**

1555

1556

1557

1558

3.4 Discussion

1559 An understanding of physiological phenotype diversity and variation of phenotypes amongst
 1560 individuals is critical to understand the impacts of thermal variability on fished populations.

1561 To accurately assess how individuals differ in environmental sensitivity, there is a need to
 1562 assess performance repeatedly in the same individual across a range of test temperatures
 1563 (Gilbert and Miles 2017) as shown in this study. The results of this chapter identified
 1564 heterogeneity in physiological performance phenotypes amongst individuals of the exploited
 1565 Noordhoek *C. laticeps* population.

1566

1567 Temperature influenced SMR, MMR and AS. Standard metabolic rate increased at warmer
 1568 temperatures due to an increase in oxygen demand (i.e. reduction in oxygen saturation), which

1569 drove variation in SMR amongst individuals at warmer temperatures only (i.e. there was a lack
1570 of significance in SMR at cold temperatures). In contrast, the relationship between MMR and
1571 temperature significantly differed amongst individuals over all test temperatures (i.e. several
1572 individuals maintained elevated MMR at low temperatures), and variation amongst individuals
1573 increased with temperature. Similarly, aerobic scope curves differed significantly amongst
1574 individuals, across all test temperatures, with the greatest variation amongst individuals at
1575 upper test temperatures. There was significant variation in the aerobic performance of high,
1576 intermediate, and low performers at higher temperatures. However, differences in performance
1577 were not significant at low temperatures, where several intermediate performers maintained
1578 high performance. The performance of some intermediate performers was only high within a
1579 narrow range (i.e. either high or low temperatures where performance was higher than the 75th
1580 percentile of the mean performance range) and physiological performance was compromised
1581 (i.e. performance was lower than the 25th percentile of mean performance range) at other
1582 temperatures outside of this range. These individuals were not high performers across variable
1583 thermal environments. Alternatively, some intermediate performers maintained moderate
1584 levels of performance across thermal contexts, whereas low performers (i.e. 25th percentile)
1585 generally only maintained moderate physiological performance at ambient temperatures

1586

1587 It is likely that the reduction in oxygen saturation appeared to be a tipping point driving
1588 differences in aerobic performance, which allowed for the categorization of individuals. This
1589 study found that variability in the shape of performance curves determined the temperature
1590 range at which individuals may function above specified performance thresholds. For example,
1591 individuals that had a broad aerobic scope (i.e. a high AS over a wide range of temperatures)
1592 maintained higher than average physiological performance (>75 % of the upper percentile
1593 determined from the aerobic performance range for the species) across a thermal gradient (10
1594 °C to 24 °C). Although it has previously been suggested that generalists may be able to perform
1595 over a wider thermal gradient but compromise performance at optimal temperatures (as found
1596 in teleost fishes by Nati et al. 2016), the findings of this study do not support this (see Figure
1597 3.8 *a* and *b* high performers). Here the high performers have the broad aerobic capacity to
1598 remain active and forage across thermal conditions (in agreement with Killen et al. 2017, 2021
1599 who reviewed these patterns in shoaling fishes).

1600

1601 The shape of performance curves can determine the range of temperatures that an individual
1602 can function above performance thresholds (Killen et al. 2021). “High” performers in

1603 temperate environments are defined by a broad aerobic scope (or a broad difference between
1604 SMR and MMR; Portner et al. 2007) to maintain normal physiological functioning across a
1605 wider thermal gradient (Portner 2010; Portner et al. 2018). In contrast, high performers in
1606 relatively stable thermal environments, such as the tropics, may monopolize on very high rates
1607 of maximum performance through a steep aerobic scope (high SMR and high MMR; Chown
1608 et al. 2010; Neubauer and Anderson 2019).

1609
1610 It has been argued that the Oxygen Capacity Limited Thermal Tolerance (OCLTT) should not
1611 be applied to tropical species with steady increases in MMR that are unlikely to reach
1612 maximum performance in natural conditions; Chown et al. 2010; Portner et al. 2018; Neubauer
1613 and Anderson 2019). However, the OCLTT is relevant to species that may reach their oxygen
1614 limits in their ecological reality, such as those living in highly variable temperate coastal
1615 environments with frequent short-term exposure to both extreme high and low temperatures
1616 (Bates et al. 2018, 2019; Portner et al. 2018). In these environments, the OCLTT can be used
1617 to assess short-term tolerance to extreme environmental changes (Portner et al. 2018). Thermal
1618 variability may impose suboptimal energy conditions where it would be disadvantageous for
1619 high performers to be characterized by a high SMR. In agreement, high performers in the
1620 present study had a broad aerobic scope (low SMR and high MMR), which provided the
1621 energetic capacity to sustain activity across changing thermal conditions, in contrast to
1622 energetically-limited low performers that experienced reductions in performance. Future
1623 physiological performance phenotypes (i.e. individuals which are likely to be successful in
1624 their own environment in the future) will be selected based on their success in the context of
1625 future environmental changes. Hence, future performance phenotypes in temperate
1626 environments can be predicted by identifying individuals that have a broad range of
1627 performance across the thermally variable conditions, which according to Bates et al. (2019)
1628 are predicted to increase in the future.

1629
1630
1631 Thermal variability (upwelling and marine heat waves) has increased in the distributional range
1632 of *C. laticeps* (Schlegel et al. 2017; Duncan et al. 2019 – reviewed in Chapter 2). The present
1633 study detected a decline in performance in *C. laticeps* at higher temperatures and this is
1634 concerning as marine heat waves are expected to occur more frequently (Schlegel et al. 2017).
1635 Duncan et al. (2019) did not identify a statistically significant decline in population-level
1636 performance at acute temperatures of 24 °C, likely due to a low sample size for the exploited

1637 population and different experimental design (i.e. the lack of repeatable measures of
1638 performance in the same individual prevented the detection of the full thermal performance
1639 range of each individual; Killen et al. 2021). However, these temperatures are close to
1640 maximum cardiac breakpoint temperatures for *C. laticeps* (i.e. 23.92 °C and 25.19 °C; Skeeles
1641 et al. 2020). High temperatures several degrees below lethal temperatures not only decrease
1642 aerobic performance in stress-compromised low performers, but can cause secondary sub-
1643 lethal effects, such as bacterial infections (Lapointe et al. 2014; Watson et al. 2020), and
1644 damage to heat shock proteins that can result in permanent oxidative damage (Iwama et al.
1645 1998; Pichaud et al. 2020). It is possible that fished populations, such as the current Noordhoek
1646 population, have fewer HPMPs than protected populations – and will therefore be less resilient
1647 to changing thermal regimes (Bates et al. 2019; Duncan et al. 2019). However, this current
1648 study identified eight HPMPs as well as several LPMPs (the latter may be attributed to the
1649 exploited nature of the population, in agreement with several studies that have found that
1650 exploited populations have fewer HPMPs; Redpath et al. 2010; Duncan et al. 2019; Taboun
1651 2020). The reduced genetic variability of metabolic traits (which have been shown to be
1652 heritable; Long et al. 2021) has consequences for physiological acclimation and
1653 transgenerational acclimation to phenotypically adapt to environmental variation (Somero
1654 2010; Munday 2014). This emphasises the importance of the spatial protection of HPMPs to
1655 maintain genetic diversity and mitigate fisheries selection against HPMPs (i.e. through spill-
1656 over of MPAs into nearby fished areas; Ward et al. 2016; Bates et al. 2018, 2019).

1657

1658

1659 The heterogeneity of physiological phenotypes within the exploited *C. laticeps* population of
1660 Noordhoek is particularly striking as this population is heavily exploited (i.e. Duncan et al.
1661 2019 found fewer high performance phenotypes in this exploited population, relative to a
1662 protected population, and attributed this to the capture of the physiologically fittest individuals
1663 by the fishery). Although *C. laticeps* is heavily exploited, their populations are less vulnerable
1664 relative to other slow growing sparid species (e.g., *Chrysoblephus cristiceps*). This may be
1665 influenced by the social behaviour of *C. laticeps* populations or their high degree of metabolic
1666 phenotype diversity. This emphasises the importance of diversity in metabolic phenotypes and
1667 the need to examine metabolic phenotypes at an individual level if we are to fully understand
1668 the notion of metabolic phenotypic diversity (i.e. the HPMP and LPMP). Additionally, there is
1669 a need to compare the physiological phenotypes of an exploited population (i.e. through
1670 repeated measures in the same individual) with that of an unexploited population to see how

1671 the distribution of phenotypes differs. This will provide greater insight into the impact of
1672 exploitation on the physiology of fish populations. Fisheries selection of metabolic traits is an
1673 important research area, given that inter-individual variation in metabolic phenotypes will
1674 determine differences in how individuals cope with environmental variation (Ward et al. 2016).

1675

1676 In conclusion, individuals with a broad aerobic scope (i.e. high AS values across a range of
1677 temperatures) are likely to be the most resilient to short-term thermal variability caused by the
1678 marine heat waves and upwelling events present in temperate coastal environments. Since the
1679 shape of thermal performance curves differs among individuals and reflects the range at which
1680 individuals can function above specified performance thresholds, individual thermal
1681 performance must be measured repeatedly in the same individual over a thermal gradient
1682 (Killen et al. 2021).

1683

1684 Performance curves serve as physiological biomarkers that are directly linked to survival and
1685 fitness. These physiological biomarkers can detect responses to environmental change long
1686 before changes to population demographics are evident (the latter are typically used in long-
1687 term fisheries datasets; Killen et al. 2021). It is important to maintain physiological phenotype
1688 diversity to allow fish populations to respond to environmental variability. Future performance
1689 phenotypes in temperate environments can be identified by matching the predicted thermal
1690 variability with individuals that have a broad range of performance across thermally variable
1691 conditions. For example, high performers likely have the aerobic capacity to cope with thermal
1692 variability through phenotypic behavioural responses (e.g. exploratory behaviour and
1693 dispersal; Wong and Candolin 2015; Beever et al. 2017; Biro et al. 2018). Given the importance
1694 of individual physiological traits in determining climate resilience, it is critical to incorporate
1695 fisheries-selection on physiological traits as part of an evolutionary-based fisheries
1696 management approach (Uusi-Heikkilä et al. 2008; Ward et al. 2016).

1697

1698 Although there may be a link between physiology and behaviour, based on the findings in
1699 Chapter 1 (with bold personality traits have been linked to a broad aerobic scope, both of which
1700 are important to explore novel areas for dispersal; (Chapter 1, Bailey et al. 2022), this has not
1701 yet been assessed in *C. laticeps*. Given the importance of *C. laticeps* in the commercial fishery,
1702 understanding the link between a broad aerobic scope and behavioural syndromes is critical to
1703 understand and predict the consequences of fisheries-induced evolution in a changing
1704 environment, and will be addressed in the following chapter (Chapter 4).

1705 **Appendix A**

1706 **Table A1: Individual fish weight (mass in kg), length (mm) and sex.**

Fish	Mass (kg)	Fork length (mm)	Sex
1	1.453	364	Male
2	0.498	242	Female
3	0.606	270	Female
4	1.49	358	Male
5	0.7	290	Female
6	0.566	253	Intersex
7	1.37	348	Male
8	0.767	292	Female
9	0.592	249	Intersex
10	1.2	329	Male
11	0.692	280	Female
12	1.46	350	Male
13	1.672	370	Male
14	0.846	280	Female
15	0.389	225	Male
16	1.321	338	Male
17	1.151	325	Intersex
18	0.691	270	Female
19	1.561	346	Male
20	1.035	329	Female
21	0.693	260	Female
22	1.414	340	Male
23	1.162	325	Female
24	0.380	215	Female
25	0.821	260	Female
26	1.365	340	Male
27	0.384	230	Female
28	0.443	249	Intersex
29	1.265	-	Male
30	0.534	250	Female
31	0.365	238	Intersex
32	1.456	350	Male
33	1.332	348	Male
34	1.068	323	Intersex
35	0.699	270	Female
36	0.76	275	Female
37	0.338	215	Female
38	0.662	265	Female
39	0.436	308	Female
40	0.48	252	Intersex
41	0.407	216	Female
42	0.642	265	Intersex
43	1.483	340	Male
44	0.685	260	Female

1707

1708

1709

1710 **Table A2: Standard metabolic rate, maximum metabolic rate and aerobic scope for each**
 1711 **individual at 10 °C, 16 °C, 21 °C and 24 °C. Individuals were grouped into high performers (>75**
 1712 **% percentile) ('HP'), intermediate performers (25 – 75 % percentile) ('IP'), and low performers**
 1713 **(<25 %) ('LP') based on the aerobic scope range available for the species.**

Fish	Performance category	Temperature (°C)	SMR (O ₂ .min ⁻¹ .kg ⁻¹)	MMR (O ₂ .min ⁻¹ .kg ⁻¹) ¹⁾	Aerobic scope (O ₂ .min ⁻¹ .kg ⁻¹)
1	HP	16	1.0533	6.918	5.864
		10	1.127	4.186	3.059
		21	1.626	6.918	5.292
2	IP	16	0.811	4.915	4.104
		10	0.527	4.156	3.629
		21	1.810	5.611	3.807
3	HP	16	1.681	7.152	5.471
		10	0.830	3.782	2.952
		21	2.299	8.175	5.885
4	HP	16	0.892	6.133	5.241
		10	0.981	3.999	3.018
		21	1.248	6.338	5.090
5	IP	16	0.996	5.105	4.109
		10	0.762	3.959	3.197
		21	2.241	6.620	4.379
6	IP	16	0.830	4.949	4.119
		21	1.439	6.358	4.919
7	LP	16	0.845	3.349	2.503
8	HP	16	1.104	5.220	4.116
		10	0.337	4.267	3.930
		21	1.819	6.710	4.891
9	HP	16	1.152	6.478	5.326
		10	0.851	4.821	3.969
		21	1.853	6.024	4.172
10	IP	16	1.129	5.463	4.334
		10	0.796	3.993	3.197
		21	1.753	6.435	4.681
11	IP	16	1.171	4.363	3.192
		10	0.937	2.597	1.660
		21	1.628	7.532	5.904
12	LP	16	0.906	3.813	2.907
		10	0.774	3.819	3.044
13	IP	16	0.689	3.421	2.732
		10	0.526	2.798	2.272
		21	1.207	7.363	6.163
14	IP	16	1.259	5.395	4.136
		10	0.989	3.247	2.258
		21	3.361	7.644	4.283
15	IP	16	1.027	4.816	3.789
		10	0.523	2.642	2.119
		21	1.870	6.248	4.378
16	IP	16	1.238	5.705	4.466
		10	0.594	3.309	2.714
		21	2.844	7.646	4.802
17	IP	16	1.806	5.413	3.608
		10	1.087	3.716	2.628
		21	2.556	7.020	4.464

18	IP	16	1.278	5.454	4.176
		10	0.767	1.330	0.563
		21	2.251	8.124	5.873
19	LP	16	0.932	2.904	1.972
		10	0.522	2.215	1.693
		21	3.748	6.734	2.986
20	IP	16	0.991	1.981	0.990
		10	0.536	2.160	1.624
		21	2.012	6.082	4.070
21	HP	16	1.211	5.476	4.266
		10	0.714	3.452	2.738
		21	1.490	7.312	5.822
22	IP	16	1.339	5.465	4.127
		10	0.770	2.910	2.140
		21	1.952	8.857	6.901
23	HP	16	1.841	7.426	5.585
		10	1.475	5.420	3.945
		21	3.718	7.971	4.253
24	IP	16	1.146	6.212	5.066
		10	0.598	3.388	2.790
25	IP	16	0.732	3.835	3.103
		10	0.403	3.569	3.167
		21	1.838	6.754	4.916
26	HP	16	1.102	4.719	3.618
		10	0.591	4.116	3.525
		21	1.453	6.723	5.270
27	IP	16	1.695	4.574	2.879
		10	0.831	3.464	2.633
		21	2.410	5.462	3.052
28	IP	16	1.057	4.534	3.478
		10	0.673	2.463	1.789
		21	2.115	7.756	5.641
29	LP	16	1.170	4.918	3.748
		10	0.641	2.130	1.489
		24	2.365	4.387	2.022
30	LP	16	1.470	3.573	2.103
		10	0.688	3.214	2.526
		24	3.532	5.630	2.098
31	IP	16	1.038	4.662	3.624
		10	0.864	2.846	1.982
		24	3.467	6.993	3.526
32	LP	16	0.936	2.976	2.040
		10	0.741	1.997	1.256
		24	1.982	3.712	1.730
33	IP	16	0.939	4.087	3.148
		10	0.714	3.340	2.626
		24	2.219	4.366	2.147
34	IP	16	0.796	5.060	4.264
		10	0.549	3.043	2.494
35	LP	16	0.928	3.433	2.505
		10	0.729	2.469	1.740
		24	2.019	3.651	1.632
36	IP	16	0.879	4.522	3.643
		10	0.698	2.679	1.981
37	IP	16	1.085	2.827	1.742

		10	0.699	2.621	1.922
		24	3.053	6.799	3.746
38	LP	16	0.716	4.295	3.579
		10	0.840	2.261	1.421
		24	0.518	0.959	0.441
39	IP	16	0.909	4.421	3.512
		10	0.705	3.055	2.350
		24	3.019	5.048	2.029
40	LP	16	1.071	4.990	3.919
		10	1.210	2.165	0.955
		24	2.236	3.397	1.161
41	LP	16	0.533	2.616	2.083
		10	1.015	1.9100	0.895
42	LP	16	0.865	3.245	2.380
		10	0.809	2.312	1.503
		24	0.580	1.270	0.690
43	IP	16	0.671	4.113	3.442
		10	0.864	2.621	1.757
		24	0.465	0.846	0.381
44	LP	16	1.038	4.597	3.559
		10	0.843	2.294	1.451

1714

1715

1716 Chapter 4

1717 Plastic behavioural responses to cope with thermal variability are 1718 determined by both bold personality and a broad aerobic scope in 1719 a temperate fish species, *Chrysolephus laticeps*

1720

1721 4.1 Introduction

1722 Global anthropogenic climate change has driven frequent short-term changes in local climate
1723 conditions within the distributional ranges of coastal fish populations (Bates et al. 2018; Bates
1724 et al. 2019; Cooke et al. 2019). Of the climate change drivers, temperature is considered to
1725 have the greatest impact on fishes (Holt and Jorgensen 2015; Cattano et al. 2018; Laubenstein
1726 et al. 2018; Laubenstein et al. 2019). While warming is expected to drive change in the tropics
1727 and cold temperate regions, it appears that variability in thermal regimes may be a greater
1728 driver of change in sub-tropical, warm-temperate and cool-temperate regions (Bates et al. 2018,
1729 Bates et al. 2019). Thermal variability is likely to have a considerable effect on fishes as it
1730 impacts physiological performance and vital (i.e metabolism, foraging and swimming style;
1731 Brownscombe et al. 2014; Johansen et al. 2014; D'Agostina et al. 2019) and non-vital (i.e.
1732 reproductive fitness; Sims et al. 2004) energetic processes.

1733 When fish are subjected to thermal stress, they may respond with a behaviour response such as
1734 behavioural thermoregulation. Species that have broad phenotypic behavioural plasticity (i.e.
1735 defined as the ability to adjust behavioural activity in presiding environmental conditions in
1736 order to remain within their optimal thermal range; Biro and Stamps 2010; Biro et al. 2018;
1737 Wong and Candolin 2015; Beever et al. 2017) may have a competitive advantage. However, if
1738 alterations in behaviour are insufficient to ensure that the individual remains within their
1739 optimal thermal range, physiological acclimation (i.e. defined as the process in which an
1740 organism adjusts to prevailing conditions by broadening their thermal performance curve so
1741 that their performance is maximized in the new thermal environment, Fry 1958; Brett 1964;
1742 Chown et al. 2010; Donelson et al. 2012; Donelson et al. 2019; Neubauer and Anderson 2019)
1743 may be required. Therefore, there is a critical link between the behaviour and thermal
1744 physiology of fishes (Tinbergen 1963), particularly in a world where they are facing increasing
1745 thermal stress.

1746

1747 Fish behavioural plasticity may take many forms. Some species may seek out thermal refugia
1748 by changing their phenology or distribution (e.g., James et al. 2008; Freitas et al. 2015; Wong
1749 and Candolin 2015; Beever et al. 2017), while others alter the timing of their seasonal (Sousa
1750 et al. 2016) and spawning migrations (Sims et al. 2004) in response to a changing environment.
1751 Although fishes can use behavioural changes to cope with climate change impacts, there does
1752 appear to be variability in the behavioural responses within species (Gosling 2001; Dingemanse
1753 et al. 2007; Sih et al. 2004; Neubauer and Anderson 2019). Here, the behavioural response may
1754 be related to animal personality types, which can be divided into syndromes, such as bold (i.e.
1755 coupled traits of boldness, aggression and high activity; Sih et al. 2004) vs timid (i.e. timid,
1756 passive and more likely to hide; Sih et al. 2004) behaviour. In many cases, the variability in the
1757 behavioural response appears to be associated with physiology. For example, the expression of
1758 behavioural personality traits (e.g. bold ‘proactive’ stress recovery vs timid and highly
1759 ‘reactive’ to stressors through a ‘freeze-hide’ response; Sih et al. 2004; Reale et al. 2007) and
1760 their energetic drivers (e.g. high performance metabolic phenotypes vs low performance
1761 metabolic phenotypes; Chapter 3) will determine differences in individual performance across
1762 changing environmental conditions (Neubauer and Anderson 2019).

1763 Bold personality traits, described as the ability to explore and colonize new environments (Sih
1764 et al. 2004; McGaugh et al. 2020) are characterized by rapid stress recovery and high ‘fight-
1765 flight’ sympathetic activity (Almeida et al. 2009; Aubin-Horth et al. 2012; Tudorache et al.
1766 2013; Li et al. 2020). However, boldness may be intricately linked to an individual’s
1767 physiology. Consequently, only some individuals may be able to sustain high rates of
1768 performance across changing environmental conditions (i.e. behavioural plasticity) with the
1769 energetic capacity provided by a broad aerobic scope (low SMR and high MMR; Portner and
1770 Knust 2007; Portner et al. 2008; Clark et al. 2017; Biro et al. 2018; Neubauer and Anderson
1771 2019).

1772
1773 Generally, individuals with high performance metabolic phenotypes (HPMPs) that are
1774 characterized by a broad aerobic scope should exhibit behavioural plasticity across a range of
1775 temperatures, and be able to quickly recover from external stressors because of their reduced
1776 energetic requirements for basic metabolism and their ability to sustain high rates of activity
1777 across changing conditions (McLean et al. 2018; Jutfelt et al. 2018; Pörtner et al. 2018;
1778 Neubauer and Anderson 2019). These individuals often have a broader thermal tolerance and
1779 are likely to be selected for in heterogeneous environments, as individuals with a narrower

1780 aerobic scope (ie. low performance metabolic phenotypes; LMPM) may exhibit reduced
1781 performance (Neubauer and Anderson 2019). High performers may have the energetic capacity
1782 to facilitate behavioural plasticity (Biro et al. 2018). Indeed, behavioural plasticity has allowed
1783 many taxa to respond to climate variability by changing their phenology or distribution (Wong
1784 and Candolin 2015; Beever et al. 2017; Biro et al. 2018).

1785 There are few studies that have used aerobic scope to predict behavioural performance
1786 parameters in fishes (see Chapter 1, published as Bailey et al. 2022). The focus of these studies
1787 has been on freshwater species (e.g., Seebacher et al. 2013; Auer et al. 2015; Gomez et al.
1788 2020) or in stable tropical environments, where individuals with a narrow aerobic scope may
1789 still maximize their performance at extreme temperatures (e.g., Biro et al. 2010; Killen et al.
1790 2014; Warren and McCormick 2019). However, there is limited research on temperate coastal
1791 species, which likely require a broader aerobic performance window (Neubauer and Anderson
1792 2019) to tolerate the intense thermal variability attributed to frequent upwelling and marine
1793 heat wave events (Goshen and Schumann 1995; Bates et al. 2018; Bates et al. 2019) (see
1794 Chapter 2). Up to now, a single study on a temperate species (*Paralichthys olivaceus*) (Rupia
1795 et al. 2016) tested whether individuals of different behavioural types differ in their absolute
1796 aerobic scope, however this was not done in the context of changing temperature. They found
1797 that although fish with bold and timid behavioural phenotypes exhibited different metabolic
1798 responses across a salinity gradient, the relationship between personality and metabolic
1799 performance did not alter across salinity gradients. To date, the relationship between aerobic
1800 scope and the capacity for behavioural plasticity in individuals has yet to be examined in fishes
1801 (Bailey et al. 2022). This lack of understanding will make it difficult to predict how fish
1802 populations will respond to climate change, particularly since behavioural plasticity is
1803 important for many long-lived, resident temperate coastal reef species, given their limited
1804 dispersal ability and slow rates of genetic adaptation to rapidly changing thermal regimes
1805 (Somero 2010; Beever et al. 2017).

1806 The aim of this chapter is to understand the behavioural responses of a temperate, coastal fish
1807 species, *Chrysoblephus laticeps* to thermal variability, as a function of individual physiological
1808 and behavioural phenotypes. This is the first study on a fish species to link individual aerobic
1809 scope phenotype (i.e. high vs low performer) to individual behavioural plasticity across a
1810 thermal gradient.

1811

1812

1813 The objectives of the chapter were to:

1814 1) Determine behavioural types (bold vs timid) of individuals in the sampled population
1815 through a series of multi-trait behaviour tests at temperatures representing optimal thermal
1816 energetic conditions.

1817 2) Determine the plasticity of individual behavioural responses to the range of thermal
1818 variability associated with the species in its native distribution.

1819 3) Assess individual behavioural plasticity in relation to the energetic capacity provided by
1820 aerobic scope phenotypes identified in Chapter 3 (across the same thermal gradient).

1821

1822 It is hypothesised that bold personality individuals will be most active at ambient temperatures
1823 (16 °C; where timid individuals are likely to hide or to exhibit lower activity rates), while only
1824 those with a broader aerobic scope curves will be able to sustain bold behaviour traits across
1825 temperatures. In addition, it is hypothesised that bold fish and timid fish with a narrow aerobic
1826 scope curves will exhibit reductions in performance across a range of temperatures.

1827

1828 **4.2 Methods**

1829 **4.2.1 Experimental set-up:**

1830 A laboratory was designed and built for behavioural experiments at the Aquatic Ecophysiology
1831 Research Platform (AERP; South African Institute for Aquatic Biodiversity) situated at the
1832 Department of Ichthyology and Fisheries Science of Rhodes University. The laboratory housed
1833 12 x 1000 L circular isolation tanks (1050 mm diameter x 1200 mm height) for individual
1834 behavioural experiments. These tanks were painted an opaque blue colour to reduce external
1835 stimuli and potential anxiety-like behaviour during experiments (de Abreu et al. 2020).
1836 Experimental tanks were connected to a filtration system made up of a 750 L slimline sump,
1837 protein skimmer (UltraZap 250 MM with submerged PT 12 000 pump), bubble bead filter
1838 (BBF-200-COMP, Wilpet Koi Products), fluidised bed biological filter (750 L slimline tank
1839 with SuperActiFlo Media) and UV steriliser (UV 55 W, UltraZap Pro UVS 55). Two pool
1840 pumps (Speck Porpoise 0.75 kW) were used to recirculate water through the system. Air was
1841 supplied to the experimental tanks and bed filter via a 2.2 kW blower outside the laboratory. A
1842 heatpump (Aquaheat SF2020P) was used to maintain control temperatures of 16 °C and
1843 manipulate experimental temperatures of 10 °C and 21 °C in the experimental isolation tanks.

1844 **4.2.2 Individual multi-trait behavioural experiments:**

1845

1846 Multi-trait behavioural tests (see description below) were used to categorize the personality of
1847 28 individuals (for which physiology information was available; see Chapter 3), along the bold-
1848 timid continuum (i.e. high-activity bold vs low-activity timid fish; Carter et al. 2013, Rupia et
1849 al. 2016) at mean environmental temperature (16 °C) and extreme temperatures (10 °C and 22
1850 °C). Prior to the start of behavioural experiments, fish were kept in their housing tanks for a
1851 period of two weeks following the physiology experiments (Chapter 3). Following this, fish
1852 were fasted for 48 hours (Bell and Stamps 2004, Carmona-Catot et al. 2013) before being
1853 moved to a 1000 L circular isolation tank (1050 mm diameter x 1200 mm height). A video
1854 camera (Sports Cam 1080 Pixel) was mounted above each tank and the rate at which the
1855 individual explored the “novel” (tank) area was recorded for 20-minutes (as per the methods
1856 of Colleter and Brown 2011, Carmona-Catot et al. 2013). TOXTRAC software (Rodriguez et
1857 al. 2017, 2018) was used to create a digitized transect overlay of the experimental arena. This
1858 software calculates exploration rate as a percentage by comparing the pixelated transect area
1859 explored during the observation period as a function of the total tank area (Kane et al. 2004,
1860 Rodriguez et al. 2017, 2018) (Figure 4.1a).

1861 After recording the exploration rate, the propensity to feed in the novel environment was
1862 recorded. Propensity to feed is often used to differentiate between behaviour types as bold fish
1863 are likely to engage in risky behaviour sooner in a novel area (Cutts et al. 2001, Sloman et al.
1864 2001, Overli et al. 2006, Castanheira et al. 2013, Rupia et al. 2016). The time taken to feed
1865 (latency) and the number of food items eaten was recorded during a 10-minute observation
1866 period. A new food item was added every 2.5 minutes, and a maximum of four food items were
1867 prepared per individual based on a mass-based growth feeding regime (of 3 % of body mass
1868 per day for a 300 g to >1000 g fish; FAO 2012, Torfi Mozanzadeh et al. 2017). Fish received
1869 a risk score of four points for hand feeding (one point for each hand-fed piece), three points for
1870 eating within one minute, and one point for first feeding within two minutes. Fish received an
1871 additional point for each food item consumed during the observation period. Fish that did not
1872 feed received no points. An individual could receive a maximum of ten points and this was
1873 converted to a percentage score (points received divided by maximum points possible).

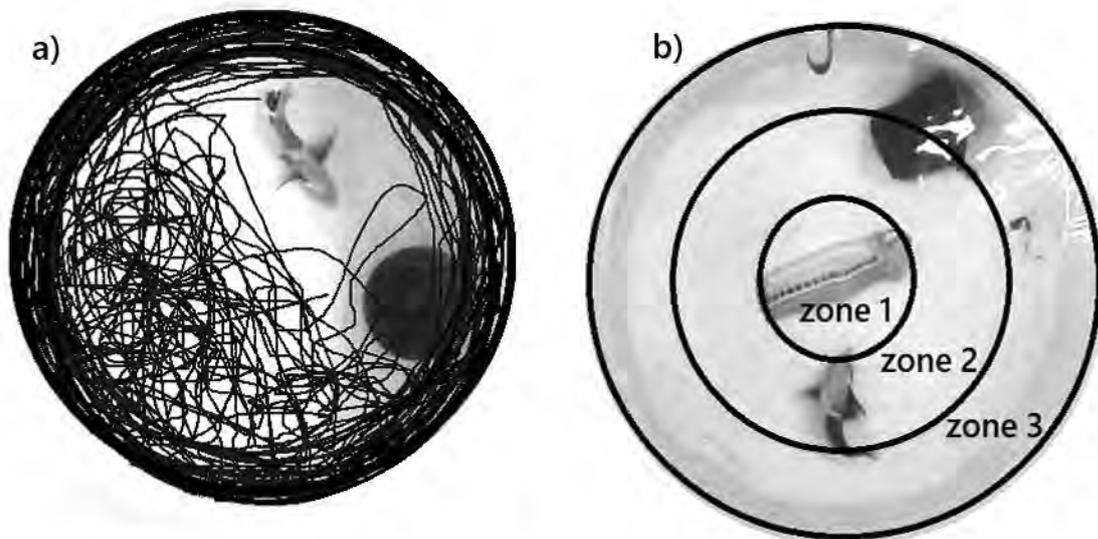
1874 After testing the propensity to feed, fish were acclimated for a period of one week to
1875 “normalize” behaviour at the mean environmental temperature (16 °C) prior to behavioural
1876 experiments. Fish were exposed to three behavioural experiments: an activity test, a novel
1877 object test and a mirror test (as per Adriaenssens and Johnsson 2013). An activity test (see
1878 description below) was done in the morning and the afternoon, and again on the morning of

1879 the following day. A novel object test (see description below) was conducted immediately after
1880 the activity test on the first morning, and a mirror test (see description below) immediately after
1881 the activity test in the afternoon. These experiments were conducted according to the repeated
1882 measures design outlined by Rupia et al. (2016).

1883 *Activity test*

1884 For the activity test, the procedure for recording individual exploration of the isolation tanks
1885 for a 30-minute observation period was repeated (Figure 4.1a). Activity recordings were
1886 repeated in the morning and the afternoon, as well as the following day. This provided the
1887 average diurnal activity level of each individual in a familiar environment where individuals
1888 displayed “natural” behaviour patterns (Cutts et al. 2001, Colleter and Brown 2011, Poulos and
1889 McCormick 2014). TOXTRAC software was used (Rodriguez et al. 2017, 2018) to create a
1890 digitized transect overlay of the experimental arena. This software calculates exploration rate
1891 as a percentage by comparing the pixelated transect area explored during the observation period
1892 as a function of the total tank area (Kane et al. 2004, Rodriguez et al. 2017, 2018) (Figure 4.1a).

1893



1894 **Figure 4.1: Graphical depiction of the calculation of exploration rate by comparing the pixelated**
1895 **transect area explored to the total tank area, using TOXTRAC software (a). Graphical depiction**
1896 **of tank zones used to calculate the proportion of time that an individual spent in each zone in**
1897 **proximity to the novel object (b).**

1899

1900

1901

1902 *Boldness test with a novel object*

1903 Boldness was quantified through a 10-minute novel object test (Carter et al. 2013, Colleter and
1904 Brown 2011, Rupia et al. 2016). The test began immediately after introducing a coloured crate
1905 (140 x 190 x 390 mm upscaled from Frost et al. 2007) to each tank. For each of the three
1906 thermal treatments, a different colour crate (orange, pink or green) was used. TOXTRAC
1907 software (Rodriguez et al. 2017, 2018) was used to create a digitized transect overlay of the
1908 experimental arena, with the tank divided into three distinct zones (Figure 4.1b). Zone one was
1909 a 30 cm radius directly surrounding the novel object, zone two was a 60 cm radius around the
1910 novel object, and zone three comprised the outer surrounding area to the tank wall (Castanheira
1911 et al. 2013) (Figure 4.1b). The latency time (in seconds) to enter the inner radius directly
1912 surrounding the novel object was measured. TOXTRAC was used to calculate the proportion
1913 of time in each of the three zones. The time spent in each zone was multiplied by a weighted
1914 score and added together to produce a final percentage score (see Table 4.1).

1915 **Table 4.1: Calculation of the proportion of time that an individual spent in proximity to the**
1916 **novel object**

Zone	Description	Weighted score
1	30 cm radius around novel object	100 % *
2	60 cm radius around novel object	85 %
3	Outer zone to tank wall	15 %

* An additional 10 % was given for immediately entering zone 1.

* An additional 5 % was given for entering zone 1 within a minute.

1917
1918

1919 *Mirror test*

1920 To measure individual aggression, a 60 cm x 40 cm mirror was placed into each tank (Figure
1921 4.2). The mirror was large enough for the individual to see throughout the 10-minute recording
1922 period. An individual received points for each aggressive behaviour, ranked from the most to
1923 least aggressive response, towards its mirrored reflection (Ros et al. 2006, Colleter and Brown
1924 2011) (see Table 4.2). Only aggressive behaviours typical of the species (as defined in Table
1925 4.2) were accounted for. An individual could receive a maximum of 100 points for the
1926 observation period and this was converted to a percentage.

1927



1937 **Figure 4.2: A *Chrysoblephus laticeps* male examining (left) and attacking (note head display;**
 1938 **right) its mirrored image.**

1939 **Table 4.2: Points given for each aggressive behaviour, ranked from the most to the least**
 1940 **aggressive response**

Aggressive behaviour	Points
Attack or bite	3
Head display	2
Charge (swims in direction of mirror)	1
Lateral display	1
Hide or flee	0

1941 On completion of the initial round of behavioural experiments at 16 °C, fish remained at control
 1942 temperatures for three days. Following this, the temperature in the tanks was decreased by ± 1
 1943 °C per hour (to reduce thermal stress, Duncan 2019) to 10 °C. Fish were acclimated for two
 1944 days before the activity, novel object (a different colour crate, viz. orange, pink or green, was
 1945 used) and mirror test was repeated. Immediately after the completion of the behavioural
 1946 experiments at 10 °C, the temperature in the tanks was increased by ± 1 °C per hour to 16 °C,
 1947 where fish remained at control temperatures for three days. Following this, the temperature in
 1948 the tanks was increased by ± 1 °C per hour to 21 °C. Fish were then acclimated for two days
 1949 before repeating the same three tests.

1950
 1951 **4.2.3 Data analysis:**

1952 **4.2.3.1. Classifying behavioural phenotypes of individuals**

1953 Behavioural assays scores for each test (i.e. exploration, propensity to feed, activity, boldness,
 1954 and aggression scores) at each temperature for each fish were calculated and analysed in a
 1955 correlation matrix using the Spearman rank's correlation coefficient (all behavioural assay
 1956 scores were converted to a percentage score to create same unit). Since behavioural assay
 1957 scores were positively correlated (i.e. positive correlations occurred between bold traits such
 1958 as high activity, boldness and high aggression; vs timid traits such as low activity, low boldness

1959 and low aggression; see the change of each trait with temperature plotted in the results below),
1960 the behavioural assays were collapsed into a single composite behavioural score for each
1961 temperature treatment using Principal Component Analysis (PCA). A PCA with the package
1962 ‘Vegan’ in R version 3.3.3 (R Core Team 2017) was used to generate a single principal
1963 component reflecting the degree of boldness for each individual. Hence, the composite
1964 behavioural score generated from the PCA (see the composite scores in Table B1 of Appendix
1965 B) was a combination of the scores for the suite of bold or timid behavioural traits.

1966 The individual composite behavioural scores for each individual at each temperature treatment
1967 were interpreted as a reflection of variation along the bold-timid continuum. To separate
1968 individuals into groups along the bold-timid continuum, a Ward’s linkage hierarchical cluster
1969 analysis was used on the principal components (Rupia et al. 2016). The silhouette function in
1970 the R package ‘cluster’ was then used to measure an individual’s degree of membership to a
1971 cluster. Individuals were assigned to a cluster based on the average distance from cluster
1972 members, and the distance from the next adjacent cluster (Borcard et al. 2011). Silhouette
1973 widths ranged from -1 to 1, where positive values indicated a tighter cluster. Behavioural types
1974 were divided into two groups (see Figure 3.3a) where PCA scores > 0 were classified as bold,
1975 while those < 0 were classified as timid.

1976

1977 **4.2.3.2 Determining individual behavioural plasticity with temperature**

1978

1979 *Activity*

1980 To examine the effect of temperature on each of the behavioural traits (i.e. activity, aggression
1981 and boldness), mixed effects models were used to account for repeated measures in individuals
1982 (i.e. each individual was measured repeatedly at each test temperature) (Bolker et al. 2009;
1983 Zuur 2009; Harrison et al. 2018). The model assumptions (i.e. for the normality of residuals)
1984 were checked using diagnostic plots (Bolker et al. 2009; Zuur 2009). To account for the
1985 bounded distribution of percentage data (i.e. percentage scores are bounded from 0 to 100,
1986 which suggests that the data does not follow a normal gaussian distribution), a mixed effects
1987 modelling approach was implemented using the *glmmTMB* package with the “beta” family and
1988 link “logit” (Brookes et al. 2017) in R version 3.3.3 (R Core Team 2017). The effect of
1989 temperature on activity was tested by modelling a second order polynomial relationship
1990 between percentage scores for activity and temperature, with a random effects structure
1991 weighted by fish ID and temperature. Hence, the variation of each individual was taken into

1992 account by including it as a random effect. The model also takes into account that each
1993 individual has a different relationship between activity levels and temperature, and this
1994 temperature effect is included as a random slope in the random effects structure with individual
1995 as the random intercept (i.e. temp|ID; Harrison et al. 2018). Fish size and sex were not
1996 significant in predicting activity data in the initial model ($p > 0.05$, $t = 2.693$, $df = 26$) and these
1997 variables were then excluded from further model analyses (i.e. data was pooled between the
1998 sexes and weight classes) (R Core Team 2017).

1999

2000 *Aggression*

2001 To examine the effect of temperature on aggression percentage scores (i.e. which do not follow
2002 a normal distribution), a mixed effects modelling approach was implemented using the
2003 *glmmTMB* package with the “beta” family and link “logit” (Brookes et al. 2017) in R version
2004 3.3.3 (R Core Team 2017). Differences in the percentage scores for aggression amongst
2005 individuals were tested by modelling a second order polynomial relationship between
2006 aggression percentage score data and temperature, with a random effects structure weighted by
2007 fish ID and temperature. Hence, the variation of each individual was accounted for by including
2008 it as a random effect. Furthermore, the model also takes into account that each individual has
2009 a different relationship between aggressive behaviour and temperature, and this temperature
2010 effect is included as a random slope in the random effects structure with individual as the
2011 random intercept (i.e. temp|ID; Harrison et al. 2018). Fish mass (kg) was included in the model
2012 as a fixed effect. Sex was not significant in predicting aggression data in the initial model ($p >$
2013 0.05 , $t = -0.807$, $df = 26$) and was then excluded from further model analyses (i.e. data was
2014 pooled between the sexes) (R Core Team 2017).

2015

2016 *Boldness*

2017 As with aggression, a mixed effects modelling approach was implemented using the *glmmTMB*
2018 package with the “beta” family and link “logit” (Brookes et al. 2017) in R version 3.3.3 (R
2019 Core Team 2017) to examine the effect of temperature on boldness percentage scores (i.e.
2020 percentage scores bounded between 0 and 100 do not follow a normal distribution). The effect
2021 of temperature on boldness was tested by modelling a second order polynomial relationship
2022 between boldness percentage score data and temperature, with a random effects structure
2023 weighted by fish ID and temperature (i.e. variation of each individual was accounted for by

2024 including it as a random effect). Similar to the model above, the model takes into account that
2025 each individual has a different relationship between temperature and boldness, and this
2026 temperature effect is included as a random slope in the random effects structure with individual
2027 as the random intercept (i.e. temp|ID; Harrison et al. 2018). Fish mass (kg) was included in the
2028 model as a fixed effect. Sex was not a significant prediction factor in the initial model ($p >$
2029 0.05 , $t = -1.512$, $df = 26$) and was then excluded from further model analyses (R Core Team
2030 2017).

2031
2032

2033 *Composite behavioural score*

2034 To interrogate overall behavioural plasticity across temperature, the above behavioural assays
2035 were combined into a single composite behavioural score for each temperature treatment (see
2036 section 4.3.2.1; Table B1 Appendix B). The model assumptions were checked using diagnostic
2037 plots (Bolker et al. 2009; Zuur 2009). Based on the diagnostic plots, a non-linear mixed effects
2038 modelling approach was implemented using the *nlme* package (Pinheiro et al. 2017) to account
2039 for the heteroscedasticity of composite behavioural scores. Inter-individual differences in
2040 behavioural plasticity were examined by modelling a second order polynomial relationship
2041 between log-transformed composite behavioural scores and temperature, and a random effects
2042 structure was fitted by random slopes weighted by fish ID and temperature (Harrison et al.
2043 2018). Individual slopes of the change in behavioural composite scores with temperature is a
2044 measure of individual behavioural plasticity (i.e. a stronger behavioural response to changing
2045 temperature; Biro et al. 2010). Sex ($p = 0.48$, $t = -0.710$, $df = 26$) and size were not significant
2046 variables ($p = 0.532$, $t = 0.634$, $df = 26$) in the initial model and were removed from the analyses
2047 (i.e. data was pooled over sexes and size classes).

2048

2049 **4.2.3.3. Linking behaviour traits with metabolic performance**

2050 Behavioural phenotypes were linked to metabolic performance using Principal Component
2051 Analyses (i.e. PCA) and cluster analyses. Individual composite behavioural scores for each
2052 temperature treatment were classified as a reflection of variation along the bold-timid
2053 continuum, and a Ward's linkage hierarchical cluster analysis was used on the principal
2054 components. Aerobic performance information (high performers (>75 % percentile),
2055 intermediate performers (25 – 75 % percentile), or low performers (<25 %) from each
2056 individual (see Chapter 3) was incorporated into the PCA. The incorporation of aerobic

2057 performance into the PCA resulted in three distinct clusters. The silhouette function in the R
2058 package ‘cluster’ was then used to measure an individual’s degree of membership to a cluster
2059 (average silhouette width of 0.81). Individuals were assigned to a cluster based on the average
2060 distance from cluster members, and the distance from the next adjacent cluster (Borcard et al.
2061 2011). Silhouette widths ranged from -1 to 1, where positive values indicated a tighter cluster.

2062

2063 **4.2.3.4. Determining individual behavioural plasticity in relation to metabolic phenotype**

2064

2065 A general linear model was used (i.e. model assumptions were checked using diagnostic plots
2066 (Bolker et al. 2009; Zuur 2009) to assess how individuals differ in their behavioural plasticity
2067 and predictability with temperature as a function of aerobic scope phenotype. Behavioural
2068 plasticity, taken by the linear slope of regression modelling the change in behaviour (using the
2069 overall behavioural composite score) with temperature (see section 4.2.3.2. above), was the
2070 response variable. Covariance was fitted separately for each aerobic phenotype category (i.e.
2071 high, intermediate vs low performer; see Chapter 3) as an interaction term with personality type
2072 (i.e. bold vs timid). The intercept of the regression was taken as a measure of behavioural
2073 predictability (i.e. whether individuals that had higher behavioural composite scores than others
2074 at one temperature also tended to maintain these high behavioural scores across other
2075 temperatures; Biro et al. 2010, 2018) (Section 4.2.3.2.). Hence, the variation of each individual
2076 was accounted for by including it as a random effect. The model output was assessed using the
2077 Dredge function with the libraries mvtnorm and MuMIn from the ‘CRAN’ R package. Weight
2078 class and sex were removed as fixed effect factors with no significant effect on the model ($p >$
2079 $0,05$; $t = -0,954$, $df = 26$).

2080

2081

2082 **4.3 Results:**

2083

2084 **4.3.1 Classifying the behavioural phenotypes of individuals**

2085 The percentage scores for the activity assay ranged between 7.00 % and 71.50 % at 10 °C,
2086 between 5.0 % and 94.0% at 16 °C, and between 8.0 % and 97.5 % at 21 °C. Boldness
2087 percentage scores ranged between at 15.0 % and 77.3 % at 10 °C, between 15.0 % and 90.0 %
2088 at 16 °C, and between 15.0 % and 89.9 % at 21 °C (Table B1 in Appendix B). The percentage
2089 scores for the aggression behavioural assay ranged between 0.1 % and 100 % at each test
2090 temperature. High percentage scores for activity, boldness and aggression were positively
2091 correlated ($p = 0.013$, $r = 0.79$, $df = 26$; Spearman’s rank correlation) and hence these

2092 behavioural assays were combined into a composite score for each individual in each thermal
 2093 context.

2094
 2095 When suites of bold and timid behavioural traits were collapsed into principal component
 2096 scores, principal component 1 (i.e. PC1) explained 79.6 % of the variation (eigenvalue =
 2097 3114.03) in behaviour (Table 4.3), while PC2 explained 10.9 % (eigenvalue = 427.04) of the
 2098 variation in behaviour, at optimal temperatures. High scores for aggression, activity and
 2099 boldness loaded positively onto PC1, while low scores loaded positively onto PC2. In other
 2100 words, the spread of timid individuals (blue) across the PC2 axis is indicating that some fish
 2101 with negative PC2 values were particularly low scoring in the exploratory trait and propensity
 2102 to feed. While those with positive PC2 were particularly low scoring in terms of aggression
 2103 and boldness. These behavioural traits constitute a suite of bold behavioural traits where bold
 2104 individuals exhibit higher levels of activity and aggression, in comparison to timid individuals.
 2105 Hence, high scores on PC1 were interpreted as high levels of boldness (Figure 4.3).

2106 Composite scores along PC1 were grouped into two distinct behavioural types, where scores
 2107 above zero were interpreted as bold, and scores below zero were interpreted as timid (Figure
 2108 4.3). Clustering within the bold and timid groups was different, with the timid group more
 2109 tightly clustered around the mean (silhouette width = 62, $df = 16$) when compared with bold
 2110 individuals (silhouette width = 55, $df = 11$) (Figure 4.3). Individual behavioural scores (i.e.
 2111 these ranged along a continuum from -82.49 to 73.74; Table B1 in Appendix B) varied across
 2112 thermal treatments.

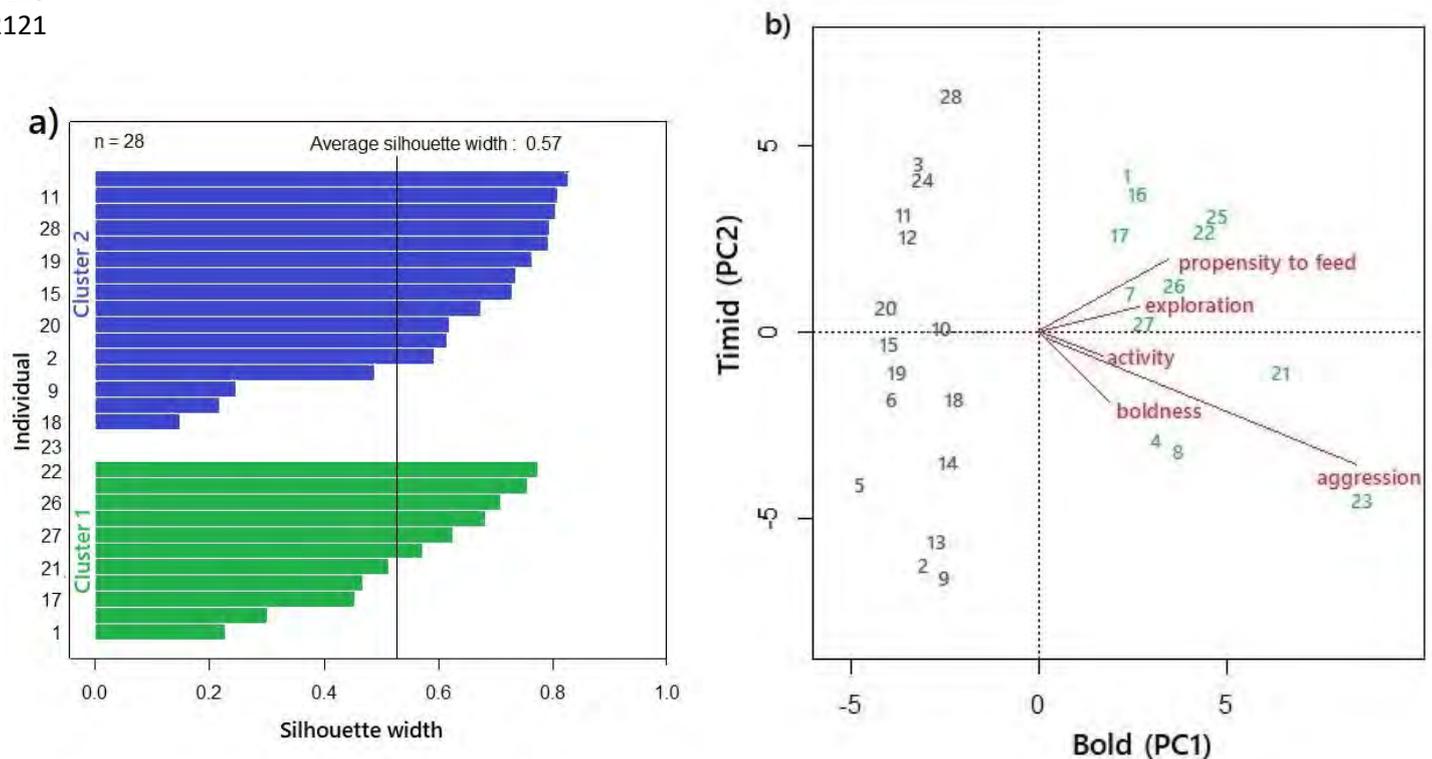
2113

2114 **Table 4.3: Results of the principal component analyses used to classify individual behavioural**
 2115 **traits of *Chrysoblephus laticeps* measured across a thermal gradient (i.e. temperatures of 10 °C,**
 2116 **16 °C, 21 °C). Correlation loadings are between PC1 (for each temperature trial) and between**
 2117 **behavioural variables: 1) activity, 2) aggression, 3) boldness, 4) exploration of the novel tank area,**
 2118 **5) feeding in a novel environment.**

2119

Principal component	% variance		Activity	Aggression	Boldness	Exploration	Feeding
PC1 16 °C	79.56	Loadings	1.717	9.146	2.060	0.953	0.994
		Correlation	0.880	0.994	0.953	0.631	0.769
PC1 10 °C	85.09	Loadings	-0.038	0.044	-0.127	-	-
		Correlation	0.846	0.937	0.986	-	-
PC1 21 °C	91.00	Loadings	-0.078	0.107	0.097	-	-
		Correlation	0.906	0.953	0.993	-	-

2120
2121



2122

2123 **Figure 4.3: Classification of *Chrysolephus laticeps* individuals into bold vs timid behavioural**
2124 **groups (a) (i.e. based on behavioural tests for boldness, aggression activity and exploration) via**
2125 **principal component analysis of individual behavioural traits (b). Note: High scores for**
2126 **aggression and activity, boldness loaded positively onto PC1, while low scores loaded positively**
2127 **onto PC2. Composite scores along PC1 were grouped into two distinct behavioural types, bold**
2128 **(cluster 1 highlighted in green) and timid (cluster 2 highlighted in blue) (a), where scores above**
2129 **0 were interpreted as bold, and scores below zero were interpreted as timid (b).**

2130

2131 4.3.2 Behavioural plasticity with temperature

2132 Activity levels were lowest at 10 °C for all individuals (Figure 4.4a). However, individuals
2133 consistently differed in activity levels at low temperatures of 10 °C, where some individuals
2134 maintained higher activity levels relative to others, as indicated by the random intercept effect
2135 (random intercept effect: $p < 0.021$; $t = 2.377$; $df = 26$). On average, individual activity rates
2136 increased by 1.75 fold from 10 °C to 21 °C and this trend was significant ($p < 0.001$, $t = 6.273$,
2137 $df = 26$, $r = 0.89$; Figure 4.4 and Figure 4.5a; Table 4.4).

2138 Average aggression also increased significantly (by 2.32 fold) from 10 °C to 21 °C ($p = 0.004$,
2139 $t = 3.013$, $df = 26$, $r = 0.61$; Figure 4.4, Figure 4.5a, Table 4.5). Size was a significant
2140 determinant of aggression, with larger individuals exhibiting the highest aggression scores (p
2141 $= 0.018$, $t = 2.521$, $df = 26$, Table 4.5). Some individuals maintained similar aggressive

2142 behaviour across thermal contexts (eg. individual three, five and 19; Figure 4.5b). Others
 2143 exhibited a steeper increase in aggression with temperature (eg. individual one, four, seven and
 2144 26; Figure 4.5b) and hence higher plasticity in aggressive behaviour.

2145 Although boldness increased by 1.03 fold with a temperature increase from 10 °C to 21 °C, this
 2146 increase was not significant ($p > 0.05$, $t = 0.127$, $df = 26$, $r = 0.59$; Figure 4.4; Figure 4.5b;
 2147 Table 4.6). Size was however a significant determinant of boldness ($p = <0.001$, $t = 4.277$, df
 2148 $=26$; Table 4.6), with larger fish receiving higher scores in the novel objects test.

2149 **Table 4.4: Mixed effects model (*glmmTMB*) results for variation in percentage scores for activity**
 2150 **data amongst individuals of an exploited population of *Chrysolephus laticeps* at temperatures of**
 2151 **10 °C, 16 °C and 21 °C. The correlation coefficient ‘*r*’ depicts the relationship between activity**
 2152 **and temperature. Bold *p*-values depict significant variation in activity data.**

2153

Random effect	Variance	SD		
Individual	0.003	0.01		
Temperature	0.002	0.01		
Dispersion parameter for beta family	11.20			
Fixed effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	-0.561	0.01	2.377	0.021
Temperature	-0.065	0.39	6.273	<0.001
Temperature ²	0.006	0.01	6.579	<0.001
<i>R</i>	0.89			
AIC	55.04			
Residual SE	14.190			
	(<i>df</i> = 26)			

2154

2155

2156 **Table 4.5: Mixed effects model (*glmmTMB*) results for variation in percentage scores for the**
 2157 **aggression test (mirror test) amongst individuals of an exploited population of *Chrysolephus***
 2158 ***laticeps* at temperatures of 10 °C, 16 °C and 21 °C. The correlation coefficient ‘*r*’ depicts the**
 2159 **relationship between aggression and temperature. Bold *p-values* depict significant variation in**
 2160 **aggression data.**

2161

Random effect	Variance	SD
Individual	0.005	0.01
Temperature	0.007	0.01

Dispersion parameter	1.10
for beta family	

Fixed effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	-4.008	0.15	-1.414	0.163
Temperature	0.398	0.01	3.013	0.004
Temperature ²	-0.010	0.03	8.551	<0.001
Size	0.191	0.01	2.521	0.018

<i>R</i>	0.61
AIC	105.72
Residual SE	0.463
	(<i>df</i> = 26)

2162

2163

2164

2165 **Table 4.6: Mixed effects model (*glmmTMB*) results for variation in percentage scores for a**
2166 **boldness test (novel object) amongst individuals of an exploited population of *Chrysolephus***
2167 ***laticeps* at temperatures of 10 °C, 16 °C and 21 °C. The correlation coefficient ‘*r*’ depicts the**
2168 **relationship between aggression and temperature. Bold *p-values* depict significant variation in**
2169 **boldness scores.**

Random effect	Variance	SD
Individual	0.003	0.06
Temperature	0.003	0.01

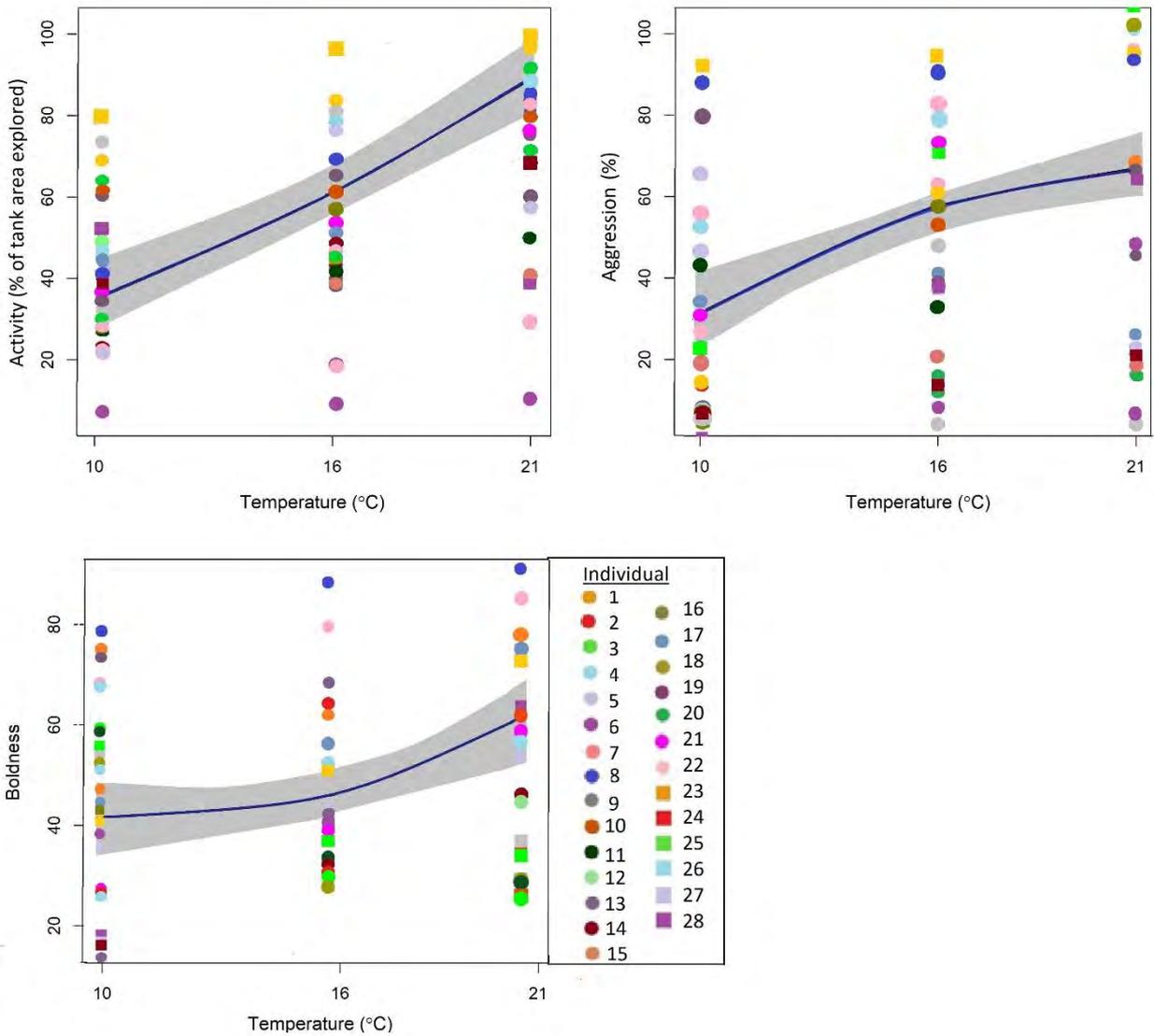
Dispersion parameter 11.7
for beta family

Fixed effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	1.616	1.00	1.017	0.313
Temperature	0.049	0.388	0.127	0.899
Temperature ²	0.117	0.110	1.064	0.292
Size	11.118	2.599	4.277	<0.001

R 0.59
AIC 46.06
Residual SE 14.08
(*df* = 26)

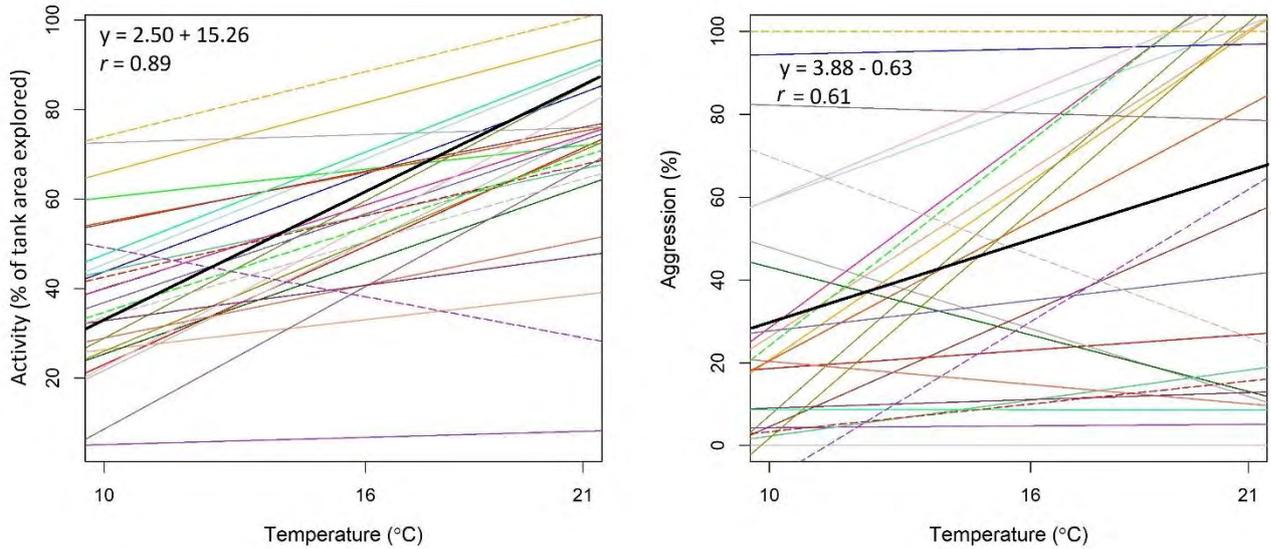
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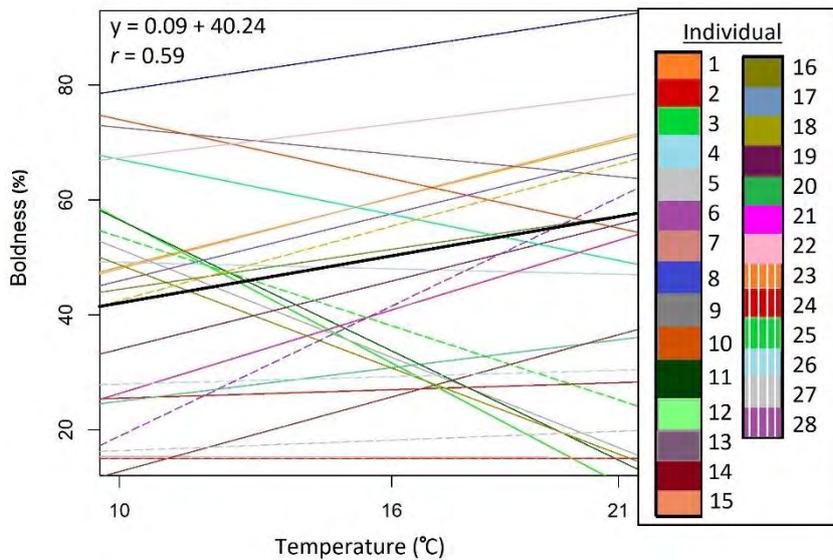
2172

2173 **Figure 4.4: The effect of temperature (10 °C, 16 °C and 21 °C) on the aggression, activity and**
 2174 **boldness of individual *Chrysolephus laticeps* from an exploited population, Noordhoek coastal**
 2175 **zone, Eastern Cape, South Africa in 2021. The curve represents the model of best fit for the**
 2176 **population with shaded areas representing a 95 % confidence interval.**



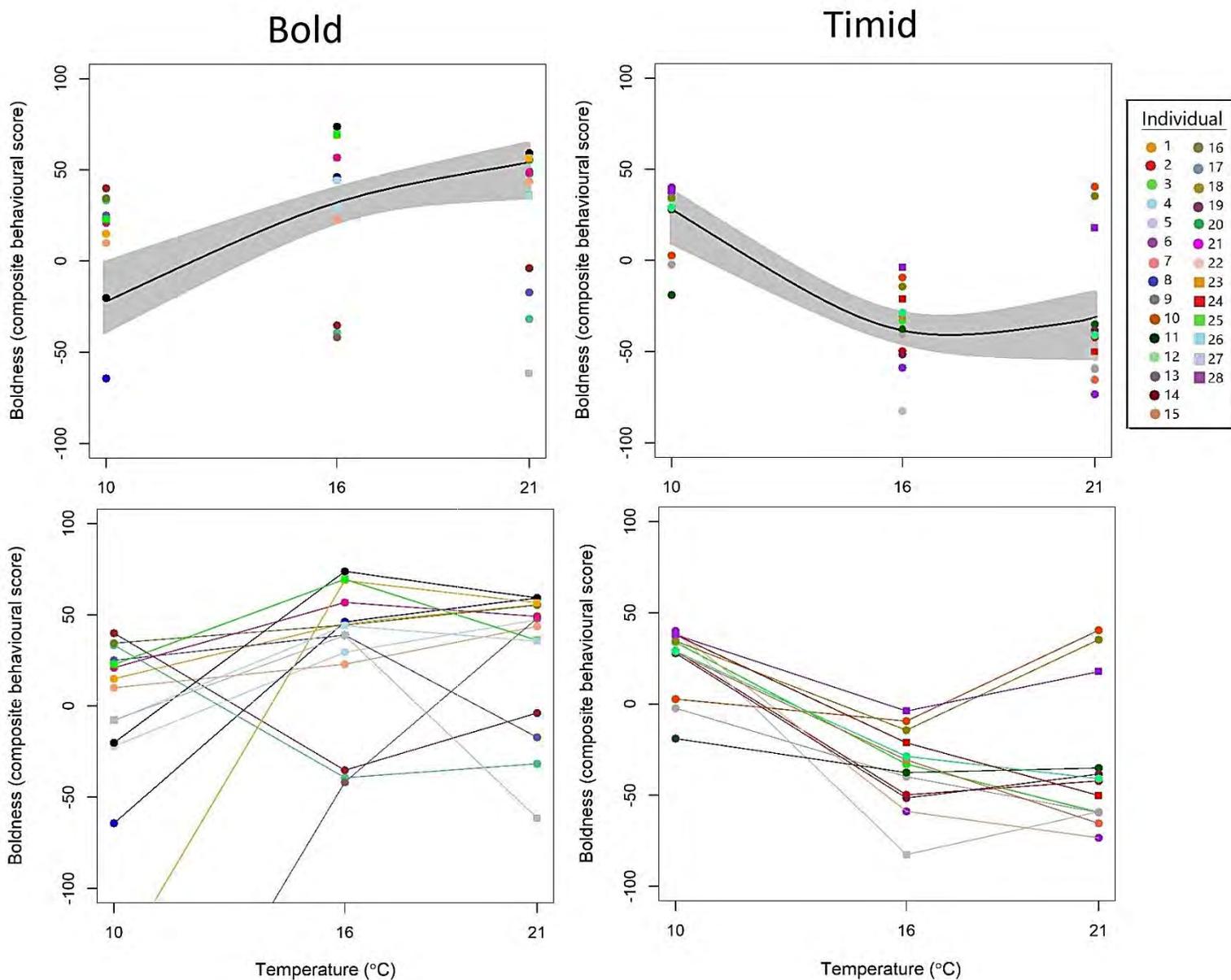
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Figure 4.5a: Individual and mean (thick black line) activity (expressed as % of the tank area explored) and aggression (expressed as a % in a mirror test) across a thermal gradient (10 °C, 16 °C and 21 °C) in an exploited population of *Chrysolephus laticeps*.



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Figure 4.5b: Relationship between individual boldness (i.e. exploration of a novel object) and temperature for an exploited population of *Chrysolephus laticeps* from Noordhoek coastal zone, Eastern Cape, South Africa. The thick black line is the population mean.



2190 **Figure 4.6: Results of the mixed effects model representing the change in boldness (i.e. high**
 2191 **composite behavioural scores for activity, aggression and boldness in approaching novel objects)**
 2192 **across temperatures of 10 °C, 16 °C and 21 °C in bold and timid individuals of *Chrysoblephus***
 2193 ***laticeps* sampled from Noordhoek coastal zone, Eastern Cape, South Africa in 2021.**

2194

2195 Individuals consistently differed in their behavioural composite scores (i.e. combined scores
 2196 for aggression, activity and boldness in approaching a novel object) at low temperatures
 2197 (random intercept effect: $p < 0.001$; $t = 6.569$; $df = 26$; Table 4.7), and the difference in this
 2198 composite score between individuals increased significantly with increasing temperature (p
 2199 0.020 ; $t = 2.388$; $df = 26$; Table 4.7).

2200

2201 **Table 4.7: Non-linear mixed effects (*nlme*) model results for variation in percentage scores for**
2202 **composite behavioural scores (i.e. combined scores for aggression, activity and boldness in**
2203 **approaching a novel object) amongst individuals of an exploited population of *Chrysoblephus***
2204 ***laticeps* at temperatures of 10 °C, 16 °C and 21 °C. The correlation coefficient ‘*r*’ depicts the**
2205 **relationship between composite behaviour scores and temperature. Bold *p*-values depict**
2206 **significant variation in composite behaviour scores.**

2207

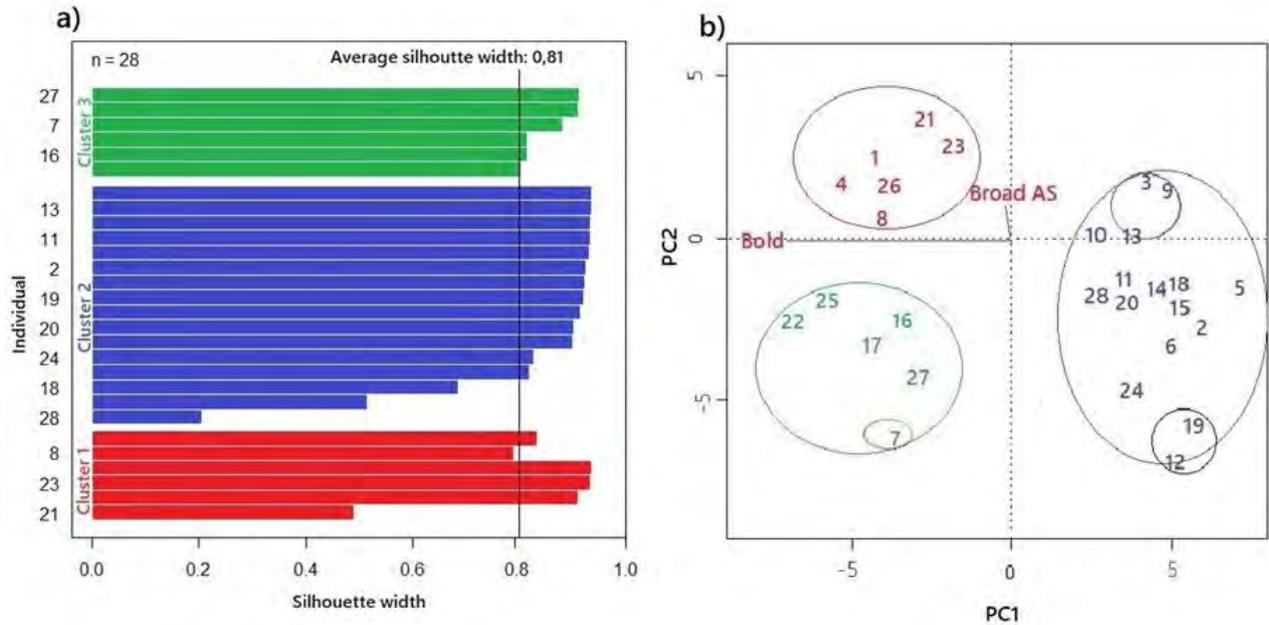
Random effect	SD			
Individual	0.39			
Temperature	0.00			
<hr/>				
Residual	0.249			
<hr/>				
Fixed effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	1.194	0.1817	6.569	<0.001
Temperature	0.020	0.008	2.388	0.020
Temperature ²	0.001	0.001	0.684	0.497
<hr/>				
<i>r</i>	0.808			
AIC	75.75535			
Residual SE	0.249 (<i>df</i> =			
	26)			

2208

2209

2210 **3.2.3. Linking behaviour traits with metabolic performance**

2211 The separation of bold and timid phenotypes (by composite score) became more apparent when
2212 metabolic performance was assigned to each individual and resulted in three distinct clusters
2213 (average silhouette width of 0.81) (Figure 4.7). Cluster one comprised bold individuals with
2214 high aerobic performance (silhouette width = 0.81), cluster two comprised timid individuals of
2215 primarily intermediate aerobic performance (silhouette width = 0.82), although it had two small
2216 subgroups of high and low performance respectively, while cluster three comprised bold
2217 individuals with intermediate performance (silhouette width = 0.82), and a single individual of
2218 low performance (Figure 4.7b).



2219

2220 **Figure 4.7 The clustering of behavioural phenotypes as a function of aerobic scope in an exploited**
 2221 **population of *Chrysoblephus laticeps* collected from Noordhoek coastal zone, Eastern Cape, South**
 2222 **Africa in 2021. Note: Cluster one (red) is comprised of bold high performers. Cluster two (blue)**
 2223 **is comprised of timid intermediate performance, as well as two small subgroups of high and low**
 2224 **performance respectively. Cluster three (green) is comprised of bold intermediate performers**
 2225 **with a single low performer.**

2226

2227 4.3.3 Determining individual behavioural plasticity in relation to metabolic phenotype

2228 Individual differences in behavioural plasticity (i.e. slope variance) were constrained by
 2229 aerobic scope ($p < 0.05$, $t = 2.076$, $df = 24$; Figure 4.8 and Figure 4.9; Table 4.8). High aerobic
 2230 performers had significantly higher behavioural plasticity (i.e. a steeper slope; $p = 0.048$; $t =$
 2231 2.076 ; Table 4.8) than intermediate aerobic performers ($p > 0.05$, $t = -0.744$; Table 4.8). While
 2232 the composite score for boldness did not influence behavioural plasticity alone ($p = 0.127$, $t =$
 2233 1.538 , $df = 24$; Table 4.8), boldness (i.e. composite score) as an interaction term with high
 2234 aerobic performance resulted in the highest behavioural plasticity ($p = 0.004$, $t = 3.185$, $df = 24$;
 2235 Table 4.8), relative to any other phenotype combination. Fish with a timid phenotype and high
 2236 aerobic scope did not have significant behavioural responses to changing temperatures ($p > 0.05$,
 2237 $t = 1.314$, $df = 24$) (Table 4.8, Figure 4.8 and 4.9).

2238 Intermediate performers did not exhibit significant behavioural plasticity ($p > 0.05$, $t = 0.744$,
 2239 $df = 24$; Table 4.8). Individuals that were on the the high end of intermediate performers had a
 2240 high intercept where high rates of boldness were predictably maintained across temperature
 2241 contexts, resulting in low plasticity (i.e. a high and flat trend line). Alternatively, the scores

2242 associated with bold behaviour decreased and altered their rank order and personality with
 2243 increases in temperature. Other intermediate performers, particularly individuals on the low
 2244 end of intermediate aerobic performance exhibited low activity and low boldness (i.e. in
 2245 approaching the novel object) across temperature contexts (i.e. a low and flat trend line; Table
 2246 4.8, Figure 4.8 and 4.9).

2247

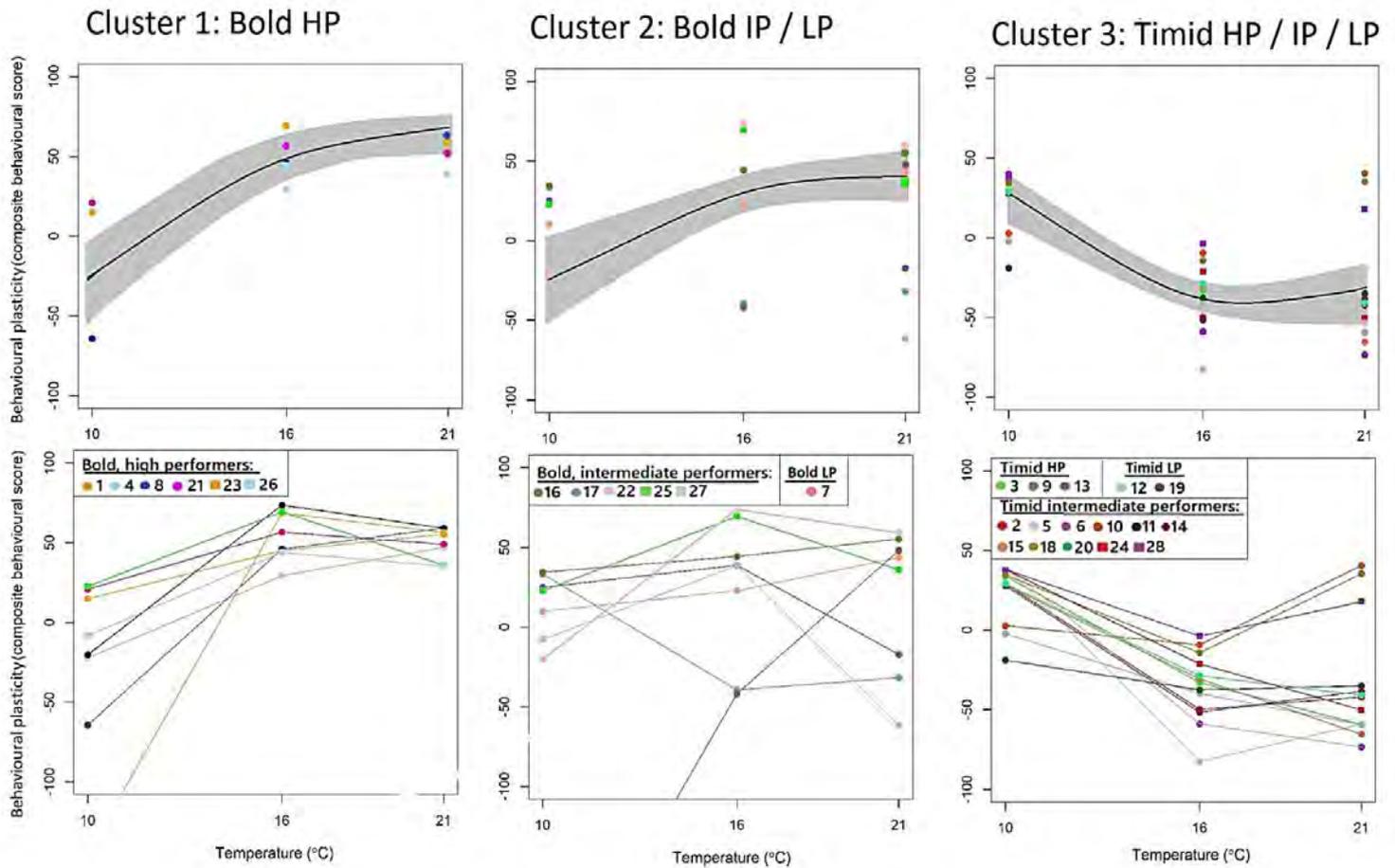
2248 **Table 4.8: Generalized linear model results for inter-individual differences in behavioural**
 2249 **plasticity (i.e. slope variance of behavioural change with temperature) by aerobic scope phenotype**
 2250 **in an exploited population of *Chrysoblephus laticeps* at temperatures of 10 °C, 16 °C and 21 °C.**
 2251 **Bold *p-values* depict significant variation in composite behaviour scores with temperature (i.e.**
 2252 **behavioural plasticity).**

Effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	-20.070	1.567	-1.281	0.212
Int. Performer	-12.94	1.740	-0.744	0.464
High performer	39.540	19.05	2.076	0.048
Boldness	20.320	1.284	1.583	0.127
Low/int. Performer: timid	0.353	2.049	0.017	0.986
Int. Performer: bold	0.6585	2.403	0.027	0.979
High performer: timid	33.764	2.569	1.314	0.202
High performer: bold	69.172	2.171	3.185	0.004
AIC	283.74			
Residual SE	3.068 (<i>df</i> = 24)			

2253

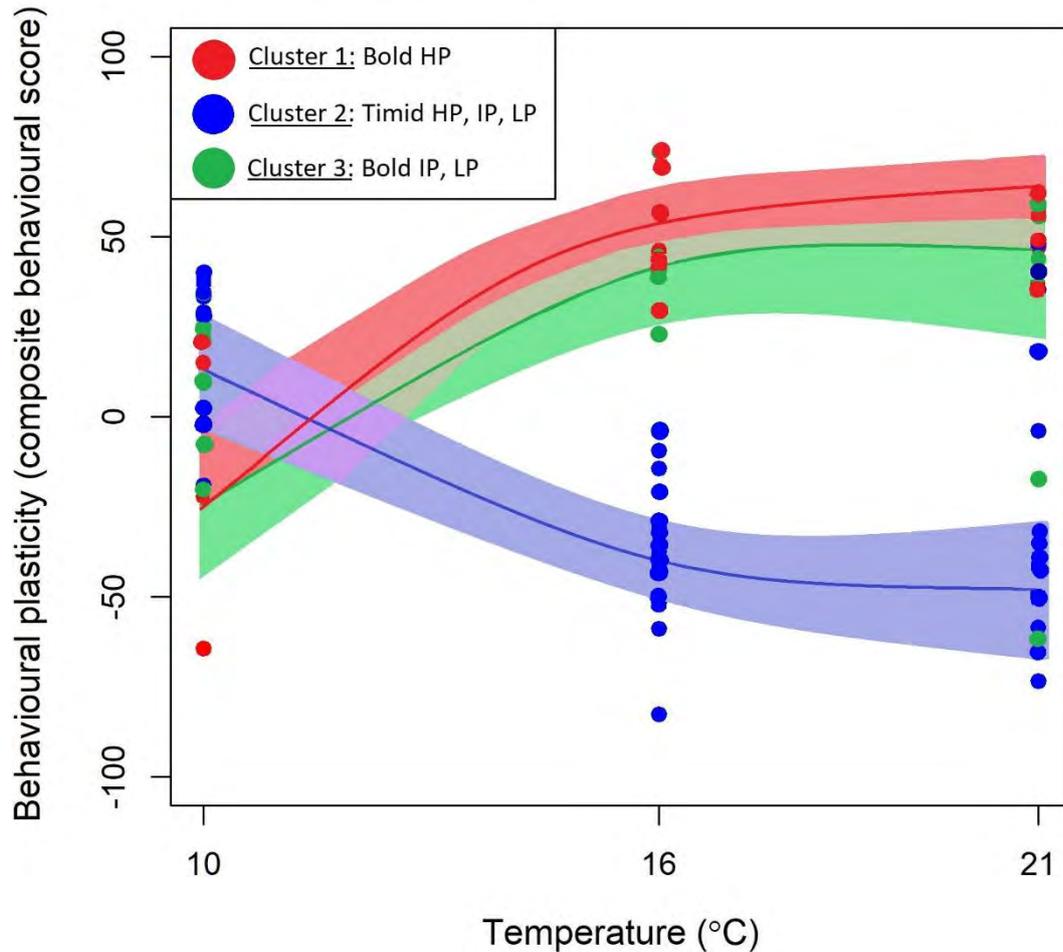
2254

2255 **Figure 4.8: Results of the mixed effects model representing the change in behavioural plasticity**



2256 (i.e, overall composite behavioural scores for activity, aggression and boldness in approaching
 2257 novel objects) across temperatures of 10 °C, 16 °C and 21 °C in bold high performers (HP; Cluster
 2258 1), bold intermediate and low performers (IP and LP; Cluster 2), and timid individuals (Cluster
 2259 3) of *Chrysolephus laticeps* sampled from Noordhoek coastal zone, Eastern cape, South Africa in
 2260 2021.

2261



2262
 2263 **Figure 4.9: Inter-individual differences in behavioural plasticity (i.e. slope variance of**
 2264 **behavioural change with temperature) by aerobic scope phenotype in an exploited population of**
 2265 ***Chrysolephus laticeps* exposed to test temperatures of 10 °C, 16 °C and 21 °C.**

2266

2267 4.4 Discussion

2268 The ability to respond to climate change through plastic behavioural responses is thought to be
 2269 dependent on physiological and behavioural phenotypic traits. Indeed, *Chrysolephus laticeps*
 2270 individuals with both a high aerobic performance phenotype and bold behavioural phenotype
 2271 had the most plastic behavioural response to thermal variability, highlighting the importance
 2272 of understanding the link between behaviour and physiology at both a population and
 2273 individual level. Bold individuals had higher levels of aggression, exploratory activity, risk
 2274 behaviour and quicker propensity to feed in a novel environment. The maintenance of these
 2275 bold personality traits at a range of temperatures (as found by Biro et al. 2010 and Warren and
 2276 McCormick 2019) were however dependent on the aerobic performance of the individual. This
 2277 suggests that metabolism may be an important driver of animal personality. Indeed, the

2278 inability of individuals with low aerobic performance to maintain bold personality traits at a
2279 range of temperatures suggests that behavioural plasticity was constrained by aerobic scope.
2280 This finding concurs with that of Biro et al (2018) who found that aerobic scope provided scope
2281 for behavioural plasticity in rodents (*Mus musculus*). In this study, bold, high aerobic
2282 performers had the capacity to sustain bold personality traits across variable temperatures, and
2283 as a result, had the ability to maintain their behavioural traits in a thermally variable
2284 environment when compared with all other combinations of physiological and behavioural
2285 phenotypes.

2286
2287 Bold individuals have been shown to survive better in response to abiotic (Long et al. 2021)
2288 and biotic stressors (Behrens et al. 2019), however this study suggests that metabolic traits
2289 influence the plastic expression of behaviour across an environmental gradient. Similarly,
2290 Enders et al. (2019 study on *Notropis percobromus*), found that thermal preferences were not
2291 related to bold and timid phenotypes, but were dependent on the oxygen limitations of aerobic
2292 metabolism. In the case of *C. laticeps*, individuals with reduced aerobic capacity for
2293 behavioural plasticity initially appeared bold at ambient temperature but were unable to
2294 maintain bold behaviours at extreme temperatures, which caused a shift to a timid personality.
2295 Similarly, Ruiz Gomez (2008) found that dominance behaviours in feeding *Oncorhynchus*
2296 *mykiss* offspring were only maintained in individuals that exhibited behavioural plasticity,
2297 while those that could not, lost the initial expression of dominance following repeated
2298 measures. Therefore, in the context of a changing climate, it is likely that bold individuals with
2299 low aerobic capacity may become timid.

2300 Changes in temperature may induce the physiological stress and increase oxygen demand in
2301 individuals with low aerobic capacity, causing the suppression of energetically expensive bold
2302 behavioural traits (i.e. aggression; Seth et al. 2013; Killen et al. 2013, or activity; D'Agostina
2303 et al. 2019). In this study, all individuals with a low aerobic scope exhibited lower rates of
2304 activity, boldness or aggression when thermal conditions moved away from optimal. In
2305 contrast, individuals with high aerobic capacity maintained their bold behavioural traits in a
2306 variable thermal environment (in agreement with Biro et al. 2010). This suggests that the ability
2307 to maintain bold behavioural traits and exhibit behavioural plasticity is linked to a greater
2308 aerobic capacity to sustain optimal rates of activity and rapidly recover from O₂ debt. A broad
2309 aerobic scope curve has previously been linked to higher rates of activity (Rupia et al. 2016),
2310 dominance and aggressive or bold behaviour (Seebacher et al. 2013; Killen et al. 2014).

2311 However, this is the first study to find a link between the maintenance of activity and high
2312 aerobic capacity across a thermal range in fishes.

2313
2314 Killen et al. (2021) found that individuals may vary in the expression of behavioural plasticity
2315 depending on the severity of the environmental stressor. In the present study on *C. laticeps*, the
2316 relationship between metabolic performance and behavioural plasticity was apparent under
2317 cold (10 °C) and warm (21 °C) thermal stress. This is within their normal thermal range.
2318 However, colder and warmer extremes may mediate this relationship. Interestingly, timid
2319 individuals had the highest dominance scores at 10 °C, in cases surpassing those of bold
2320 individuals (Figure 4.9). This suggests that foraging success for these individuals may be
2321 greatest at cold temperatures. However, it is possible that this pattern may be masked at lower
2322 temperatures, particularly since Duncan et al. (2019) found that *C. laticeps* populations entered
2323 cold shock at 8 °C. Similarly, extreme warm temperatures (24 °C) reduced the physiological
2324 performance in this species (see Chapter 3). Therefore, since extreme temperatures may impact
2325 the performance of individuals regardless of phenotype (Killen et al. 2013, 2014), it is critical
2326 to conserve high performers that are more likely to have the capacity to respond to the predicted
2327 increase in the frequency and intensity of upwelling events and heat waves in temperate coastal
2328 zones (Bates et al. 2019).

2329 This study provides empirical evidence that high performers are linked to bold phenotypes,
2330 supporting the previous findings that bold, fitter individuals are more vulnerable to capture
2331 (Alos et al. 2012; Koeck et al. 2018). Indeed, fishing may reduce the resilience of fished
2332 populations to environmental variation by selecting for the removal of bold high performers
2333 that are likely to encounter and bite fishing gear (Alos et al. 2012; Koeck et al. 2018; Duncan
2334 et al. 2019). These are the same individuals that are likely to exhibit behavioural plasticity, as
2335 was observed in this study, and were indeed associated with exploratory risk behaviour in
2336 approaching and biting novel objects. Fishing may reduce the diversity of behavioural
2337 phenotypes (Cooke et al. 2007) by selecting for a timidity syndrome in fished populations and
2338 this may be linked to high stress reactivity and reduced exploratory behaviour (Arlinghaus et
2339 al. 2017; Moynes et al. 2019; Alioravainen 2020; Satterfield et al. 2020). However, for fishing-
2340 induced evolution to occur on physiological (eg. Duncan et al. 2019) and behavioural traits
2341 (Cooke et al. 2007; Arlinghaus et al. 2017; Moynes et al. 2019), these traits would need to be
2342 heritable. Researchers have recently isolated genes linked to the expression of metabolic traits
2343 associated with heat stress (Beemelmanns et al. 2020; Taboun 2020) and hypoxia (Zou et al.

2344 2022), as well as behavioural traits (i.e. mirror elicited aggression; Baran and Streelman 2020,
2345 amongst others; Ariyomo et al. 2013; Edenbrow and Croft 2013; Laine et al. 2014). For
2346 example, Zou et al. (2021) found that bold and timid *Paralichthys olivaceus* differed in the
2347 expression of 144 genes related to personality and metabolism. Long et al. (2021) found that
2348 offspring of the same species contained a mix of bold and timid phenotypes irrespective of
2349 maternal line, however behavioural traits were linked to metabolic traits, which were partly
2350 heritable due to maternal effects. Both bold and timid offspring from the bold maternal line
2351 had the advantage of a higher metabolic rate and the ability to respond to environmental
2352 stressors (Long et al. 2021). Muller (2022) provided evidence for the heritability of metabolic
2353 traits in *C. laticeps*. Therefore, the selection of heritable physiological and behavioural traits
2354 that are related to behavioural plasticity by fishery suggests that evolutionary-based
2355 management approaches are necessary (Ward et al. 2016). For example, marine protected areas
2356 can prioritize the protection of the fittest individuals with the aerobic capacity to respond to
2357 climate variability through behavioural plasticity, allowing these individuals to reproduce and
2358 supply nearby fished areas (Ward et al. 2016; Moynes et al. 2019).

2359
2360 In conclusion, this study provided evidence that high performance metabolic traits provide the
2361 scope for plasticity in bold behavioural responses to thermal variability. This emphasises the
2362 importance of protecting the fittest individuals with the aerobic capacity to respond to climate
2363 variability through behavioural plasticity. The expression of individual metabolic and
2364 behavioural phenotypes consistently determined performance across contexts, suggesting that
2365 individual traits can be used to predict performance in social groups (Castenheira et al. 2013;
2366 Hansen et al. 2020). However, previous research has shown that a social context may modulate
2367 the links between foraging activity and behaviour (Hansen et al. 2020). Hence, competitive
2368 foraging behaviour should be measured within a social hierarchy in relation to individual
2369 physiological and behavioural phenotype. Additionally, the validation of laboratory studies in
2370 the field is necessary and can be achieved using acoustic telemetry studies (Metcalf et al.
2371 2012; Killen et al. 2013). These kinds of studies will assist in assessing the coupled impacts of
2372 multiple climate stressors, biotic stressors and overexploitation on phenotypic traits.

2373

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2377

2378 **Appendix B**

2379 **Table B1: Behavioural assay scores for each fish at each temperature treatment. Final**
 2380 **composite scores for each individual at each temperature treatment were created by combining**
 2381 **behavioural assay scores in a principal component analysis.**

2382 **Note: Aggression scores were cut off at a maximum of 100 points (to note, exceptionally**
 2383 **aggressive individuals that received more than double these points are highlighted in bold).**
 2384

Fish ID	Temp (°C)	Propensity to feed (% score)	Exploration (% score)	Activity (% score)	Aggression (% score)	Boldness (% score)	Composite score from PCA
1	16	80.00	74.00	79.00	63.00	60.40	45.18
	10			67.00	21.00	48.30	14.86
	21			96.00	100.00	70.25	55.42
2	16	0.10	3.00	54.00	42.00	31.00	-49.75
	10			21.00	10.00	23.68	29.04
	21			69.00	16.50	26.00	-42.09
3	16	40.00	65.00	63.00	0.10	21.20	-32.95
	10			62.00	0.10	61.38	33.87
	21			74.00	0.10	16.51	-59.40
4	16	60.00	35.00	59.00	85.00	44.80	29.49
	10			50.00	58.00	50.62	-22.12
	21			94.00	100.00 (269 points)	48.77	47.17
5	16	0.10	3.00	43.00	0.10	15.57	-82.49
	10			25.00	0.10	15.23	39.94
	21			78.00	0.10	15.00	-59.09
6	16	30.00	7.00	7.00	14.00	15.00	-58.87
	10			5.00	0.10	15.00	40.00
	21			8.00	0.10	15.00	-73.44
7	16	70.00	36.00	36.00	67.00	60.82	22.84
	10			25.00	26.00	47.84	10.00
	21			37.00	100.00	70.43	43.51
8	16	40.00	75.00	76.00	90.00	89.98	46.08
	10			39.00	97.00	77.29	-64.26
	21			78.00	100.00	89.90	59.11
9	16	0.10	3.00	78.00	50.00	35.00	-39.92
	10			71.00	38.00	50.35	-2.31
	21			74.00	0.10	15.60	-59.60
10	16	60.00	18.00	59.00	33.00	65.29	-9.36
	10			58.00	30.00	73.26	2.65
	21			79.00	93.50	54.20	40.33
11	16	60.00	22.00	40.00	5.00	15.00	-37.60
	10			28.00	53.00	65.05	-19.04
	21			66.00	25.00	25.03	-35.15
12	16	40.00	42.00	45.00	5.00	24.35	-39.38
	10			49.00	5.00	27.86	33.36
	21			73.00	21.50	39.17	-31.66
13	16	0.10	17.00	16.50	41.00	78.21	-41.89
	10			19.50	100.00 (289 points)	67.94	-53.39
	21			80.00	100.00 (215 points)	58.42	48.05
14	16	0.10	43.00	55.30	42.00	20.75	-35.30
	10			59.50	0.10	15.00	39.87
	21			82.00	50.00	39.27	-3.90

15	16	0.10	76.33	49.33	33.00	15.00	-30.64
	10			25.00	12.00	15.00	28.12
	21			46.00	0.10	15.00	-65.43
16	16	65.00	89.00	51.66	78.00	23.17	44.29
	10			32.50	0.10	57.28	34.39
	21			89.50	100.00	72.63	55.30
17	16	70.00	71.00	37.67	74.00	41.31	38.72
	10			45.50	10.00	53.34	25.06
	21			83.50	20.00	76.23	-17.12
18	16	5.00	66.00	37.30	60.00	15.00	-14.30
	10			32.00	0.10	55.91	34.56
	21			78.00	100.00	24.45	35.25
19	16	0.10	52.17	40.33	9.00	50.92	-51.63
	10			33.00	10.00	31.69	27.89
	21			47.50	14.00	52.96	-38.46
20	16	0.10	80.00	81.67	19.00	50.92	-28.77
	10			42.50	4.00	70.03	28.82
	21			83.50	3.00	53.03	-41.00
21	16	80.00	58.00	44.33	100.00	28.30	56.76
	10			46.50	17.00	32.04	20.88
	21			82.00	100.00 (214 points)	59.78	49.14
22	16	100.00	59.00	44.25	100.00	60.59	73.74
	10			27.00	53.00	73.08	-20.14
	21			86.00	100.00	84.98	59.26
23	16	70.00	80.00	94.00	100.00 (249 points)	46.73	68.79
	10			71.50	100.00	46.45	-56.65
	21			97.50	100.00 (289 points)	70.93	59.26
24	16	40.00	67.00	74.00	13.00	15.00	-21.25
	10			34.50	2.00	15.00	37.97
	21			58.00	14.00	15.00	-50.16
25	16	90.00	73.33	46.33	100.00	32.60	69.49
	10			38.00	12.00	56.04	22.70
	21			73.50	100.00	28.27	35.89
26	16	60.00	65.67	58.00	89.00	36.52	43.95
	10			38.50	47.00	26.34	-8.14
	21			77.50	100.00	24.64	35.40
27	16	40.00	77.33	67.00	94.00	18.27	38.70
	10			26.00	48.00	16.28	-7.80
	21			55.5	0.10	19.67	-61.49
28	16	70	80.33	42.00	11.00	17.27	-3.93
	10			47.50	0.10	29.88	37.88
	21			27.00	72.00	73.62	17.71

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2392 **Chapter 5**

2393 **Social dominance across thermally variable conditions is** 2394 **predicted by high metabolic performance in a bidirectional** 2395 **hermaphroditic fish**

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2397

2398 **5.1 Introduction**

2399

2400 The coupled effects of climate change and unsustainable fishing practices act to degrade marine
2401 habitats and alter the competitive interactions for finite resources within reef assemblages and
2402 amongst members of fish social groups (Munday et al. 2008; Biro et al. 2009, Biro et al. 2010;
2403 Seebacher et al. 2013; Wong & Buston 2013; Wong & Candolin et al. 2015; Warren et al.
2404 2016; Killen et al. 2017; Warren and McCormick 2019). The ability of fishes to capture and
2405 compete for resources in an increasingly variable thermal climate will be dependent on the
2406 plasticity of their metabolic and social behavioural traits, such as activity, aggression and
2407 boldness (Biro et al. 2010; Wong & Buston 2013; Wong & Candolin et al. 2015; Warren et al.
2408 2016; Pruitt et al. 2018). For example, moderate increases in temperature can raise metabolic
2409 rate and increase aggressive competition for food or mates amongst conspecifics by two to six-
2410 fold (Biro et al. 2009; Biro et al. 2010, Warren et al. 2016, Warren and McCormick 2019). This
2411 may have a considerable impact on competitive dominance hierarchies of fishes.

2412

2413 Dominance hierarchies are thought to have evolved due to resource competition between
2414 individuals with asymmetrical physiological (i.e. high vs low performer) and behavioural traits
2415 (i.e. bold aggressive, proactive stress recovery vs timid and reactive to stressors) (Härdling et
2416 al. 2001; Warren and McCormick 2019). The reason that phenotypic variation is maintained
2417 amongst shoal mates is due to the social benefits that individuals with consistent differences in
2418 physiological and behavioural traits provide (Nadler et al. 2016; Killen et al. 2017; Krause and
2419 Seebacher 2018). Individuals with the capability of seeking out preferable environments and
2420 resources often occupy leadership positions in shoals. High performance individuals leading a
2421 shoal may provide hydrodynamic benefits (i.e. using fewer tail beats to maintain speed) for fish
2422 with low aerobic capacity at the rear of the shoal. These leaders ultimately reduce group
2423 metabolic locomotory costs for exploration and dispersal (Seebacher et al. 2013; Marras et al.
2424 2015; Nadler et al. 2016; Killen et al. 2017; Huang et al. 2020; Rodriguez Santiago 2020). In
2425 contrast, subordinates at the rear of the shoal maintain group consensus behaviour and provide

2426 a buffer against predators (Day et al. 2001; Nadler et al. 2016). Group movement plays an
2427 important role in leadership and consensus behaviour, however these social aspects may be
2428 sensitive to environmental change (Jolles et al. 2017; Killen et al. 2021).

2429

2430 The sensitivity of social groups to environmental variability depends on the type of social
2431 hierarchy (Barrett et al. 2019; Hasenjager et al. 2020; Piefke et al. 2021). Linear dominance
2432 hierarchies are the most common and are established as a large individual aggressively
2433 dominates over subordinates through competitive interactions for resources (Gurnery and
2434 Nisbet 1979; Bessa et al. 2021). Here, the mechanism driving dominance can be caused by the
2435 greater energetic requirements of a large body size or sex-related, where dominance would
2436 allow access to mates in the case of a harem hierarchical system (Day et al. 2001; Nadler et al.
2437 2016). The ability to compete for resources is dependent on physiological sensory perception
2438 of the resource and the aerobic performance to engage in energetically-costly aggressive
2439 interactions (Seebacher et al. 2013; Killen et al. 2017, 2021). However, changing
2440 environmental conditions may amplify differences in metabolic costs amongst shoal mates,
2441 where differences in aerobic performance may determine when certain individuals no longer
2442 benefit from remaining in the social group (Killen et al. 2017, 2021).

2443

2444 Thermal variability can exacerbate the energetic cost of activity unevenly amongst individuals
2445 (Chapter 3). Physiological traits are thermally sensitive and the extra metabolic costs imposed
2446 by changing environmental conditions can influence the capacity to express competitive
2447 behaviours (Härdling et al. 2001; Nadler et al. 2016, Killen et al. 2017, 2021). This may impact
2448 the competitive encounters and dominant positions of individuals within the social hierarchy
2449 of fishes, as individuals with physiological and behavioural phenotypes that are competitive
2450 across thermally variable conditions will be dominant (Fausch 1984; Härdling et al. 2001; Biro
2451 et al. 2009, Biro et al. 2010; Warren et al. 2016; Neubauer and Anderson 2019; Warren and
2452 McCormick 2019). These differences in individual physiological performance can affect social
2453 group behaviour by altering the rank order of dominance hierarchies under thermal variability
2454 (as reviewed by Killen et al. 2021). For example, although individuals with low physiological
2455 performance may dominate a social hierarchy under optimal environmental conditions, they
2456 may be physiologically constrained from occupying dominance positions across changing
2457 conditions, which may induce a change in the rank order of the social hierarchy (Killen et al.
2458 2017, 2021). Shifts in the rank order of the dominant fish in the social hierarchy may influence
2459 group level success if predator avoidance by the group is influenced by a leader (i.e. a leader

2460 with a broad aerobic scope has rapid swimming speeds and the stamina to lead the group away
2461 from predators; Killen et al. 2017, 2021). In a highly variable environment, group leaders that
2462 ascend to dominance ranks will require the metabolic capacity to sustain high rates of
2463 locomotor performance and risk behaviour at shoal frontal positions, to influence group
2464 movement and foraging benefits (Jolles et al. 2017; Seebacher and Krause 2017; Killen et al.
2465 2017).

2466

2467 Rapid rates of anthropogenic environmental change and exploitation are predicted to cause
2468 instability in social structures and the splitting of social groups (Jolles et al. 2017; Killen et al.
2469 2021). Under these conditions, dominant fish may move to a new optimal environment (or be
2470 replaced by a high performer that can relocate), and subordinates follow the group leader or
2471 split from the group. For example, subordinates with a narrow range of aerobic performance
2472 may be physiologically constrained from remaining in the group (i.e. these individuals may not
2473 be able to match the average swimming speeds of the group or may be unable to cross thermal
2474 barriers outside of their optimum range). This lack of consensus behaviour in the social group
2475 may result in the formation of homogeneous groups with individuals of similar physiological
2476 and behavioural phenotypic traits (Killen et al. 2017, 2021).

2477 The transfer of individuals between social groups may enhance the spread of diseases in
2478 homogenous stress-compromised low performance groups, which lack the energetic capacity
2479 to match their behaviour to rapidly changing thermal conditions without the presence of high
2480 performers (Krause and Seebacher 2018; Sosna et al. 2019; Warren and McCormick 2019).
2481 However, if high-performers conform to the physiological and environmental niche
2482 requirements of low performance group members to keep the social group intact, then the entire
2483 social group will be limited in their response to environmental change (Killen et al. 2017,
2484 2021).

2485 Dominance hierarchies are an important factor for population stability (i.e. influencing rates of
2486 predation and the transfer of information amongst individuals; Barrett et al. 2019; Hasenjager
2487 et al. 2020; Piefke et al. 2021) and the maintenance of the social hierarchy is critical for the
2488 survival of social species. This is particularly important in the anthropocene where fishing
2489 pressure may alter social dominance by changing the proportions of physiological (Duncan et
2490 al. 2019) and behavioural (Alos et al. 2012) phenotypes within fished populations.

2491

2492 Thus, understanding the effect of thermal variability on individual performance will provide
2493 insight as to how the hierarchical structure of dominance hierarchies may change under thermal
2494 variability, and how this will affect the vulnerability of fishes with dominance hierarchies in a
2495 changing climate (Warren and McCormick 2019). Thermally-induced changes to social
2496 competitive interactions have been measured in freshwater (De Staso and Rahel 1994;
2497 Taniguchi et al. 1998; Reese and Harvey 2002) and tropical marine systems (Pruitt et al. 2018;
2498 Warren and McCormick 2019). These studies found that competitive interactions increased
2499 with increases in temperature. However, this is the first study to assess how changes to social
2500 structure may be related to individual aerobic scope and behavioural phenotype in a temperate
2501 species experiencing extreme short-term thermal variability.

2502
2503 *Chrysoblephus laticeps* is the ideal model species to measure changes in competitive and
2504 hierarchical structure under climate change, owing to their highly resident nature, life history
2505 traits, behavioural traits and complex hierarchical social structure (Kerwath et al. 2007; Götz
2506 et al. 2008). *C. laticeps* has a small home range (Kerwath et al. 2007) and lives in hierarchically
2507 structured social groups in temperate coastal waters that experience frequent thermal variability
2508 (Brander 2010). Here, the species resides in hierarchically structured social groups, where the
2509 largest dominant male will change sex (when between 27-30cm in length) and dominate over
2510 a harem of females (Götz et al. 2008). This bidirectional hermaphroditic nature can make the
2511 species particularly susceptible to changes in social structure. For example, upon removal of
2512 the dominant male, aggressive interactions will increase amongst the largest remaining females
2513 to vie for the dominant position (Kerwath et al. 2007). Such a scenario is likely as fishing
2514 pressures and thermal variability can exert synergistic pressures on the hierarchical social
2515 structure of this highly resident and socially-dependent species.

2516

2517 The aim of this chapter is to assess how social competition for resources is influenced by
2518 individual physiological and behavioural phenotype in *C. laticeps*, and whether this will drive
2519 the restructuring of hierarchical dominance ranks by phenotype under thermal variability. To
2520 do this, high performers, intermediate performers and low performers (identified in Chapter 3
2521 and 4), were subjected to sized-matched duels across a thermal gradient. It is hypothesised that
2522 bold individuals are likely to outcompete timid individuals, and that only the bold high aerobic
2523 performers will sustain their competitive dominance across changing thermal conditions.

2524

2525 **5.2 Methods**

2526 **5.2.1 Pre-contest isolation and duel allocation**

2527 Prior to duel contests, 24 individuals (eight high performers, 12 intermediate performers and
2528 four low performers) were each housed in their own 1000 L circular tank (1050 mm diameter
2529 x 1200 mm height) to reduce the possibility of pre-established hierarchy effects (Killen et al.
2530 2014; Warren and McCormick 2019). After one week of acclimation at 16 °C, individuals were
2531 fasted for a 24-hour period before two individuals were simultaneously relocated to an empty
2532 1000 L circular tank for the duel.

2533 To determine how behavioural and physiological phenotypes may influence competitive
2534 interactions across variable temperatures, similar-sized individuals, previously categorised by
2535 physiological and behavioural phenotype (i.e. bold with high aerobic performance (HP), bold
2536 with intermediate (IP) to low (LP) aerobic performance, timid with intermediate-low aerobic
2537 performance, timid with high aerobic performance; see Chapter 4) were selected for each duel.
2538 The order of duels was randomized and contests between a pair of individuals were staged
2539 consecutively (Table C1 Appendix C). Between 28 and 33 paired duels (five bold HP vs bold
2540 IP, two bold HP vs timid LP, eight bold IP vs timid IP, two bold IP vs timid LP, two timid HP
2541 vs timid IP, seven timid IP vs timid IP, one timid IP vs timid LP, one bold IP vs bold IP) were
2542 conducted for each temperature treatment (see Table C1 in Appendix C).

2543

2544 **5.2.2 Competitive feeding duels**

2545 All duels were staged in daylight hours between 07:00 and 17:00. For each duel, each
2546 competitor was placed on either side of a removable opaque plastic divider within an opaque
2547 1000 L circular duel tank (1050 mm diameter x 1200 mm height) mounted with a video camera
2548 to record the duel (Sports Cam 1080 Pixel). Following removal of the barrier, competitive
2549 interactions were recorded for a 10-minute period and later analysed. Fish were habituated to
2550 the duel arena for 2-5 minutes prior to removing the divider with minimal disturbance. The
2551 tank divider was kept on standby so that the experimenter could intervene in the case of severe
2552 aggression (Warren and McCormick 2019). One food item (i.e. a 1 cm by 1cm piece of squid,
2553 *Loligo* spp.) was placed at the centre of the tank to stimulate aggressive competition for food
2554 and space and this was replaced once eaten (see the tank setup in Figure 5.1).

2555 Duels were staged at optimal temperatures for the species (16 °C). After duels at optimal
2556 temperatures, fish were removed from the duel tank, placed in their holding tank and the

2557 temperature was adjusted by 1 °C per hour to either 10 °C or 21 °C (1 day). Fish were then
2558 acclimated at the new test temperature for two days before the duel experiments were repeated
2559 at 10 °C and 21 °C. The three-day period between duels was to reduce possible winner-loser
2560 effects (as per the methods of Colleter and Brown 2011; Poulos and McCormick 2014; Warren
2561 and McCormick 2019). Individuals were euthanized at the end of the duel experiments for a
2562 full biological examination (i.e. otolith removal, sexing and gonad staging).

2563
2564



2565 **Figure 5.1: Paired duel competitive contest for dominance in two male red roman,**
2566 ***Chrysolephus laticeps***
2567

2568 **5.2.3 Scoring of feeding duels**

2569 **5.2.3.1 Aggressive interactions**

2570 Aggressive behaviours are a good indicator of a duel outcome and hence were used as a proxy
2571 for competitive performance (as per the methods of Colleter and Brown 2011; McCormick and
2572 Weaver 2012). The duel initiator was given a bonus of ten points, and each competitor received
2573 points for each consecutive aggressive behaviour towards its opponent. Four aggressive
2574 behaviours typical of the species were quantified (based on observations and the literature;
2575 Götz et al. 2008), and the points given for each behaviour were ranked from the most to least
2576 aggressive response, namely; (i) attacks, defined as a chase and biting of the opponent (ii) head
2577 flare, defined as flaring of the gill operculum, with or without displaying of teeth, (iii) charging
2578 in the direction of the opponent, and (iv) body or lateral fin flare in the direction of the opponent
2579 (Table 5.1). For each duel, each competitor was scored based on aggressive behaviours as well
2580 as feeding, which was used to stimulate aggressive encounters, and each fish's proximity to the
2581 food source.

2582

2583 **5.2.3.2 Feeding and tank position in proximity to the food source**

2584 The first competitor to feed in each duel was given a bonus of five points. Each competitor
2585 received a point for each consecutive food item eaten, and points were given to each competitor
2586 based on proximity to the food source for the duration of the duel (as per the methods of Sloman
2587 et al. 2001). To measure proximity to the food source, TOXTRAC video analysis (Rodriguez
2588 et al. 2017, 2018) was used to create a digitized transect overlay of the duel arena and to divide
2589 the tank into three distinct zones. Zone one was a 30 cm radius directly around the food source
2590 in the tank centre, zone two was a 60 cm radius around the food source, and zone three
2591 comprised the outer surrounding area to the tank wall (Castanheira et al. 2013). The latency
2592 time (seconds) for each competitor to enter the inner radius directly surrounding the food
2593 source was measured. TOXTRAC was used to calculate the proportion of time that each
2594 competitor spent in each of the three zones. The time spent in each zone was multiplied by a
2595 weighted score (i.e. where the individual received higher scores for time spent in zones of close
2596 proximity to the novel object, relative to the zones furthest from the novel object) and added
2597 together to produce a percentage score of tank dominance (see Table 5.1 for calculation of the
2598 weighted score).

2599 **Table 5.1: Calculation of individual dominance scores for the winner and loser of each**
 2600 **competitive feeding duel, where aggression, feeding and proximity to the food source were used**
 2601 **to measure the extent that each competitor participated in the feeding duel. Duels were repeated**
 2602 **in size-matched pairs of competitors across a thermal gradient (i.e. temperatures of 10 °C, 16 °C**
 2603 **and 21 °C).**
 2604

Behaviour	Description	Point
<u>Aggressive interaction</u>		
Attack or bite	In contact with body of competitor	
Head display	Fish displays gill flare towards competitor	
Charge	Swims in direction of competitor	3
Head or lateral display	Fish swims laterally alongside competitor with fins extended	2
Hide or flee	Fish avoids competitor	1
Initiator of duel	* <i>Additional 10 % given to duel initiator, additional 5 % given for initiating the duel within 30 seconds</i>	1
	TOTAL converted to percentage /100	0
<u>Feeding</u>		
First to eat first food item		5
Piece eaten	Additional point for each piece eaten	1
	TOTAL (x6) converted to percentage /100	
<u>Tank dominance</u> (i.e. time spent in proximity to food source)		
	<i>The time spent in each zone was multiplied by a weighted score and added together to produce a percentage score of tank dominance</i>	
Zone 1	30 cm radius around food source (centre)	
Zone 2	60 cm radius around food source	Weighted score
Zone 3	Outer zone to tank wall	100 % *
	* <i>An additional 10 % was given for immediately entering zone 1.</i>	85 %
	* <i>An additional 5 % was given for entering zone 1 within a minute.</i>	15 %
	TOTAL maximum /100	

2605 5.2.5 Statistical analysis

2606 5.2.5.1 PCA generated composite behavioural score to determine the winner and loser of 2607 each duel

2608 Principal Component Analysis (PCA) was used to generate a single principal component score
 2609 (from each of the behavioural assay scores - aggressive behaviour, tank position and feeding)
 2610 reflecting the degree of dominance in which an individual was willing to engage in the

2611 competitive feeding duel. Each individual received a maximum of 100 points for aggressive
2612 behaviour (note that a few outliers received aggression scores greater than 100, however these
2613 points were cut off at 100 to prevent the data set from being skewed by aggression scores), 100
2614 points for tank position in proximity to the food source and 100 points for feeding (see how
2615 points were given in Table 5.1). These scores were converted to percentages. High scores for
2616 aggression, feeding and tank dominance (i.e. in proximity to the food source) were positively
2617 correlated (via Spearman's rank correlation) and interpreted as dominance of the feeding duel.

2618

2619 For each temperature treatment, each individual received a dominance score by combining the
2620 total scores for food intake, tank position and aggressive interactions in each duel as variables
2621 using a PCA (as per the methods of Sloman et al. 2000) with the package 'Vegan' in R version
2622 3.3.3 (R Core Team 2017). Each behavioural assay percentage score was arcsine transformed
2623 for input into the PCA. High scores for aggression, feeding and tank position loaded positively
2624 onto PC1, while low scores loaded positively onto PC2. Hence, high composite scores (see the
2625 composite scores in Table C1 of Appendix C) generated from PC1 were interpreted as high
2626 levels of dominance. For each treatment, the individual with the higher dominance score was
2627 deemed dominant and the contest winner for that pair, while the individual with the lower
2628 composite dominance score was deemed the loser of the contest.

2629

2630 **5.2.5.2. Dominance scores across temperatures**

2631

2632 To assess how dual scores for each behavioural metric (i.e. aggression, feeding and tank
2633 dominance) varied among phenotype groups (i.e. bold high performers, bold intermediate
2634 performer, timid high and intermediate performers and timid and bold low performers) and
2635 temperature, the percentage behaviour score calculated for each fish belonging to each
2636 phenotype group was averaged for each temperature and presented graphically in bar plots. To
2637 quantitatively assess how dominance scores varied across a thermal gradient, the PCA generated
2638 single composite behavioural score (see section 5.2.5.1), calculated for each fish (Table C1
2639 Appendix C) was modelled against each temperature treatment (10, 16 and 21 °C). A non-
2640 linear mixed effects modelling approach was implemented using the *nlme* package (Pinheiro
2641 et al. 2017) to account for heteroscedasticity in the composite dominance scores. Model
2642 assumptions were checked using diagnostic plots (Bolker et al. 2009; Zuur 2009). Log-
2643 transformed dominance scores were modelled against phenotype group (i.e. bold high
2644 performer, bold intermediate performer, timid high and intermediate performers and timid and

2645 bold low performers) as an interaction term with temperature. Fish sex (i.e. as a factor for the
2646 group; male, female or intersex) and mass (i.e. as a factor for the group; >1000 grams, or <1000
2647 g to 700 g, or <700g) were also included in the model as fixed effects. Phenotypic groups with
2648 only one individual were pooled with the closest phenotypic group (e.g., the single bold LP
2649 individual was pooled with bold intermediate performers for comparison with timid low
2650 performers). The model included fish ID as a random effect to account for repeated measures
2651 in each fish (Harrison et al. 2018). Since sex ($p = 0.0808$, $t = -0.243$, $df = 31$) and mass ($p =$
2652 0.446 , $t = 0.787$, $df = 31$) were not significant variables in the initial full model, they were
2653 removed from the analyses. Post-hoc analyses were conducted using the R package, lsmeans
2654 (Lenth et al. 2017). All modelling was conducted in R version 3.3.3 (R Core Team 2017)

2655

2656 ***5.2.5.3 Assessing the probability of wins by each phenotype groups with changes in*** 2657 ***temperature***

2658

2659 To examine the probability of the different phenotype groups winning across temperatures, a
2660 binomial mixed effects modelling approach was implemented using the *glmmTMB* package
2661 with the “binomial” family and link “logit” (Brookes et al. 2017) in R version 3.3.3 (R Core
2662 Team 2017). The model was checked using diagnostic plots (Bolker et al. 2009; Zuur 2009).
2663 The probability of the different phenotype groups winning across temperatures was tested by
2664 modelling a second order polynomial relationship of temperature as a predictor of win
2665 probability (i.e. a binomial response variable, where; 1 = win, 0 = lose). Here, the behavioural
2666 and physiological phenotype combination (i.e. bold high performer, bold intermediate
2667 performer, timid high and intermediate performers and timid and bold low performers) was
2668 added as a fixed effect. Phenotypic groups with only one individual were pooled with the
2669 closest phenotypic group (e.g., the single bold LP individual was pooled with bold intermediate
2670 performers for comparison with timid low performers). Sex (i.e. as a factor for the group; male,
2671 female or intersex) and mass (i.e. as a factor for the group; >1000 grams, or <1000 g to 700 g,
2672 or <700g) were also included as fixed effects in the model. Fish ID (i.e. individual one to 24)
2673 was included as a random effect to account for repeated measures in each fish (Harrison et al.
2674 2018).

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2676

2677 **5.3 Results**

2678

2679 **5.3.1 Dominance scores**

2680

2681 The percentage scores for aggression and feeding ranged between 0.1 % and 100.0 % at each
 2682 test temperature. However, the percentage scores for tank position in proximity to the food
 2683 source ranged between 15.0 % and 100.0 % at each test temperature (scores for individuals are
 2684 provided in Table C1 of Appendix C).

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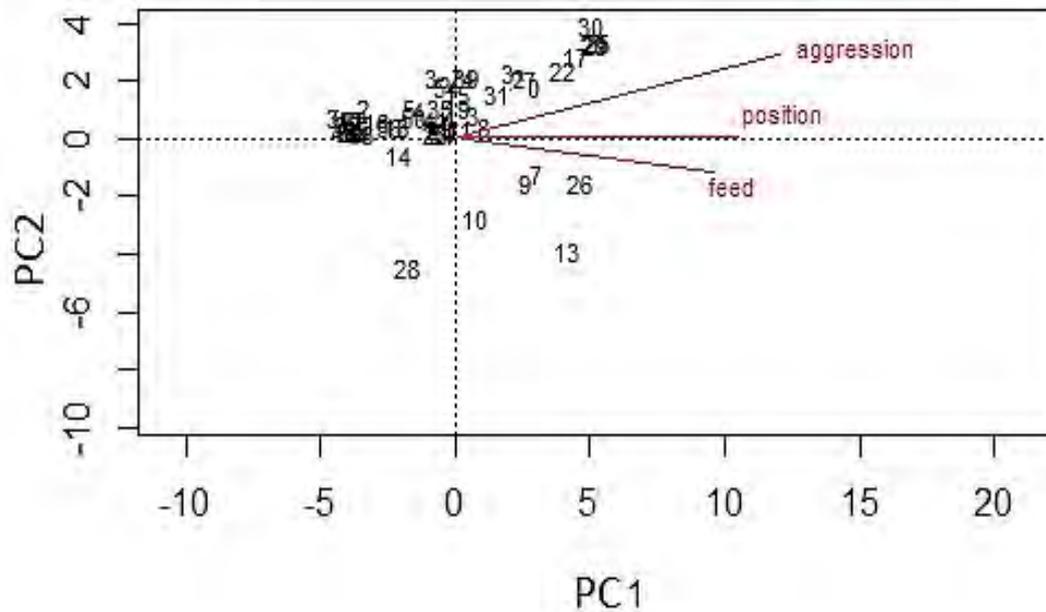
2686 High percentage scores for aggression, feeding and tank position in proximity to the food
 2687 source were positively correlated ($r = 0.7$; $p < 0.05$, $t = 2.277$, $df = 24$; Spearman's rank
 2688 correlation) and hence these behavioural assays were combined into a composite dominance
 2689 score for each individual in each thermal context. Principal component 1 (i.e. PC1) explained
 2690 90.21 % of the variation (eigenvalue = 2301.72) in behaviour, while PC2 explained 13.04 %
 2691 (eigenvalue = 863.05) of the variation in behaviour (Table 5.2). High dominance scores for
 2692 aggression, feeding and tank dominance loaded positively onto PC1, while low scores loaded
 2693 positively onto PC2 (Figure 5.2).

2694

2695 **Table 5.2: Results of the principal component analyses used to determine individual dominance**
 2696 **scores of *Chrysoblephus laticeps* participating in competitive feeding duels across a thermal**
 2697 **gradient (i.e. temperatures of 10 °C, 16 °C, 21 °C). Correlation loadings are between PC1 (for**
 2698 **each temperature trial) and between behavioural variables: 1) aggression, 2) tank position in**
 2699 **proximity to the food source and 3) feeding.**

2700

Principal component	% variance		Aggression	Tank position	Feeding
PC1 16 °C	90.21	Loadings	0.370	0.442	-0.021
		Correlation	0.485	0.902	0.485
PC1 10 °C	87.96	Loadings	0.555	0.277	0.155
		Correlation	0.640	0.881	0.241
PC1 21 °C	92.81	Loadings	0.554	0.277	0.155
		Correlation	0.723	0.930	0.205



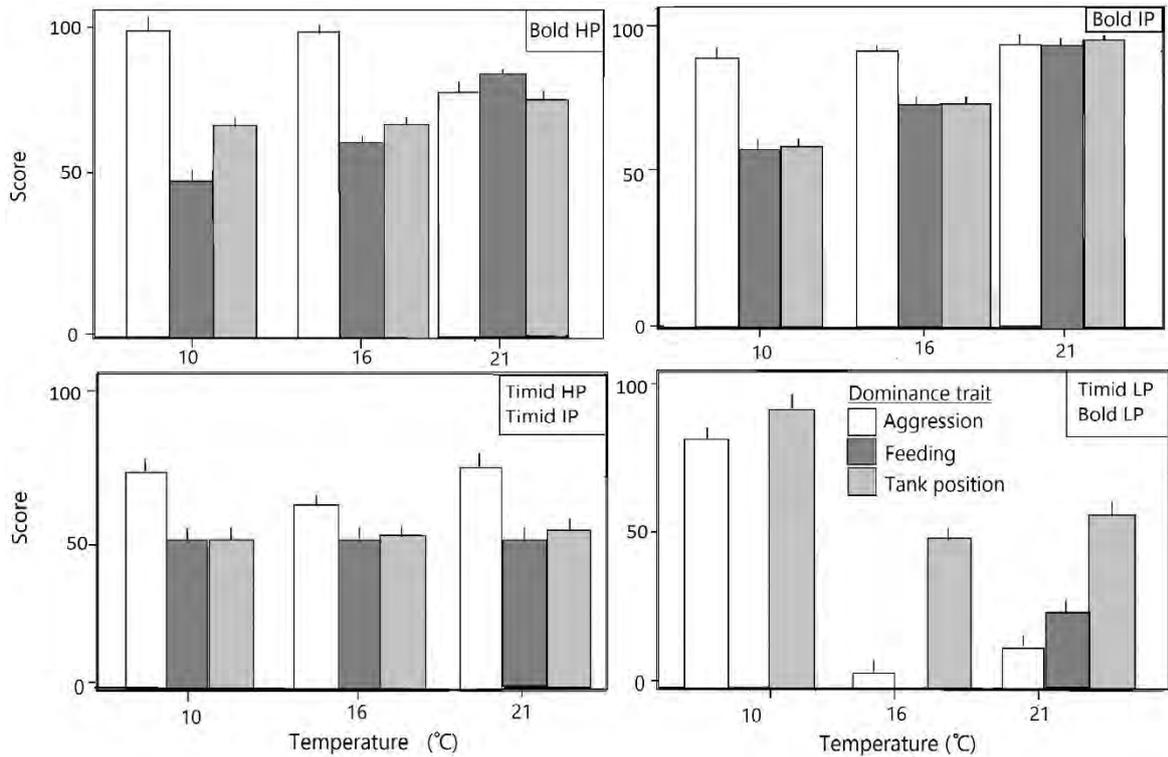
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Figure 5.2: Results of the principal component analyses used to determine individual dominance scores of *Chrysoblephus laticeps* participating in paired competitive feeding duels across a thermal gradient (i.e. temperatures of 10 °C, 16 °C, 21 °C). Correlation loadings are between PC1 (for each temperature trial) and between behavioural variables: 1) aggression, 2) tank position in proximity to the food source and 3) feeding. High scores for aggression, tank position in proximity to the food source and feeding were positively correlated.

2712 5.3.2 Dominance scores across temperature

2713 Both bold high performers (Bold HP) and bold intermediate performers (Bold IP) had the
2714 highest levels of aggression, feeding and tank dominance (Figure 5.3). High performers and
2715 intermediate performers were generally able to maintain these traits associated with dominance
2716 at all temperatures, although there were differences between high performers and intermediate
2717 performers in the expression of these traits (Figure 5.3). Bold high performers appeared to
2718 reduce aggressive behaviours at the high temperature of 21 °C, whereas bold intermediate
2719 performers increased aggression at this temperature (Figure 5.3). In contrast, both bold and
2720 timid low performers (LP) exhibited the lowest levels of these traits associated with dominance
2721 (i.e. aggression, feeding and tank dominance) at 21 °C (Figure 5.3). At cold temperatures (10
2722 °C), however, the results indicated that low performers had the greatest dominance when
2723 compared to the high-performance bold fish, which were not as active and were less dominant
2724 (Figure 5.3).

2725



2726
 2727 **Figure 5.3: Mean±SD aggression, feeding and tank dominance scores among phenotype groups (bold high performers, bold intermediate performers, timid high and intermediate performers, and timid and bold low performers) of *Chrysolephus laticeps* participating in competitive feeding**
 2728 **duels across a thermal gradient (i.e. temperatures of 10 °C, 16 °C, 21 °C).**
 2729
 2730

2731
 2732 Model results (Table 5.3) showed that Bold HP and Bold IP outperformed timid and bold low
 2733 performers at optimal and high temperatures ($p = 0.005$, $t = -2.871$, $df = 24$). Low performers
 2734 exhibited a significantly lower dominance score at both ambient (16 °C; $p = 0.003$, $t = -1.250$,
 2735 $df = 4$) and elevated temperatures (21 °C; $p = 0.021$, $t = -2.023$, $df = 4$) when compared to other
 2736 phenotypic groups (Figure 5.4). However, it was at low temperatures of 10 °C that bold HPs
 2737 had similar performance to low performers (i.e. dominance scores did not statistically differ
 2738 between these groups; $p > 0.05$; $t = -1.258$, $df = 16$).

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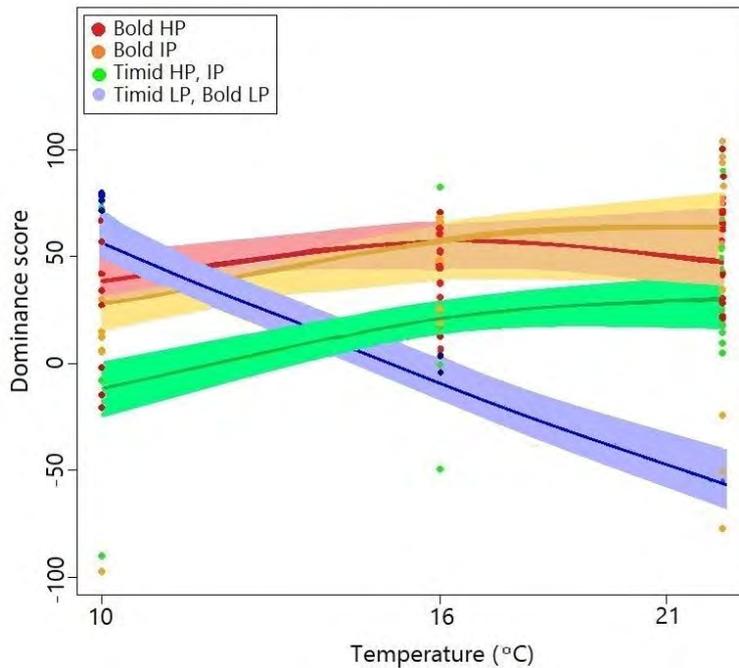
2745 **Table 5.3: Mixed effects model results for the difference in dominance scores between phenotype**
 2746 **group combinations (i.e. behavioural phenotype: bold vs timid; and physiological phenotype: high**
 2747 **performer, intermediate performer, or low performer) of *Chrysoblephus laticeps* participating in**
 2748 **paired competitive feeding duels across a thermal gradient (i.e. temperatures of 10 °C, 16 °C, 21**
 2749 **°C).**
 2750
 2751

Random effect	Variance	SD		
Individual	2.130	0.54		
Fixed effect	Estimate	SE	<i>t</i> -value	<i>p</i> -value
Intercept	1.639	4.868	3.367	0.001
Bold HP	2.179	2.628	-2.221	0.043
Bold IP	2.153	5.421	-2.736	0.016
Timid HP, IP	2.154	3.966	-2.242	0.042
Bold, Timid LP	-1.139	4.516	-3.977	0.001
Bold HP: temp	10.899	3.657	2.503	0.013
Bold IP: temp	14.994	3.121	3.522	0.001
Timid HP, IP: temp	9.154	5.665	2.629	0.009
Bold, Timid LP: temp	-14.712	3.154	4.664	0.001
Temperature	2.266	2.249	1.186	0.179
AIC	239.05			
Residual SE	0.5404			
	<i>(df</i> = 31)			

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2756 **Figure 5.4: Model fit for the population level variance in dominance scores of phenotypic groups**
 2757 **(i.e. bold high performers in red; bold intermediate performers in orange; timid high and**
 2758 **intermediate performers in green; and timid and bold low performers in blue) of *Chrysolephus***
 2759 ***laticeps* participating in competitive feeding duels across a thermal gradient (i.e. temperatures of**
 2760 **10 °C, 16 °C, 21 °C).**

2761

2762 5.3.3 Probability of winning by each phenotypic group across a thermal gradient

2763 Bold and timid low performers had the highest proportion of wins at 10 °C, bold intermediate
 2764 and high performers had the highest proportion of wins at 16 °C, and bold intermediate
 2765 performers had the highest proportion of wins at 21 °C (Figure 5.5). Bold high performers had
 2766 a significantly higher probability of winning duel contests at optimal temperatures ($p = 0.013$,
 2767 $z = 1.982$, $df = 8$), while bold intermediate performers had a significantly higher probability of
 2768 winning as temperatures increased ($p = 0.013$, $z = 2.494$, $df = 12$; Table 5.4). In contrast, the
 2769 probability of winning by low performers was only significant at low temperatures ($p = 0.011$,
 2770 $z = 2.532$, $df = 4$; Table 5.4). Additionally, sex and mass were also significant influencers of
 2771 the outcome of paired duels, where large males dominated over competitors with heightened
 2772 aggressive behaviour ($p = 0.020$, $df = 7$; $z = -2.326$; Table 5.4).

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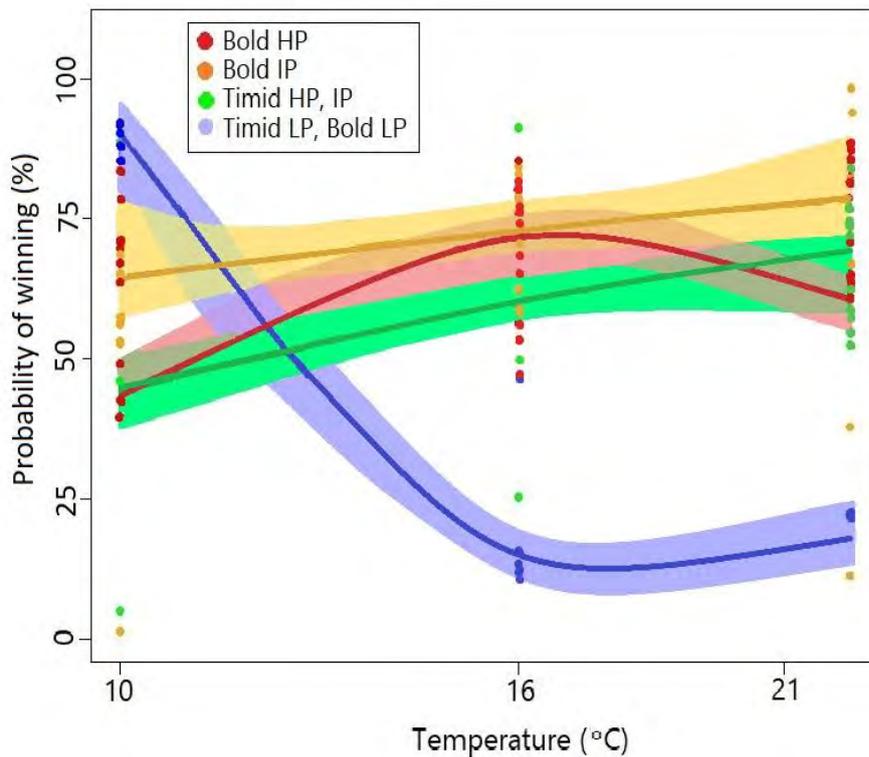
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2779 **Table 5.4: The probability of winning by phenotype groups (i.e. behavioural phenotype: bold vs**
 2780 **timid; and physiological phenotype: high performer, intermediate performer, or low performer)**
 2781 **of *Chrysolephus laticeps* participating in paired competitive feeding duels across a thermal**
 2782 **gradient (i.e. temperatures of 10 °C, 16 °C, 21 °C).**
 2783

Random effect	Variance	SD		
Individual	0.001	0.00		
Fixed effect	Estimate	SE	z-value	p-value
Intercept	-0.804	2.29	-0.351	0.726
Temperature	-0.004	0.31	-0.014	0.989
Temperature ²	0.104	2.09	0.050	0.960
HP Bold	0.510	0.65	0.789	0.430
HP Timid	1.283	1.21	1.144	0.253
IP Bold	1.561	0.63	2.494	0.013
IP Timid	1.025	0.62	1.656	0.098
LP Timid	0.191	0.01	1.461	0.144
HP Bold: temp	0.380	0.19	1.982	0.047
HP, IP Timid: temp	0.595	0.28	2.158	0.031
IP Bold: temp	0.314	0.18	1.757	0.078
LP bold, timid: temp	0.454	0.18	2.532	0.011
Mass >1000 g	2.412	1.10	2.199	0.028
Mass 1000 – 700 g	-0.735	0.48	-1.522	0.128
Mass <700 g	-0.501	0.52	-0.967	0.334
Male	-2.585	1.11	-2.326	0.020
Female	-0.261	0.39	-0.677	0.499
AIC	319.54			
Residual SE	0.209 (df=19)			

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2789 **Figure 5.5: The probability of winning for phenotypic groups (i.e. bold high performers in red;**
2790 **bold intermediate performers in orange; timid high and intermediate performers in green;**
2791 **and timid and bold low performers in blue) of *Chrysolephus laticeps* participating in competitive**
2792 **feeding duels across a thermal gradient (i.e. temperatures of 10 °C, 16 °C, 21 °C).**

2793

2794 **5.4 Discussion**

2795

2796 This study found that both physiological phenotype and behavioural phenotype are important
2797 in determining dominance in *Chrysolephus laticeps*, with bold high and intermediate
2798 performers having the highest probability of winning dual contests at normal and warming
2799 temperatures. Both bold and timid low performers lost duels as temperatures increased, and as
2800 such, physiological phenotype may ultimately be more important than behavioural phenotype
2801 in determining dominance and competitive access to food resources as temperatures increase.
2802 There was less variation in the expression of physiological phenotypes between all individuals
2803 at cold temperatures. However, low performers were comparatively more dominant and just as
2804 likely to win duels. These findings not only provide insight into the role of physiology and
2805 behaviour in the social structure of fishes, but also emphasize the importance of maintaining
2806 phenotype diversity in rapidly changing climates.

2807

2808 Rivas et al. (2020) and Bessa et al. (2021) suggested that changes to the ranking of dominance
2809 hierarchies in fish residing in thermally variable environments will primarily be facilitated by
2810 aerobic scope and body size. The findings of this study align with these suggestions and also
2811 with Killen et al (2014), who suggested that social dominance may be predicted by aerobic
2812 scope. Furthermore, both bold and shy high performers that occupied subdominant ranks have
2813 the aerobic potential to adjust their behaviour to respond to thermal stress (Chapter 3 and 4).
2814 Hence, the largest male high performers are likely to be selected for upper dominance rank
2815 positions, and may have the highest fitness potential through their energetic budget to sustain
2816 dominance over food, territory and mates across a thermal gradient (e.g. Härdling et al. 2001;
2817 Killen et al. 2021).

2818

2819 The increased dominance of low performers at the lowest test temperature was somewhat
2820 surprising in this study and deserves consideration. It is important to emphasise that both bold
2821 and timid low performers had similar, or higher, physiological attributes at the lowest test
2822 temperature when compared with the intermediate and high performers (Chapter 3 and 4). This
2823 may be an adaptive strategy to allow them to obtain food resources as they are completely
2824 outcompeted at normal and high temperatures. As upwelling events are predicted to increase
2825 in frequency and intensity (Roualt et al. 2010, Szekeres et al. 2016; Bates et al. 2019), low
2826 performers may have a competitive advantage at low temperatures, but may experience very
2827 high physiological costs at warmer temperatures in between upwelling events.

2828

2829 In the present study, high performers (HP) and intermediate performers (IPs) had the greatest
2830 proportion of wins. Owing to the similarities in performance between HPs and IPs, the latter
2831 may be motivated to compete for upper dominance positions at warm temperatures. Indeed,
2832 IPs had the greatest dominance at warm temperatures in this study at 21 °C, but appear to
2833 occupy subordinate positions at 16 °C. Increased competition for dominance is very likely at
2834 warm temperatures because the associated increase in aggressive interactions can destabilize
2835 the presiding social hierarchy (Leiser et al. 2004; Bessa et al. 2021; Dioguardi et al. 2021,
2836 Killen et al. 2021). Here, IPs may be particularly motivated to compete for alpha dominance at
2837 high temperatures because subdominant positions can be the most disadvantageous position
2838 within the social hierarchy. This is because subdominant positions have considerable metabolic

2839 costs (i.e. increasing aggressive interactions to contend for dominance positions by raising
2840 RMR by 3.3 fold; Grantner and Taborsky 1998), without gaining the competitive access to
2841 resources and mates that are secured by the alpha dominant (Leiser et al. 2004; Bessa et al.
2842 2021; Dioguardi et al. 2021, Killen et al. 2021). Given the similarities in performance between
2843 HPs and IPs, it is understandable that IPs were able to succeed at competing for dominance
2844 positions, particularly at high temperatures where the presiding social hierarchy is unstable.

2845

2846 Thermal variability can be extensive enough to destabilize a social hierarchy by changing the
2847 rank order of performance phenotypes that determine dominance (Killen et al. 2021). Based on
2848 the findings of this study, there may be considerable changes to the social structure of *C.*
2849 *laticeps* in the rapidly changing thermal environment off the southern coast of South Africa.
2850 Warming and cooling are predicted to increase in frequency and intensity (Bates et al. 2019),
2851 particularly in dynamic upwelling zones where *C. laticeps* resides and this may have
2852 consequences for the social structure of the species.

2853

2854 Warming temperature may raise the metabolic rates of group members, which will increase the
2855 aggressive competitive interactions of individuals with broad aerobic scope (in agreement with
2856 Killen et al. 2014; Warren and McCormick 2019). This was observed in the present study.
2857 Elevated temperatures may therefore increase the variation in the expression of physiological
2858 phenotype and individuals with the lowest aerobic scope will become more subordinate (i.e.
2859 ranked at the lowest subordinate position of the social hierarchy; Border et al. 2021; Miln et al.
2860 2021). Social defeat following the competition for resources can induce a reactive stress
2861 response accompanied by physiological changes of increased cortisol, lowered blood oxygen
2862 carrying capacity, lowered immune response, and reduced RNA synthesis to repair oxidative
2863 stress (Bessa et al. 2021; Wei et al. 2021; Zou et al. 2021). These competitive interactions for
2864 dominance can exacerbate the effects of thermal stress on subordinates in an unstable
2865 hierarchy, which have a significantly higher number of stress hormones and reactive oxygen
2866 species than their counterparts in stable hierarchies (Dioguardi et al. 2021).

2867

2868 In contrast, there was low variation in individual performance and dominance at cooler
2869 temperatures of 10 °C in this study. This may suggest that cooler temperatures may increase
2870 group cohesion (i.e., as a function related of risk related to reductions in swimming ability).

2871 This conclusion was also reached by Killen et al. (2021) on their research on the effects of
2872 environmental gradients on physiological performance and social group behaviour. However,
2873 severe declines in performance of the intermediate and high performers is likely as
2874 temperatures move away from ambient or warm temperatures during intense wind-driven
2875 upwelling events where temperatures can drop to 8 °C over several hours and cause cold shock
2876 (Goshen and Schumann 1995; Rouault et al. 2010; Bates et al. 2019; Duncan 2019). Such
2877 thermal extremes may further amplify differences in metabolic performance (Killen et al. 2014;
2878 Dioguardi et al. 2021).

2879

2880 Based on these findings, there may be resource partitioning that is driven by physiology, as
2881 well as due to increasing upwelling. There is evidence that the high-intermediate performance
2882 bold fish do not perform as well, are not as active and are less dominant at cold temperatures.
2883 Hence, with increased upwelling, it is possible that low performers may become more
2884 competitive with more opportunities for feeding. This is a key result in terms of resilience and
2885 maintenance of phenotypic diversity. However, it is bold high-intermediate performers that
2886 have the aerobic capacity and high rates of activity to sustain dominance at the warmer
2887 temperatures. These bold high performers are needed for the social group to respond to thermal
2888 variability (i.e. migratory species may rely on bold high performers to relocate the social group
2889 to thermally optimal species; Bessa et al. 2021, Killen et al. 2021; perhaps this may occur in
2890 resident red roman during the settlement stage).

2891

2892 This social instability can be accelerated through the direct removal of the dominant group
2893 leader through angling (Louison et al. 2019). For example, Duncan et al. (2019) found that an
2894 exploited population of *C. laticeps* had fewer high performers, relative to a protected
2895 population, and this was attributed to the capture of the physiologically fittest fish by the
2896 fishery. The present study established the link between physiological performance and social
2897 dominance, particularly at high temperatures (where HPs and IPs dominated competitive
2898 interactions). This suggests that angling will likely remove dominant fish from the group,
2899 particularly at normal and elevated temperatures. Furthermore, as an example, an increase in
2900 aggressive interactions is particularly likely to occur when large individuals may contend for
2901 the alpha position after the previous alpha male has been fished (Louison et al. 2019; Piefke et
2902 al. 2021). Once a dominance hierarchy becomes unstable (i.e. through an increase in aggressive

2903 interactions contending for alpha dominance), physiological performance overtakes social
2904 status in determining dominance rank (Border et al. 2021; Miln et al. 2021).

2905

2906 Although angling may place additional stress on social hierarchical structure by selecting
2907 against bold personality traits and high-performance metabolic traits that are associated with
2908 dominance, the genetic potential of high performers can be conserved in nearby marine
2909 protected areas. Their offspring can then disperse into nearby fished areas to replace high
2910 performance phenotypes with the greatest fitness potential to respond to climate change (Ward
2911 et al. 2016). Without this mechanism, social groups may be without the hierarchical dominance
2912 of a bold high performer. This may have consequences for the social group as a bold high
2913 performing leader may facilitate the relocating able subordinates to suitable areas in response
2914 to thermal change (Krause and Seebacher 2018; Sosna et al. 2019; Killen et al. 2021).

2915

2916 This study found that low performers had the greatest decline in competitive behaviour and
2917 could not match the behaviour of group members across thermal conditions. Low performers
2918 lack the aerobic capacity to follow a high-performance leader across conditions where their
2919 performance may be further compromised. Without a high performance leader, low performers
2920 may have reduced foraging opportunities and be limited in their response to climate change.
2921 Stress-compromised low performers may be limited to finite microrefugia along with other
2922 homogenous shoal mates, with whom they are likely to experience increased competition
2923 owing to their shared high-energetic demands (Härdling et al. 2001; Killen et al. 2017; Warren
2924 and McCormick 2019). In the context of climate-variability, low performers may fall away
2925 from social groups. Hence, the spatial protection of individuals with high performance traits
2926 associated with dominance is critical to prevent shifts in the rank dominance of phenotypic
2927 traits, which may alter the behavioural responses of a social group to climate change (Killen et
2928 al. 2017, 2021).

2929

2930 In conclusion, the results from this chapter emphasises the need to determine the effect of
2931 temperature on the individual physiological and behavioural phenotype of group members to
2932 predict how social hierarchies will change in response to thermal variability. Indeed, as
2933 temperatures become more variable, reef hierarchies may be restructured for dominance by
2934 high performers that are able to lead the social group across variable temperatures (Warren and

2935 McCormick 2019; Killen et al. 2021). In particular, this study highlights the importance of
2936 individual performance phenotype to predict the restructuring of dominance hierarchies in
2937 territorial reef species facing climate change. This is because of the observed relationship
2938 between the physiology and behavioural phenotype of individuals. Experiments that combine
2939 individual physiological performance and behavioural assessments should be measured
2940 repeatedly in the same individual across an environmental gradient and repeated in a social
2941 setting to predict the future climate success or vulnerability of reef fishes. Shifts in dominance
2942 will impact the ability of social groups to colonize new areas and should be combined with
2943 species-specific thermal tolerance data to predict future species distributions (Ward et al. 2018;
2944 Warren and McCormick 2019). Individual variability within populations, observed in this
2945 study, suggests that data on the relationship between dominance and temperature for multiple
2946 species would better illustrate how climate change may drive dominance shifts in the social
2947 networks of reef assemblages at particular geographic locations. Furthermore, the link between
2948 physiological performance and social dominance observed in this study suggests that the
2949 behavioural responses of fish social groups to climate change may be impacted by passive
2950 fisheries that select against high performance phenotypes associated with dominance (as has
2951 been suggested by Duncan et al. 2019; Louison et al. 2019).

2952
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2954

2955 **Appendix C**

2956 **Table C1: Total dominance scores (derived from the PCA) of *Chrysoblephus laticeps* individuals participating in paired competitive**
 2957 **feeding duels across a thermal gradient (i.e. temperatures of 10 °C, 16 °C, 21 °C). Dominance scores were calculated via PCA by**
 2958 **collapsing the scores for aggression, tank position in proximity to the food source and feeding scores into a single principal component**
 2959 **(PC1).**

2960 * **Note: Duels numbers indicate paired duels for each temp treatment (not the order of duels conducted)**

Duel	Competitor Fish ID	Performance category	Behavioural category	Fork Length (mm)	Sex	Rank	Temperature (°C)	Aggression (%)	Tank position (%)	Feeding (%)	Total dominance score (PCA)	Winner / Loser
1	6	IP	Timid	253	Intersex	3	16	0.10	100.00	0.10	-74.365	Loser
	11	IP	Timid	280	Female	3		56.00	34.60	0.10	6.755	Winner
	6						10	13.00	32.97	0.10	67.314	Winner
	11							49.00	88.06	0.10	3.291	Loser
	6						21	0.10	27.69	0.10	-81.422	Loser
	11							94.00	92.25	0.10	41.844	Winner
2	6	IP	Timid	253	Intersex	3	16	15.00	58.40	0.10	-48.806	Loser
	9	HP	Timid	249	Intersex	3		78.00	97.08	48.00	52.339	Winner
	6						10	40.00	58.40	0.10	27.198	Winner
	9							60.00	97.08	0.10	-12.385	Loser
	6						21	2.00	66.25	0.10	-67.369	Loser
	9							112.00	100.00	0.10	71.611	Winner
3	1	HP	Bold	364	Male	1	16	22.00	100.00	84.00	24.763	Winner
	12	LP	Timid	350	Male	4		17.00	45.23	0.10	-53.840	Loser
	1						10	39.00	49.82	0.10	32.485	Loser
	12							6.00	15.84	0.10	82.955	Winner
	1						21	75.00	54.83	0.10	9.346	Winner
	12							32.00	48.05	48.00	-31.967	Loser

4	9	HP	Timid	249	Intersex	3	16	100.00	61.91	0.10	46.401	Winner
	11	IP	Timid	280	Female	3		56.00	90.91	60.00	35.874	Loser
	9						10	98.00	95.58	35.00	-58.181	Loser
	11							65.00	100.00	6.00	-20.645	Winner
	9						21	0.10	60.74	0.10	-71.168	Loser
	11							100.00	100.00	60.00	129.214	Winner
5	1	HP	Bold	364	Male	1	16	61.00	59.99	0.01	-7.069	Loser
	10	IP	Timid	329	Male	3		93.00	48.23	30.00	30.986	Winner
	1						10	90.00	96.78	36.00	-50.866	Loser
	10							52.00	100.00	36.00	-14.907	Winner
	1						21	12.00	76.83	0.10	-53.091	Loser
	10							100.00	94.04	72.00	160.051	Winner
6	10	IP	Timid	253	Male	3	16	58.00	90.09	78.00	46.663	Winner
	12	LP	Timid	350		4		11.00	22.25	0.10	-71.058	Loser
	10						10	47.00	100.00	0.10	-3.786	Loser
	12							8.00	25.63	0.10	76.049	Winner
	10						21	100.00	100.00	0.10	70.685	Winner
	12							25.00	50.31	0.10	-47.029	Loser
7	15	IP	Timid	225	Male	3	16	51.00	20.02	0.10	-36.636	Loser
	27	IP	Bold	230	Male	2		88.00	99.30	0.60	68.675	Winner
	15						10	100.00	88.08	72.00	-81.122	Loser
	27							9.00	93.13	0.10	41.45724	Winner
	15						21	39.00	79.24	72.00	-11.651	Loser
	27							100.00	97.08	0.10	157.682	Winner
8	15	IP	Timid	225	Male	3	16	2.00	15.00	0.10	-82.813	Loser
	24	IP	Timid	215	Female	3		16.00	86.35	54.00	-5.206	Winner
	15						10	64.00	66.09	0.10	-1.042	Loser
	24							18.00	43.73	0.10	56.875	Winner
	15						21	2.00	28.61	0.10	-79.048	Loser
	24							100.00	99.50	0.10	135.344	Winner

9	28	IP	Timid	249	Intersex	3	16	28.00	97.35	54.00	11.156	Loser
	24	IP	Timid	215	Female	3		91.00	46.28	0.10	12.523	Winner
	28						10	100.00	100.00	0.10	-87.433	Loser
	24							23.00	62.27	0.10	42.567	Winner
	28						21	0.10	100.00	0.10	-57.466	Loser
	24							100.00	38.65	0.10	74.687	Winner
10	15	IP	Timid	225	Male	3	16	34.00	31.57	0.10	-45.782	Loser
	28	IP	Timid	249	Intersex	3		100.00	0.10	98.95	70.893	Winner
	15						10	57.00	82.50	0.10	-2.084	Winner
	28							145.00	98.46	0.10	-99.543	Loser
	15						21	0.10	26.11	0.10	-81.912	Loser
	28							100.00	100.00	0.10	65.261	Winner
11	27	IP	Bold	230	Female	2	16	15	92.96	0.10	-30.934	Loser
	28	IP	Timid	249	Intersex	3		86.00	100.00	0.10	37.797	Winner
	27						10	38.00	92.59	0.10	12.226	Winner
	28							100.00	100.00	0.10	-77.391	Loser
	27						21	73.00	96.36	0.10	20.032	Loser
	28							100.00	100.00	0.01	62.663	Winner
12	27	IP	Bold	230	Female	2	16	70.00	100.00	0.01	25.479	Winner
	24	IP	Timid	215	Female	3		14.00	93.94	0.01	-31.314	Loser
	27						10	35.00	93.48	0.10	14.835	Winner
	24							75.00	52.66	0.10	-5.552	Loser
	27						21	75.00	100.00	60.00	34.037	Winner
	24							25.00	84.14	6.00	-35.538	Loser
13	28	IP	Timid	249	Intersex	3	16	100	98.95	0.01	52.213	Winner
	21	HP	Bold	260	Female	1		3.00	53.10	66.00	-27.673	Loser
							10	100.00	100.00	0.01	-102.580	Loser
								100.00	96.24	48.00	-89.934	Winner
							21	100.00	100.00	48.00	77.718	Winner
							20.00	71.54	100.00	-29.114	Loser	

14	28	IP	Timid	249	Intersex	3	16	100.00	96.13	0.10	60.536	Winner
	18	IP	Timid	270	Female	3		14.00	56.18	100.00	1.528	Loser
	28						10	99.00	92.52	0.10	-49.792	Loser
	18							14.00	75.73	48.00	34.207	Winner
	28						21	80.00	94.66	6.00	28.193	Winner
	18							2.00	54.67	100.00	-54.140	Loser
15	28	IP	Timid	249	Intersex	3	16	54.00	72.85	0.10	-6.641	Loser
	25	IP	Bold	260		2		100.00	78.56	48.00	66.778	Winner
	28						10	100.00	99.52	0.10	-101.089	Loser
	25							100.00	78.27	0.10	-97.640	Winner
	28						21	100.00	78.36	0.10	166.165	Winner
	25							51.00	74.85	0.10	-10.830	Loser
16	13	IP	Timid	370	Male	3	16	42.00	92.70	100.00	45.317	Winner
	26	HP	Bold	340	Male	1		7.00	76.63	18.00	-37.108	Loser
	13						10	81.00	90.66	0.10	-30.561	Loser
	26							5.00	29.00	0.10	77.426	Winner
	13						21	78.00	85.38	0.10	22.120	Winner
	26							7.00	62.79	0.10	-62.945	Loser
17	13	IP	Timid	370	Male	3	16	62.00	93.00	100.00	63.261	Winner
	19	LP	Timid	346	Male	4		0.01	0.01	33.42	-74.978	Loser
	13						10	73.00	100.00	100.00	-50.880	Loser
	19							5.00	15.00	0.10	84.390	Winner
	13						21	90.00	100.00	100.00	56.827	Winner
	19							6.00	58.31	0.10	-65.435	Loser
18	19	LP	Timid	346	Male	4	16	13.00	84.15	0.10	-37.268	Loser
	17	IP	Bold	325	Intersex	2		100.00	81.50	0.10	57.420	Winner
	19						10	50.00	70.57	0.10	10.973	Loser
	17							66.00	34.73	0.10	12.520	Winner
	19						21	10.00	61.16	0.10	-60.167	Loser
	17							34.00	91.92	0.10	-24.224	Winner
19	22	IP	Bold	340	Male	2	16	49.00	100.00	100.00	56.456	Winner

	17	IP	Bold	325	Intersex	2		1.00	77.28	0.10	-51.49	Loser
	22						10	40.00	100.00	0.01	6.452	Winner
	17							100.00	46.69	100.00	-58.726	Loser
	22						21	100.00	100.00	100.00	100.096	Winner
	17							1.00	69.48	0.10	-67.465	Loser
20	26	HP	Bold	340	Male	1	16	18.00	58.83	0.10	-45.913	Loser
	22	IP	Bold	340	Male	2		58.00	52.008	0.10	65.090	Winner
	26						10	77.00	53.57	0.10	-8.038	Winner
	22							97.00	100.00	0.10	-52.856	Loser
	26						21	5.00	15.00	0.10	-79.972	Loser
	22							100.00	86.81	0.10	66.540	Winner
21	26	HP	Bold	340	Male	1	16	18.00	52.01	0.10	-49.443	Winner
	19	LP	Timid	346	Male	4		2.00	67.53	0.10	-55.644	Loser
	26						10	42.00	80.57	0.10	14.137	Loser
	19							18.00	15.70	0.10	70.817	Winner
	26						21	17.00	24.57	0.10	-63.811	Loser
	19							6.00	91.01	0.10	-55.285	Winner
22	13	IP	Timid	370	Male	3	16	38.00	100.00	100.00	46.483	Winner
	17	IP	Bold	325	Male	2		0.10	39.33	0.01	-71.918	Loser
	13						10	46.00	91.58	84.00	-14.368	Loser
	17							4.00	44.54	0.10	70.713	Winner
	13						21	65.00	100.00	100.00	30.585	Winner
	17							1.00	54.17	0.10	-72.218	Loser
23	13	IP	Timid	370	Male	3	16	48.00	95.13	100.00	51.912	Winner
	22	IP	Bold	340	Male	2		60.00	54.80	0.10	-10.643	Loser
	13						10	78.00	100.00	100.00	-55.050	Loser
	22							6.00	46.99	0.10	67.460	Winner
	13						21	57.00	100.00	100.00	21.144	Winner
	22							2.00	53.04	0.10	-71.467	Loser
24	22	IP	Bold	340	Male	2	16	21.00	78.91	100.00	19.507	Winner

	19	LP	Timid	346	Male	4		5.00	71.78	0.10	-50.778	Loser
	22						10	3.00	100.00	90.00	22.992	Loser
	19							0.10	31.82	0.10	81.010	Winner
	22						21	100.00	93.63	0.10	123.627	Winner
	19							6.50	76.72	0.10	-59.174	Loser
25	26	HP	Bold	340	Male	1	16	47.00	96.67	0.10	-0.554	Winner
	17	IP	Bold	325	Intersex	2		3.00	72.97	0.10	-51.942	Loser
	26						10	40.00	90.89	0.10	11.036	Loser
	17							35.00	62.35	0.10	30.320	Winner
	26						21	13.50	45.89	0.10	-61.043	Loser
	17							7.00	100.00	0.10	-50.159	Winner
26	21	HP	Bold	260	Male	1	16	100.00	63.69	0.10	43.761	Winner
	18	IP	Timid	270	Female	3		27.00	49.10	0.10	-42.940	Loser
	21						10	38.00	99.95	0.10	76.391	Winner
	18							2.00	37.21	0.10	8.565	Loser
	21						21	87.00	93.26	0.10	34.461	Winner
	18							0.10	46.23	0.10	-75.669	Loser
27	21	HP	Bold	260	Female	1	16	100.00	100.00	0.10	82.4867025	Winner
	25	IP	Bold	260	Female	2		54.00	94.68	0.10	4.6462748	Loser
	21						10	94.00	70.03	0.10	-33.522	Loser
	25							64.00	52.95	0.10	5.494	Winner
	21						21	96.00	89.05	0.10	43.050	Winner
	25							0.10	81.24	0.10	-64.807	Loser
28	18	IP	Timid	270	Female	3	16	5.00	55.28	0.10	-59.316	Loser
	25	IP	Bold	260	Female	2		100.00	96.23	0.10	62.367	Winner
	18						10	6.00	39.93	0.10	70.971	Winner
	25							21.00	57.75	0.10	46.845	Loser
	18						21	2.00	25.02	0.10	-80.163	Loser
	25							0.10	41.20	0.10	-77.230	Winner
29	14	IP	Timid	280	Female	3	16	0.10	33.83	36.00	-55.943	Loser
	17	IP	Bold	325	Intersex	2		97.00	92.68	0.01	41.8572	Winner
30	18	IP	Timid	270	Female	3	16	8.00	54.12	0.10	-57.247	Loser
	14	IP	Timid	280	Female	3		46.00	91.97	100.00	48.496	Winner
31	25	IP	Bold	260	Female	2	16	13.00	78.13	0.10	-40.379	Loser
	14	IP	Timid	280	Female	3		65.00	100.00	100.00	70.583	Winner

32	14	IP	Timid	280	Female	3	16	23.00	44.03	0.10	-49.120	Loser
	26	HP	Bold	340	Male	1		71.00	89.18	0.10	16.922	Winner
33	14	IP	Timid	280	Female	3	16	7.00	33.12	0.10	-68.996	Loser
	17	IP	Timid	325	Intersex	2		52.00	100.00	0.10	5.837	Winner

2961

2962 Chapter 6

2963 Management of phenotypic diversity and promoting the climate 2964 resilience of fished stocks

2965 6.1 Main findings

2966 This is the first body of research to show how individual aerobic scope is linked to behavioural
2967 plasticity across a thermal gradient, and the first to assess how these traits influence social
2968 dominance in an exploited fish species. A broad aerobic scope provided the scope to exhibit
2969 behaviourally plastic responses across a thermal gradient. Individual performance was assessed
2970 by conducting a repeated measure on the same individual over a thermal gradient, as recommended
2971 by Killen et al (2021). This study found that using the repeated measures design was indeed
2972 necessary. This was because some individuals that performed well at high temperatures performed
2973 poorly at lower temperatures and thus only individuals with a broad aerobic scope across the
2974 thermal gradient were identified as the physiologically fittest individuals with the greatest
2975 resilience to thermal variability.

2976 In addition to the identification of high, intermediate, and low performers, some general patterns
2977 were observed. As temperatures increased from 16 °C to 24°C resembling the downwelling of
2978 warm surface waters, there was a significant deviation in the physiological performance of high
2979 and intermediate-low performers. High performers did better than intermediate and low
2980 performers as temperatures increased. This highlights the importance of maintaining phenotypic
2981 diversity and the presence of high performers in fished populations, in order for these to survive
2982 climate change effects. In contrast, there was no significant deviation in the physiological
2983 performance of any of the performance groups as temperatures decreased from 16 °C to 10 °C (i.e.
2984 cold temperatures indicative of upwelling events). Although intermediate and low performers
2985 generally had higher levels of performance at the lowest temperatures, all phenotypes had reduced
2986 physiological performance when compared to optimal and high temperatures. Duncan et al.
2987 (2019) suggested that these low temperatures of 10 °C are close to the lower limit of the tolerance
2988 range of *C. laticeps*. Indeed, they found that this species entered cold shock as temperatures
2989 dropped to 8 °C. Based on the findings of this study, it is possible that the most important climate-
2990 driven selection pressure may be the predicted increase in the frequency and intensity of upwelling
2991 events in the region (Duncan et al 2019) and this may select against the high physiological
2992 performers. This finding is not surprising as increasing thermal variability has been predicted to
2993 have a greater impact on fishes than large-scale warming (Bates et al. 2019). This is because

2994 environmental variability will select across the full thermal range (and performance capabilities)
2995 of individuals and only those with broad aerobic performance may be able sustain the
2996 physiological processes.

2997 There will be considerable consequences for reduced physiological performance of fishes in terms
2998 of their behavioural responses to a thermally variable environment. In terms of behaviour, bold
2999 personality traits have been linked to increased chances of survival when exposed to both abiotic
3000 (i.e. *Paralichthys olivaceus* exposed to a thermal gradient; Long et al. 2021) and biotic stressors
3001 (i.e. *Neogobius melanostomus* exposed to intraspecific competition; Behrens et al. 2019).
3002 However, this study suggests that the plastic expression of bold traits across an environmental
3003 gradient are determined by the aerobic scope. For example, individuals with reduced aerobic
3004 capacity for behavioural plasticity initially appeared bold at control temperatures of 16 °C, but
3005 were unable to maintain bold behaviour at extreme temperatures, which caused a shift to timidity.
3006 Thermal variability may induce physiological stress and increase oxygen demand in fish with
3007 narrow aerobic capacity, causing the suppression of energetically expensive bold behavioural
3008 traits (i.e. aggression; Seth et al. 2013, Killen et al. 2013, or activity; D'Agostina et al. 2019). In
3009 this study, low performers similarly suppressed the expression of bold behavioural traits in
3010 response to thermal stress outside of their narrow optimal temperature range. In contrast, high
3011 performers did respond to temperature change with dramatically higher rates of activity, boldness
3012 or aggression.

3013 Several studies have suggested that High Performance Metabolic Phenotypes (HPMPs) with a
3014 broad aerobic scope may also have a greater energetic capacity to remain active across a broader
3015 range of environmental conditions (Killen et al. 2017, Claireaux and Lefrancois 2007, Ferrer et al.
3016 2020) and facilitate plastic behavioural responses to climate stressors, such as exploring novel
3017 resources for dispersal (Castanheira et al. 2013, Beever et al. 2017, McGaugh et al. 2020).
3018 However, this is the first study to provide empirical evidence for behavioural plasticity across a
3019 thermal gradient in a fish species and suggests that there is a link between aerobic scope and the
3020 thermal behavioural plasticity in a fish species, with high performer able to sustain optimal rates
3021 of activity and rapidly recover from O₂ debt across thermal contexts.

3022 Individual variation in physiological performance and behaviour may impact the social rank order
3023 of resident temperate reef species residing in dynamic upwelling zones (Chapter 5). This is
3024 concerning given that warming and cooling are predicted to increase in frequency and intensity
3025 (Bates et al. 2019). Indeed, model results from Chapter 5 suggested that social dominance could

3026 be predicted by a combination of aerobic scope and bold behaviour, where bold high and
3027 intermediate performers occupied upper dominance ranks as temperatures increased. Additionally,
3028 the findings showed that the largest high/intermediate performers are likely to occupy dominance
3029 rank positions and this may be attributed to their high physiological performance, which allows
3030 them to maintain dominance for food, territory and mates across a thermal gradient (Figure 5.4).
3031 Similarly, Killen et al. (2021; review on several social species) found that dominance was
3032 attributed to individuals with high rates of swimming performance (i.e. a proxy for aerobic scope).
3033 In this study, the dominance of the intermediate/high performers was however not evident at the
3034 coldest temperatures (Figure 5.6), where the low performers were able to match their competitive
3035 behaviour. This may suggest that periods of low temperature may be a period for food acquisition
3036 for the low performers and therefore for the maintenance of the diversity of the social structure of
3037 these populations.

3038 Resident fish populations may rely heavily on the presence of large dominant intermediate and
3039 high performers that have the aerobic capacity to respond to thermally variable conditions, and
3040 the bold behaviour to explore thermally optimal areas (Bessa et al. 2021, Killen et al. 2021).
3041 However, size-selection by capture fisheries has been associated with a decrease in risk-taking
3042 behaviour in fished populations, suggesting that size-selective mortality can have consequences
3043 for behavioural and physiological processes (Sbragaglia et al. 2021). This emphasises the
3044 importance of a physiological-based conservation approach to fisheries management, without
3045 which biomass predictions may be unreliable due to unforeseen stock declines or range shifts
3046 (Ward et al. 2016, Killen et al. 2021, Sbragaglia et al. 2021). For the sustainable management of
3047 fished stocks, the spatial protection of the physiologically fittest individuals can restock nearby
3048 fished areas and preserve the phenotypic diversity needed for social groups to respond to climate
3049 change (Ward et al. 2016).

3050

3051 **6.2 The relevance of this study to fisheries decision makers**

3052 **6.2.1. Fishery selection on heritable physiological and behavioural traits**

3053

3054 This study has highlighted the importance of physiological and behavioural traits in predicting the
3055 survival of fished populations to thermal variability. This is particularly important in the context
3056 of fisheries management, as both physiological and behavioural traits are under selection by
3057 fisheries. Based on the findings of Duncan et al (2019), it is likely that hook and line exploitation
3058 is more likely to remove the high and intermediate performers of *C. laticeps*, particularly at normal

3059 and elevated temperatures. When one considers the results of the present study, where boldness is
3060 linked to increased aerobic capacity, it appears that exploitation will likely selectively remove, the
3061 intermediate and bold high performers of the *C. laticeps* population, which are also likely to be
3062 the dominant individuals in the social structure. This is likely to have negative impacts on the
3063 resilience of this species as dominance of the lower performance individuals may not be retained
3064 at warm temperatures and the social structure may break down, with potentially negative
3065 consequences for reproductive success (Priede 1977). Fisheries may therefore drive fished
3066 populations to a lower resilient state through their primary selection of individual aerobic scope
3067 traits.

3068 One of the mechanisms driving fish populations to a lower resilient state is the selective removal
3069 of individuals with a broad aerobic scope because they have the energetic capacity to remain active
3070 and forage across environmental conditions (Portner et al. 2004, Claireaux and Lefrancois 2007,
3071 Killen et al. 2017) over a larger home range. This not only increases their susceptibility to, but
3072 also their likelihood of encountering passive fishing gear. This primary selection on aerobic scope
3073 physiology (Duncan 2019), may also be linked to a secondary selection on behaviour where the
3074 boldest fish exhibit greater risk in approaching and biting fishing gear (Alos et al. 2012, Koeck et
3075 al. 2019). Indeed, bold personality traits have been linked to a broad aerobic scope (Seebacher et
3076 al. 2013, Killen et al. 2014, Rupia et al. 2016), both of which are important to explore novel areas
3077 for dispersal (Warnock and Rasmussen 2014, Seebacher and Krause 2017). Additionally,
3078 behavioural selection by fishing pressure has been shown to reduce the diversity of behavioural
3079 phenotypes in largemouth bass *Micropterus salmoides* (Cooke et al. 2007), and fished populations
3080 may have greater proportions of timid phenotypes (Arlinghaus et al. 2017). However, for fishing-
3081 induced evolution to occur on physiological (eg. Duncan et al. 2019) and behavioural traits (Cooke
3082 et al. 2007, Arlinghaus et al. 2017, Moynes et al. 2019), these traits would need to be heritable.

3083
3084 Researchers have recently isolated genes linked to the expression of metabolic traits associated
3085 with heat stress (Beemelmans et al. 2020, Taboun 2020) and hypoxia (Zou et al. 2022), as well
3086 as behavioural traits (i.e. mirror elicited aggression; Baran and Streelman 2020, amongst others;
3087 Ariyomo et al. 2013, Edenbrow and Croft 2013, Laine et al. 2014). For example, Zou et al. (2021)
3088 found that bold and timid *Paralichthys olivaceus* differed in the expression of 144 genes related
3089 to personality and metabolism. Long et al. (2021) found that offspring of the same species
3090 contained a mix of bold and timid phenotypes irrespective of maternal line, however behavioural
3091 traits were linked to metabolic traits, which were partly heritable due to maternal effects. Both

3092 bold and timid offspring from the bold maternal line had the advantage of a higher metabolic rate
3093 and the ability to respond to environmental stressors (Long et al. 2021). In *Crysolephus laticeps*,
3094 Muller (2022) found that larvae from populations that were protected from exploitation were
3095 physiologically more tolerant of climate stressors, relative to exploited populations. Therefore, by
3096 removing high-performance aerobic phenotypes and bold traits, hook and line fishing may reduce
3097 the resilience of fished populations to environmental variation. This suggests that a mechanistic
3098 conservation approach (i.e. the conservation of heritable phenotypes) is necessary to promote the
3099 resilience of fish populations in the Anthropocene (Ward et al. 2016; Cooke et al. 2023).

3100

3101 **6.2.2. Physiological and behaviour-based conservation strategies for fisheries management**

3102 The diversity of physiological and behavioural traits is needed for the resilience of fish populations
3103 to thermal variability, according to the findings of this study. In particular, it is important to
3104 conserve large dominant intermediate and high performers that have the aerobic capacity to
3105 behaviourally respond to thermally variable conditions (Bessa et al. 2021, Killen et al. 2021).
3106 Hence, the implementation of physiological and behaviour-based conservation strategies is critical
3107 for the resilience of fished stocks to climate change (Maynard et al. 2010, Levy and Ban 2013,
3108 Beever et al. 2017). As physiological biomarkers are directly linked to survival and fitness
3109 endpoints, they allow fisheries scientists to detect early warning signs of the cause and effect
3110 behind stock declines attributed to thermal variability. These physiological assessments should be
3111 done rapidly before largescale changes to population demographics, such as those driven by
3112 behavioural distribution shifts, are observed (Killen et al. 2021 Brosset et al. 2021). The
3113 incorporation of physiology biomarkers will improve the reliability of fisheries biomass
3114 predictions (Sbragaglia et al. 2021) because of their known mechanistic basis but should be
3115 incorporated at time scales that are relevant for management (Killen et al. 2021 Brosset et al.
3116 2021). While laboratory techniques can provide useful physiological biomarkers, coupling these
3117 data with physiological measurements of *in situ* metabolic rate, through field respirometry (Chabot
3118 et al. 2016) or electronic heart rate loggers (Metcalf et al. 2016, Skeeles et al. 2020), while
3119 collecting routine fisheries data would no doubt provide better resolution for stock assessment and
3120 management.

3121 *In situ* techniques offer the further advantage of accounting for behaviours such as activity,
3122 exploration, and angling interactions (Ward et al. 2016, Killen et al. 2021 Brosset et al. 2021).
3123 This kind of ecophysiological data can assist in predictions of individual fitness and changing

3124 population demographics in the context of climate change (Ward et al. 2016, Killen et al. 2021).
3125 By using these tools, researchers can link information on physiological tolerance limits with
3126 predictive climatic models to understand future patterns of fish distributions and abundance. These
3127 kinds of physiological-based approaches will add reliability to the management and conservation
3128 of fish stocks in a climate change context and as the body of knowledge expands, can be
3129 extrapolated across species residing in different geographic locations overtime (Killen et al. 2021).

3130

3131 Although physiological biomarkers have rarely been used in fisheries management to identify the
3132 cause of stock declines, the Canadian salmon fishery is one of the few examples where rigorous
3133 physiological experimental protocol has been applied to fisheries management (Cooke and Connor
3134 2010, Cooke et al. 2012, McKenzie et al. 2016). Following public outcry against *Oncorhynchus*
3135 sp. mortalities during their summer upstream spawning migrations, scientists identified thermal
3136 thresholds (ie. through aerobic scope and cardiac output) and monitored pre-spawning behaviour
3137 and spatial use. Behavioural- and physiological-based conservation strategies were used to
3138 implement the inclusion of cool-water refugia in modified upstream passageways, catch levels
3139 were limited to allow for sufficient spawning escapements, and access to fishing stock was
3140 prevented when water temperatures passed thermal thresholds (Farrell et al. 2008, Hasler et al.
3141 2012, Coristine et al. 2014). Additionally, fishing policy enforced gillnet boats to have recovery
3142 boxes on board, in which bycatch could be housed in aerated optimal conditions for 1-2 hours to
3143 assist in physiological recovery for post-release survival (this is compatible with in-field
3144 measurements that show a decrease cortisol and lactate with recovery time; Farrell et al. 2008).

3145

3146 The Canadian example illustrates the importance of the identification of thermal thresholds (i.e.
3147 beyond which aerobic performance is compromised) while accounting for the energy required for
3148 maintenance metabolism, growth, dispersal and reproduction in each ecological situation (Pörtner
3149 and Knust 2007, Bozinovic and Pörtner 2015). Such physiologically-based life cycle models can
3150 also be linked with climatic data to predict future population demographics, including range shifts
3151 or climate vulnerability. These kinds of predictions are not only important for the sustainable
3152 management of fisheries, but they can also be used to identify the causal mechanisms behind stock
3153 declines or changes to the distribution of phenotypic traits. This information can also be
3154 incorporated into risk assessments, which are necessary for all species, but particularly vulnerable
3155 endemic species, such as many of the South African linefishes.

3156

3157 **6.2.2. Incorporation a physiologically-based management approach into South African**
3158 **fisheries policy**

3159 This study emphasises the need to conserve physiological and behavioural traits for the survival
3160 of exploited *C. laticeps* stocks facing thermal variability, which is predicted to increase in
3161 frequency and intensity in their home range. Indeed, South Africa is a climate-change hotspot with
3162 exploited fishery stocks, both of which have led to the need for climate-adaptive management
3163 (FAO 2000, Hobday and Pecl 2014). South African linefish stocks have shown some recovery
3164 after policy intervention following the state of emergency declared in 2000 (FAO 2000, Attwood
3165 et al. 2013, Parker et al. 2016). This emergency prompted a number of regulatory changes,
3166 including amendments to the bag and size limits for many linefish species. Despite these stricter
3167 measures, recovery has only been observed for a few target species (DAFF 2016, DEFF 2020).
3168 The poor status of many linefish species in South Africa is exacerbated by increasing thermal
3169 variability along many parts of the coastline (Duncan et al 2018). Recognising this threat, Ortega-
3170 Cisneros et al. (2018) reviewed the likely sensitivity of 40 of South Africa's commercial linefish
3171 species to change. They categorised *C. laticeps* as a medium-high sensitive species, attributing
3172 much of their sensitivity to the intense pressure by the small-scale boat-based sector. However,
3173 since their methodology did not incorporate any physiological metrics, the true sensitivity to the
3174 changing thermal environment has not been adequately assessed.

3175 Duncan et al (2018) used growth, distribution and metabolic data to predict the future response of
3176 *C. laticeps* to climate change. They concluded that *C. laticeps* is physiologically robust and will
3177 persist in its core range and in its most productive commercial fishing grounds, which have been
3178 defined as between False Bay and Arniston (Griffiths 2000, Kerwath et al. 2013b). Given that an
3179 understanding of the physiological limits of fish is key to predict their responses to climate change,
3180 it is critical that information from this thesis (and other similar work) be incorporated into South
3181 African fisheries management structures. Indeed, the FAO (2012) recommended that climate
3182 management must be physiologically and behaviourally-based and this is critical, given the
3183 economic importance of the linefishery.

3184 The Department of Agriculture, Forestry and Fisheries' (DAFF) Climate Change Adaptation and
3185 Mitigation Plan (CCAMP), for improving adaptive management of the linefishery to maximize
3186 economic benefit, has identified small-scale fishing communities as most vulnerable to climate
3187 change effects (DAFF 2016, Hampton et al. 2017). Small-scale fisher households rely heavily on

3188 fisheries resources, particularly sparid reef communities, and are limited in their ability to adapt
3189 to climate-driven changes in resource availability (DAFF 2016, Hampton et al. 2017). Future
3190 assessments of fisher vulnerability, should however, not only consider where the fishers are
3191 vulnerable, but where the fish populations may be exposed to conditions beyond their
3192 physiological limits. Using physiological metrics, Duncan et al. (2018) identified future range
3193 contraction of *C. laticeps*, and likely other similar sparid reef species, between the areas of
3194 Arniston and Knysna, as well as east of St Francis. These areas are important for small-scale
3195 fisheries (Hampton et al. 2017) and may require the implementation of adaptation measures for
3196 increasing fishing efficiency, such as an upgrade to vessels that can travel longer distances and
3197 track fish population distribution shifts. Other suggested adaptation measures include the
3198 promulgation of additional Marine Protected Areas (MPA's) and the improved efficiency of
3199 existing MPA's (Hampton et al. 2017). This is important as climate-driven stock declines of *C.*
3200 *laticeps* are predicted in the Dwesa-Cebe, Amathole and Bird Island MPAs. The predicted declines
3201 of fish stocks in these MPA's are problematic for the most vulnerable small-scale communities
3202 that rely on these MPAs for the recruitment of fish stocks into nearby fishing areas (Duncan 2018).

3203
3204 South Africa has linked the sustainability of ocean resources and protection of marine services
3205 under Operation Phakisa (Harris et al. 2014). Here, 21 new MPAs have been proposed with an
3206 ultimate goal of protecting 20 % of South Africa's coastal zone within the next 20 years
3207 (Government of South Africa 2010, Harris et al. 2014). The goal is to conserve populations that
3208 can be resilient to future climate change. For example, *C. laticeps* populations residing from False
3209 Bay to Arniston and from Knysna to St Francis Bay are unlikely to be impacted by climate change
3210 until 2100 (based on metabolic data; Duncan 2018). This range also includes the major commercial
3211 fishing grounds of the species and several MPAs such as Tsitsikamma, Robberg, Goukamma and
3212 Betty's Bay (Harris et al. 2014, Duncan 2018).

3213
3214 The maintenance of MPAs in the primary fishing area is important. The findings from this thesis
3215 have shown that the physiologically and behaviourally fittest individuals appear to have the
3216 greatest resilience to climate variability. When this information is combined with Duncan et al's
3217 (2019) findings which suggested that populations protected from exploitation had improved
3218 physiological performance when compared with those that were exploited and Muller's (2022)
3219 study that found that larvae from populations that were protected from exploitation were
3220 physiologically more tolerant of climate stressors, it appears that these MPAs will be critical to
3221 preserve *C. laticeps* populations and the fisheries resources that they provide in this area. In

3222 addition, the promulgation of additional MPAs, to protect the bold, high performers in areas where
3223 *C. laticeps* may be susceptible in the future may be necessary. The incorporation of physiological
3224 information into conservation strategies has been made elsewhere. For example, Maynard et al.
3225 (2010) and Levy and Ban (2013) recommended that the principals of conservation physiology be
3226 fundamentally incorporated into MPA design to preserve fisheries resources.

3227
3228 For resident fishes, such as *C. laticeps*, MPA's offer a unique opportunity to protect the
3229 physiologically and behaviourally fittest phenotypes. Depending on their egg and larval dispersal
3230 strategies, the adults of these fishes have the potential to contribute their offspring to the
3231 surrounding exploited areas. This is considered critical for maintaining physiological diversity
3232 (Duncan et al 2019), genetic diversity and catchability in nearby fished areas (Cooke et al. 2007,
3233 Gingerich et al. 2007) where the resilient physiological and behavioural phenotypes have been
3234 removed (e.g. reduced aerobic scope and activity; Duncan et al. 2019, Alos et al. 2012, Enberg et
3235 al. 2012, Koeck et al. 2018). Understanding these concepts and incorporating them into climate
3236 adaptation plans should be an essential component of South Africa's fisheries policy. However,
3237 while the basic mechanism driving the selection of certain physiological phenotypes is understood,
3238 much research is necessary to refine and improve our understanding of this process and how to
3239 improve the status quo.

3240

3241 **6.3. Limitations of this study**

3242 Coupling physiological function with behaviour provides a better scope of ecological processes
3243 (Scott and Sloman 2004), however laboratory-based predications may differ from ecological
3244 reality. Domestication (including netting, capture, transport and husbandry) can change fish
3245 physiological and behavioural phenotypes (as reviewed by Sylvain et al. 2020). However, the
3246 extent of behavioural and physiological changes varies amongst species. *Chrysoblephus laticeps*
3247 individuals were very robust to laboratory conditions and began feeding the following day after
3248 introduction to the laboratory, inferring that domestication-induced behavioural changes may
3249 occur to a lesser extent in this species.

3250 One of the concerns in the present study was the consequences of exposure to very warm
3251 temperatures during the experiments. *Chrysoblephus laticeps* were initially exposed to 24°C
3252 following a standardised experimental design (Duncan et al. 2019). However, in the present
3253 study's repeated measured design, fish suffered poor health (including bacterial infection and
3254 mortality) after this exposure and the experiment had to be terminated. Following this, a new batch

3255 of individuals were subjected to a slightly lower thermal maximum (21 °C). The detrimental effect
3256 of the 24 °C went unnoticed by Duncan et al. (2019) as they did not perform repeated measures
3257 on the same fish. The need for repeated measures must be acknowledged when performing thermal
3258 physiological studies at an individual level, in comparison to a population level. Indeed, the
3259 exposure to high temperatures may result in a reduction in aerobic scope of an individual (Portner
3260 et al. 2004), or a bacterial infection caused by physiological stress or injury from capture (Steeger
3261 et al. 1994, Lapointe et al. 2014, Watson et al. 2020, Sylvain et al 2020). In an ecological reality,
3262 several abiotic and biotic components (ie. sensory ability, perception of risk, or residency shifts to
3263 avoid unfavourable conditions; Giske et al. 1998, Stankowich and Blumstein 2005, Nilsson and
3264 Ostlund-Nilsson 2008) may interact to impact physiological performance, and individual or social
3265 behaviour (Killen et al. 2021). These could not be evaluated in this study.

3266 Assessing the impact of temperature and phenotypic differentiation in the context of social
3267 hierarchy can be challenging in a lab setting. In this study, the formation of social groups of three
3268 individuals per 1000 L tank was attempted, but high levels of aggression occurred to the point of
3269 mortalities. Hence, individuals were subjected to paired duels. Future studies should measure
3270 complex social interactions beyond paired duels (for example, a typical harem of around eight
3271 individuals in a larger housing tank equipped with cameras to record behaviour), such as plastic
3272 changes in the group behaviour of multiple subordinates following the removal of the dominant
3273 individual. This is because the behavioural response of individuals may vary between paired duels
3274 versus a complex social setting. For example, losers of dyadic duels may have much higher cortisol
3275 when facing the dominant individual head on, as opposed to lower stress shared between multiple
3276 subordinates under a single dominant competitor in ecological reality (Rivas and White 2020).
3277 The physiological underpinning of sociality is under researched, but there is increasing
3278 understanding that the variation of physiological traits amongst individuals is a critical driver of
3279 social organization (Seebacher and Krause 2017, Killen et al. 2021). There is a need to examine
3280 how individual physiology within a social group context can change social group responses to
3281 environmental variation (Jolles et al. 2017, Killen et al. 2021). For example, a social hierarchy
3282 can be shifted by an individual's behaviour within the group, and this will impact interactions
3283 between other group members and group function as a whole (Jolles et al. 2017, Killen et al. 2021).
3284 While individual physiological performance should be measured repeatedly for the same
3285 individual across an environmental gradient as was done in this study, these measurements should
3286 be repeated within a social group context to predict the ecologically relevant future climate success
3287 or vulnerability of reef fishes.

3288 Additionally, this study assessed ecologically relevant short-term tolerance to thermal variability,
3289 which is important as it is often argued that simulated laboratory conditions differ from the realized
3290 niche, particularly in the context of the OCLTT theory (Oxygen Capacity Limited Thermal
3291 Tolerance; Jutfelt et al. 2018, Portner et al. 2018). Indeed, this study used the variability in
3292 metabolic phenotypes and height of performance curves to assess ecologically relevant short-term
3293 tolerance to extreme thermal variation. In particular, the OCLTT is under debate as to whether
3294 optimum performance temperatures estimated in laboratory experiments correspond to
3295 temperatures where aerobic performance is maximised in ecological reality (Jutfelt et al. 2018,
3296 Portner et al. 2018). Hence, it has been argued that the OCLTT should not be applied to species
3297 whose MMR increases steadily to reach maximum performance in natural conditions (Portner et
3298 al. 2018). This would include species from stable tropical environments that may capitalise on
3299 very high rates of maximum performance through a steep aerobic scope curve (Chown et al. 2010,
3300 Killen et al. 2014, Neubauer and Anderson 2019).

3301
3302 Payne et al. (2016) found that laboratory data on optimal performance temperatures matched *in*
3303 *situ* environmental thermal tolerance in several tropical and temperate species. They suggested
3304 that thermal performance curves may be applied to an individual's realised thermal niche. Despite
3305 this, owing to the debate, optimal aerobic performance was not used to infer optimum temperature
3306 for *C. laticeps* in the present study, but rather the variability in metabolic phenotypes and height
3307 of performance curves was used to assess short-term tolerance to extreme thermal variation (as
3308 suggested by Portner et al. 2018). Accordingly, the OCLTT may be more relevant to species that
3309 may reach their oxygen limits in their ecological reality (Portner et al. 2018), such as those
3310 (including *C. laticeps*) living in highly variable coastal environments with frequent short-term
3311 exposure to heat waves and upwelling events (Bates et al. 2018, 2019, Portner et al. 2018).

3312
3313 The present study focussed on ecologically relevant short-term temperate variation, and the
3314 associated short-term thermal acclimation, rather than on long-term physiological acclimation.
3315 However, long term physiological acclimation is an important response to thermal variability
3316 through the broadening of thermal performance curves, or genetic adaptation (over several
3317 generations) so that performance curves are maximized in the new thermal environment (Donelson
3318 et al. 2012, Munday 2014, Chown et al. 2010, Donelson et al. 2019, Neubauer and Anderson
3319 2019).

3320

3321

3322 **6.4. Future research priorities to understand the link between behaviour and**
3323 **physiology in the Anthropocene**

3324

3325 This study has highlighted the importance of linked physiological and behavioural traits in
3326 predicting the survival of fished *C. laticeps* populations to climate change. However, this research
3327 is in the early stages and there is currently limited information on how fisheries select for coupled
3328 behavioural and physiological traits for most species (Uusi-Heikkilä et al. 2008). Such information
3329 is important as physiological and behavioural plasticity are likely to govern the adaptive potential
3330 of fish populations. A focus of future studies should be to understand the coupled effects of
3331 exploitation and climate stressors on fish physiology and behaviour (Gingerich et al. 2007) to
3332 optimise the governance of exploited angling species at risk of stock collapse, due to their
3333 ecological, economic and social importance (FAO 2012). The selection for behaviour and
3334 underlying physiological traits by fisheries is identified as one of the most crucial research areas
3335 in the study of fishing-induced evolution (Uusi-Heikkilä et al. 2008). Within this general research
3336 area, there are several future research priorities (outlined below) that are required to provide
3337 information to maximize the survival and fitness of fished populations for effective management
3338 (McKenzie et al. 2016, Ward et al. 2016, Campillay-Llanos et al. 2021).

3339

3340 **6.4.1. Fishing selection on physiological and behavioural phenotypes.**

3341 As exploitation and climate change are expected to operate at the level of genotype through natural
3342 selection, whole-genome sequencing approaches to identify quantitative trait loci related to
3343 aerobic scope and behaviour are required. By comparing exploited and unexploited populations
3344 (for example those found inside and outside Marine Protected Areas) and populations inside and
3345 outside environmental change hotspots, it may be possible to assess the genetic basis for the
3346 physiological and behavioural traits of interest, and to assess how directional selection for these
3347 traits can vary under different pressures. For example, bold individuals may be favoured under
3348 climate stressors but selected against by exploitation.

3349

3350 To gain a better understanding of the influence of exploitation, future research should aim to
3351 combine catchability experiments with telemetry to monitor behaviour, spatial use (e.g. Whitlock
3352 et al. 2015) and survival of released fish (Cooke et al. 2016). These biotelemetry studies should

3353 be extended to include physiological variables (e.g. heart rate or field metabolic rate; Metcalfe and
3354 Arnold 1997, Skeeles et al. 2020) and these can be related to environmental conditions in the wild.
3355 These physiological data can not only be used to define critical thresholds (e.g. temperature and
3356 oxygen concentration), while accounting for energy used in vital metabolic processes (e.g.
3357 locomotion, foraging) and biotic interactions (e.g. social competition, predation evasion), but will
3358 also provide information on the selective nature of exploitation. This information may be valuable
3359 to inform fisheries policy that mitigates the effects of fishery-induced evolution for physiological
3360 and behaviour traits (McKenzie et al. 2016) in both catch and release and catch and kill contexts.
3361 Additionally, data obtained on the abundance and spatial use of individuals with certain
3362 behavioural and physiological traits could be used to determine the effectiveness of Marine
3363 Protected Areas for conserving the fittest phenotypes (Cooke et al. 2016, McKenzie et al. 2016,
3364 Ward et al. 2016).

3365

3366 **6.4.2. Assessment of the plasticity and predictability of phenotypic trait expression, across** 3367 **a range of stressors of differing intensity.**

3368 It is crucial to predict how populations may respond to environmental variation by determining
3369 which physiological and behavioural phenotypic traits can be expressed across a range of
3370 environmental conditions (Careau et al. 2008). Within this context there is also a need to account
3371 for various life history stages as these may have different energy budgets that may determine their
3372 sensitivity to environmental change. These must also be assessed across populations, as local
3373 acclimation and adaptation may impact growth, survival, fitness and genetic drift. This thesis has
3374 collected important data on the importance of linked physiological and behavioural traits for the
3375 survival of fished populations to thermal variability. However, there is a lack of information on
3376 the expression of physiological traits on behavioural phenotypes across a range of stressors and
3377 species and area-specific research is required (McKenzie et al. 2016, Ward et al. 2016).

3378 To add to the data collected in this study on the expression of linked physiological and behavioural
3379 traits across a thermal gradient, future studies need to characterize the expression of physiological
3380 and behavioural phenotypic traits across interacting environmental gradients. These include
3381 temperature variability, pH, dissolved gases (hypoxia and hypercapnia) and salinity. To better
3382 understand trait plasticity and differentiate between high and low performers, it is critical to
3383 categorize the expression of phenotypic traits at both optimal and extreme environmental
3384 thresholds, where performance, survival or reproduction are impaired. For example, studies on

3385 how aerobic scope varies with temperature is lacking for numerous fish species. Assessing the
3386 expression of physiological and behavioural traits across interacting environmental gradients for
3387 numerous species is a large undertaking, which will require linking laboratory and field studies,
3388 as well as physiology-based models (McKenzie et al. 2016, Ward et al. 2016). However, these
3389 data can be used to produce mechanistic thermal envelope models, for the projection of the
3390 sensitivity of species to global change, in relation to functional indicators such as bioenergetics
3391 and life history traits (Holt and Jorgensen 2015).

3392

3393 **6.4.3 Impact of fishing pressure on social hierarchy.**

3394 This study found that physiological and behavioural traits determined social dominance, which
3395 can change under thermally variable conditions. Given that that these traits are under selection by
3396 fisheries (Alos et al. 2012, Duncan 2019), fisheries are likely to impact the structure of social
3397 groups and their ability to respond to climate change (Killen et al. 2021). Future research on the
3398 fishery-induced selection on behavioural and physiological traits in a social group context is
3399 therefore important to preserve fish stocks and the catchability of these stocks. For example,
3400 exploitation pressures in hook and line fisheries may cause prolonged fission of populations by
3401 removing bold individuals (Alos et al. 2012) that have the aerobic capacity for behavioural change
3402 in the population (Killen et al. 2017, Seebacher and Krause 2017, Pörtner et al. 2018).
3403 Alternatively, trawl fishing has been shown to reduce group cohesion (and hence, catchability of
3404 these stocks) by removing fish likely to school (Hollins et al. 2019). Fishing-induced alterations
3405 to social group structure is an important modulator of locomotion, foraging, and predation-evasion
3406 costs and may be problematic for many social species (Killen et al. 2017, Hansen et al. 2020).

3407

3408 To better predict the consequences of fishing-induced alterations on the social structure of fishes,
3409 we need to improve our understanding of how physiology and behaviour (e.g. risk taking,
3410 foraging, locomotion, activity) act together to determine the structure of fish shoals. For example,
3411 fish may form groups with individuals maintaining similar swimming speeds and sharing similar
3412 metabolic costs within the environment (Killen et al. 2017, Seebacher and Krause 2017).
3413 Furthermore, there is a lack of information as to how individuals use sensory cues to identify
3414 appropriate social groups (with similar physiological phenotypes), although Metcalfe and
3415 Thompson (1995) suggested that fish can identify the competitive ability of conspecifics and may
3416 choose to group with less competitive individuals. Killen et al. (2017) suggested that fish may also
3417 be able to identify the physiological traits of individuals, which may determine social group

3418 structure. In particular, more information is needed on species that form harems (i.e. the largest
3419 male dominates over a harem of females; as is the case in *C. laticeps*), and how this type of
3420 hierarchy may change following the capture of the dominant male.

3421
3422 A key to predicting the impact of fisheries-induced evolution on group structure is the
3423 development of an understanding of which physiological and behavioural phenotypes influence
3424 the susceptibility of fishes to capture. This can be done by measuring individual physiological and
3425 behavioural traits in fish, assigning these fish to social groups and subjecting groups to fishing
3426 simulations. An example of this kind of study was conducted by Hollins et al. (2019), who used a
3427 trawl simulation in a swim tunnel to assess which physiological phenotypes were most likely to
3428 be captured. Future research will need to determine the susceptibility of physiological and
3429 behavioural phenotypes to capture by a range of active and passive fishing gears. Fishing-induced
3430 changes to group social structure can be simulated by assigning different phenotypic trait
3431 compositions to social groups and assessing the cohesion of these groups under environmental
3432 variability. Changes to group cohesion can be assessed through the measurement of changing
3433 behavioural interactions and aerobic capacity (e.g. swim tunnel experiments) within the group,
3434 under changing environmental conditions. Behavioural preference tests should be used to evaluate
3435 whether individuals favour associating with familiar or unfamiliar shoal mates, and this should be
3436 related to the physiological phenotypes of shoal members. Models can be used to predict future
3437 rates of change to the social structure of fished populations by combining data on fishery-specific
3438 phenotypic trait selection with environmental data and annual catch rates. The prediction of the
3439 future structure of fished populations will be important for management and policy intervention.

3440

3441 **6.4.4. Long-term data collection to account for micro-evolutionary time scales**

3442 Long-term data sets will provide evidence for increases in fishing mortality and its associated
3443 impacts on life history characteristics such as the age or size at maturation. For example, Andersen
3444 and Beyer (2015) using long-term datasets found that a late maturing life history strategy increased
3445 a populations' susceptibility to the effects of fishing. However, reference points as to how different
3446 metabolic phenotypes influence catchability are still needed. Long-term data sets spanning
3447 multiple generations will assist in answering key questions on the heritability of different
3448 phenotypic traits associated with metabolism and swimming performance. Long-term, detailed
3449 records of the heritability of phenotypic traits are required to detect shifts in physiological and

3450 behavioural trait diversity caused by fishing-induced micro-evolutionary processes, together with
3451 their capacity to alter ecological interactions (Ward et al. 2016).

3452
3453 Long-term monitoring of angling effort, catch rates and fished population structure is required.
3454 Furthermore, the recording of long-term environmental data (e.g. temperature, dissolved oxygen
3455 and pH) is equally important. Long-term environmental datasets can be related to changes in
3456 growth overtime, for example by obtaining otoliths from subsamples of harvested individuals
3457 (Morrongiello et al. 2012). Telemetry can be used to relate how individuals perform
3458 physiologically (e.g. electrocardiogram or acceleration; Metcalfe and Arnold 1997, Hunter et al.
3459 2004) to prevailing environmental conditions in the wild. Physiological traits must be related to
3460 susceptibility to capture. The spatial tracking of tagged individuals, from which physiological data
3461 is collected, can be used to identify when these individuals engage in anthropogenic interactions
3462 (e.g. harvest or catch-and-release fishing; Cooke et al. 2016). Together, this information would
3463 provide an indication on the historical and contemporary physiological and behavioural phenotype
3464 structure of fish populations and could be used to model future scenarios.

3465
3466 **6.4.5. Measuring fitness to assess the heritability of physiological and behavioural**
3467 **phenotypic traits.**

3468 Inter-individual variation in metabolic traits has been attributed to a genetic basis in several taxa
3469 (Zub et al. 2012, Mathot et al. 2013). Among fishes, several studies (Lahti et al. 2002, Seppänen
3470 et al. 2009, Metcalfe et al. 2016) have suggested inter-individual variation in metabolic traits may
3471 be under genetic control. Several genes have been linked to general metabolic processes (i.e.
3472 proteolysis and antioxidants) associated with heat stress in *Salmo salar* (Beemelmans et al. 2020).
3473 With the genotype influencing the physiological and behavioural phenotypes, it is critical to gain
3474 an understanding of heritability. Researchers have recently isolated genes linked to the expression
3475 of metabolic traits associated with heat stress (Beemelmans et al. 2020, Taboun 2020) and
3476 hypoxia (Zou et al. 2022), as well as behavioural traits (Abeliovich et al. 1993, Chen et al. 1994,
3477 Iguchi et al. 2001, Baran and Streelman 2020, amongst others; Ariyomo et al. 2013, Edenbrow
3478 and Croft 2013, Laine et al. 2014). As mentioned previously (see Section 6.3), Zou et al. (2021)
3479 found that bold and timid *Paralichthys olivaceus* differed in the expression of 144 genes related
3480 to personality and metabolism. In particular, it is necessary to gain understanding of whether inter-
3481 individual differences in stress responses, (i.e. attributed to the expression of physiological and
3482 behavioural phenotypic traits) may be related to reproductive fitness. For example, Careau et al.

3483 (2020) is the first study to have quantified metabolic trait reaction norms in relation to fitness. This
3484 was done to understand the evolutionary importance of physiological and behavioural traits in
3485 response to anthropogenic stressors. They found that differences in physiological and behavioural
3486 trait expression did not affect the reproductive fitness of male zebra finches (*Taeniopygia guttata*)
3487 exposed to a novel environment. However, an understanding of the heritability of behavioural and
3488 physiological traits is needed among the fishes. Specifically, this research should focus on whether
3489 differences in trait expression are related to fitness by determining different stress responses. The
3490 first study to do this was by Long et al. (2021), who found that *P. olivaceus* offspring contained a
3491 mix of bold and timid phenotypes irrespective of maternal line, however behavioural traits were
3492 linked to metabolic traits, which were partly heritable due to maternal effects. Both bold and timid
3493 offspring from the bold maternal line had the advantage of a higher metabolic rate and the ability
3494 to respond to environmental stressors (Long et al. 2021). Epi-genetics is considered to be an ideal
3495 tool to examine the heritability of metabolic and behavioural phenotypic traits and the co-
3496 existence, of behavioural and metabolic phenotypic traits (Long et al. 2021).

3497 In addition to employing epigenetic techniques, chemical tags can be used to express or prevent
3498 the expression of genes to expose which genes may be linked to behavioural and physiological
3499 phenotypes, as well as which of these phenotypes can co-exist. To determine the evolutionary
3500 consequences of variability in physiological and behavioural traits, future studies need to measure
3501 changes in trait frequency under simulated stressors overtime (Biro and Post 2008). Studies will
3502 also need to account for the selective nature of fisheries on the relative frequency of physiological
3503 and behavioural phenotypic traits overtime. For example, Redpath et al. (2010) used two bred lines
3504 of largemouth bass *Micropterus salmoides*, with different vulnerability to angling and correlated
3505 these with metabolic traits.

3506
3507 Critically, when any of the abovementioned research is conducted using wild fish populations, the
3508 method of capture has to be closely considered. This is because individuals with certain
3509 behavioural (eg. Alós et al. 2012) or physiological characteristics (eg. Duncan et al 2019) may be
3510 more susceptible to capture in a single gear and may therefore be overrepresented in
3511 experimentation. Researchers will have to reduce this potential bias and may be able to do this by
3512 using a range of sampling methods (Biro and Dingemanse 2009), including active and passive
3513 techniques when capturing individuals for these experiments. While this may complicate
3514 experiments, researchers are urged to embrace this challenge and contribute to the sparse

3515 information base on how fisheries select for coupled behavioural and physiological traits (Uus-
3516 Heikkila et al. 2008).

3517

3518 **6.5 Conclusion**

3519 In conclusion, physiological and behavioural traits are crucial to predict the survival of fished
3520 populations to thermal variability. The scientific community has the capacity to inform fisheries
3521 policy using data collected on the coupled effects of exploitation and climate stressors on fish
3522 metabolic physiology and behaviour. Fisheries scientists need to collaborate with government
3523 authorities to apply such knowledge to develop regulatory frameworks that optimize the
3524 management of exploited fishes and maintain the resilience of the complex socio-ecological
3525 systems associated with their fisheries (FAO 2012). It is critical to preserve physiological traits
3526 linked to behavioural plasticity as these traits are likely to govern the adaptive potential of fished
3527 populations and facilitate vital ecological and evolutionary processes (Ward et al. 2016).
3528 Preserving the diversity of physiological and behavioural phenotypes in fished populations will
3529 promote climate-resilience and hence, falls within the scope of an ecosystem-based fisheries
3530 management approach (Schindler and Hilborn 2015, Ward et al. 2016). By implementing a
3531 management approach that considers the protection of physiological and behavioural diversity,
3532 fisheries managers will maximize ecosystem services in a rapidly changing climate (Schindler and
3533 Hilborn 2015).

3534

3535

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