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The Role of Intraspecific Variation in Physiological Traits in Determining Vulnerability to Capture in Fish

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ABSTRACT

Impacts of fisheries induced evolution (FIE) may extend beyond life history traits to more cryptic aspects of biology, such as behaviour and physiology. Understanding roles of physiological traits in determining individual susceptibility to capture in fishing gears, and how these mechanisms change across contexts is essential to evaluate the capacity of commercial fisheries to elicit phenotypic change in exploited populations. In particular, physiological traits related to metabolism, bioenergetics, and swim performance may affect the probability of fish interacting with a fishing gear, or successfully escaping it once it has been encountered, and so may also be under selection in commercial and recreational fisheries. Selection on these traits has the capacity to alter the physiological composition of exploited fish populations in response to fishing pressure, with consequences for the viability of fish stocks, and the sustainability of fisheries exploitation. Evaluating the capacity of fisheries to elicit phenotypic change in exploited fish stocks is complicated by the myriad different fishing gears used around the world, and their contrasting mechanisms of capture, as well as the modulating effect of environment on relationships between individual traits and capture vulnerability. This thesis made use of both laboratory and field-based experiments, alongside data collected from commercially important species in a real world fisheries context to establish mechanistic links between individual physiological traits and capture vulnerability in different gears, the degree to which these relationships may be modulated by the environment, and how fisheries selection may alter the ecological niche of exploited species.

Using laboratory experiments, I investigated the role of environmental context in determining relationships between individual physiological traits and capture vulnerabilities in different gear types. Trawling simulations conducted on groups of Minnows comprised of individuals familiar with one another, and of individuals which had never seen each other before showed that social context can alter relationships between individual traits and capture vulnerability. When swimming among familiar conspecifics, a negative relationship between trawl capture vulnerability and anaerobic metabolic capacity was found, while no relationship between individual traits and capture vulnerability was found when fish faced the trawl alongside unfamiliar shoalmates. In contrast, a subsequent experiment investigating links between physiological traits of minnows and capture vulnerability in replicated trawl and trap trials found no relationship between metabolic traits and capture vulnerability in either gear at any temperature. However, the trawl still selected on fish behaviour with high activity fish at less risk of capture at all temperatures tested.

These laboratory experiments are accompanied by two studies of fisheries selection in the wild. The first used a combination of lab based behavioural assays, respirometry and acoustic telemetry to investigate the capacity for two different fishing methods (gill netting and angling) to select on the physiological and behavioural traits of perch. This study found that gillnetted perch showed broader patterns of habitat use than their angled conspecifics, suggesting that gill nets selected on the spatial traits of wild fish. No differences in physiological traits between gear types was found. Finally, a similar comparative approach was used to investigate the capacity for trawling and jigging to select on contrasting ecological traits of wild cod. Jigging was found to selectively remove fish with low $\delta^{15}N$ values, most likely through a mechanism of feeding motivation, while the trawl was found to be less selective on ecological traits.

These results highlight the capacity for fishing gears to select on cryptic aspects of fish biology, such as patterns of space use, feeding motivation, and swim performance, but also show that these relationships can be strongly dependent on the external environment.

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Author’s Declaration

The results presented in this thesis are the culmination of experiments and field work conducted between March of 2016 and July of 2018, supervised by Professor Shaun Killen and Doctor David Bailey. Writing of the thesis took place under guidance from Professor Shaun Killen and Doctor David Bailey. This research has not been submitted for any other degree at the University of Glasgow or any other institution. The experiments were conducted by myself, with assistance in data collection and conducting experiments from Davide Thambithurai (Chapter 2), Barbara Koeck (Chapters 3,4,5) , Amelie Crespel (Chapter 3), Travis Van Leeuwen (Chapter 2,4) , and Brooke Allan (Chapter 2). All data analysis was performed by myself. Additional support was provided by Matt Guzzo and Matt Newton in the maintenance of the telemetry array used in Chapter 4, and by Jason Newton in the operation of the mass spectrometer at the LSMSF. Davide Thambithurai, Barbara Koeck, Brooke Allan, Steven J. Cooke, Jan Lindström, Kevin J. Parsons, Shaun Killen and David Bailey contributed to the writing of Chapter 1 (Sections 1.1-1.2.4), and its subsequent publication. Davide Thambithurai, Barbara Koeck, Travis Van Leeuwen, Brooke Allan, Shaun Killen and David Bailey also contributed to the writing and subsequent publication of Chapter 2.

Jack Hollins

1. GENERAL INTRODUCTION

1.1 A PHYSIOLOGICAL PERSPECTIVE ON FISHERIES SELECTION

Commercial and recreational fishing are changing the phenotypic composition of exploited fish stocks, particularly in traits related to life-histories and reproduction (Enberg *et al.* 2009a; Enberg *et al.* 2012; Hard *et al.* 2008; Heino *et al.* 2013b; Jørgensen *et al.* 2007). Where the high mortality imposed by fishing extends to immature life history stages, fishing selects for individuals which reproduce at an earlier age (Law and Grey 1989; Heino 1998; Law 2000; Ernande et al. 2004; Jørgensen et al. 2006; 2009). Consequently, exploited stocks can become predominantly comprised of individuals that mature earlier and at smaller sizes. These effects can become exacerbated when there is direct size-selectivity by fisheries in which larger fish are preferentially targeted (Conover and Munch, 2002; Edley and Law, 1998; Handford et al. 1977; Rijnsdorp 1993;van Wijk et al. 2013) The capacity for size-based fisheries selection to elicit evolutionary change in wild fish populations was first noted by Cloudsley Rutter (1904). In a study of the Chinook salmon (*Oncorhynchus tshawytscha*) from the Sacramento river, it was postulated that the use of gillnet mesh sizes designed to allow small male Chinook salmon to evade capture was counterintuitive, allowing only smaller individuals to breed and ultimately leading to a deterioration in salmon size (Rutter, 1904). If the traits under selection by fisheries have a heritable component, then evolutionary change in exploited populations may occur, a phenomenon known as fisheries-induced evolution (FIE). As evidence of fisheries-induced evolution has accumulated, focus has shifted from determining whether or not FIE is occurring, to assessing the rate at which these changes occur and the potential for reversibility (Enberg *et al.* 2012; Heino *et al.* 2013b). It is now recognised that quantifying and predicting these evolutionary responses will be important in maintaining the economic and ecological viability of fisheries (Laugen *et al.* 2014a). This, in turn, requires a thorough understanding of the mechanisms of fish capture, and how individual traits influence susceptibility to capture for individual fish.

Intraspecific variation in traits related to physiology and behaviour have recently received increased research attention in the wider field of biology (Killen *et al.* 2017a; Williams 2008). The study of intraspecific variation in behavioural traits has shown that differences are stable over time and across contexts (Bell *et al.* 2009; Wolf and Weissing 2012), in a diverse array of taxa including fishes (Sih *et al.* 2004). Differences in behaviour among individuals are often correlated with other, more cryptic aspects of an individual's biology, from physiological traits, such as metabolic phenotype (Metcalfe *et al.* 2016c), to whole-animal measures of performance and fitness (Biro and Stamps 2008; Careau and Garland 2012). In the context of fisheries, where these traits influence an individual's susceptibility to capture in a given fishery, and are also heritable this constitutes a mechanism through which harvest-associated selection could occur and narrow the phenotypic composition of exploited populations (Heino and Godø, 2002). While the role of individual variation in behaviour has been considered in terms of making some fish more vulnerable to capture by fisheries(Biro and Post 2008b; Diaz Pauli and Sih 2017b; Uusi-Heikkilä *et al.* 2008a), overall there has been comparatively little effort to examine how traits other than size at age might make some individual fish more vulnerable to capture than others, particularly the role of physiological traits (Enberg et al. 2012). Furthermore, there have been few direct investigations of how increased mortality and altered life-histories stemming from harvest may have indirect effects on the physiological traits present within populations (Jorgensen and Fiksen, 2010; Duffy et al. 2013; Jorgensen and Holt 2013).

Physiological traits related to bioenergetics and swim performance are especially likely to affect the probability that a fish will be captured by fishing gear or survive after escaping. For example, minimum metabolic rate (i.e. standard metabolic rate in ectotherms; SMR) is a heritable trait that shows wide, repeatable intra-specific variation (Burton *et al.* 2011b; Rønning *et al.* 2007). SMR influences demand for food and oxygen and is related to various aspects of foraging and predator avoidance (Killen *et al.* 2012a; Killen 2011; Millidine *et al.* 2006), which could include avoidance of fishing gear. This estimate of basal energetic demand is sometimes also referred to as resting metabolic rate (RMR). Aerobic scope (AS) is the difference between maximum metabolic rate (MMR) and SMR and is the capacity for aerobic metabolism above that required for maintenance. It sets the limit for the number of aerobic processes that can be performed simultaneously (e.g. activity, growth, digestion) and may affect various aspects of behavioural ecology and the geographical distributions of species (Jørgensen *et al.* 2012; Killen *et al.* 2017c; Killen *et al.* 2012d; Marras *et al.* 2015; Pörtner and Farrell 2008). In fishes, AS is also correlated with swimming endurance, maximum sustainable speed, and recovery rate after exhaustive exercise (Killen *et al.* 2012d; Marras *et al.* 2010c), all of which may be relevant to a fish's ability to evade capture by fishing. After controlling for factors such as body size and temperature, it is common for metabolic rates to differ by 2-3 fold among individuals of the same species (Burton *et al.* 2011b; Norin and Malte 2011b; Norin and Malte 2012). There is also evidence that metabolic rates are at least partially heritable, and so could be targets for harvest-associated selection (Ward et al. 2016).

Variation in sensory ability, neuroendocrinology, and cognition among individual fish may also influence fish vulnerability to capture. For example, intraspecific variation in the visual capabilities of fish (e.g. opsin expression in the retina, Fuller at al. 2005; Flamarique et al. 2013; Sandkam et al. 2015) can manifest as differences in how individuals perceive colour, identify shapes, and distinguish objects. In addition to the role vision plays in determining whether a gear is perceived by a fish, these traits may also play a role in determining whether fish adopt specific behaviours upon encountering a gear (Kim and Wardle, 2003). Chemosensory ability (e.g., expression of receptor proteins within the olfactory bulb, or the relative size of the telencephalon or bulb itself) and circulating hormone levels (e.g., ghrelin, a regulator of appetite) may also determine whether fish adopt behaviours associated with susceptibility to capture in fishing gears (e.g. active search/foraging behaviour). Broad measures of sensory physiology (e.g. brain size and morphology) show intraspecific variation (Kihslinger, Lema and Nevitt, 2006; Gonda, Herczeg and Merila, 2011) and have also been found to correlate with the likelihood of a fish expressing behaviours potentially related to capture vulnerability (Wilson and McLaughlin, 2010), in addition to cognitive capacity and aspects of decision making in fish (Burns and Rodd, 2008). These latter traits relate to an individual's capacity to locate potential escape routes in a trawl, or the entry to a trap (Klefoth et al. 2017; Monk and Arlinghaus 2017). While circulating levels of hormones, and the expression of receptor proteins within the olfactory bulb also play important roles in determining whether certain behaviours are adopted, these are often linked to physiological condition (Hoskins et al. 2008; Volkoff et al. 2009; Maruska and Fernald, 2010). In these cases, these characteristics may represent a component of the mechanism through which energy demand may affect vulnerability to capture, but may not directly alter susceptibility in their own right.

Fishing may well be causing unnoticed changes to the intrinsic physiological traits of fish which could be influencing species' life-history traits, geographic distributions, and capacity to respond to environmental change or recover from overexploitation. The current failure to consider these underlying physiological mechanisms in the context of FIE also precludes the development of effective mitigation strategies that refine harvest techniques or gear implementation to better understand the effects of harvest-induced selection. Understanding the mechanistic links between individual fish traits and capture vulnerability throughout the capture process is a fundamental first step in assessing the capacity for fishing to elicit phenotypic change in exploited fish populations. The following section describes the mechanisms of capture of different fishing gears (Figure 1.1), and the degree to which intraspecific variation in physiological traits may influence capture vulnerability at each stage of the capture process (Figure 1.2).

1.2 THE CAPTURE PROCESS AND SELECTION ON PHYSIOLOGICAL TRAITS

There is great diversity in fishing gears used around the globe by the commercial and recreational fishing sectors spanning marine and freshwater systems. Fishing gears are often divided into passive or active gears. In reality, however, many fishing gears lie along a continuum between these two extremes (Figure 1.1) and rely on a mixture of stimuli that elicit various behavioural and physiological responses in fish that facilitate their capture. At one end of this continuum, passive gears rely on fish to find the deployed gear, exploiting fish active behaviours, such as foraging and exploratory behaviour and their underlying physiological traits. These would include metabolic demand and hormonal cues underlying foraging motivation, and also sensory systems related to detecting and finding food sources (e.g. sight and olfactory systems). At the other end of the continuum, active gears pursue targeted fish, with vulnerability potentially depending on fish escape ability. This could relate to a range of physiological traits associated with locomotor ability as well as threat detection and evasion (e.g. auditory and visual cues). Differences in capture methods may therefore give rise to differences in selectivity and how that selectivity may be mitigated.

The capture success for any type of gear is determined by the cumulative probability of outcomes along a set sequence of decision points (Figure 1.2) (Rudstam *et al.* 1984; Sampson 2014). Each of these stages is associated with a specific mechanism of selectivity occurring over increasingly fine spatial and temporal scales (Millar and Fryer 1999) that may act together to determine an individual's overall vulnerability to capture. The outcome at each stage has the potential to be influenced by the physiological traits of individual fish.

1.2.1 Selection via Habitat Use

The broadest spatial scale of selection occurs with the initial deployment of the gear: only those individuals within the active space of a given gear will be available to the fishery. Within-species differences in habitat use have been observed in fishes (Elliott *et al.* 2017; Kobler *et al.* 2008) and can vary based on size, sex or reproductive stage (Sólmundsson *et al.* 2015). The role of physiological traits in determining habitat use in fishes has received little attention so far but are very likely to affect capture vulnerability at broad spatial scales because parameters that affect gear deployment such as depth, distance from shore, and sea bed types are linked to variation in food abundance, predation risk, temperature, oxygenation, and water velocity. Just as population level processes are the result of the cumulative patterns of habitat selection and behaviour expressed by a population's individual members, these individual-level processes are in turn governed by physiological responses to environmental conditions determining individual fitness and performance (Cooke et al. 2014; Horodysky et al. 2015). Intraspecific variation in physiological responses to environmental conditions, and other associated physiological traits may therefore influence the habitat selection of individual fish and determine whether they overlap with a deployed fishing gear. SMR can influence food and oxygen requirements in fish (Killen *et al.* 2012a; Killen 2011), for example, and both SMR and AS are strongly dependent on temperature (Biro and Stamps 2010; Claireaux and Lefrancois

2007; Fry 1971). These temperature effects on metabolic physiology could in turn influence habitat use by individual fish and their likelihood of encountering deployed gears. For example, physiological responses to environmental change underpin seasonal southward migrations of Pacific bluefin tuna (*Thunnus orientalis*) (Whitlock et al. 2015), and diurnal patterns of habitat use in small spotted catsharks (*Scyliorhinus canicula*) (Sims et al. 2006), as individuals seek to avoid now energetically costly hunting grounds, and maximise the efficiency of feeding and subsequent digestion. Variation in temperature preference and habitat use may also be directly linked to individual SMR and the maximisation of aerobic scope and capacity for growth (Killen 2014). Similarly, fish often use specific habitats for certain behaviours, such as foraging (Sims et al. 2005; Bernal et al. 2010; 2017 Schaefer et al. 2007; Thorrold et al. 2014), and so individual differences in the frequency or duration of those behaviours may contribute to intraspecific differences in habitat use. For example, high SMR fish may meet their elevated energetic demands through increased use of foraging grounds. Differential use of habitat among individual fish led to increased capture vulnerability of timid bluegill sunfish (a trait which can correlate with SMR (Huntingford et al. 2010, Killen, Marras and Mckenzie, 2011; Killen, Marras, Ryan et al. 2012), as angling gears targeted habitat adjacent to available shelters (Wilson et al. 2011).

Physiological traits may also determine the extent to which individual fish exploit vertical habitats. In the open ocean, fish often experience cold, hypoxic conditions during oscillatory dives which approach or extend beyond the depths at which the mixed layer ends, and the oxygen minimum zone begins (Bernal et al. 2010). Segregation of vertical habitat use of open ocean fishes is driven by the physiological ability of species to maintain sufficient cardiorespiratory capacity for active behaviours under these challenging conditions (Bernal et al. 2010; 2017) a trait governed by a suite of physiological factors which are known to show interindividual variation (Ollivier et al. 2015; Joyce et al. 2016; Ozolina et al. 2016). This variation may ultimately manifest as differences in the maximum depth attainable by individual fish, or the amount of time fish spend at a given depth, and so give rise to intraspecific differences in vertical habitat use (Quayle et al. 2009; Cosgrove et al. 2014; Vaudo et al. 2014), with implications for being available to gears deployed at specific depths (Olsen et al. 2012). Links between physiological traits and habitat use may also manifest indirectly. For example, recent research on pumpkinseed sunfish captured from littoral and limnetic habitats revealed divergent sensitivity of the hypothalamic–pituitary–interrenal axis to stressors (Belanger *et al.* 2017a) emphasizing potential for spatially-structured fisheries to select for stress responsiveness

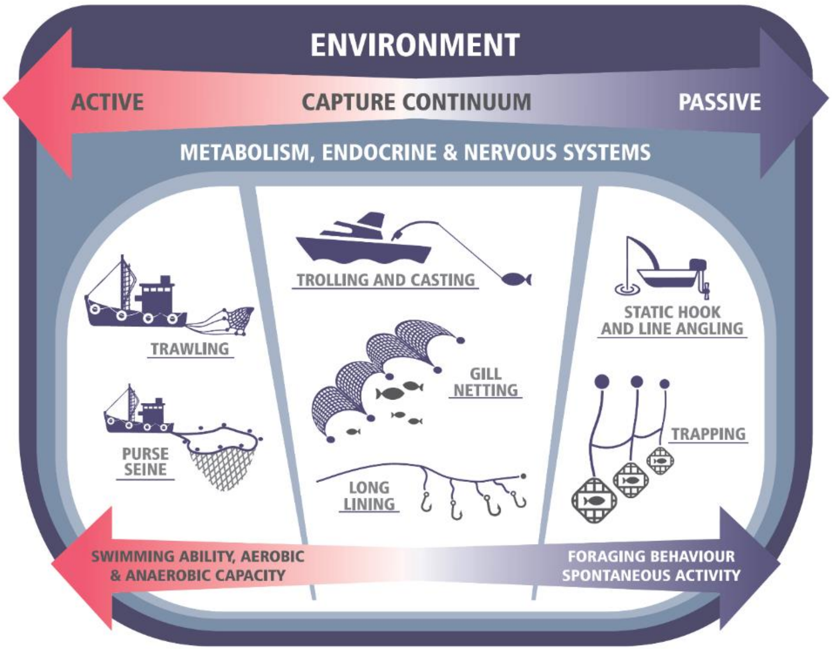

Figure 1.1. The continuum of fisheries harvest techniques between active and passive gears and practices. Techniques toward the passive end of this continuum are more likely to select on traits associated with foraging behaviour, including hormonal regulation of hunger and exploratory behaviours, as well as sensory ability. Techniques toward the active end of the continuum are more likely to select on traits related to locomotor and escape ability. Broadly spanning the entire continuum are physiological traits related to whole-animal metabolic traits, which can be directly or indirectly linked to foraging, body size, and locomotor ability. The environment will also have an over-riding influence along all points of the continuum, modulating fish vulnerability to capture and the strength of potential links with physiological traits (also published in Hollins et al. (2018).

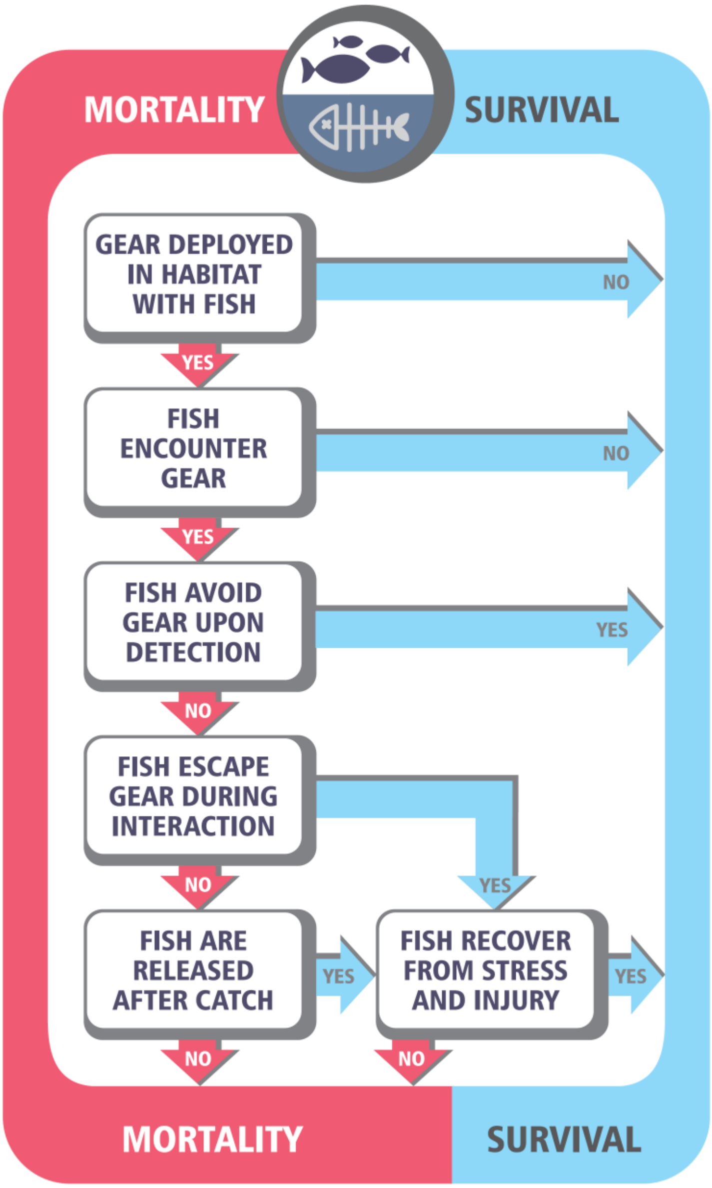

Figure 1.2. Stages during fishing leading to mortality or survival for targeted fish. Physiological traits are likely to play a role in determining the path taken at each decision point (also published in Hollins et al. 2018).

1.2.2 Selection via Gear Encounter Rate

Although gear encounter rate will necessarily have some overlap with traits affecting habitat selection, there is an important distinction to be made between selective processes occurring at these two scales. Even if gear and fish co-occur in the same broad habitat, fish must actually encounter the gear to have any chance at being captured. Individual fish vary in spontaneous activity, boldness, and exploration, and those that are more active will have higher encounter rates with fishing gears (Biro and Post 2008b; Koeck *et al.* 2018; Uusi-Heikkilä *et al.* 2008a). This could be due to random encounters during exploration or, particularly when considering passive gears, due to directed movements toward the deployed gear after initial detection. Indeed, bold or more active phenotypes are often associated with higher vulnerability to capture by angling or gill netting(Biro and Post 2008b; Cooke *et al.* 2017; Härkönen *et al.* 2014; Kekäläinen *et al.* 2014; Klefoth *et al.* 2013; Klefoth *et al.* ; Koeck *et al.* 2018; but see Wilson *et al.* 2011), but these mechanisms are also likely to increase the probability of a fish being in the path of an oncoming trawl, or beneath a towed lure, at any point in time.

Importantly, the drivers of these behavioural differences may be linked with underlying physiological traits, at least in some contexts (Biro and Stamps 2010; Killen *et al.* 2013). Fish that are more active and exploratory, for example, have also been shown to have lower hypothalamus-interrenal-pituitary and parasympathetic reactivity (Øverli *et al.* 2006; Verbeek *et al.* 2008), increased sympathetic reactivity (Verbeek *et al.* 2008), and increased metabolic rates (Killen 2011). More active fish may also possess an increased AS to accommodate this active lifestyle (Killen *et al.* 2010; Killen *et al.* 2012d), suggesting a mechanism by which passive gears may preferentially capture individuals with a high aerobic capacity. A high AS may also permit prolonged or more active bouts of swimming behaviour in fish, or be associated with increased maintenance requirements and foraging demands (Auer *et al.* 2015; Killen *et al.* 2016c), thus increasing their likelihood of encountering gears (Redpath *et al.* 2010a).Such mechanisms may partly explain why largemouth bass (*Micropterus salmoides)* bred for high vulnerability to angling also exhibited higher AS (Redpath *et al.* 2010a).

For active gears, encounter rate will be largely dependent on the movement of the gear by fishers, but sonar location can direct boats toward shoals or schools of fish. Gregarious individuals could thus be more likely to be targeted by trawls, producing selection against any metabolic or endocrine traits that promote social behaviour (Killen *et al.* 2016b).

1.2.3 Selection via Gear Avoidance

Fish still have the opportunity to avoid gears after an initial encounter or detection. For passive gears, traps catch only a small proportion of fish that come within a close proximity because some fish enter traps more readily than others (Thomsen *et al.* 2010).This could depend on a number of physiological factors, including physiological traits that underlie decision-making and risk-assessment (Andersen *et al.* 2016b; Giske *et al.* 2013; Höglund *et al.* 2005; Øverli *et al.* 2002; Øverli *et al.* 2005; Winberg and Thörnqvist 2016). For passive gears, it has been suggested that decision-making after the initial gear encounter is a greater determinant of individual vulnerability to capture than encounter rate itself (Monk and Arlinghaus 2017b). In largemouth bass, individuals with low stress responsiveness are more vulnerable to capture by angling, though the exact stage of the capture process that is affected by endocrine traits was not identified (Louison *et al.* 2017). The opposite trend was found by Koeck et al. (2018), where more stress resilient rainbow trout (*Oncorhynchus mykiss*) were more vulnerable to capture by rod and reel. Louison *et al.* (2017) also found that boldness and metabolic traits did not influence capture vulnerability, providing evidence that the decision to engage with the deployed gear after discovery was at least partially detached from foraging requirements, exploration, or risk-taking *per se*. Again, this is somewhat in contrast to the findings of Koeck et al. (2018), who found that stress resilient, capture-vulnerable rainbow trout were also more active, and so in this instance, selection via rod and reel was not independent of fish engaging in risky, exploratory behaviours (Koeck *et al.* 2018). Still, hunger increases willingness to approach and enter baited traps after an initial encounter, as does environmental temperature (Stoner 2004; Stoner *et al.* 2006; Thomsen *et al.* 2010).

While appetite is inherently labile, high energetic demand associated with high MR (Killen et al. 2011) will increase the probability of a fish being hungry and responsive to baits at any one point in time. However, effects of the environment, particularly temperature, are often observed on the vulnerability of fish via the cumulative effects of increased activity and feeding motivation (Stehfest *et al.* 2015; Stoner 2004; Stoner *et al.* 2006). By allowing the expression of extreme phenotypes, this plasticity should inherently weaken selection on the heritable genetic basis of the traits underlying fish vulnerability to capture.

Although individuals with enhanced sensory capacity would presumably be better able to avoid certain gears or find baited hooks (Lennox *et al.* 2017a), we are unaware of any empirical work directly examining this possibility. For active gears, fish often flee oncoming active gears upon first visual or auditory detection (Handegard and Tjøstheim 2005). However, there is variation in reaction distance, speed, and directionality of this response among individuals that may be related to various aspects of sensory physiology (Winger *et al.* 2004). Many gear types encourage high densities of fish within their immediate vicinity, potentially exaggerating the importance of social interactions and associated physiological traits in determining responses to gear (Winger *et al.* 2010). Should high densities of fish be present around a gear already, asocial fish may be dissuaded from approaching, reducing their capture vulnerability and indirectly selecting on underlying physiological traits related to sociability (Killen *et al.* 2016b) .

Traits related to how fish perceive risk are also likely to be important in determining whether individuals avoid a detected gear. Avoidance of active gears shows interesting parallels with optimal escape theory for avoidance of natural pursuit predators – fleeing too early can result in lost foraging opportunities while fleeing too late can result in mortality (Winger *et al.* 2010; Ydenberg and Dill 1986). The costs of lost foraging opportunities may be higher for individuals with higher SMR, causing them to have shorter reaction distance and increased risk of fishing mortality (Finstad *et al.* 2007; Killen 2011). Individuals with a higher foraging demand may be more likely to perceive the benefit of investigating a food source as outweighing the risk posed by foreign objects such as hooks or traps. Metabolic traits of fish have been shown to correlate with boldness (Huntingford *et al.* 2010; Killen *et al.* 2012a; Killen 2011), which in turn has been shown to correlate with susceptibility to capture in passive gears (Biro and Post 2008b; Diaz Pauli *et al.* 2015b; Klefoth *et al.*). It has also been demonstrated that cardiac output and RMR were directly correlated with vulnerability to capture in largemouth bass (Cooke *et al.* 2007; Redpath *et al.* 2010a). Such mechanism may partly explain the presence of 'timidity syndromes' (Arlinghaus *et al.* 2017b), where bolder individuals are apparently extirpated from populations first owing to their increased vulnerability to capture, leaving a population comprised of more shy individuals. This is corroborated by observations that fish populations subjected to recreational fishing pressure also exhibit lower RMR than their unfished conspecifics, implying a removal of high RMR phenotypes by recreational fishing (Hessenauer *et al.* 2015).

1.2.4 Selection via Escape from Gear

Even when capture seems inevitable, fish often escape gears by employing behaviours that are likely linked to aerobic and anaerobic capacity. This is particularly true for active gears such as trawls, which herd fish as they attempt to swim and hold station in front of the trawl mouth. They eventually fatigue, fall back further into the net and finally into the codend, where they are retained (Winger *et al.* 2010). There may also be a behavioural decision-making component to this form of capture whereby a fish "voluntarily" ceases swimming before complete exhaustion or follow shoal mates into the trawl. During the final moments of the trawl, free-swimming fish within the body of the net may also be retained as the gear is hauled to the surface, and accelerates as it lifts from the sea floor. Fish 'scooped up' in this fashion do not have to have succumbed to fatigue to be caught. Fish can escape by swimming faster than the trawl, or moving around the outside of the trawl mouth, making it likely that faster swimming fish, or those with a greater capacity for short-bursts of anaerobic swimming, escape capture. This effect has been illustrated in laboratory-based trawling simulations with a direct positive correlation between the capacity for burst-type anaerobic swimming and the ability to avoid being captured (Killen *et al.* 2015a). Fish can also escape capture once inside the trawl net by passing through the mesh. Escape through mesh is size-selective but there may well be a large influence of swimming endurance and anaerobic capacity on escape ability at this stage (Winger *et al.* 2010), because fish will require bursts of anaerobic swimming while changing their vector relative to the path of the trawl.

It is also completely unknown whether the metabolic costs of prior feeding and digestion affect vulnerability to capture via reductions in swimming performance. In fish, there is a temporary post-feeding increase in metabolic rate associated with digestion and nutrient assimilation (Fu *et al.* 2008; Jobling 1995; Secor 2009), referred to as specific dynamic action, that can reduce swim performance (McLean *et al.* 2018) and possibly decrease the ability to outswim a trawl. Fish with a larger AS, however, might maintain an excess capacity for swimming even while processing a meal, providing another means by which individuals with a higher AS may be less catchable by trawl.

The relevance of this swim performance based mode of selectivity is dependent on fish engaging in an optomotor response (a reflexive behaviour thought to re-orient a swimming fish after displacement from its desired horizontal course) (Kim and Wardle 2003) in which they swim and maintain station with the trawl, often oriented adjacent to the trawl doors, until they drop back within the net. While this is often observed (Rose 1995; Kim and Wardle 2003) individual variation in the response to gears is also frequent (Yanase, Eayrs, and Arimoto 2009; Underwood et al. 2015)and often predict the chances of capture for individual fish. Whether these behavioural responses represent, or correlate with, inherent physiological traits remains unclear, although individual's orientation prior interaction with the trawl gear, and density of conspecifics have all been noted to influence fish responses to approaching trawls (Rose 1995; Underwood et al. 2015). This would suggest that such responses are context-specific, heavily influenced by external environment, and so could dampen selection on traits correlated with swim performance. Kim and Wardle (2003) noted that erratic responses, characterised by burst swimming and haphazard, rapid changes in orientation, acceleration and swim velocity, lead to opportunistic use of potential escape routes around trawls. Fish with greater anaerobic capacity may be expected to engage in such behaviours more readily, or for longer periods, and so be less catchable.

Finally, there is wide intraspecific variation in stress responsiveness within fish species (Höglund *et al.* 2005; Pankhurst 2011),and so individuals may vary widely in the extent to which they can recover from fishing-stress and physical trauma even after they escape from a fishing gear. Out swimming a trawl may result in a severe physiological disturbance due to intense exercise, as may fighting on a fishing rod or longline. Even gears considered to be comparatively benign, like traps can induce a stress response from confinement (Colotelo *et al.* 2013). During recovery from these stressors, fish may be more vulnerable to predation or less likely to forage or participate in reproductive activities (Winberg and Thörnqvist 2016). There is some evidence that increased AS may facilitate faster recovery from acute stress (Killen *et al.* 2014b) but much more information is needed in this area. Overall, mortality occurring in fish post-escape from fishing gears could constitute another potential avenue for selection on physiological traits to occur.

1.3 ENVIRONMENTAL MODULATION OF RELATIONSHIPS BETWEEN PHYSIOLOGICAL TRAITS AND CAPTURE VULNERABILITY

The behavioural and underlying physiological traits which may influence the capture vulnerability of individual fish can be highly plastic, and can be modulated by both the physical (Claireaux *et al.* 2006; Domenici *et al.* 2013; Farrell 2016; Johansen and Jones 2011; Johansen *et al.* 2014; Meuthen *et al.* 2019) and social (Rose 1995; Sloman *et al.* 2000; Thambithurai *et al.* 2018; Winger 2010) environment. This influences the capacity for fishing gears to select on individual fish traits by influencing relationships among traits themselves, (Killen *et al.* 2013; Killen *et al.* 2012b), changing which fish are vulnerable to capture by context (Killen *et al.* 2016a) and by directly altering the diversity of phenotypic traits in a fish population, limiting or broadening scope for selection to occur. This environmental modulation of selectivity may be the reason that previous work has found mixed evidence for whether fishing gears can select on physiological and behavioural traits, and highlights the need for empirical demonstrations linking individual fish traits with capture vulnerability across environmental contexts.

Environmental temperature has the capacity to influence the expression of physiological and behavioural traits relevant to determining capture vulnerability in both passive and active gears. Physiological traits underpinning fish feeding motivation and the likelihood of a fish engaging in risky behaviours (e.g. SMR) (Killen *et al.* 2011; Killen *et al.* 2012b) are thought to be particularly relevant in determining the capture vulnerability of fish in passive gears (Arlinghaus *et al.* 2017a; Biro and Post 2008a; Redpath *et al.* 2010b) and strongly influenced by temperature. SMRs of ectothermic fish generally increase with temperature, in turn increasing baseline energetic demand. This may increase the likelihood of a fish responding to a perceived bait used by a fishing gear, with knock-on consequences for the capacity of that gear to select on individual physiological and behavioural traits. For example, in a food-saturated environment fish may in general be less catchable by a baited fishing gear, as fish are unlikely to risk interacting with a novel and potentially threatening object like a hook or trap while other food resources are readily available. However, should temperatures increase, or available food decrease, a relationship between individual SMR and likelihood of attacking a bait may appear, as high SMR individuals now require greater access to resources, diminishing the perceived risk of approaching a bait relative to the benefits it provides. Environmental factors may therefore have the capacity to mask or reveal relationships between individual physiological and behavioural traits and capture vulnerability (Killen *et al.* 2016a; Killen *et al.* 2013). Plasticity of behavioural and physiological traits may also influence the vulnerability of fish to capture at the population – level, determining the magnitude of any fisheries selection which can occur. Temperature mediated increases in activity and feeding motivation, for example, can lead to sharp increases in catch per unit effort (CPUE) of fish in passive gears (Stehfest *et al.* 2015; Stoner 2004; Stoner *et al.* 2006), potentially dampening any selection on individual traits. Similar effects may be expected in fisheries employing active gears, where traits related to swim performance and escape responses are likely involved in determining probability of capture (Killen *et al.* 2015b; Kim and Wardle 2003). Swim performance in fish can be strongly influenced by temperature and oxygen availability (Claireaux *et al.* 2006; Domenici *et al.* 2013; Hvas *et al.* 2017), through both physical effects on muscle contraction speeds (Rome 1990; Rome *et al.* 1992), and influencing the metabolic capacities of individual fish. Increased muscle contraction speeds driven by higher temperatures will increase the efficiency of aerobically fuelled red-muscle fibres, potentially delaying the recruitment of anaerobic muscle and subsequent onset of fatigue in fish pursued by a trawl. This direct effect of temperature on swimming efficiency may weaken the capacity of a trawl to select on individual swim performance. Trawl fisheries targeting fish at the high and low ends of their thermal range may also have diminished capacity to select on individual traits, as low temperatures inhibit muscle contraction speeds and swim performance, while high temperatures reduce metabolic scope, and the energetic resources available for swimming, potentially rendering all available fish vulnerable to trawl capture (Ryer and Barnett 2006; Winger 2010), decreasing selectivity. Plastic responses of individual traits narrowing the phenotypic variation present in a fish population in this way will reduce the capacity of fisheries selection to occur, or otherwise shift capture vulnerability in a manner directly related to the sensitivity to thermal shifts of individual fish, and subsequent corresponding effects on performance(Killen *et al.* 2016a).

Both active and passive fishing gears often cause high fish densities in their vicinity, potentially exaggerating any effects of social interactions on relationships between individual traits and capture vulnerability. Intraspecific competition between fish has been observed were multiple fish converge on a bait, with submissive individuals hesitating to attack in the presence of more dominant fish (Stoner 2004), potentially disrupting selection on feeding motivation by baited gears, once they have been encountered by the fish. The presence of competitors at a bait does not always dissuade submissive individuals from attacking however, and social facilitation of fish attack baits can also occur. For example, in salmon being targeted using trolling lures, the number of attacks per individual on the lures increased as fish density increased (Shardlow 1993), elevating the capture vulnerability of all present fish. A similar effect was observed in Pacific halibut (*Hippoglossus stenolepis*), which located bait items faster, made more attacks per individual, and reduced latency between location of a bait and a subsequent strike when fish were in groups compared to individually (Stoner and Ottmar 2004). Both intraspecific competition and socially facilitated feeding around baits may therefore weaken selection on physiological traits underlying feeding motivation.

Where fish must engage in escape behaviours to avoid capture when being pursued by an active gear, then the emergent collective behaviours of pursued fish shoals may also influence the capture vulnerability of their members independently of individual fish's traits (Magnhagen and Staffan 2004; Marras *et al.* 2011). In trawls, while there is experimental evidence that collective behaviours can lead to fish making more efficient use of escape routes around a trawl and avoiding capture (Brown and Warburton 1999), *in-situ* observations of fish behaviour ahead of the trawl show that these responses can be maladaptive, with fish following one another into the net leading to mass capture (Rose 1995; Winger 2010). These behavioural responses are often exploited by trawls to increase capture efficiency, with trawl components specifically designed to concentrate fish together ahead of the trawl mouth in dense groups (Ryer *et al.* 2009; Ryer 2008). This could lead to a mechanism where capture vulnerability is more strongly dependent on traits related to individual swim performance when fish encounter the trawl individually or in loose groups (Killen *et al.* 2015b; Kim and Wardle 2003), but becomes more strongly determined by group-level coordinated behaviours as fish are aggregated and concentrated in denser and denser groups. Social interactions among fish ahead of a pursuing active gear may therefore modulate any relationships between individual traits and capture vulnerability, with consequences for selectivity.

While competitive interactions, social facilitation, and fish engaging in collective behaviours may all have the capacity to influence the selectivity regime of fishing gears during the final stages of capture, social interactions among fish may also play a role in determining capture vulnerability over broader scales as well. Indirect experience of conspecific fish being caught in angling gear can induce stress responses in nearby fish (Lovén Wallerius *et al.* 2019), and experiencing a capture event directly can decrease capture vulnerability during subsequent gear exposures (Fernö and Huse

1983). These behavioural impacts of fishing activities can decrease capture vulnerability of fish populations as a whole, particularly where fishing effort is high (Koeck *et al.* 2019). In these instances, the probability of a fish responding to, and attacking a perceived bait may become decoupled from individual feeding motivation or boldness, and more closely linked with individual variation in stress responses (Belanger *et al.* 2017b; Koeck *et al.* 2018).

1.4 THESIS AIMS AND OVERVIEW

Despite several studies investigating links among physiological traits and vulnerability to capture in fishing gears, evidence for the capacity of fisheries to select on fish physiological traits remains mixed. Laboratory experiments and recreations of small scale fisheries permit tight control over environmental conditions not otherwise possible (Conover and Baumann 2009). These experimental approaches can allow for strong conclusions to be drawn regarding the mechanistic links between individual fish's physiological traits and their vulnerability to capture (Horodysky *et al.* 2015; Klefoth *et al.* 2017b). However, so far only one such study has demonstrated links between physiological traits and capture vulnerability in a simulated active gear (Killen *et al.* 2015b), while a mechanistic relationship between physiological traits and capture vulnerability in passive gears has yet to be empirically demonstrated (Louison *et al.* 2018b; Thambithurai *et al.* 2018; Väätäinen *et al.* 2018). Determining mechanistic links between individual physiological traits and capture vulnerability, as opposed to purely correlational approaches, will be an important component of assessing the feasibility of managing selectivity via modifications to existing fishing gears, and also in predicting the selectivity regimes of different fishing gears across different contexts (Horodysky *et al.* 2015; Killen *et al.* 2016a). Further important evidence for fishing gears selecting on physiological traits of fish has been provided by wild (Hessenauer *et al.* 2015), mesoscale (Koeck *et al.* 2018), and selection line studies (Prokkola *et al.* 2019; Redpath *et al.* 2010b; Steven J. Cooke *et al.* 2007). While the design of these larger scale studies limits the conclusions which can be drawn when mechanistically linking individual traits with capture vulnerability, they are also critically important to demonstrate that fisheries selection can elicit phenotypic change in the physiological traits of fish populations. There is clearly a requirement for further empirical investigations of relationships among individual physiological traits, and their relevance for determining capture vulnerability in fish, alongside studies investigating how these relationships may manifest in the wild. Furthermore, the ecological consequences of fisheries selection on individual physiological traits are completely unknown. Expanding upon existing approaches investigating fisheries selection to include measures of individual fish's ecological traits (using stable isotope analysis, for example) in addition to their behavioural or physiological traits could provide invaluable information in this regard. This thesis aims to expand upon the current understanding of the role of intraspecific variation in physiological traits in determining fish vulnerability to capture using a combination of small-scale fisheries recreations in the lab alongside larger scale experiments in the wild, under real fisheries scenarios. Specifically, Chapters 2 and 3 investigate relationships between individual physiological traits and capture vulnerability across contexts using small scale recreations of fishing gear, while chapters 4 and 5 use a comparative approach to investigate the capacity for different fishing gears to select on physiological, behavioural and ecological traits of fish in the wild.

1.4.1 Chapter 2: Shoal familiarity modulates effects of individual metabolism on vulnerability to capture by trawling

In this laboratory-based experiment, I investigated the capacity for changing social context to disrupt relationships between individual fish's metabolic traits and capture vulnerability in a replica trawl. European minnows (*Phoxinus phoxinus*) were profiled for their metabolic phenotype, including their SMR, AS, MMR and EPOC, and then subjected to simulated trawl capture three times in each of two social contexts; alongside familiar shoalmates, and alongside unfamiliar fish which had never encountered each other before.

1.4.2 Chapter 3: Does thermal plasticity affect susceptibility to capture? Insights from a simulated trap and trawl fishery.

This experiment investigated the capacity for fishing gears employing contrasting mechanisms of capture to select on individual behavioural and physiological traits across three temperature treatments. European minnows (*Phoxinus phoxinus*) were profiled for their metabolic phenotype (SMR, AS, MMR), behavioural traits, and swim performance, then either maintained at 16°C, or acclimated to 20°C and 24°C sequentially. At each temperature, all traits were measured again, and fish subjected to both a simulated trapping and trawling event to investigate how behavioural and physiological thermal plasticity influenced the capacity for each gear type to select on individual traits.

1.4.3 Chapter 4: Does capture method predict metabolic, behavioural and space use traits of wild perch?

By comparing the metabolic, behavioural, and space use traits of wild perch (*Perca fluviatilis*) caught by angling to those caught by gill net, I investigated the capacity for two different passive gear types to exhibit contrasting patterns of selectivity in the wild. Fish were captured from identical habitat in a small lake, then taken to a lab where they were subjected to a behavioural assay and respirometry. Fish were then implanted with acoustic transmitters, and released back into the lake they were collected from where their movements were monitored using a high resolution acoustic telemetry array.

1.4.4 Chapter 5: Does Capture Method Predict Ecological Niche of Skagerrak Atlantic Cod?

In this study, I compared the ecological niche of trawled Skagerrak cod (*Gadus morhua*) to that of cod caught via rod and reel-based jigging using stable isotope analysis. Absolute values of $\delta^{13}C$ and $\delta^{15}N$ were directly compared between gear types, and also used to generate estimates of the ecological niche occupied by both trawl and jigging vulnerable cod. This allowed us to determine whether fishing gears employing contrasting mechanisms of capture have the capacity to select on different ecological traits of wild fish.

2. SHOAL FAMILIARITY MODULATES EFFECTS OF INDIVIDUAL METABOLISM ON VULNERABILITY TO CAPTURE BY TRAWLING

2.1 INTRODUCTION

High mortality and selective removal of fish caused by fishing can induce changes in the phenotypic composition of fish stocks (Enberg *et al.* 2012; Heino *et al.* 2015). Selective removal of specific phenotypes can erode overall trait diversity, and if traits under selection have a heritable component, evolutionary change can occur in a process known as fisheries induced evolution (FIE) (Heino *et al.* 2013a; Heino *et al.* 2015; Redpath *et al.* 2010b; Richard 2007). While the impacts and mechanisms of FIE are most frequently considered in a life-history context, specific behavioural and physiological traits can also render fish more susceptible to capture and may themselves be under selection in exploited fish stocks (Arlinghaus *et al.* 2017a; Diaz Pauli and Sih 2017a; Enberg *et al.* 2012; Hollins *et al.* 2018). Physiological and behavioural traits have been shown to correlate with susceptibility to capture in laboratory and field studies (Diaz Pauli *et al.* 2015a; Killen *et al.* 2015b; Koeck *et al.* 2018; Monk and Arlinghaus 2017a; Redpath *et al.* 2010b). However, these relationships can be inconsistent (Biro and Post 2008a; Louison *et al.* 2018b; Redpath *et al.* 2010b; Vainikka *et al.* 2016; Wilson *et al.* 2011), suggesting variation among species and/or context-dependency of relationships between phenotype and susceptibility to capture by fishing gears.

Understanding mechanistic links between individual traits and susceptibility to capture is essential for predicting the capacity of fishing gears to elicit phenotypic change in exploited populations (Hollins *et al.* 2018; Horodysky *et al.* 2015; Ward *et al.* 2016) and provide effective fisheries management (Laugen *et al.* 2014b). Active gears (including trawls and seine nets) pursue or encircle targeted fish with nets, and exploit fish behavioural responses, including shoaling, to elicit capture. Physiological traits, such as individual swimming ability, may in this instance be linked to gear avoidance (Killen *et al.* 2015b; Kim and Wardle 2003), which in turn may be related to traits determining individual aerobic and anaerobic metabolic capacity. Specifically, aerobic scope (AS; the difference between an animal's minimum (standard metabolic rate, SMR) and maximum rate of aerobic metabolism (maximum metabolic rate, MMR)) represents an individual’s capacity to supply oxygen to physiological processes beyond those required for maintenance, including aerobically powered ‘steady state’ swimming, and recovery from exhaustive exercise. Additionally, the capacity to perform anaerobic metabolism may also be important for evading capture from active gear types as it represents an individual’s ability to perform rapid bouts of burst swimming, often employed in escaping predators, or performing other high-speed manoeuvres (Marras *et al.* 2010a).

Fish pursued by a trawl net may escape capture by sustaining high swim speeds, or by exploiting potential escape routes to remove themselves from the path of pursuing gear. Individual fish with greater aerobic or anaerobic capacity may be more able to manoeuvre outside the path of active gear, or endure the pace of a pursuing trawl net without succumbing to fatigue and falling back into the net (Hollins *et al.* 2018; Killen *et al.* 2015b; Winger 2010) and thus maximising available opportunities for escape. Active gears may therefore selectively remove slower swimming fish or those with a lower capacity for aerobic or anaerobic metabolism from exploited populations. Individual variation in the behavioural response to fishing gears has also been observed, (Rose 1995; Underwood *et al.* 2015; Yanase *et al.* 2009), with certain fish using escape routes to avoid an approaching trawl net (Brown and Warburton 1999; Diaz Pauli *et al.* 2015a; Winger 2010). The use of escape routes, rather than swimming to the point of fatigue in front of a trawl net, could modulate the relationship between metabolism and susceptibility to capture, however, the extent to which this occurs is currently unknown. It is also unknown whether the tendency to utilise escape routes is a repeatable characteristic of individual fish, and whether social information may influence fish behaviour and encourage individuals to remain cohesive with conspecifics as the group swims ahead of the trawl net, falls back toward the oncoming net, or as localised subgroups of individuals swim toward escape routes.

Behavioural responses of fish to active gears are influenced by extrinsic factors, including social interactions amongst the fish themselves (Rose 1995; Winger 2010). Conformity of behaviour within a fish shoal can occur where members respond to stimuli, and these responses subsequently propagate through the shoal, manifesting as a collective behaviour (Brown and Laland 2002; Magnhagen and Staffan 2004; Marras *et al.* 2011). While behavioural conformity may enable groups of fish to efficiently exploit escape routes in pursuing gears (Brown and Warburton 1999) through a 'follow the leader' type principle, there is also evidence that it may increase susceptibility to capture of shoaling fish when the collective decision of a shoal is to voluntarily enter fishing gear, as opposed to escaping it (Rose 1995; Thambithurai *et al.* 2018). Trawls often exploit this behaviour to increase capture efficiency (Ryer 2008) with gear components specifically designed to concentrate pursued fish ahead of a trawl mouth in a behaviour known as herding (Ryer *et al.* 2009). Herding increases the density of fish in pre-existing shoals, and of shoals created by aggregating fish encountered individually, or in smaller groups (Winger *et al.* 2010). High densities of fish may exacerbate the role of social interactions in determining fish behaviour, and lead to shoals of fish comprised of individuals not normally associated with one another and/or are unfamiliar to each other. Shoals comprised of individuals unfamiliar with each other may be less cohesive (*i.e*. show greater between-individual distances) and therefore less likely to exhibit coordinated group-level responses (Atton *et al.* 2014; Chivers *et al.* 1995), or learn potential escape routes from conspecifics (Brown and Laland 2002; Swaney *et al.* 2001). This could generate a mechanism whereby the relationship between an individual's phenotype and susceptibility to capture is modulated by the degree of familiarity with shoal-mates. For example, a fish surrounded by unfamiliar individuals may be less influenced by its neighbours, and so its vulnerability to capture may be determined by its own intrinsic traits, such as swimming ability.

By replicating the final moments of the capture sequence in a trawl fishery, using shoals of wild minnow (*Phoxinus phoxinus*), we investigate the role of individual metabolic traits in determining susceptibility to capture among shoals of either familiar or unfamiliar conspecifics. Trawling simulations were conducted within a laboratory swim tunnel, where fish were forced to swim ahead of a miniature trawl net. The degree of familiarity among shoal-mates could influence the relationship between individual metabolic traits and vulnerability to capture in several ways. In shoals comprised of unfamiliar individuals, low shoal cohesion and decreased conformity of swimming behaviour may emphasise the importance of individual traits in determining vulnerability to capture. Alternatively, among familiar shoals, consistent leader/follow dynamics may lead to more repeatable behaviour around the trawl, and so strengthen relationships between individual traits and vulnerability to capture.

2.2 MATERIALS AND METHODS

2.2.1 Experimental animals

All minnows *P. phoxinus* used in the study were sourced from the wild and collected using dip nets from the River Kelvin, UK. From the individuals collected, a total of 40 minnows were subsequently split across 10 aerated tanks (50 x 40 x 40cm) so that each tank housed 4 individuals. All fish were acclimated to the laboratory for 7 months prior to experiments. Tanks were supplied with recirculating, UV-treated water maintained at 14°C. Each tank contained a shelter, gravel substrate and plastic plants, and all fish were kept on a 12L: 12D photoperiod . All tanks were shielded with opaque plastic blinds, preventing fish from interacting and observing individuals in neighbouring tanks. During this time, minnows were fed *ad libitum* a combination of commercial feed and bloodworm. Three months prior to the start of trawl trials and respirometry measurements, individual fish were sedated using benzocaine, and given a unique combination of coloured VIE elastomer (Northwest Marine Technology Inc) to allow individual identification during trawl trials. We used common minnow (*Phoxinus phoxinus*) as the study species because they are a small shoaling fish (Magurran and Girling 1986; Pitcher *et al.* 1986) which lives in close association with the substrate, making this species a suitable representation of commercially targeted bentho-pelagic species.

2.2.2 Familiar and Unfamiliar Trawl Trials

Fish were subjected to a total of 6 trawl trials in groups of 4 fish: 3 trials with familiar fish and 3 trials with unfamiliar fish. Individual fish were haphazardly assigned to different 'unfamiliar shoals' before the beginning of the experiment and were assembled from fish in different tanks shortly before the start of each unfamiliar trial. Familiar shoals were assembled from fish housed in the same tank. Half of all fish encountered the trawl net in a 'familiar' context first, while the other half first encountered the trawl net in an 'unfamiliar' context. In all cases, fish within each shoal had encountered the trawl net an equal number of times as shoal mates, and so within each shoal individual fish had the same degree of experience to trawling.

Trawling simulations followed a similar design to that of Killen et al. (2015a) and were conducted in a 90 l Steffensen-type swim tunnel (Loligo systems, Tjele, Denmark), designed to exercise fish at controlled speeds in laminar flow with a uniform velocity profile, thermoregulated to 14 ± 0.1°C. The working section of the swim tunnel was 70 long x 20 deep x 20 wide cm. A modified lid with a slit cut 30 cm from the front of the swim tunnel was used to allow for a perforated plastic divider to be placed between the fish and trawl net. This allowed the net to remain hidden from test fish during their settling period (see below) prior to the trial. The swim tunnel was calibrated using a vane wheel flow meter (Flowtherm NT, Höntzch, Waiblingen, Germany), with both the divider present and absent and with the trawl net in a deployed position to account for the added drag of the net on water velocity. Lastly, the setup was shielded from view by an opaque plastic blind to further minimise fish disturbance.

Trawl trials consisted of introducing shoals of 4 individuals to the swim tunnel with the divider in place, preventing fish from interacting with the trawl prior to the start of the trial. With the lid firmly in place, water flow was increased to a speed of ~0.5 body lengths (BLs) per second (~2.5 cm s^{-1}), based on the mean standard length of the minnows used. Fish were allowed to settle in the swim tunnel for 30 min. Following the settling period, water velocity was gradually increased

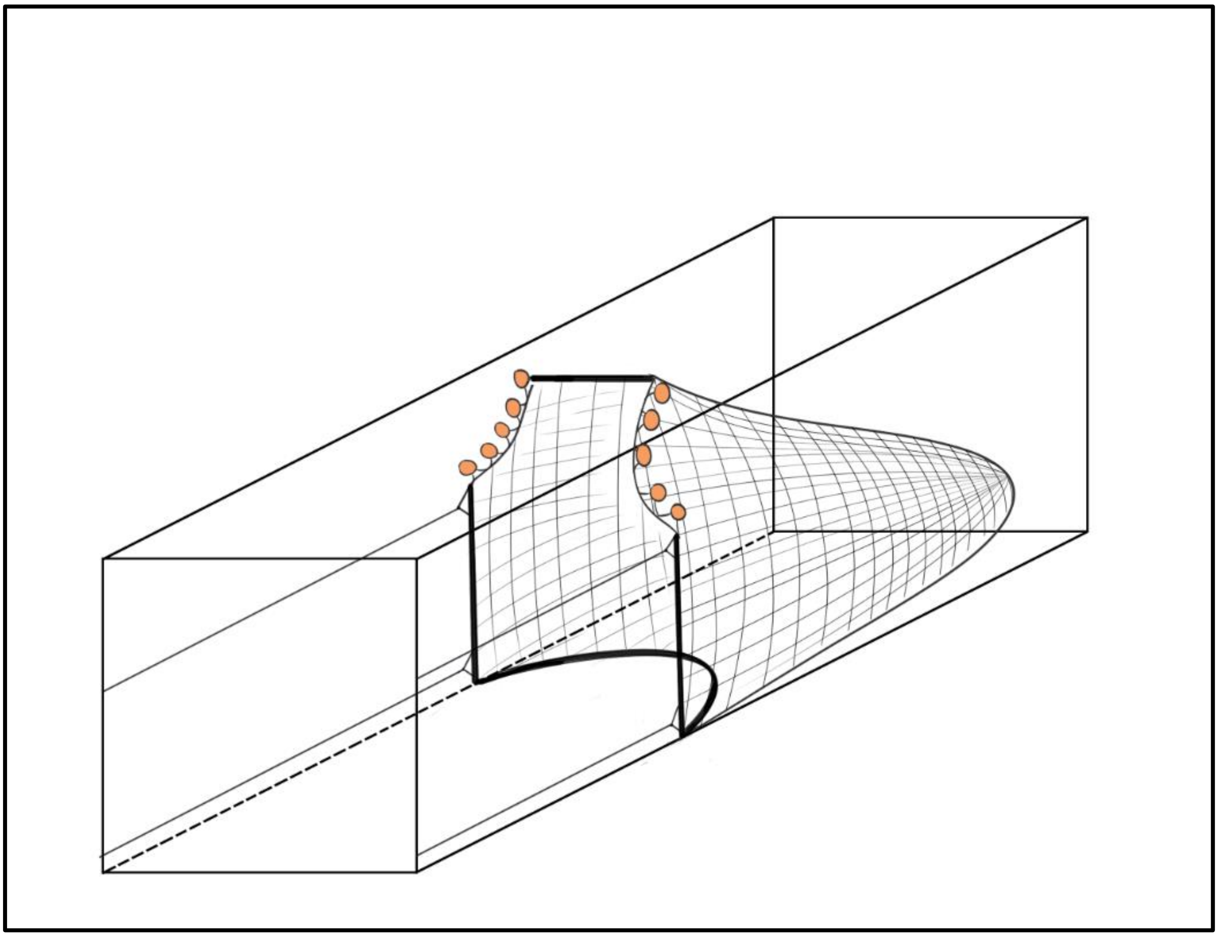

Figure 2.1: Layout of the miniature trawl net in the working section of the swim tunnel. Thick black lines indicate portions of the net which are flush with the walls of the swim tunnel, while portions of the net mouth bordered with small orange buoys indicate available escape routes.

from ~2.5 cm $s^{-1}$to ~66.5 cm s^{-1} over a period of 30 s, while the divider between the fish and trawl net was raised and the trawl net deployed. A custom-made scaled replica trawl net (Marine Institute, Memorial University of Newfoundland, Figure 2.1) was used to simulate the final stages of capture in a trawl. Steel wire was threaded through the mesh along the mouth of the net to help maintain its shape and to ensure the sides of the net remained flush with the walls of the swim tunnel during trials. Two possible escape routes for fish were left in the top right and left corners of the swim tunnel (Figure 2.1), each equal to approximately 6 cm^2, or a third of the total cross-sectional area of the swim tunnel. Fish could swim freely back and forth through these routes for the duration of the trial. However, fish behind the net were still subjected to the oncoming flow of the swim tunnel but could partially avoid it by positioning themselves behind the footrope of the trawl. The bottom of the trawl net included rubber washers to simulate the rollers present on the footrope and provide weight to prevent the net from lifting during the trial. The top of the net included several orange beads spaced approximately 2cm apart to replicate the appearance of floats along the headrope in a commercial trawl and provide a potential visual queue for fish to orient near the front of the net. The trawl net was deployed externally behind the swimming shoal of fish by pulling a PVC handle attached to the trawl net by fishing wire. Once the net was 20 cm from the front of the swim tunnel it was secured to prevent the net from slipping backwards during the trial.

Once the trawl net was deployed, fish were left to swim for 10 min. Swimming activity ahead of and within the trawl net, along with use of escape routes was recorded using high definition video cameras (GoPro Hero 4 16:9 Full HD, 720p; GoPro, San Mateo, California, USA) mounted directly above and to the side of the swim tunnel. Fish were allowed a minimum 42-h recovery period between trials with no individuals used on two consecutive days. No adverse behaviours or fin damage was observed following the trawling trials and all fish resumed feeding once returned to their respective holding tanks.

2.2.3 Analysis of Fish Behaviour Around the Trawl

To investigate the role of individual traits in determining time spent in the trawl net (a proxy of fishing vulnerability) and the degree of coordination among shoal members, video recordings of trials for each individual fish within each shoal were analysed by recording the cumulative time individual fish spent inside the net, as well as the number of successful escapes around the net (Table 2.1).

Behaviour/Event	Description
Escape	Whole fish body passes behind net via an escape route, and remains behind the net, below escape route for 3s
Re-Entry	Whole fish body re-enters the swim tunnel anterior to the trawl mouth via an escape route
In Net	Fish snout drops behind the mouth of the trawl
Out of Net	Fish tail moves ahead of trawl mouth

Table 2.1. Different behaviours exhibited by fish in the trawl trials. Where an escape occurred, the timestamp was taken from the beginning of the 3s period.

2.2.4 Measurement of Metabolic Traits

Once trawling trials were complete, all fish were subjected to intermittent flow respirometry after a 24 h fasting period to provide estimates of metabolic phenotype (SMR, MMR, AS and EPOC). Respirometry was undertaken at least 7 d after the cessation of trawl trials, with all respirometry completed within 12 d of the final trawl trial. Shoals of 4 individuals were removed from their holding tanks using dip nets, and 2 shoals (8 individuals total) were tested through respirometry concurrently. Estimates of maximum metabolic rate (MMR) were achieved by manually chasing individual fish to exhaustion in a circular tank (50 cm diameter). Exhaustion was determined as the point at which fish were no longer receptive to the chase stimulus (mean chase time = 96 s, ± 34 s). The use of manual chase is assumed to elicit maximum rates of oxygen uptake as fish recover from prolonged anaerobic exercise (Killen *et al.* 2017d). Once exhausted, fish were quickly transferred to individual cylindrical glass respirometry chambers (75 mL volume) attached to an intermittent flow respirometry system. Oxygen content of water within the closed respirometry circuit was recorded every 2 s using a firesting 4-channel oxygen meter and associated sensors (PyroScience GmbH, Aschen, Germany). The circuit itself comprised of a glass cylinder, and a length of gas impermeable tubing, through which water was constantly recirculated using a peristaltic pump. Respirometry chambers were submerged in an air saturated, temperature-regulated water bath (14°C ± 0.1°C; 50 l) and were shielded from disturbance and direct light via an opaque plastic blind. Every 8 min, an automated flush pump was programmed to turn on for 3 min and flush chambers with oxygenated water, and then switch off, sealing the respirometers to allow decreases in oxygen content due to fish respiration to be measured. Estimates of MMR were obtained by calculating rates of oxygen uptake for each 3 min time interval throughout the first 30 min of recovery immediately following exhaustive exercise. MMR (mg O_2 h^{-1}) was taken as the highest rate of aerobic metabolism during this period. After measurement of MMR, fish remained in their respective respirometry chambers overnight to allow for estimation of SMR and RMR. Individuals were removed from their chambers the following morning at around 09:00, having remained in the respirometers for approximately 17 h total. Once removed from respirometry chambers, fish mass and standard length were measured. Whole animal SMR (mg O_2 h^{-1}) was estimated as the lowest 10th percentile of measurements taken throughout the measurement period, while RMR was measured as the mean level of oxygen uptake, excluding the recovery period used for MMR estimation, and the 4.5 hrs thereafter (Svendsen *et al.,* 2013). Excess post-exercise oxygen consumption (EPOC) for each fish was calculated from the area under the exponential recovery function, above RMR, until the time at which fitted values were equal to RMR. EPOC represents the increase in oxygen consumption above routine levels which occurs during recovery from a bout of exhaustive anaerobic exercise and is proportional to the anaerobic capacity of an animal (Killen *et al.* 2015b; Lee *et al.* 2003). Absolute aerobic scope (AS) was calculated as the difference between MMR and SMR.

2.2.5 Statistical Analyses

All statistical analyses were performed in R.3.5.1 (R Development Core Team) using the lme4 (Bates et al. 2016), MuMIn (Barton, 2015) and rptR (Stoffel *et al.* 2017) packages. Time in net (T) was log (T+1) transformed and used as the response variable for both repeatability estimates (hereafter T_i), and statistical models investigating individual fish's time in the trawl net. The effect of shoal composition (familiar vs unfamiliar) on time spent in the net was investigated using a linear mixed effect model (LME) via the function lmer, with log transformed time in net as the response variable, and log mass, log SMR, log AS, log MMR, log EPOC and shoal composition (categorical variable with two levels: familiar, unfamiliar) as explanatory variables. All possible interactions between individual metabolic traits and shoal composition were also included, with trial number (1-6) and Fish ID nested within tank as random effects. Models of best fit were determined using maximum likelihood estimation, although wherever a metabolic trait (SMR, AS, MMR, EPOC) remained in the model, mass was also retained to account for allometric scaling of metabolic rates regardless of AIC. Non-significant interactions were dropped sequentially, starting with those with the smallest t values, but were retained if their removal resulted in higher AIC values (ΔAIC >2 (Arnold 2010)). Assumptions of homoscedasticity and normality of residuals were examined by visual inspection of residual plots. Significance testing, alongside model r^2 values were used to indicate the strength of observed patterns. R^2 values included marginal (r_m^2) and conditional (r_c^2) r^2 values which indicate the variance explained by fixed factors, and by both fixed and random factors, respectively (Nakagawa and Schielzeth, 2013). Across-context repeatability of T_i was calculated as adjusted repeatability, as described by Stoffel, Nakagawa and Schielzeth (2017) using variances calculated with LMEs and including fish ID as a random effect. Repeatabilities of T_i were also calculated at the shoal level for familiar and unfamiliar shoals as a measure of similarity of performance among fish within a given shoal.

To investigate whether fish behaviours around the trawl were synchronised within trials and between different shoal compositions, coefficients of dispersion (CD) for each behaviour were calculated for each 10 min trial (Chapman and Chapman 1994; Hastie *et al.* 2003; Killen *et al.* 2018). Trials were split into 5 s time intervals, and the mean number of each type of event occurring within that interval recorded, alongside the variance around that mean. CD was then calculated as the variance/mean ratio across intervals, with values greater than 1 indicating temporally clustered events, and values less than 1 indicating events uniformly distributed in time.

2.3 RESULTS

From 240 observations of individual fish behaviour in groups around the trawl, a total of 138 entries into the net were observed. Of these, 65 were within the familiar treatment, and 73 within the unfamiliar treatment, with fish spending a mean time of 92 (± 151) and 70 (± 130) seconds in the trawl net, respectively. These means were not statistically different (t=-1.029, p=0.3) and there was a great degree of variation among individuals within each treatment. The number of total recorded escapes was also similar between treatments, with a total of 162 escape events recorded in familiar trials and 177 escapes recorded in the unfamiliar trials.

Adjusted repeatability for individual time in the trawl net was significant (R = 0.303, 95 % CI: 0.16 - 0.44 p < 0.001), as were unadjusted repeatabilities calculated within each treatment (R=0.26, 95% CI:0.01-0.4, p=0.004 and R=0.23, 95% CI:0.06-0.45, p=0.01, for familiar and unfamiliar shoals, respectively) Repeatability of T_i calculated within each trial, (*i.e.* indicating similarity between the time spent in the trawl by a fish as compared to its shoal mates) were comparatively low and similar between each treatment (R = 0.13, 95 % CI: 0 - 0.33, p = 0.06 and R = 0.03, 95 % CI: 0 - 0.18, p = 0.4 for familiar and unfamiliar shoals, respectively). There was a significant interaction between log(EPOC) and shoal composition (P = 0.045), with log(EPOC) showing a weak negative association with time spent in the net when in a familiar shoal, but no relationship with time spent in the net when in an unfamiliar shoal (Table 2.1; Figure 2.2) There were no relationships between any other individual-level traits and time in the net in either familiar or unfamiliar trials (Table 2.1; figure 2.2).

Successive behaviours of the same type (escapes, re-entries, entering the net, and leaving the net) but performed by different individuals were found to be temporally clustered (Figure 2.2). Clustering of events was recorded in a higher proportion of familiar than unfamiliar trials in all event types. However, these differences in clustering were generally small, except for entries into the net. In this instance, 20% more clustered fall-backs into the net were observed in familiar than unfamiliar trials.

Term	**Estimate**	***SE***	***df***	***T***	***p***	r_m^2	r_c^2
Intercept	6.258	6.242	45.412	1.003	0.321	0.041	0.450
log(Mass)	-0.362	1.405	34	-0.258	0.798		
log(SMR)	1.558	2.352	46.524	0.662	0.511		
log(AS)	6.846	8.090	50.032	0.846	0.401		
log(MMR)	-8.024	10.200	50.117	-0.787	0.435		
log(EPOC)	-0.046	0.745	50.751	-0.061	0.951		
Shoal Composition	-2.700	4.691	169.446	-0.576	0.566		
log(SMR)*Shoal Composition	-0.554	1.834	169.446	-0.302	0.763		
log(AS)*Shoal Composition	-2.730	6.956	169.447	-0.392	0.695		
log(MMR)*Shoal Composition	4.297	8.793	169.447	0.489	0.626		
log(EPOC)*Shoal Composition	-1.297	0.641	169.448	-2.025	0.045		

Table 2.2 Results of linear mixed effects models examining the role of metabolic traits and shoal composition on time spent in the net by individual fish.

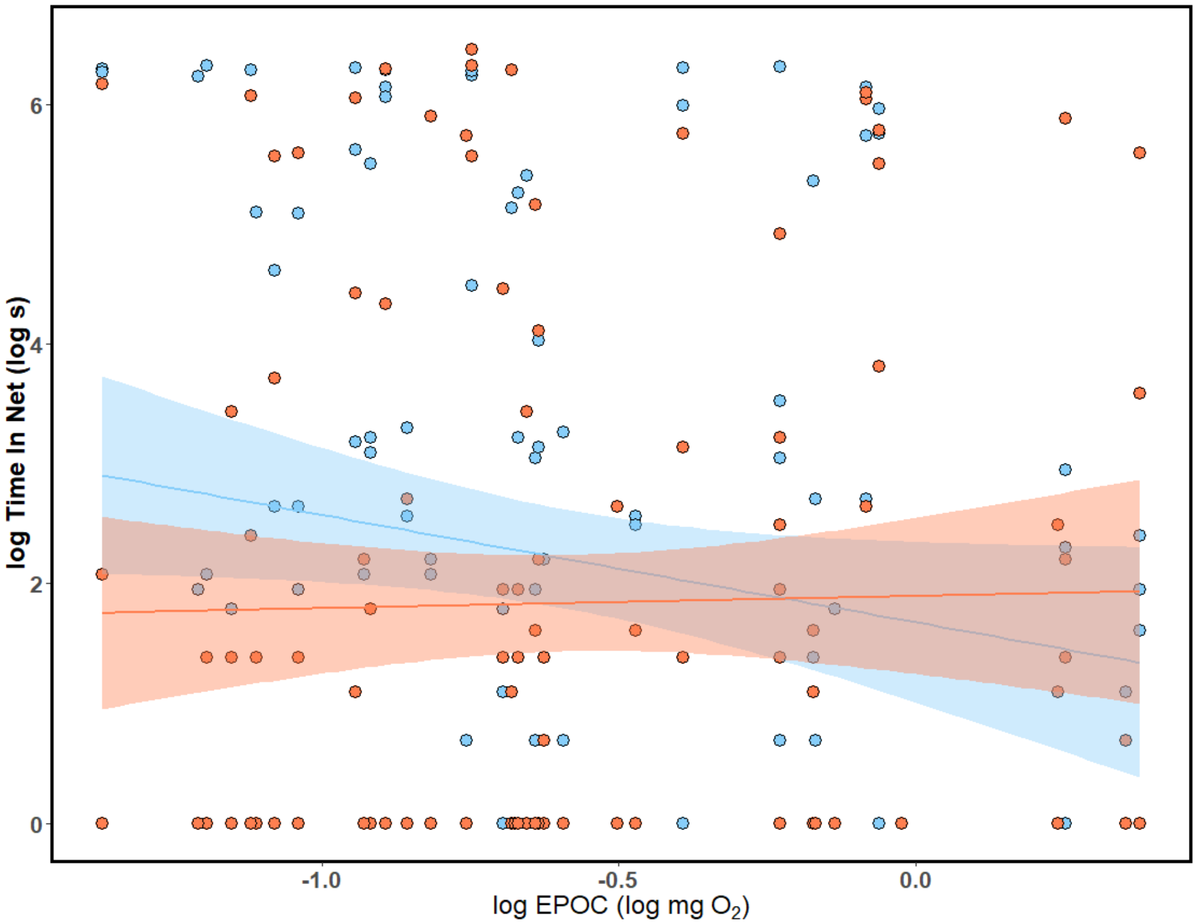

Figure 2.2: Relationship between anaerobic metabolic capacity (EPOC) and time spent in the net in familiar (blue) and unfamiliar (orange) shoals. Lines represent linear regression between log(EPOC) and log (Time in Net), for each shoal composition, while the shaded area corresponds to 95% confidence intervals. Three replicates are shown for each fish (n = 40) in both familiar (blue) and unfamiliar treatments (orange).

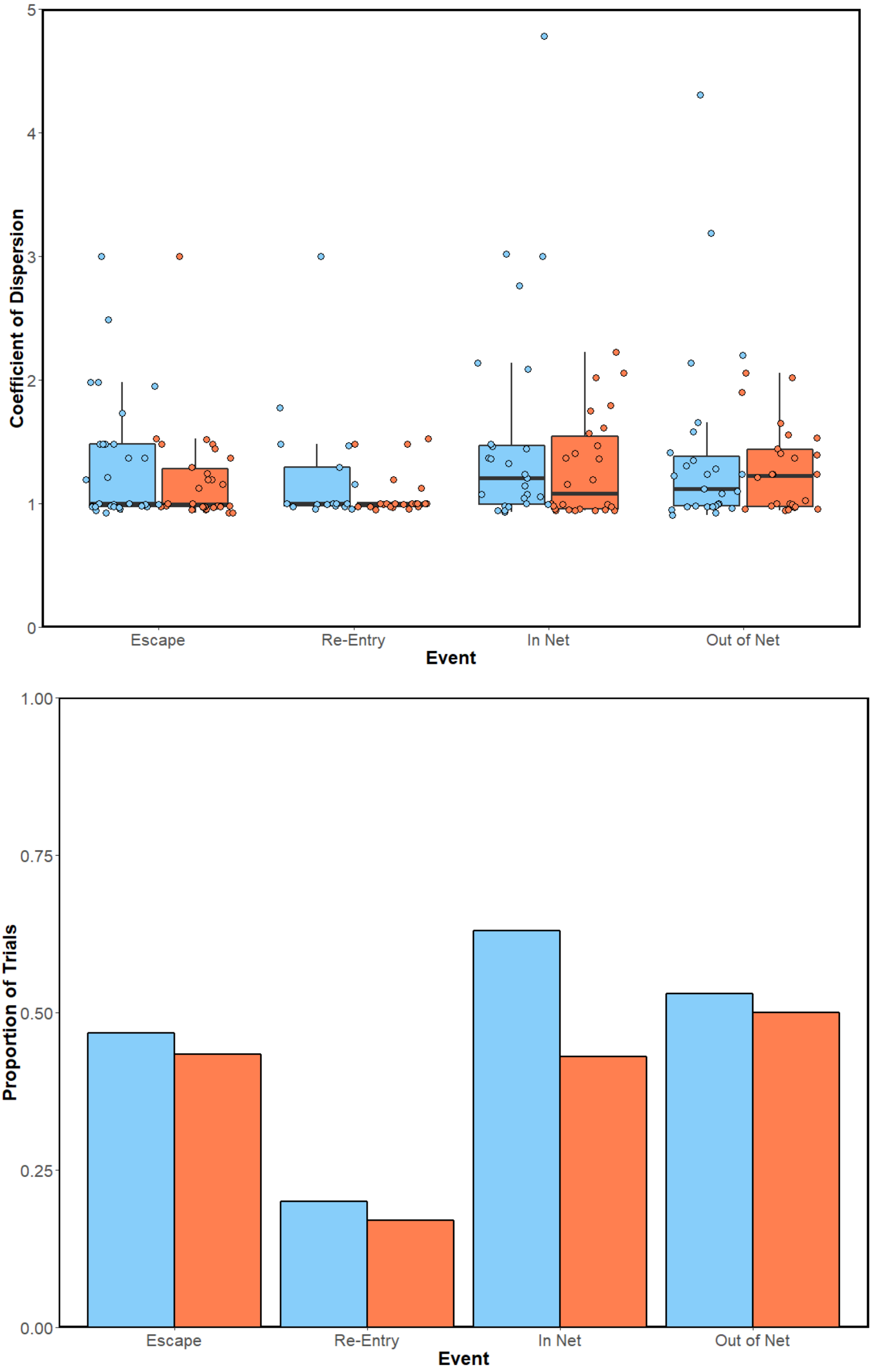

Figure 2.3: Temporal synchronisation of the 4 behaviours within a 5s window (Escapes, Re-Entries, In Net, Out of Net) among 4 fish in familiar (blue) and unfamiliar (orange) trawl trials, as shown by coefficient of dispersion (CD) ratios. Top: boxplot of coefficients of dispersion for each behaviour. Each overlaid dot represents the CD calculated for one trial. Values >1 represent events clustered in time. Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of

datapoints between each hinge, and 1.5x the difference between 25th and 75th percentiles. Bottom: bar chart showing the proportions of trials where CD ratio for each behaviour was >1 (ie the number of trials were clustering for that behaviour was identified).

2.4 DISCUSSION

Establishing mechanistic links between individual phenotypic traits and vulnerability to capture is an important component of fisheries management (Horodysky *et al.* 2015; Laugen *et al.* 2014b; Ward *et al.* 2016). In our study, we found that fish with higher anaerobic capacity spent less time swimming within the trawl net, in accordance with previous experimental work (Killen *et al.* 2015b). However, the relationship was context specific and only present when fish were tested alongside familiar shoal-mates. Evidence of synchronisation in behaviour around the trawl net was present in both familiar and unfamiliar shoals, suggesting that individuals within shoals are likely using a form of information transfer among individuals to avoid capture, as has been observed in previous experiments using trawl simulations (Brown and Warburton 1999) and novel-avoidance tasks (Brown and Laland 2002). This result supports the notion that while active gears have the capacity to selectively remove the slowest swimming fish, and drive phenotypic change in exploited fish stocks, extrinsic social factors may play a role in modulating this effect (Hollins *et al.* 2018; Thambithurai *et al.* 2018).

A negative relationship between individual anaerobic capacity (EPOC) and time spent in the trawl net was found in fish tested with familiar shoal mates only. Anaerobically powered, burst swimming is employed by fish during escapes from natural predators (Plaut 2001) and is often observed *in-situ* in fish pursued by trawls (Bayse *et al.* 2016; Rose 1995; Ryer *et al.* 2009). In the present study, fish actively swam against the oncoming flow of water, using intermittent bursts of anaerobic swimming amidst periods of aerobic steady state swimming (Killen *et al.* 2015b; Svendsen *et al.* 2015). As trials progressed, fish gradually dropped further back where they would either begin to fall into the trawl net, or rise and make use of escape routes. Within the trawl mouth, fish would often employ successive bursts to move ahead of the trawl net, however, given the excessively high swim speeds and energy required to out swim the trawl net this proved to be unsustainable as fish often made several passes into the mouth of the net over the duration of the trial.

Differences in the synchronisation of behaviours between fish in familiar and unfamiliar shoals may help explain the absence of relationship between anaerobic capacity and susceptibility to capture among unfamiliar shoals. Fish entering the net showed greater evidence of synchronisation in familiar shoals. This is likely attributable to greater shoal cohesion among fish swimming in familiar shoals (Chivers *et al.* 1995), which would also explain why time spent in the net was more similar among fish within familiar than unfamiliar shoals. When swimming in a familiar shoal, the presence of conspecifics swimming ahead of the trawl net may provide added motivation for fish to leave the net once they drop behind the mouth (Atton *et al.* 2014; Barber and Wright 2001). As the shoal drops back into the net, individual fish may be more likely to engage in energetically costly anaerobic burst swimming to maintain cohesion with familiar conspecifics than if the shoal were comprised of unfamiliar individuals. The capacity for individual fish within a familiar shoal to regain a position ahead of the trawl net mouth subsequently becomes limitied by individual anaerobic capacity. In an unfamiliar shoal, the perceived benefits of maintaining shoal cohesion may be reduced (Atton *et al.* 2014) and so individual fish may be less willing to incur the costly metabolic debt strenuous swimming generates (Killen *et al.* 2015b). However, if fish in unfamiliar shoals were less inclined to enagage in anaerobic swimming to maintain a minimal distance from conspecifics, it would be expected that they would spend more time in the net on average than those swimming among a familiar shoal, as they would drop back into the net before the onset of fatigue. In our study, the opposite trend was observed, with average time in net being 22 s longer in familiar shoals, although the large degree of variability within both treatments makes interpreation difficult. An alternative explanation for the lack of relationship between anaerobic capacity and time in the net in unfamiliar shoals may be that decreased cohesion or coordination among unfamiliar shoals may emphasise the importance of stochastic processes, such as position of the fish relative to the trawl, in determining time spent in the net. A less cohesive shoal will collectively occupy more space than a more cohesive one, increasing the likelihood of a given fish swimming in close proximity to a potential escape route. In this instance, a fatigued fish falling back toward the trawl net may have greater opportunity to access an escape route purely by chance, effectively missing the net. This presents a mechanism whereby a fatigued fish may completely avoid spending time in the net, weakening the relationship between metabolic traits and susceptibility to capture, and also decreasing synchronisation of fish successively entering the trawl mouth.

Fish pursued by a trawl net likely do so among an assortment of other species and a mixture of familiar and unfamiliar conspecifics (Rose 1995; Ryer 2008; Underwood *et al.* 2015). In this experiment, we show that simply altering the composition of a shoal can influence gear selectivity and phenotypic drivers of fishing selection. However, the cues eliciting herding in our experiment differ from those experienced by pursued fish in a trawl in the wild. In our experiment, the on-coming flow of the swim tunnel provides a strong cue for fish to orient themselves perpendicular to the trawl mouth and maintain forward swimming. In the wild, while herding cues provided by trawl doors and sediment plumes caused by the trawl sweeps' contact with the seafloor encourage fish to aggregate together, (Winger 2010), their orientation and swimming direction relative to different parts of the trawl can vary widely (Ryer 2008; Underwood *et al.* 2015; Winger 2010; Yanase *et al.* 2009). As a result, in the wild, fish may turn headfirst into a pursuing trawl, (Brown and Warburton 1999; Rose 1995; Underwood *et al.* 2015), increasing capture and leading to the entry of fish not yet fatigued (Rose 1995; Yanase *et al.* 2009). Fish may also turn headfirst into pursuing trawls in an effort to maintain minimal distance from, or keep visual contact with shoalmates, also leading to the capture of non-exhausted fish (Day *et al.* 2001). To study the effect of fish entering a net head-first the use of remotely controlled artificial fish could be adopted in a laboratory setting (Bierbach *et al.* 2018; Faria *et al.* 2010), and would provide an interesting avenue for further research. The trawl used in this experiment was static, and simulated the pursuit of fish using an on-coming flow of water. As such, this experiment does not replicate the hydrodynamic disturbances caused by a full-scale trawl as it moves through the water, which may provide additional cues for fish to exploit when avoiding capture. These effects could not be replicated in the experimental approach used here, and their effects on fish behaviour and capacity to escape a pursuing trawl warrant further research. In addition to aggregating fish unfamiliar with one another within a pursued shoal, trawls may also cause shoals with phenotypic compositions that are unusual (for example, a shoal largely comprised of asocial individuals, (Cote *et al.* 2012)), or would normally not arise in natural settings. Specifically investigating how varying the phenotypic composition of a shoal influences the vulnerability of its respective members to capture (Bevan *et al.* 2018; Killen *et al.* 2017b) would be a useful next step. While there was no evidence of fish learning to avoid trawl capture in this study, fish have shown the capacity to learn trawl avoidance (Özbilgin and Glass 2004; Pyanov 1993), and the numerous negative stimuli provided by a trawl (e.g. vessel noise, forced exhaustive swimming) may provide sufficient negative reinforcement for fish to learn escape behaviours in the wild. Investigating how the inclusion of fish exhibiting learned trawl escape behaviours influences shoalmates' vulnerablity to capture, and how this may influence selection on physiological traits therefore warrants further study.

Neither SMR, MMR or aerobic scope were related to vulnerability to capture in either familiar or unfamiliar shoals. Aerobically powered red muscle fibres contribute to fish swimming performance once the fish has begun to swim beyond its gait transition speed (McKenzie 2011). While this contribution at high swim speeds is comparatively small, a fish with greater aerobic capacity may postpone the recruitment of anaerobic muscle fibres in its efforts to maintain station ahead of the trawl net, and thus delay its eventual fatigue resulting in decreased time in the net. In this experiment, AS had further capacity to influence vulnerability to capture, determining the available metabolic budget which could be allocated to the restoration of homeostasis after engaging in strenuous exercise (Killen *et al.* 2015c; McKenzie 2011). The fact that no relationship between susceptibility to capture and either AS or MMR was found, suggests that within familiar shoals anaerobic capacity was a more important influence in determining time fish spent in the net.

The results of this study support the notion that commercial harvest using active gears has the potential to alter the phenotypic composition of exploited fish stocks by selectively removing the poorest swimming fish (Hollins *et al.* 2018; Killen *et al.* 2015b). However, this experiment also shows that this effect is context specific, making the strength of this selectivity in the wild difficult to determine. The impact of this erosion of phenotypic diversity is difficult to predict, but evolutionary impacts of fisheries harvest has implications for the recovery and sustainability of exploited fish stocks (Enberg *et al.* 2009a; Heino *et al.* 2013a; Laugen *et al.* 2014b), as well as the economic viability of fisheries themselves (Eikeset *et al.* 2013). Considering the role of anaerobic metabolism in predator prey dynamics (Kaufman *et al.* 2006; Killen *et al.* 2015b), selective removal of slow swimming individuals could result in exploited fish stocks becoming less available to predators, or otherwise alter food web dynamics (Claireaux *et al.* 2018). Fish exhibiting high exercise performance can also exhibit prolonged recovery times after engaging in exhaustive exercise experienced during predator avoidance or catch and release angling (Clark *et al.* 2017), likely attributable to the excessive metabolic debt these high performance fish can incur. The high performance swimmers exhibiting high anaerobic metabolic capacity which are more likely to escape trawl capture may therefore also be those most likely to succumb to delayed mortality after exhaustive exercise (Clark *et al.* 2017), particularly under future scenarios of climate warming (Clark *et al.* 2017; McLean *et al.* 2016; Wilson *et al.* 2014). Selection for high performance phenotypes driven by active fisheries may therefore leave exploited stocks particularly maladapted to the effects of climate change, with further implications for catch and release fisheries targeting species which are also subject to harvest by active gears, such as Atlantic cod (*Gadus morhua*).

To summarise, vulnerability to trawling was linked to individual anaerobic capacity in fish swimming among familiar conspecifics, but this relationship was absent when fish faced the trawl alongside an unfamiliar shoal. This pattern seems to be driven by differences in shoal cohesion or coodination, and subsequent collective behaviour of fish. While vulnerability to capture showed significant across-context repeatability, as well as a context specific relationship with anaerobic capacity, both these trends were weaker than those observed in previous experimental work (Killen *et al.* 2015b). This is likely attributable to the inclusion of escape routes around the trawl, allowing behavioural responses beyond keeping pace in front of the trawl to contribute to lowering individual time in the net. This study demonstrates a mechanism where relationships between a fish's metabolic traits and vulnerability to capture in a trawl may be modulated by a individual's social context. These results have implications for determining the potential strength of selection on individual fish traits by active gears, and how these relationships may be modulated by extrinsic factors.

3. DOES THERMAL PLASTICITY AFFECT SUSCEPTIBILITY TO CAPTURE? INSIGHTS FROM A SIMULATED TRAP AND TRAWL FISHERY

3.1 INTRODUCTION

In fishes, physiological and behavioural traits often correlate with an individual's vulnerability to capture by fishing gears (Diaz Pauli *et al.* 2015a; Killen *et al.* 2015b; Koeck *et al.* 2018; Monk and Arlinghaus 2017a; Redpath *et al.* 2010b). These traits may therefore be under selection in exploited fish populations. Selective removal of fish exhibiting specific behavioural or physiological traits may drive shifts in the phenotypic composition of fish populations by eroding overall trait diversity (Arlinghaus *et al.* 2017a; Diaz Pauli and Sih 2017a), but may also drive evolutionary responses if traits under selection are heritable (Arnold 2010; Diaz Pauli and Sih 2017a; Enberg *et al.* 2012; Heino *et al.* 2015; Hollins *et al.* 2018). Assessing the capacity of fisheries to drive phenotypic change in wild fish populations is of increasing conservation and management concern (Dunlop *et al.* 2009; Laugen *et al.* 2014b; Ward *et al.* 2016), but requires comprehensive understanding of the mechanisms of capture employed by different fishing gears, how individual traits influence vulnerability to capture in these gears, and how these relationships are modulated by the environment (Diaz Pauli *et al.* 2015a; Hollins *et al.* 2018; Horodysky *et al.* 2015).

Fishing gears can be categorised as either active or passive, based on their mechanism of capture. Active gears, (*e.g.* trawls) pursue or encircle target fish, while passive gears (*e.g.* traps) rely on fish to approach and interact with the fishing gear to be captured. These contrasting mechanisms of capture mean that traits which correlate positively with susceptibility to capture in one gear may show the opposite or no relationship with capture vulnerability in another (Diaz Pauli *et al.* 2015a). For active gears, physiological traits linked to individual swim performance may be particularly relevant in terms of determining capture vulnerability (Killen *et al.* 2015c; Kim and Wardle 2003; Marras *et al.* 2010b). Trawl nets employed by fishers are towed at a speed chosen to progressively exhaust pursued fish, causing fish in the path of a trawl to engage in burst-and-coast swimming to maintain station ahead of pursuing nets, before eventually succumbing to fatigue and being caught

(Rose 1995; Ryer *et al.* 2009; Underwood *et al.* 2015; Winger 2010; Yanase *et al.* 2009). Pursued fish have also been observed entering trawls head-first (Rose 1995; Underwood *et al.* 2015), which has the potential to disrupt selection on swim performance (Hollins *et al.* 2019), although the mechanisms underlying this behaviour are unclear. Individual burst-swimming performance is linked with anaerobic metabolic capacity (Killen *et al.* 2015b; McKenzie 2011; Svendsen *et al.* 2015), and it has been shown that fish exhibiting high anaerobic metabolic capacity may be less vulnerable to capture by trawls while swimming in groups (Hollins *et al.* 2019; Killen *et al.* 2015b). Traits related to aerobic metabolism also have the capacity to influence individual fish's vulnerability to capture in active gears. Aerobic scope (AS) is the difference between an animal's minimum and maximum rate of aerobic metabolism (standard metabolic rate, SMR and maximum metabolic rate, MMR, respectively), and so represents the capacity of an organism to simultaneously deliver oxygen to physiological processes beyond those required for maintenance. While previous experiments have not found relationships between AS and vulnerability to trawl capture (Hollins *et al.* 2019; Killen *et al.* 2015b), relationships between physiological traits and capture vulnerability may only arise under specific contexts. For example, where fish are pursued by a trawl in temperatures beyond the thermal optima for AS, high AS individuals may be at an advantage, as they may have sufficient AS remaining to fuel aerobic swimming, or recovery from exhaustive exercise.

Physiological traits may also underpin a range of behaviours which can influence individual fish's susceptibility to capture in passive fishing gears (Andersen *et al.* 2016a; Arlinghaus *et al.* 2017a; Diaz Pauli and Sih 2017a; Metcalfe *et al.* 2016b). SMR is a physiological trait which shows wide intraspecific variation (Burton *et al.* 2011a; Metcalfe *et al.* 2016b) and is intrinsically linked with individual fish's energetic demands and, in some contexts, behavioural traits related to boldness and foraging activity (Killen *et al.* 2011; Killen *et al.* 2012b). Individual fish with high SMRs may therefore be more likely to engage in foraging behaviour at any given time, and so be more likely to encounter fishing gears (Hollins *et al.* 2018), or to inspect bait in a passive gear once it has been encountered (Biro and Post 2008a; Hessenauer *et al.* 2015; Hollins *et al.* 2018; Klefoth *et al.* 2017b; Svendsen *et* *al.* 2015). Fish that display these active, risk-prone behaviours may also possess increased AS to accommodate the energetic demand of a more active lifestyle (Killen *et al.* 2012c; Killen *et al.* 2014a; Redpath *et al.* 2010b). Therefore, AS may also influence individual vulnerability to capture in passive gears.

While behavioural and physiological traits can correlate with capture vulnerability in both laboratory and field studies (Biro and Post 2008a; Diaz Pauli *et al.* 2015a; Koeck *et al.* 2018; Monk and Arlinghaus 2017a; Redpath *et al.* 2010b; Wilson *et al.* 2011), these relationships can be inconsistent (Louison *et al.* 2018a; Vainikka *et al.* 2016). For example, Klefoth *et al.* (2017) found that bold carp (*Cyprinus carpio*) were selectively removed by angling, while Wilson *et al.* (2011) reported the opposite trend in bluegill sunfish (*Lepomis macrochirus*), and no relationship between the two was found in perch (*Perca fluviatilis*) by Vainikka *et al*. (2016). This could in part be due to the influence of environmental factors on relationships among traits (Killen *et al.* 2013). Many traits which may influence individual fish's susceptibility to capture are labile, and environmental conditions can act to constrain the expression of these traits among fish populations (Domenici *et al.* 2013; Johansen *et al.* 2014; Meuthen *et al.* 2019; Stoner 2004), or otherwise alter relationships between expressed traits (Killen *et al.* 2013). More information is needed on how environmental factors alter correlations among labile traits in the context of fisheries, because this form of plasticity could alter which traits are available as targets for direct or correlated selection.

Environmental temperature is especially likely to alter relationships among metabolic and behavioural traits which in turn may affect susceptibility to capture in fish. Metabolic rates of ectothermic animals increase with temperature, in turn increasing baseline energetic demand. Increased demand for resources may subsequently alter individual behaviour, if fish must spend more time foraging or be more aggressive to secure sufficient resources. If any increase in SMR due to warming is not met with commensurate increases in MMR, then AS will be reduced, reducing the capacity to perform simultaneous aerobic physiological processes. These constrained metabolic budgets may limit the capacity for fish to express traits, reducing phenotypic diversity of fish populations, and therefore the capacity of fishing gears to select on specific traits. Elevated environmental temperature can also influence individual traits independently of effects on AS, particularly those related to swim performance (Hvas *et al.* 2017). Elevated temperatures increase the maximum contraction velocity and power output of red muscle fibres (Rome 1990; Rome *et al.* 1992), postponing the recruitment of anaerobic white muscle when swimming at high speeds, delaying the onset of fish fatigue, for example. Finally, it is unlikely that reaction norms for a trait determining vulnerability to capture across temperatures will be identical for all fish within a population (Cavieres and Sabat 2008; Maldonado *et al.* 2012). Accordingly, as temperature changes, so may the individuals which exhibit the greatest vulnerability to capture.

Experimental lab-based approaches to studying fisheries selection permit precise control over the myriad factors which may influence fish capture vulnerability, allowing us to isolate the contribution of specific factors of interest (Thambithurai *et al.* 2018). Similarly, small scale recreations of fisheries permit control over the capture process itself, allowing us to facilitate encounters between fish and fishing gears, and focus on how selection operates at specific stages of the capture process (Hollins *et al.* 2018). Surrogate species have been used in a number of experimental approaches to studying fisheries selection (Conover and Baumann 2009; Reznick and Ghalambor 2005), and provide several advantages when compared studying wild, commercial species. In this study, we used European Minnow (*Phoxinus phoxinus*) to investigate the effects of thermal plasticity on the capacity for trap and trawl fisheries to select on behavioural and physiological traits. Using this approach, we aim to address the following questions: i) Does acclimation temperature affect vulnerability to capture in active and passive fishing gears? ii) Does acclimation temperature affect which traits are related to capture vulnerability in active and passive gears?

3.2 METHODS

All minnows were initially held at 16°C, at which point baseline measurements of physiological and behavioural traits were taken (Figure 3.1). Fish were then haphazardly assigned to one of two groups, dividing the population in half. Half of the fish were subsequently kept at a constant 16°C throughout the remainder of the study, while the remaining half were sequentially acclimated to 20 and 24°C. European minnow occupy freshwater environments at temperatures of 2-20°C ,and so while both the control and first acclimation temperatures represent conditions likely experienced by wild fish, 24°C was anticipated to constrain the aerobic metabolic capacity of experimental fish. After each acclimation period, both the acclimated and control fish had all physiological and behavioural measurements repeated, in addition to being subjected to both a simulated trawl and trap fishery.

3.2.1 Experimental Animals

All minnows *P. phoxinus* used in this study were sourced from the wild during October 2016, collected via a large dip-net from the River Kelvin. Fish were then kept in aerated tanks (100x40x40cm) supplied with recirculating UV treated water maintained at 14-16°C for 6 months before experimental procedures began. A total of 72 similar sized minnows (7.45± 0.56cm and 4.84± 0.64g, mean length/mass ± SD) were subsequently split across 6 aerated tanks (50 x 40 x 40cm) so that each tank housed 12 individuals. These tanks were supplied with recirculating, UV-treated water maintained at 16°C, before temperature treatments began. Each tank received identical water, contained a shelter, gravel substrate and plastic plants, and all fish were kept on a 12L: 12D light cycle. During this time, minnows were kept on an *ad libitum* feeding regime, and were fed a mixture of commercial feed and bloodworm. Once fish were assigned to their respective tanks, they were anaesthetised using benzocaine, and implanted with individually coded PIT tags, to allow identification. Fish were then allowed 1 week to recover before experimental procedures began.

3.2.2 Temperature Acclimation and Measurement of Individual Traits

At each acclimation temperature, measurements of behaviour, swim performance, and physiological traits were taken. In all cases fish were fasted for 48 h before each procedure. The order of testing the tanks was haphazard but conformed to a general pattern of alternating between tanks assigned to the 'control' and 'warm acclimation' treatments on successive days. Fish were assayed for swim performance first, with half the fish from each of two tanks trialled per day. Respirometry and activity assays were conducted one tank at a time, with activity assayed during the day, and fish subsequently placed in respirometers overnight. Once these procedures had all been completed at 16°C for all fish, temperature acclimation began. Tanks 1-3 were maintained at 16°C for the duration of the experiment (table 3.1), and so tank conditions remained exactly as described above. Tanks 4-6 were incrementally warmed to 20 °C over a period of a week, and then left to acclimate at a constant 20°C for 4 weeks before traits were re-measured, alongside trap and trawl vulnerability (Fgure 3.1). Tanks were selected for testing in the same way as the previous round of measurements, although all respirometry, activity assays and fishing vulnerability assays were now conducted at the tank's respective acclimation temperature. Two tanks of fish were subjected to the fisheries simulations per day, with half of each tank exposed to the trawl, and the other half to the trap, so that half of each tank encountered a different gear type first. After a period of at least 3 days, all fish were then profiled for vulnerability to capture in whichever gear they had not yet faced. Additionally, swim performance tests were now conducted one tank at a time, to avoid having to change swim tunnel temperatures halfway through the day. Once all assays were complete, fish were maintained at their acclimated temperatures for 2 months (16°C and 20°C), before a final temperature increase could begin (figure 3.1). Again, tanks 1-3 remained at 16°C, while tanks 4-6 were incrementally warmed from 20°C to 24°C over a week, before being left to acclimate at their warmer temperature for a month. After this time, fish were assayed again, following an identical schedule to that described for sampling at T2 (figure 3.1).

3.2.3 Fish Behaviour

Individual fish activity was determined using an open field assay using an 80x20cm behavioural arena divided into 2 sections separated by a removable plastic divider. All activity assays were conducted within a metal frame covered with opaque curtains which minimised potential disturbance to the fish. Each divider was attached to a simple pully system using fishing line which allowed it to be lifted and lowered from outside of the frame, without disturbing fish. 4 arenas were placed side-by-side within the frame so 4 fish could be profiled simultaneously. Fish activity throughout these trials was recorded using two Logitech, C920 HD Pro Webcam cameras fixed to the top of the frame so that each camera had 2 tanks in frame. The first section of the behavioural arena consisted of a small acclimation area (10x20cm), with gravel substrate, where fish were placed at the beginning of the trial. Here, fish were allowed to acclimate for 10 minutes, before the first plastic divider was withdrawn, and the second section of the arena became visible to fish. This second 70x20cm section consisted of an open field, with no substrate or shelter present. Fish were given up to 20 minutes to enter the open field of their own volition, after which time the divider was closed behind the fish, so that it could not re-enter the starting shelter. If the fish did not leave the shelter during this time, it was encouraged into the open field using a small dip net. Once behavioural trials were complete, fish were transferred to a holding tank, before being subjected to respirometry that afternoon. Activity of fish was subsequently quantified from recorded videos and determined as the amount of time fish spent active in the open field section of the arena during the middle 10 minute portion of the activity trial. A fish was defined as ‘active’ once it had moved 1 body length away from its starting stationary position and was ‘inactive’ once the fish remained stationary (*i.e.* resting on the tank bottom with no tail movement) for 5 seconds. The middle 10-minute section of the video was used to quantify activity to minimise the potential impact of removing/replacing the arena dividers on fish behaviour.

3.2.4 Swim Performance

Individual swim performance was determined for each fish using a constant acceleration test (CAT, Farell, 2008; Killen et al. 2015). Fish were placed into the working section (45x14x14cm) of a 30-l Steffensen type swim tunnel (Loligo systems, Tjele, Denmark), designed to exercise fish at controlled speeds in non-turbulent water with a uniform velocity profile. All CATs were performed at the individual fish's acclimation temperature. Once within the swim tunnel, the lid was tightly bolted on, and the fish left to acclimate for 30 minutes at a water velocity of 5cm s^{-1}, approximately 1 BL s^{-1}. Once acclimation was complete, water velocity was then increased by 2.5cm s^{-1} every minute. Fish swimming patterns were then closely observed through an opening in an opaque sheet to identify gait transition speed (U_{gt}). Gait transition occurs at the point where fish begin to rely on anaerobic, non-steady burst swimming as opposed to steady swimming powered by slow twitch, oxidative muscle fibres. This switch in swimming behaviour was determined as the point where 4 successive swimming 'bursts' were observed within a 1-min increment. The corresponding speed at the beginning of this increment was then taken as the fish's U_{gt} and was taken as the fish's maximum aerobic swimming speed. Once U_{gt} was identified, water velocity continued to be increased until the fish fell against the retaining grid at the back of the working section of the swim tunnel and did not resume swimming for 5 s. The speed at which this occurred was taken as each individual's maximum swim speed (U_{max}) and represents the fish's maximal anaerobic swim performance.

3.2.5 Respirometry

After behavioural assays for a tank of fish were complete, all fish were subjected to intermittent flow respirometry to provide estimates of metabolic phenotype (SMR, MMR, and AS) one tank at a time. Estimates of maximum metabolic rate (MMR) were achieved by manually chasing individual fish to exhaustion for a period of 2 minutes in a circular plastic tank (50 cm diameter) with a water depth of 10 cm. By the end of the chase period, all fish ceased attempting to escape from being chased and were determined exhausted, and so were exhibiting maximal rates of oxygen uptake as fish recover from prolonged anaerobic exercise (Killen, Norin and Halsey, 2017). Once exhausted, fish were quickly transferred to individual cylindrical glass respirometry chambers (75 mL volume) attached to an intermittent flow respirometry system (Killen, Nati and Suski, 2015; Thambithurai et al., 2018). Oxygen content of the water within the closed respirometry circuit was quantified once every 2 s using a Firesting 4-channel oxygen meter and associated sensors (PyroScience GmbH, Aschen, Germany). The circuit itself comprised of the glass cylinder, and a length of gas impermeable tubing, through which water was constantly recirculated using a peristaltic pump. Respirometry chambers were kept within an aerated, rectangular, temperature-regulated water bath (at the tank acclimation temperature ± 0.1°C; 50 l) and were shielded from disturbance and direct light via an opaque plastic blind. Every 8 min, an automated flush pump would switch on for 3 minutes to flush chambers with fresh oxygenated water, and then switched off, sealing the respirometers to allow decreases in oxygen content to be determined and used in the estimate of rates of oxygen consumption.

Estimates of MMR were obtained by calculating rates of oxygen uptake for each 3-minute time interval throughout the first 30 mins of recovery immediately following exhaustive exercise. MMR ($mg.O_2.h^{-1}$) was taken as the highest rate of aerobic metabolism during this period. After measurement of MMR, fish remained in their respective respirometry chambers overnight to allow estimation of SMR. Individuals were removed from their chambers the following morning at around 09:00, having remained in the respirometers for approximately 17 hours total. Once retrieved from the respirometry chambers, fish were measured for wet mass and standard length. Whole animal SMR ($mg\ O_2\ h^{-1}$) was estimated as the lowest 20th percentile of measurements taken throughout the measurement period (Chabot *et al.* 2016). Absolute aerobic scope (AS) was calculated as the difference between MMR and SMR.

3.2.6 Fishery Simulations

All fish were individually subjected to a simulated trawl and trap fishery. All simulations were designed to replicate the final moments of the capture process (Hollins et al. 2018), after fish had already encountered fishing gears.

3.2.6.1 *Trap Simulations*

Trapping simulations were performed in a rectangular 120x60x60 cm arena filled to a depth of 14 cm, housed within a frame covered with opaque curtains to minimise disturbance to the fish. Fish behaviour throughout the trial was recorded using a Logitech, C920 HD Pro Webcam mounted in the centre of the top of the frame and attached to a laptop computer. This allowed us to unobtrusively monitor fish movements in real time. In this study, we used a replica trap measuring 12x12x17 cm made from a metal frame and green mesh to simulate the final moments of capture in a trap fishery: when a fish has encountered a gear and is deciding whether to approach and subsequently enter the trap. The trap had one inverted conical entrance of a diameter of 2 cm at one end, while a bait canister was at the other. The bait canister consisted of a 10 cm^3 plastic cylinder with several openings covered with a fine mesh, to allow the scent of the bait to diffuse into the behavioural arena, without spreading the bait itself. This canister was attached to a bloodworm-filled syringe kept outside of the frame of the behavioural arena via a length of rubber tubing. At the beginning of the trial, the fish was held in a clear plastic shelter with an opaque top at the end of the tank furthest from the trap. Here, the fish was given an acclimation period of 10 min before the trial began. Just before the acclimation period was over, the plunger on the bait syringe was pushed, releasing an odour cloud for the trap to act as an attractant. The shelter was then lifted from around the fish, and the fish allowed to explore the arena and interact with the trap. The fish was given a maximum of 30 minutes to enter the trap, at which point the trial was stopped and the fish recorded as ‘caught’, and the time until capture noted if it entered the trap, and ‘uncaught’ if the fish did not enter the trap at any point for the duration of the trial. Once the trial was complete, the fish were returned to their holding tanks and fed, and the water in the arena completely drained and replaced.

3.2.6.2 *Trawl Simulations*

Trawling simulations were conducted in a 90 l Steffensen-type swim tunnel (Loligo systems, Tjele, Denmark), designed to exercise fish at controlled speeds in laminar flow with a uniform velocity profile, thermoregulated at each tested fish's acclimation temperature ± 0.1°. The working section of the tunnel was 70 long x 20 x 20 wide cm, and with a 3cm thick foam false bottom fitted along its length. A modified lid for the working section was constructed, with a slit cut 30 cm from the front of the lid. This allowed a perforated plastic divider to be placed into the working section of the tunnel, dividing the working section into a 30cm front portion and a 40 cm rear portion. This allowed for the net to remain hidden from test fish during their acclimation period (see below). Prior to the first trawl trial, the swim tunnel was calibrated using a vane wheel flow meter (Flowtherm NT, Höntzch, Waiblingen, Germany), with both the divider present and absent. Trawl trials began with single fish introduced to the front half of the working section, ahead of the trawl net, and then allowed to acclimate for 30 minutes at a speed approximating 0.5 body lengths per second (BLs^{-1}). Following this acclimation period, water velocity was gradually increased to 58.25cm s^{-1} over a period of ~30s, while the divider was slowly pulled up, exposing the fish to the trawl net in the latter portion of the working section of the tunnel. In this study, a custom-made scale replica trawl net (Marine Institute, Memorial University of Newfoundland) was used to simulate the final stages of capture in a commercial trawl: the pursuit of fish as they attempt to maintain station ahead of the trawl mouth, and resist falling back into the net. A solid metal frame was used to hold the mouth of the trawl open, and ensure its shape held during and between trials, while ensuring that the sides of the net were flush with the working section of the flume, and the centre of the top of the net flush with the underside of the lid. Two possible escape routes were left in the top right and left corners of the working section of the tunnel, each encompassing an area of 3x3cm. The trawl included escape routes to allow fish to avoid spending time in the net by passing past it, as well as swimming ahead of it. The bottom of the net included black rubber washers to imitate the rollers present on the footrope of a trawl and was weighted to prevent it lifting during a trial and presenting an alternative escape route. The top of the net included several orange beads spaced approximately 2cm apart along its length to replicate the appearance of buoys along the headrope in a commercial trawl and to provide a potential visual queue for orienting near the front of the net. Once the divider was up, and the trial speed attained, fish were left to swim at 58.25 cm s^{-1} in front of the trawl for a maximum of 10 minutes. If fish fell back into the trawl against the net mesh and did not resume swimming for 5 s, the trial was stopped and the fish recorded as 'caught' whereas if it dropped back past the net through one of the potential escape route, the trial was stopped and the fish recorded as 'escaped'.

3.2.7 Statistical Analyses

All statistical analyses were performed in R.3.5.1 (R Development Core Team) using the survival (Therneau and Lumley, 2009), lme4 (Bates et al. 2016), MuMIn (Barton, 2015) and rptR (Stoffel *et al.* 2017) packages. For estimates of repeatability and Linear Mixed Effects (LME) models, all behavioural traits were log(n+1) transformed, while measures of swim performance were normalised to BL s^{-1} to account for growth between trial times. Similarly, metabolic traits (SMR, AS, and MMR) were adjusted for mass by calculating the residuals from the linear regression of each metabolic trait against log transformed mass, and adding calculated residuals to the predicted value of that metabolic trait at the mean mass of all fish. The inverse log of these values was then taken, and used to account for effects of body mass and growth between successive measurements (McLean *et al.* 2018). Each transformed trait was used as the response variable in individual LMEs investigating the effects of treatment and time on the distribution of traits in our experimental fish using the function lmer, using 'Treatment' (a categorical variable with two levels: control and warmed) and 'Time' (a categorical variable with 3 levels, 'T1', 'T2' and 'T3') as fixed effects, and Fish

ID as a random effect. Models of best fit were determined using maximum likelihood estimation, non-significant interactions were dropped sequentially, starting with those with the smallest t values, but were retained if their removal resulted in higher AIC values (ΔAIC >2 (Arnold 2010)). Assumptions of homoscedasticity and normality of residuals were examined by visual inspection of residual plots. Significance testing, alongside model r^2 values were used to indicate the strength of observed patterns. R^2 values included marginal (r_m^2) and conditional (r_c^2) r^2 values which indicate the variance explained by fixed factors, and by both fixed and random factors, respectively (Nakagawa and Schielzeth, 2013). Adjusted repeatability of each trait was calculated using transformed traits, as described by Stoffel, Nakagawa and Schielzeth (2017) using variances calculated with LMEs and including fish ID as a random effect. Agreement repeatability of capture vulnerability was also calculated using binary caught/uncaught data, using fish ID as a random effect .The vulnerability of individual fish to capture in trawl and trap fisheries across temperatures was assessed using semiparametric Cox proportional hazard models (Cox PH), with time until capture and whether the fish was caught or escaped as response variables. Comparisons of overall survival were first made between each gear type, within each temperature treatment, to investigate differences in catch efficiencies of the two gears, and how temperature effects vulnerability to capture overall. The role of individual traits in determining vulnerability to capture was also assessed using Cox PH models, fitted to each fishery simulation individually. In each case, log(n+1) transformed behavioural traits, and adjusted metabolic traits were used as predictor variables, while log-transformed absolute max swim speed (cm s^{-1}) was used in place of swim speed normalised to BL s^{-1}. Cox PH models of best fit were determined using the same protocol as outlines for LMEs above, with assumptions of proportional hazards assessed using the cox.zph function within the survival package in R. Repeatability of capture vulnerability was calculated using binary caught/uncaught data.

	Time		
Tank ID	T1	T2	T3
1 2 3	16°C Swim Performance Metabolic Phenotype Activity	16°C Swim Performance Metabolic Phenotype Activity Trap/Trawl Vulnerability	16°C Swim Performance Metabolic Phenotype Activity Trap/Trawl Vulnerability
4 5 6	16°C Swim Performance Metabolic Phenotype Activity	20°C Swim Performance Metabolic Phenotype Activity Trap/Trawl Vulnerability	24°C Swim Performance Metabolic Phenotype Activity Trap/Trawl Vulnerability

Figure 3.1: Timeline showing the acclimation of fish to different temperatures. In each case, fish were allowed to acclimate to each temperature for 4 weeks before measurements of individual traits began. At T1 fish were profiled for metabolic phenotype, swim performance, and behavioural traits, while each of these measurements was also repeated at T2 and T3. At T2 and T3, fish were additionally assayed for vulnerability to capture in both a trawl and trap simulated fishery. Note that during the final acclimation, a total of 9 fish died before respirometry or capture vulnerability assays could be performed at 24°C.

3.3 RESULTS

3.3.1 Does acclimation temperature affect vulnerability to capture in active and passive fishing gears?

Risk of capture only increased in response to temperature for the trawl, not for the trap, and this effect of temperature on trawling vulnerability was only apparent at 24°C. Probability of capture did not differ between 16°C and 20°C in either the trawl (HR=-0.077, p = 0.83), or trap (HR=0.34, p=0.2). Trawls conducted at 16°C caught 50% of fish (median chase time = 149 s), and similarly trawls at 20°C caught 46.9% of fish (median chase time = 120 s, Figure 3.4). In contrast, fish probability of capture in the trawl was higher at 24°C than at 16°C, where 66.6% of fish were caught (median chase time = 38 s, Figure 3.4). Trapping at 16 and 20 °C caught 77.1% and 93.8% of fish (median capture times = 61 and 71 s, respectively, Figure 3.4). Risk of capture was unchanged in the trap at 24°C compared to 16°C, where 80% of fish were caught (median capture time = 280 s, Figure 3.4).

3.3.2 Does acclimation temperature affect which traits are related to capture vulnerability in active and passive gears?

More active fish were less likely to be caught in the trawl at all temperatures, ($p=0.04$, $p=0.025$, for both trawl trials conducted at 16°C, and $p=0.005$, $p=0.03$ for trials conducted at 20°C and 24°C, Figures 3.4,3.5; Table 3.4), but there were no relationships between trawl vulnerability and any other trait. This selectivity regime was maintained across temperatures despite significant effects of temperature on activity (Figures 3.2,3.5; Table 3.2). Activity increased with temperature up until 20°C, before decreasing at 24°C. Although activity was consistently correlated with capture vulnerability in the trawl, trawl capture vulnerability itself was not repeatable across or within temperatures (Table 3.3), indicating that while selection on activity was consistent, capture vulnerability was not. In contrast, no relationship between any individual trait and capture vulnerability was found in the trap at any acclimation temperature, except at 24°C, where fish with higher swim performance were at significantly lower risk of capture in the trap ($p=0.008$, Table 3.4). This relationship between swimming performance and trap capture vulnerability was accompanied by a significant decrease in the swimming performance of fish at 24°C, while no differences in swim performance were recorded between 16°C and 20°C (Figure 3.2, Table 3.2). Vulnerability to trap capture was not found to be repeatable across temperatures (Table 3.3). Significantly higher SMRs, which drove decreases in AS with temperature, were observed in fish acclimated to 24°C, although SMR, AS and MMR did not correlate with capture vulnerability in either gear at any temperature (Tables 3.2,3.4, Figure 3.3).

Trait	*Adj. R*	*SE*	*CI*	*p*
Activity	0.462	0.078	0.296, 0.621	<0.001
Umax (BLs^{-1})	0.119	0.076	0, 0.272	0.069
Adj(SMR)	0	*NA*	*NA*	*NA*
Adj(AS)	0.298	0.082	0.145, 0.459	<0.001
Adj(MMR)	0.299	0.08	0.147, 0.456	<0.001

Table 3.1: Across context repeatabilities of individual behavioural and physiological traits assessed using LMEs. Repeatability was calculated for each individual trait using the trait of interest as a response variable, and acclimation temperature and fish ID as fixed and random effects, respectively.

Trait	Term	Estimate	*SE*	*df*	*t*	*p*	r_m^2	r_c^2
Activity	Intercept	391.26	48.734	5.292	8.028	<0.001	0.047	0.586
	Treatment	-13.729	68.705	5.226	-0.2	0.85		
	Time T2	-24.846	32.08	121.732	-0.775	0.44		
	Time T3	-21.664	32.08	121.732	-0.675	0.5		
	Treatment:T2	96.803	45.503	122.226	2.127	0.035		
	Treatment:T3	-62.824	46.956	123.607	-1.338	0.183		
Swim Performance (BL s^{-1})	Intercept	53.973	4.012	5.951	13.452	<0.001	0.255	0.448
	Treatment	9.096	5.674	5.951	1.603	0.16		
	Time T2	14.417	3.04	125.827	4.743	<0.001		
	Time T3	26.765	3.04	125.827	8.805	<0.001		
	Treatment:T2	-6.145	4.281	125.148	-1.436	0.154		
	Treatment:T3	-17.496	4.527	130.805	-3.857	<0.001		
Adj(SMR)	Intercept	0.571	0.013	191.834	42.663	<0.001	0.56	0.57
	Treatment	-0.021	0.019	191.834	-1.088	0.277		
	Time T2	-0.016	0.019	130.926	-0.835	0.405		
	Time T3	-0.056	0.019	130.926	-2.928	0.004		
	Treatment:T2	0.042	0.027	130.28	1.584	0.116		
	Treatment:T3	0.309	0.027	134.478	11.227	<0.001		
Adj(AS)	Intercept	86.026	12.074	6.994	7.125	<0.001	0.026	0.357
	Treatment	13.853	17.076	6.994	0.811	0.444		
	Time T2	16.444	10.932	127.592	1.504	0.134		
	Time T3	14.982	10.932	127.592	1.37	0.172		
	Treatment:T2	-11.678	15.385	126.886	-0.759	0.449		
	Treatment:T3	-35.144	15.893	129.39	-2.211	0.029		
Adj(MMR)	Intercept	2.9117	0.157	7.093	18.597	<0.001	0.026	0.301
	Treatment	0.167	0.221	7.093	0.754	0.475		
	Time T2	0.276	0.143	129.374	1.937	0.054		
	Time T3	0.363	0.143	129.374	2.544	0.012		
	Treatment:T2	-0.209	0.201	128.671	-1.042	0.299		
	Treatment:T3	-0.325	0.207	131.464	-1.566	0.12		

Table 3.2: Results of linear mixed effects models examining the effect of time and treatment on individual metabolic and behavioural traits. In each case, the trait of interest was the response

variable, while temperature treatment, time, and an interaction term between each treatment and time were used as predictors.

Trait	***Agreement R***	***SE***	***CI***	***p***
Trawl Capture	0.19	0.148	0, 0.525	0.129
Trap Capture	0	1.76	0,7.117	0.5
Trawl Capture (16°C)	0.268	0.191	0, 0.639	0.122
Trap Capture (16°C)	0.017	0.336	0, 0.979	0.496

Table 3.3: Agreement repeatabilities of capture in each fishing gear. Binary caught/uncaught data for each gear type were used for the response variable in each case, using individual fish ID as a random effect.

Model	**Term**	**β**	**z**	***p***
Trawl 16T2	*adj(AS)*	4.51	1.829	0.067
	adj(MMR)	-4.36	-1.823	0.068
	SGR	-4.03	-1.244	0.213
	Log(Activity)	-0.371	-2.049	0.04
Trawl 16T3	*Log(Activity)*	-0.531	-2.278	0.025
Trap 16T2	*adj(SMR)*	-7.833	4.757	0.091
	adj(AS)	-4.199	2.643	0.117
	adj(MMR)	5.091	3.147	0.111
	SGR	3.327	1.886	0.084
Trap16T3	*SGR*	4.335	1.674	0.079
Trawl 20T2	*Log(Activity)*	-0.946	-2.34	0.005
Trap 20T2	*Null Model*	NA	NA	NA
Trawl 24T3	*Log(Activity)*	-0.358	-2.164	0.03
Trap 24T3	*Log (Umax)*	-0.04	-2.68	0.008

Table 3.4: Results of Cox proportional hazards models examining the role of individual behavioural traits in determining probability of capture in trap and trawl fishing gears.

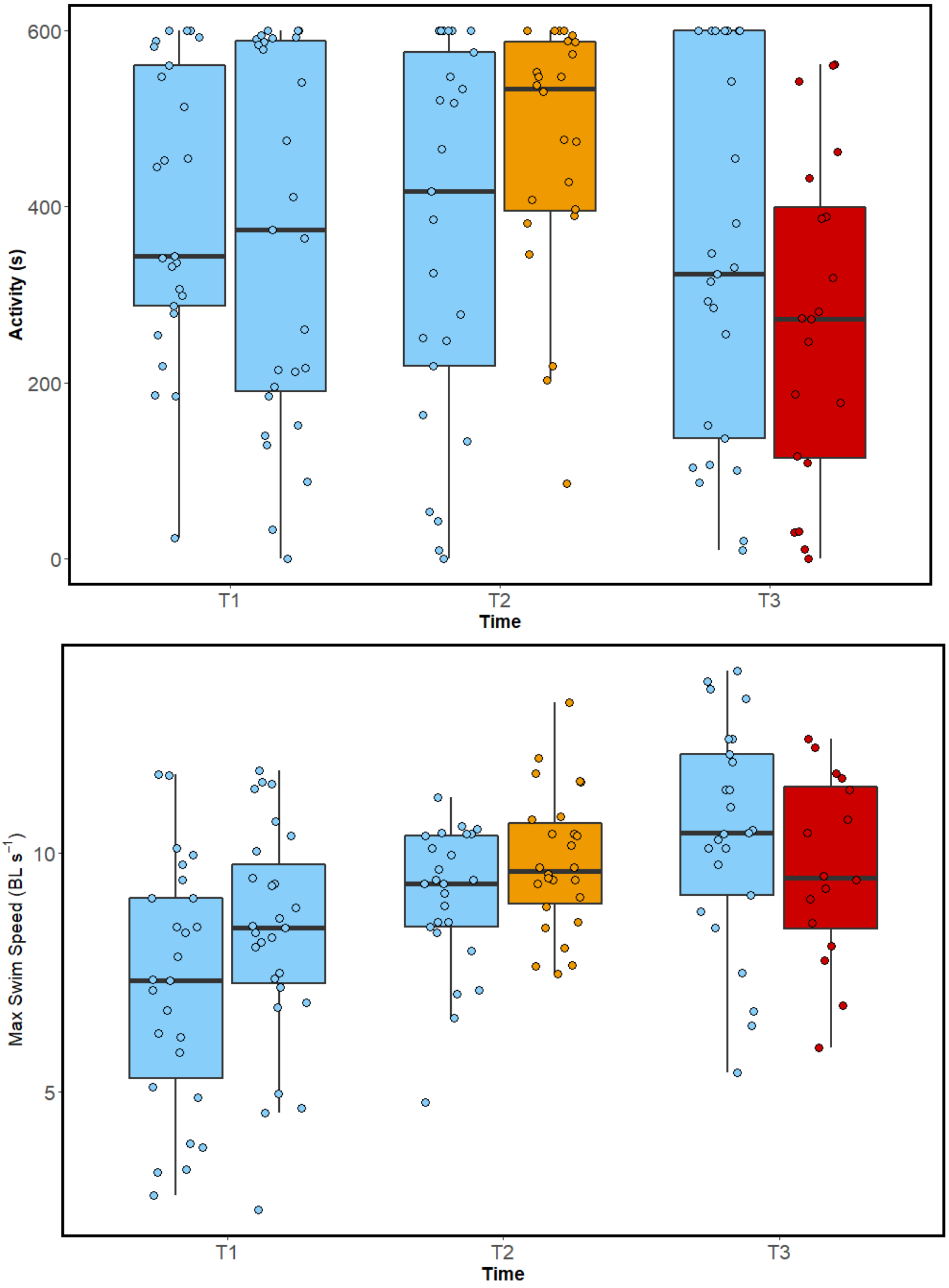

Figure 3.2: Boxplots behavioural and swim performance trait distributions at each temperature and time of measurement. Blue, orange and red plots are traits recorded at 16,20 and 24°C, respectively. Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of datapoints between each hinge, and 1.5x the difference between 25th and 75th percentiles, while data beyond this range are outliers and not plotted.T1 16°C control n= 35, warm n=35; T2 16°C n=32, 20°C n=32; T3 16°C n=32, 24°C n=27.

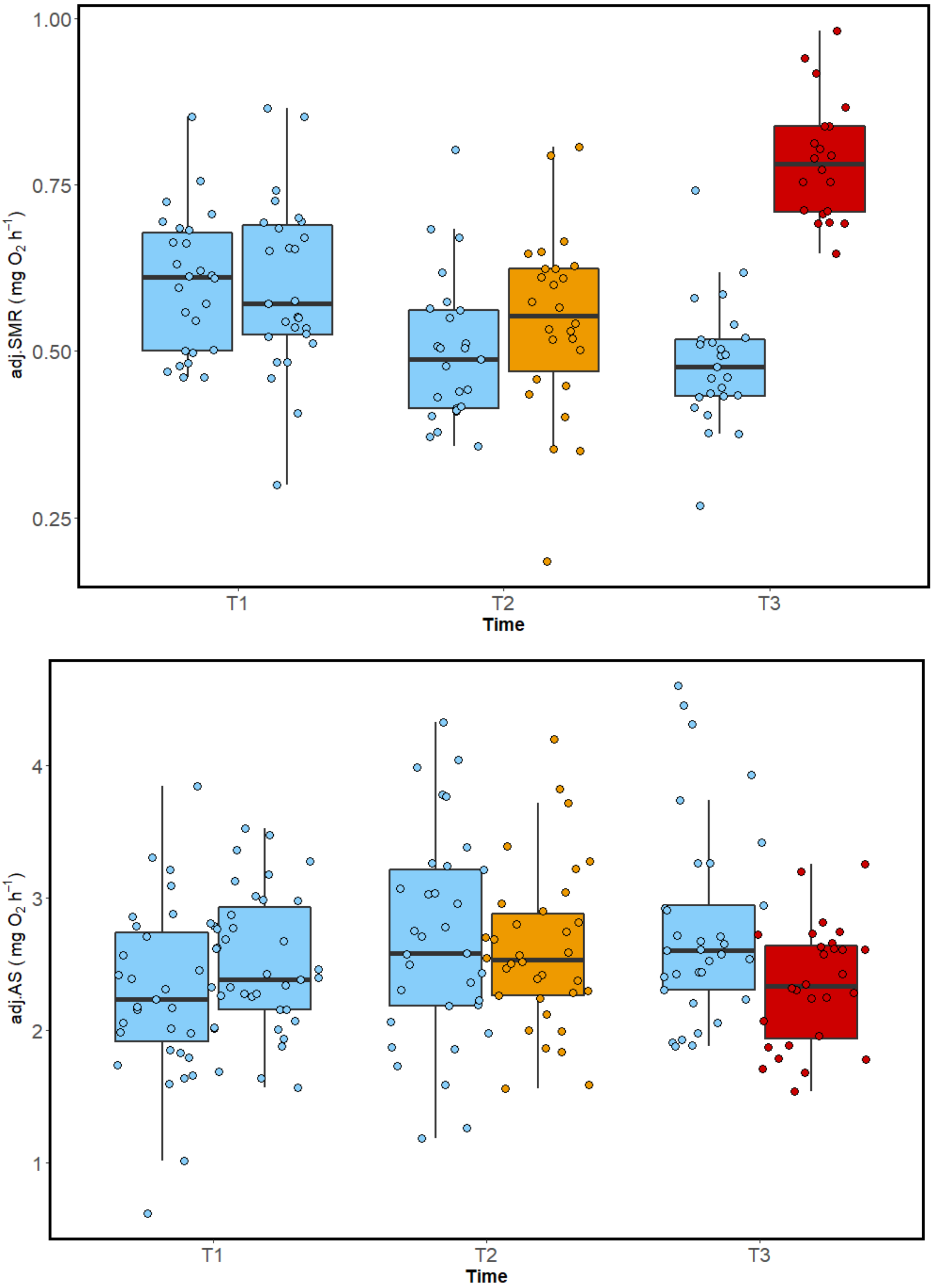

Figure 3.3: Boxplots of physiological trait distributions at each temperature and time of measurement. Blue, orange and red plots are traits recorded at 16,20 and 24°C, respectively. Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of datapoints between each hinge, and 1.5x the difference between 25th and 75th percentiles, while data beyond this range are outliers and not plotted. T1 16°C control n= 35, warm n=35; T2 16°C n=32, 20°C n=32; T3 16°C n=32, 24°C n=22.

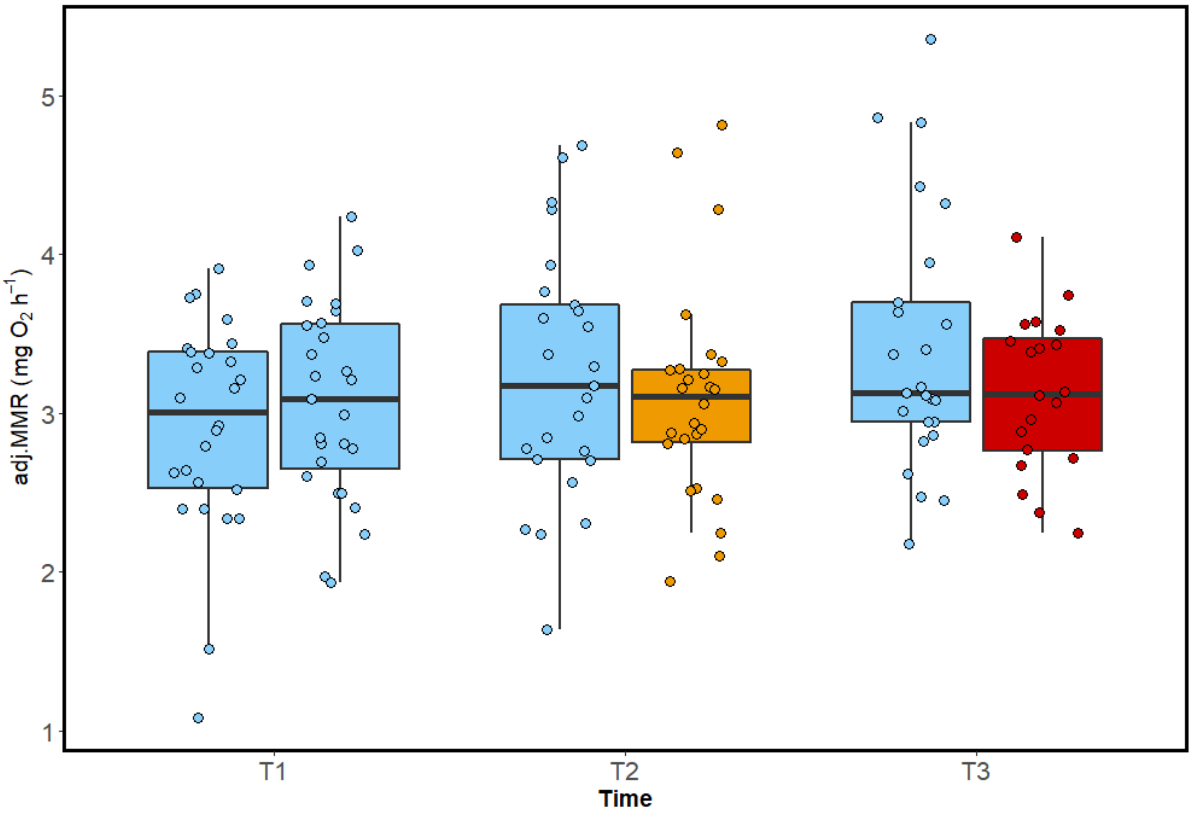

Figure 3.3 (cont): Boxplots of physiological trait distributions at each temperature and time of measurement. Blue, orange and red plots are traits recorded at 16,20 and 24°C, respectively. Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of datapoints between each hinge, and 1.5x the difference between 25th and 75th percentiles, while data beyond this range are outliers and not plotted. T1 16°C control n= 35, warm n=35; T2 16°C n=32, 20°C n=32; T3 16°C n=32, 24°C n=22.

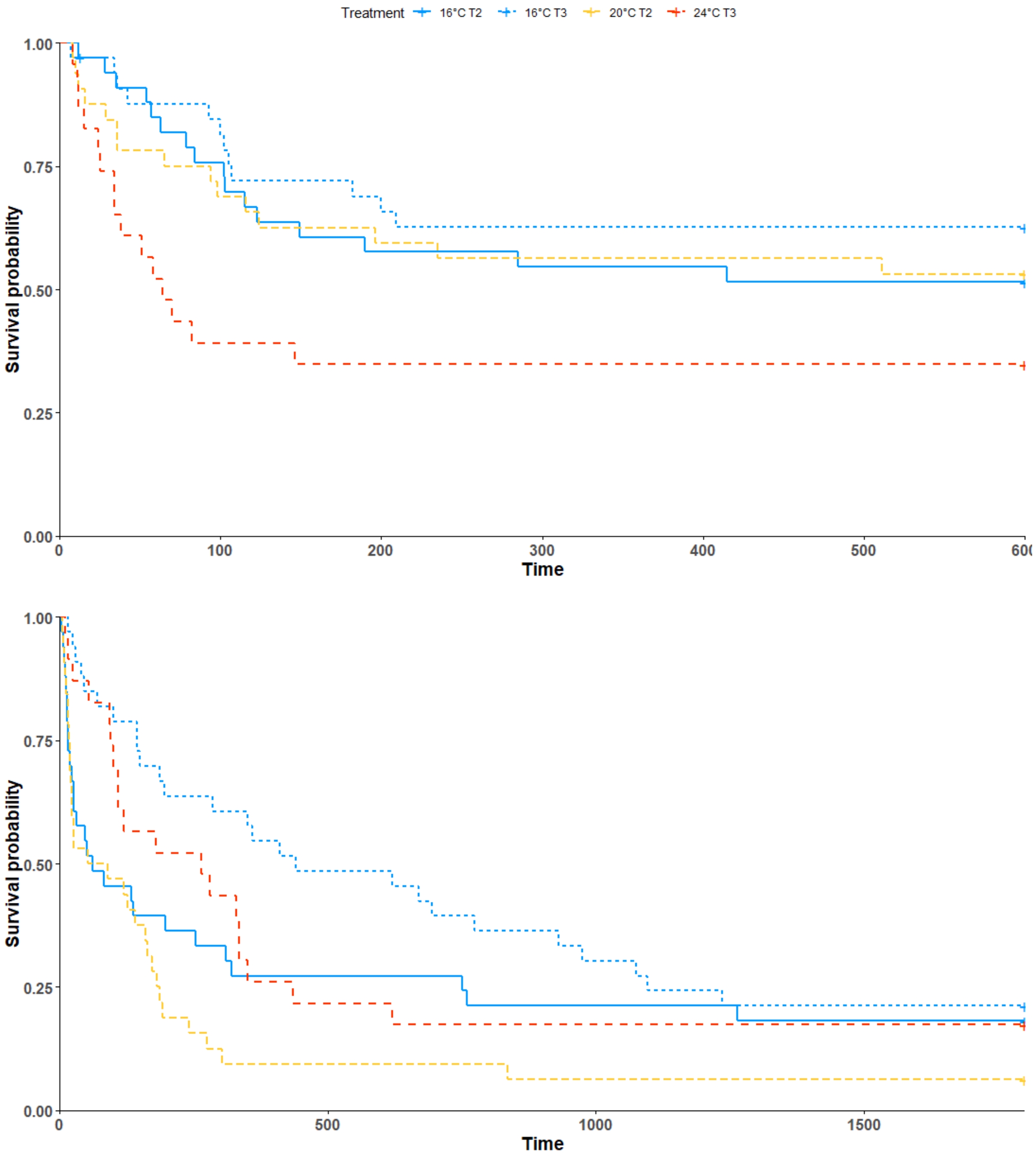

Figure 3.4: Survival curves of minnow within simulated trawl (top) and trap (bottom) fisheries.

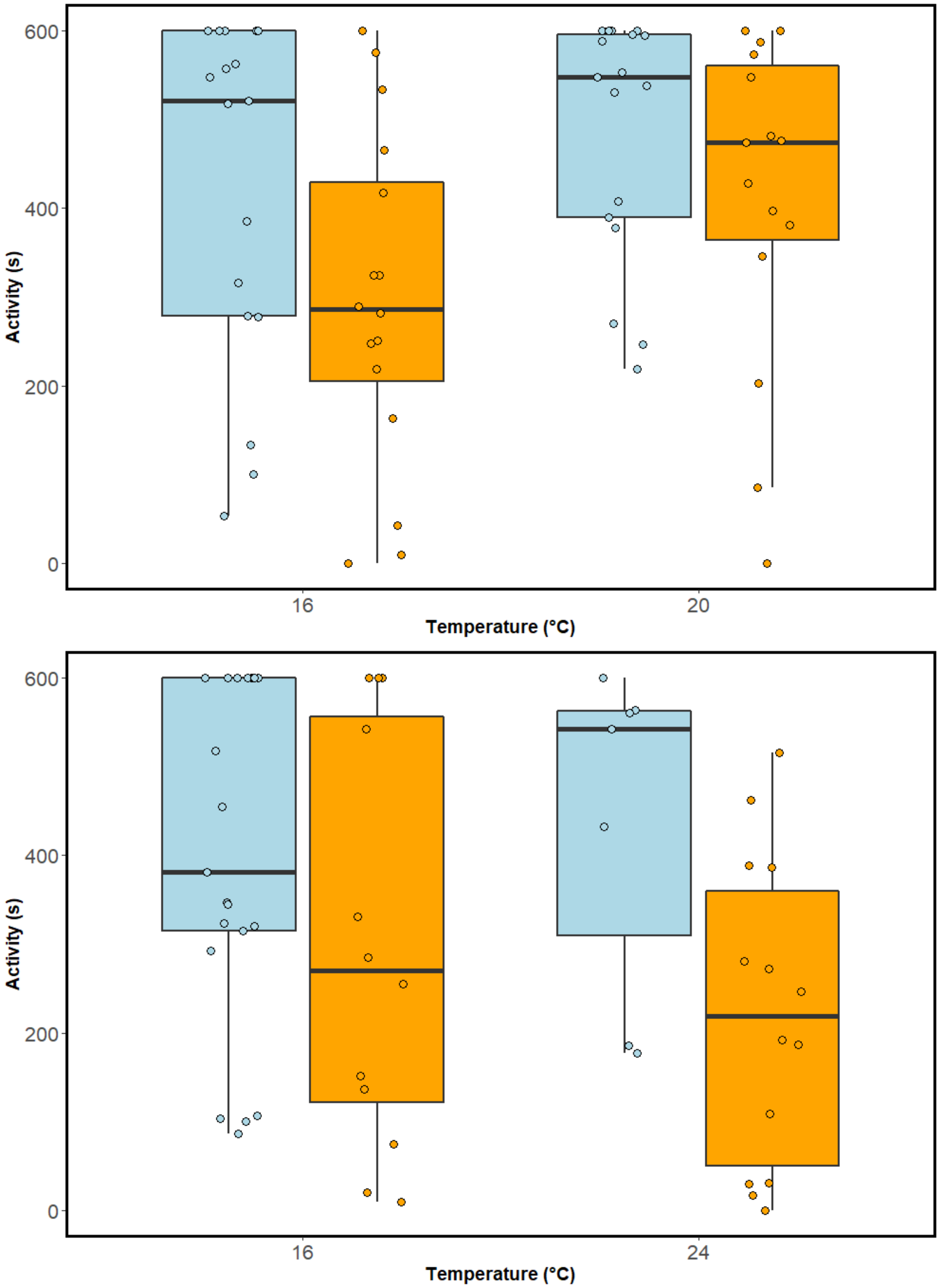

Figure 3.5: Comparison of of uncaught (blue) and caught (orange) fish activities in the trawl at 16 vs 20°C (top), and 16 vs 24°C (bottom)

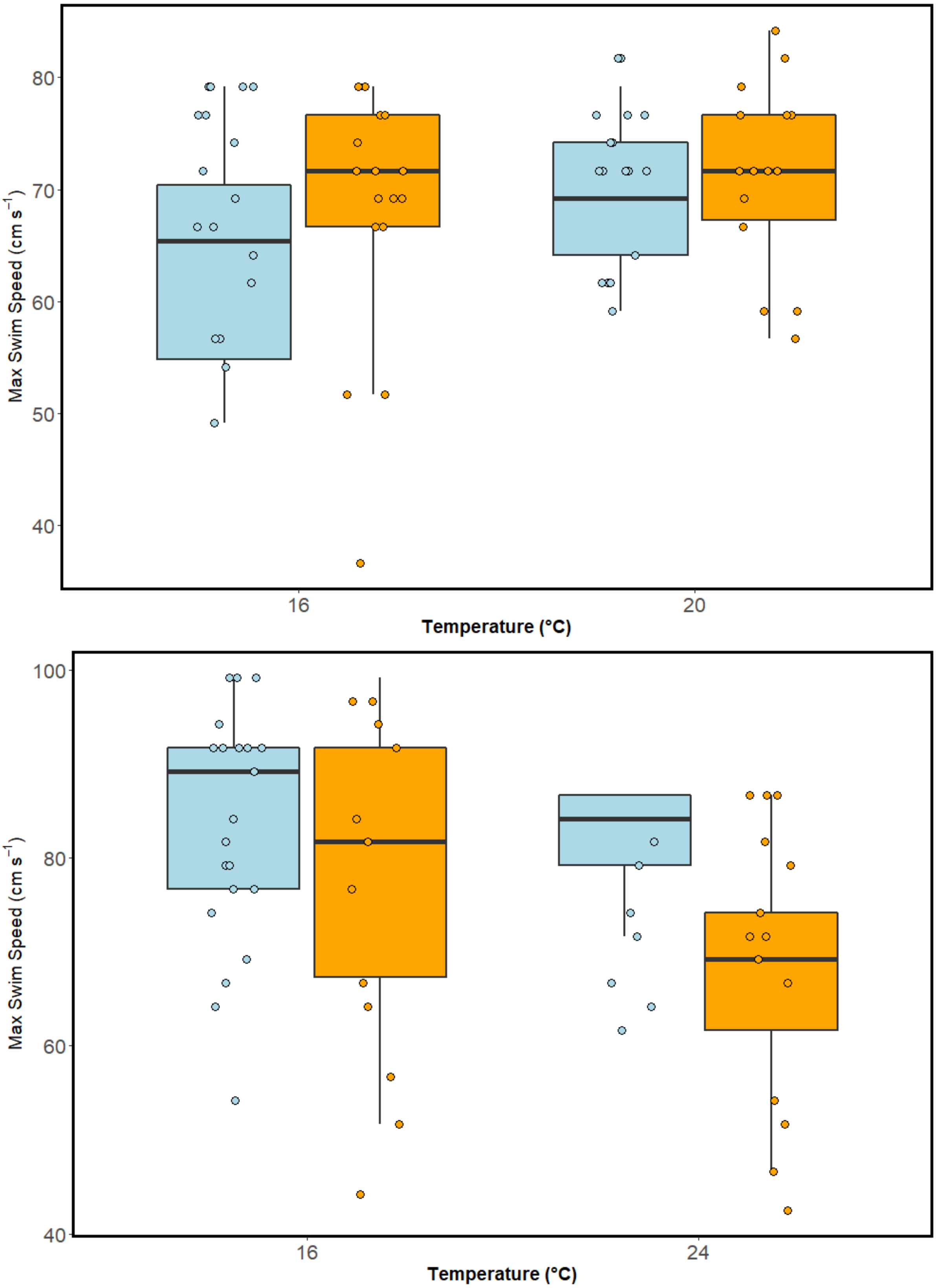

Figure 3.6: Comparison of of uncaught (blue) and caught (orange) fish swim speeds in the trap at 16 vs 20°C (top), and 16 vs 24°C (bottom)

3.4 DISCUSSION

The results here suggest that, during the critical phase of capture when fish are interacting with a deployed gear, acclimation temperature has only a modest effect on risk for fish to be captured by either trapping or trawling. Specifically, there was an increase in the proportion of fish captured by trawling at only the warmest temperature tested and there was no noticeable effect of temperature on vulnerability to capture by trap. We also found differences in the traits associated with risk of capture between active and passive gears, supporting the notion that different fishing gears can select on contrasting phenotypes (Arlinghaus *et al.* 2017a; Diaz Pauli *et al.* 2015a; Uusi-Heikkilä *et al.* 2008b). While physiological traits were not correlated with vulnerability to capture by either gear at any temperature, fish that were more active were less likely to be captured by trawl across all temperatures, and fish with a higher swimming capacity were less likely to be caught by trap at the warmest temperature. Establishing the capacity for fishing gears to select on physiological and behavioural traits in fish populations, and how this is modulated by the environment is key for sustainable fisheries management (Horodysky *et al.* 2015; Laugen *et al.* 2014b; Ward *et al.* 2016). The results here highlight the capacity for environmental variability to interact with fisheries-selection to yield phenotypic change in exploited fish populations.

We found no relationship between any of SMR, MMR, or AS and risk of capture by either gear at any acclimation temperature (Table 3.4). Metabolic phenotype has received considerable attention as a potential trait influencing susceptibility to capture in fish, particularly in passive gears (Hessenauer *et al.* 2015; Hollins *et al.* 2018; Louison *et al.* 2018b; Redpath *et al.* 2010b; Thambithurai *et al.* 2018). Interestingly, swimming performance also showed no relationship with capture vulnerability in the trawl, in contrast with the findings of Hollins et al. (2019) and Killen et al. (2015). In the current study, however, selection on anaerobic metabolic traits in the trawl would be most likely an indirect effect of selection on swimming performance. As no relationship between swimming performance and trawl capture vulnerability was found in this study, there was likely limited scope for the trawl to select on anaerobic metabolic traits. The disparity between these results may be attributable to the design of the trawling simulations in each case. Both Hollins et al. (2019) and Killen et al. (2015) tested fish trawl vulnerability in groups, while this study tested fish individually. This may have partially decoupled trawl vulnerability from swimming performance, as it was found in the Hollins *et al.* (2019) study that the relationship between anaerobic metabolic and capture vulnerability in the trawl was only present when fish were tested alongside familiar conspecifics. Putatively, this pattern was driven by a mechanism of familiar shoal mates providing stronger impetus for fish to engage in strenuous, anaerobic swimming, than that provided by unfamiliar shoals, strengthening selection on swimming performance. The inclusion of escape routes around the trawl in this study, which were not included in the Killen *et al.* (2015) experiment, also had the potential to disrupt selection on swimming performance, by providing opportunity for escape unrelated to the ability to solely maintain position ahead of the trawl net.

In this study, fish with a lower level of spontaneous activity had a higher risk of capture by trawl (Table 3.4; Figure 3.5), agreeing with the findings of Diaz Pauli et al. (2015). This relationship between individual activity and vulnerability to capture may be driven by more active individuals making use of more space in front of the trawl, therefore being more likely to locate and make use of escape routes. Although some fish were able to maintain sufficient swim speed to remain ahead of the trawl for the entire trial duration, most uncaught fish avoided capture by utilising escape routes, therefore dampening the potential for swimming ability to be a target for selectivity in this experiment. Interestingly, despite this reduced capacity for swimming performance to influence capture vulnerability, risk of trawl capture was higher at 24°C, coinciding with a reduction in swim performance seen in 24°C acclimated fish (Table 3.2; Figure 3.2). This reduction in overall swimming performance may have driven the high capture rate in the trawl at 24°C (Figure 3.4), potentially masking any selection on individual swimming performance which would have been present (Killen *et al.* 2013). While this is possible, decreases in overall fish activity were also recorded at 24°C which is also likely to have increased overall capture probability, as fish become less likely to locate and make use of available escape routes, due to decreased use of available space.

The relatively high vulnerability to capture by trap at 20°C (Figure 3.4), may have in part been driven by the particularly high activity of fish at this temperature (Figure 3.2), increasing the likelihood of a fish interacting with the trap and being caught. The high activity and vulnerability to trapping at 20°C may have ameliorated selection on other traits at the individual level. While population level increases in activity found at 20°C may have driven overall levels of capture risk in the trap, individual level activity was not associated with trap capture vulnerability in any instance. This is surprising considering the potential links between traits related to activity and the likelihood of a fish encountering and being caught by a fishing gear (Diaz Pauli *et al.* 2015a). Selection on individual minnow's spontaneous activity may have been weakened by the design of the fisheries simulations, which replicated the final stages of fisheries capture (Hollins *et al.* 2018). This may have decreased the capacity for individual fish's activity to influence susceptibility to capture, as this trait would be more relevant in determining capture vulnerability during earlier stages in the capture process not examined in the present study, by determining encounter rate, for instance. If individual activity is an important trait in determining capture vulnerability earlier in the capture process, then highest encounter rates with gears in the wild may be expected at temperatures at where spontaneous activity is maximised, in this instance 20°C, before declining again as temperatures exceed thermal optima. Traits related to space use and activity in fish can be under selection in passive fisheries (Monk and Arlinghaus 2017a), although this is not necessarily driven through a mechanism of more active fish encountering fish gears more frequently, as many fish encountering gears fail to be subsequently caught (Monk and Arlinghaus 2017b). In this experiment, therefore, individual traits related to risk perception (Klefoth *et al.* 2017b) may be more relevant in determining susceptibility to capture, as our assays were focussed on interactions between fish and fishing gears after gears had initially been encountered. We found no relationship between any trait and risk of capture in the trap, except at 24°C, where a negative relationship between swimming performance and capture vulnerability was apparent (Table 3.4). This is despite traits related to foraging and exploration being thought to be particularly relevant in determining vulnerability to capture by passive gears (Biro and Post 2008a; Hessenauer *et al.* 2015; Hollins *et al.* 2018; Klefoth *et al.* 2017b; Koeck *et al.* 2018; Monk and Arlinghaus 2017a; Monk and Arlinghaus 2017b). The negative relationship between swim performance and capture vulnerability in the trap found at 24°C is difficult to explain, as no mechanism by which poor swimming fish would be more likely to be caught by a trap is clear. It is possible that selection on swimming performance by trapping is indirect, and instead related to a separate trait not measured in this study but correlated with swim performance.

In contrast to previous experiments investigating links between individual traits and capture vulnerability, capture vulnerability across temperatures was not found to be a repeatable trait in its own right in either the trap or trawl (Table 3.3). The reason capture vulnerability was not repeatable in this instance is not clear, but repeatability would likely have been reduced by the different temperatures that capture vulnerability was tested within (Stoffel *et al.* 2017). If this were the sole cause, however, it would be expected that capture vulnerability would be repeatable for fish maintained at 16°C, however this was not the case for either gear type .Furthermore, previous experiments have tested trawl capture vulnerability in several fish simultaneously (Hollins *et al.* 2019; Killen *et al.* 2015b), which may have ameliorated any stochastic effects on capture probability, increasing repeatability of capture vulnerability. Non-repeatable trap capture vulnerability may have contributed to the lack of selection on individual traits observed in the trap, with the exception of at 24°C. While low or absent repeatability of capture vulnerability in both gears may weaken the capacity for fisheries to select on individual traits, individual activity was consistently associated with trawl vulnerability across all temperatures. As such, while low activity fish were consistently at greater risk of capture in the trawl, the same fish are not caught each time. As temperature differences between trawl and trap vulnerability trials seem the most likely cause of a lack of repeatability in this study, this suggests that depending on acclimation temperature, different individuals were the most likely to be captured by either trawl or trap. Repeated capture vulnerability trials within each acclimation temperature would be required in future work investigating the degree to which capture vulnerability is repeatable within as opposed to across thermal regimes.

While experimental approaches using simulated fisheries allow precise control over the factors influencing fish capture vulnerability, the small scale at which they must be conducted means careful consideration must be given to how the data can be interpreted and used to inform fisheries in the wild and studies at larger scales. Recreating all stages of fisheries capture (Hollins *et al.* 2018) is generally beyond the scope of experimental approaches. For example, individual traits determining habitat selection are likely relevant during early stages of fisheries capture, as these will determine which fish overlap with a deployed fishing gear (Olsen *et al.* 2012; Villegas-Ríos *et al.* 2018). Further issues of scale arise regarding the size of the fishing gears relative to the fish themselves. While the size of the trap relative to the minnows used in this experiment is comparable to that seen in trap fisheries in the wild (Königson *et al.* 2015), the relative size of the trawl is much smaller than what would be expected in real-world fishery. This likely exacerbated the impact of escape routes being present around the trawl in disrupting any potential selection on swimming performance. While fish can escape capture by manoeuvring outside of the path of a pursuing trawl, the fish which do are typically already close to the edges of the trawl mouth (Winger 2010). More typically, fish targeted by the trawl are herded into the centre of the pursuing net mouth by the trawl sweeps (Rose 1995; Ryer *et al.* 2009; Ryer 2008; Winger 2010), where the size of the trawl mouth relative to these pursued fish makes escape via manoeuvring outside of the path of the trawl more difficult.

To summarise, we found evidence that active and passive fishing gears exhibit distinct patterns of selection on fish behavioural traits, but no evidence of fisheries selection on physiological traits was found. Trawl simulations consistently selected on individual fish activity, while traps tended to be non-selective on individual traits until fishing trials were conducted at the highest acclimation temperature. Selection in both the trawl and trap fishery was altered at 24°C, driven by a combination of temperature effects on gear capture efficiency, and on underlying traits of the fish themselves. This study highlights the capacity for different fishing gears to select on distinct groups of phenotypic traits, but also shows that relationships between individual traits and vulnerability to capture may be modulated by environmental conditions.

4. DOES CAPTURE METHOD PREDICT METABOLIC, BEHAVIOURAL, AND SPACE USE TRAITS OF WILD PERCH?

4.1 INTRODUCTION

It has been established that fisheries selection has the capacity to drive evolutionary change in the life history traits of exploited fish populations (Enberg *et al.* 2012; Heino *et al.* 2015; Richard 2007), in a phenomenon known as fisheries induced evolution (FIE). However, there is increasing evidence that in addition to life history traits, behavioural and physiological traits of individual fish may also be under selection in fisheries (Arlinghaus *et al.* 2017a; Biro and Post 2008a; Enberg *et al.* 2012; Hollins *et al.* 2018; Koeck *et al.* 2018; Uusi-Heikkilä *et al.* 2008b). Selection on these traits has the capacity to erode behavioural and physiological diversity in fish stocks, influencing population resource requirements, resilience to environmental change, and species distributions (Claireaux *et al.* 2018; Hollins *et al.* 2018). Accounting for the evolutionary responses of fish populations to commercial and recreational fisheries harvest is critical to effective fisheries management (Laugen *et al.* 2014b), but requires comprehensive understanding of the links between fish behavioural and physiological traits and capture vulnerability in fishing gears. This is complicated by the fact that contrasting capture mechanisms of different fishing gears exploit different aspects of fish behaviour to facilitate capture (Hollins *et al.* 2018). As such, traits relevant to determining capture vulnerability in one fishing gear type may not be relevant in another (Diaz Pauli *et al.* 2015a; Hollins *et al.* 2018), giving rise to patterns of selection and phenotypic change which are likely gear-specific.

Fishing gears can be classified as either ‘active’ or ‘passive’ based on their mechanisms of capture. Active fishing gears are mobile, and pursue or encircle target fish using nets, exploiting behaviours related to shoaling and escape responses (Hollins *et al.* 2018; Hollins *et al.* 2019; Killen *et al.* 2015b; Kim and Wardle 2003; Ryer *et al.* 2009). In contrast, passive fishing gears are static, and rely on fish to approach and interact with the gear to be caught (Arlinghaus *et al.* 2017a; Diaz Pauli *et al.* 2015a; Hollins *et al.* 2018).Despite these similarities within each broadly defined gear type, subtle distinctions between mechanisms of capture for different fishing gears exist within each of these categories. For example, some relatively passive capture methods, including angling, facilitate interactions with fish using baits or lures designed to imitate the appearance, sound, or chemical stimuli of potential food resources. In contrast, other passive gear types rely on being undetectable by target fish. Gill nets, for example, rely on being undetected by nearby fish, capturing fish which attempt to swim through the mesh while engaged in routine, spontaneous activity. As such, while a fish exhibiting more active behaviours may be more likely to encounter both deployed gill nets and the lures/baits of line and hooks (Biro and Post 2008a; Monk and Arlinghaus 2017a; Monk and Arlinghaus 2017b), traits related to threat perception, or willingness to investigate or attack a potential prey item may only be relevant for determining vulnerability to angling. (Klefoth *et al.* 2017a; Lennox *et al.* 2017b; Monk and Arlinghaus 2017b). More active fish may therefore be more likely to be removed from wild populations by both rod and reel and gill nets due to increased probability of encounter, with rod and reel exerting further selection on individual fish's proclivity to approach and interact with a foreign object once the encounter has occurred (Monk and Arlinghaus 2017b). Correlations between behavioural traits and vulnerability to capture have been recorded in several fish species in both laboratory and field settings (Biro and Post 2008a; Diaz Pauli *et al.* 2015a; Koeck *et al.* 2018; Monk and Arlinghaus 2017a; Redpath *et al.* 2010b; Wilson *et al.* 2011). Notably, the strength and direction of these relationships varies, and are likely context-dependent (Killen *et al.* 2013). For example, studies have reported both positive (Klefoth *et al.* 2007) and negative (Wilson *et al.* 2011) relationships between 'boldness' and capture vulnerability in rod and reel, and these relationships may also be absent altogether (Vainikka *et al.* 2016).

If gill netting and angling selectively remove more active or bold individuals, this may not only alter the phenotypic composition of exploited fish populations, but may also elicit other indirect phenotypic changes through correlational selection. In particular, the energetic demand of individual fish may influence frequency and duration of active behaviours, such as foraging, and the likelihood of a fish attacking an encountered fishing hook. For example, standard metabolic rate (SMR) is a heritable trait which shows repeatable variation within fish populations (Burton et al. 2011; Metcalfe et al. 2016), and has received attention as a candidate trait for selection by passive fishing gears (Hessenauer *et al.* 2015; Louison *et al.* 2018b; Redpath *et al.* 2010b; Thambithurai *et al.* 2018). SMR is the minimum metabolic cost incurred from routine maintenance of homeostasis and sets baseline energetic demand for survival. A fish with a high SMR may therefore spend more time foraging, or behaving more aggressively, to help secure available resources. Correlations between SMR and traits related to foraging, exploration, and other risk-taking behaviours have been recorded in a range of fish species (Finstad et al. 2007; Killen et al. 2011; Killen et al. 2012b; Régnier et al. 2012), with high SMR fish often more likely to engage in riskier behaviours (Metcalfe *et al.* 2016b). These high SMR fish may therefore be at greater risk of encountering a fishing gear, or more likely to decide to approach and interact with it once detected. The capacity for fish to utilise energy resources beyond SMR may also play a role in determining whether a fish will display behaviours determining capture vulnerability. Aerobic Scope (AS) is the difference between an animal's minimum (SMR) and maximum metabolic (MMR) rates and represents the capacity of an animal to simultaneously allocate oxygen to aerobic physiological processes beyond those required for maintenance. A high AS may allow fish to engage in more active lifestyles, as the costs of swimming or maintaining vigilance in potentially risky environments are more easily accommodated than in fish with a lower AS (Killen *et al.* 2015c; Redpath *et al.* 2010b). In comparison to links between behaviour and capture vulnerability, there have been few attempts to link physiological traits to likelihood of capture in passive gears, although the studies that exist provide mixed evidence. Largemouth bass (*Micropterus salmoides*) selectively bred to exhibit high angling vulnerability were shown to exhibit high SMR, AS, and MMRs compared to their low-vulnerability conspecifics (Redpath *et al.* 2010b; Steven J. Cooke *et al.* 2007), suggesting a metabolic basis for angling vulnerability. This is corroborated by the results of Hessenauer *et al.* (2015), who recorded elevated metabolic rates in *M. salmoides* collected from lakes closed to fishing, compared to those collected from lakes where recreational fishing occurs, a pattern which could be driven by fisheries selection removing individuals exhibiting high metabolic rate. However, experimental approaches directly linking individual susceptibility to capture in passive gears with metabolic phenotype have found no evidence of a relationship (Louison *et al.* 2018a; Thambithurai *et al.* 2018), highlighting the need for further investigation.

It is still unknown to what extent different fishing gears select on the same traits in the wild (Arlinghaus *et al.* 2017a; Hollins *et al.* 2018), despite contrasting mechanisms of capture and the presence of experimental evidence suggesting the contrary (Diaz-Pauli *et al.* 2015, Hollins *et al. in press)*. Further research on the mechanisms of selection present in different fishing gear types is required to evaluate the capacity of fisheries to drive phenotypic change in wild fish populations and help inform effective fisheries management. As traits related to spontaneous activity and patterns of space use have the capacity to influence a fish's capture vulnerability in the wild, (Arlinghaus *et al.* 2017a; Diaz Pauli *et al.* 2015a; Monk and Arlinghaus 2017a), fisheries selection may directly alter the spatial ecology of exploited fish populations. Due to the widespread presence of fisheries throughout the world's oceans (Kroodsma *et al.* 2018), it is possible that many fish populations already exhibit altered patterns of habitat selection, space use or dispersal (Olsen *et al.* 2012). As fisheries management practices are often informed by population-level values of traits related to space use derived from exploited fish populations (Balbar and Metaxas 2019; Carr *et al.* 2017; Ward *et al.* 2016; Weeks *et al.* 2017), not considering the degree to which fisheries selection may have altered these traits may reduce the effectiveness of spatial closures to fishing, or otherwise undermine conservation efforts. For example, if a fish population exhibits reduced average home ranges as a result of fisheries driven phenotypic change, and a marine protected area is implemented using these altered trait values, then the MPA itself may constitute a selective pressure, selecting individuals with home ranges smaller than the MPA itself, or with lower dispersal distances. This could act to further fragment fish wild populations, hampering the potential for stock recovery (Carr *et al.* 2017). Considering the role that physiological processes play in linking environmental conditions with species survival and fitness (Cooke *et al.* 2014; Cucco *et al.* 2012; Farrell 2016; Horodysky *et al.* 2015), fisheries selection on traits related to individual fish's spatial ecology could also indirectly select on individual physiological traits (Hollins *et al.* 2018). In this study, we investigated the potential for lure-based angling and gill netting to select on individual traits related to metabolic phenotype, habitat use, and behaviour in wild perch (*Perca fluviatilis*) using a combination of lab based respirometry and behavioural assays, alongside acoustic telemetry in the wild. By doing this, we hoped to accomplish the following: 1)determine and compare the traits of wild gill-net vulnerable and angling-vulnerable perch in a real fishery scenario, 2) quantify the degree and repeatability of intraspecific variation in patterns of space use and behaviour in wild perch and 3) investigate correlations between individual lab derived physiological and behavioural traits, and patterns of movement and behaviour in the wild.

4.2 METHODS

4.2.1 Fish Collection, Study Site, and Husbandry

Fishing was conducted in the Dubh Lochan (56.13169861,-4.61367424, Scotland) between 27th July and August 16th 2016 using both gill nets and angling deployed from a small power-driven vessel. The Dubh Lochan is a 10 ha natural lake with a mean and maximum depth of 5 and 12m, respectively, with a fine sediment substratum enclosed by a 1-2m macrophyte boundary. The fish community is comprised largely of European perch, which are preyed upon by Northern pike (*Esox lucius*) also present in the lake, with European eel (*Anguilla anguilla*) also present. The site is closed to public fishing, although it is possible some illegal fishing has occurred, and fishing activity for research purposes on the lake has been small and infrequent (1-2 days out of the year). As such, it can be assumed that fish are largely naïve to rod and reel and gillnet fishing gears, and that minimal fisheries selection had occurred within this population at the beginning of this experiment. Fishing was conducted during daylight hours (05:12-21:31, 05:50-20:49 at the beginning and end of the fishing period, respectively), with both gill nets and lures deployed simultaneously, specifically targeting the inner most edge of the macrophyte boundary. Fishing began between 8-10:00 and was concluded no later than 16:00. To avoid sample biases driven by intraspecific differences in habitat use and potential confounding effects of having two gears deployed very close to one another, gears were rotated between the Northern and Southern portions of the lake alternately, so that while gill nets were deployed in the Southern portion of the lake, angling was conducted in the Northern portion. Gill nets (4 x 38mm single panel and 4x 45mm single panel) were deployed parallel to the macrophyte boundary for 1.5-3 hrs at a time on the lake bottom, targeting fish as they move in and out of the macrophyte boundary, and retaining them in the mesh by entanglement. During this time, fish were also targeted via angling by trolling spoons (concave metal lures which move erratically when pulled through the water, imitating the movement of an injured prey item) along the lake bottom. Casts targeted the macrophyte boundary's inner edge, similarly to gill nets, and were continually reset throughout the fishing period to help ensure equal fishing hours between the two gears. Once caught, perch were kept in an on-board holding-tub filled with water collected from the lake. Perch were kept on board until all gill nets had been checked and/or angling had ceased for a given session, at which time they were transferred to a small mesh holding pen, with vertical divisions to keep angled and gill netted fish separate, situated on the lake bottom. During this time, water in the holding tub was manually replenished with fresh lake water frequently to minimise temperature increases and hypoxia. Once fishing for the day was complete, fish were transferred from the mesh holding pen in the lake to one of two 150x150x80cm holding tanks, depending on their method of capture, in the wetlab facilities at the Scottish Centre for Ecology and the Natural Environment (SCENE), situated ~150m from the Dubh Lochan shore. The same holding tub used to hold fish on board the research vessel was used to transfer fish from holding pen to the wetlab. Perch holding tanks were always covered with a large, opaque lid, and continuously supplied with UV-treated water directly from nearby Loch Lomond (approximately 80m from SCENE) and aerated using multiple air stones. Wetlab lights were synchronised with dawn/dusk to provide fish with a light regime approximating that experienced in the wild, and were all fed an *ad libitum* diet of commercial fish pellet and live earthworm (*Lumbricina* sp.). Once fish were housed in their respective holding tanks, they were given a minimum of 1 week to recover from capture before experimental procedures began.

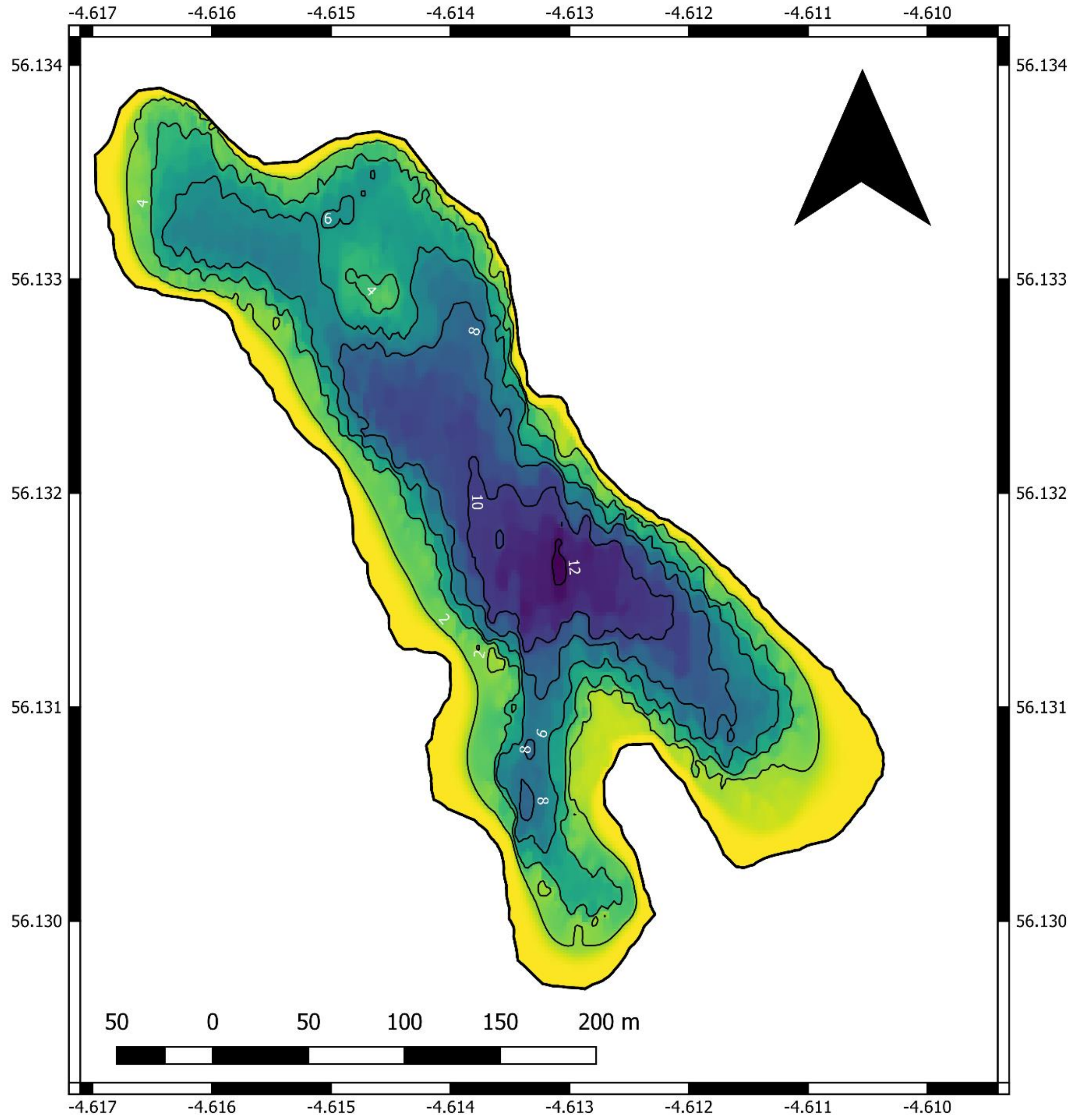

Figure 4.1: Bathymetric map of the Dubh Lochan (projection: longlat, datum: WGS84), produced using QGIS 2.18.13 (QGIS Development Team, 2014) with the in-build raster grid inverse-distance to a power interpolation algorithm (power=5.0, smoothing=2.0) based on depth measures sampled by sonar (Humminbird Helix 9) following equally spaced transects. Additional isobaths contours were fitted at 2m depth intervals.

4.2.2 Respirometry

Metabolic traits of captured perch were quantified using intermittent flow respirometry. Perch were run through respirometry 8 fish at a time, with the exception of the final fish which was run individually. In order to quantify individual MMR, fish were subjected to a chase protocol before being transferred to the respirometry chambers. The chase protocol was conducted in circular tub (57cm diameter) filled with Loch-Lomond sourced water to a depth of 20cm. Fish were chased by hand to exhaustion, which was determined as the point at which fish were no longer receptive to the chase stimulus. The manual chase is assumed to elicit maximum rates of oxygen consumption as fish recover from prolonged aerobic exercise (Killen *et al.* 2017d). Once exhausted, fish were quickly transferred to individual respirometry chambers (2 l volume) attached to the intermittent flow respirometry circuit. The respirometry circuit itself comprised of a length of silicon tubing attached to the respirometry chamber through which water was constantly recirculated using a 5-watt pump. Oxygen concentration of the water within the closed respirometry circuit was recorded every 2s using a Firesting 4-channel oxygen meter and associated sensors (Pyroscience GmbH, Aschen, Germany). Respirometry chambers were submerged in an air saturated, temperature-regulated water trough (16°C ± 0.5°C), and shielded from direct overhead light using an opaque plastic blind. Every 7 minutes, an automated flush pump turned on for 4 mins to flush chambers with oxygenated water, and then switch off to seal the respirometry circuit and allow for the decline in oxygen concentration due to fish respiration to be measured. Estimates of MMR were obtained using the rates of oxygen uptake for each 3-min time interval of the ‘closed’ portion of the respirometry cycle throughout the first 30 mins immediately following transfer to the respirometry chamber. During this time, fish were still recovering from the exhaustive chase protocol, and MMR (mg O_2 h^{-1}) was taken at the highest rate of aerobic metabolism during this period. Fish remained in the respirometry chambers overnight to allow estimation of SMR and were removed the following morning at approximately 09:00-10:00, having spent approximately 20 h in the chambers in total. Once fish were removed from the chambers, their masses were recorded to allow accurate normalisation of metabolic rate to body mass. Whole animal SMR was then estimated as the lowest 20th percentile of measurements taken throughout the measurement period. Absolute AS was calculated as the difference between MMR and SMR.

4.2.3 Behavioural Assays

Individual fish boldness was assessed twice for each fish using an open field test. A subsection of a large holding tank was used, demarcated using PVC panels fitted with plastic mesh, to provide fish with an arena of 70x300 cm, filled to a water depth of 50 cm. The arena itself was devoid of any other structure, and no gravel or substrate was provided for the fish. Trials were conducted one fish at a time, and each fish was assayed twice, 6 days apart. Fish were transferred from their holding tanks and introduced to the centre of the arena enclosed within a weighted, transparent container which prevented fish exploring the arena. Fish were left to acclimate within this holding area for 20 minutes before the trial began, at which time the container was carefully removed from around the fish, allowing fish to freely explore the arena. Fish were allowed to swim freely around the arena for 10 minutes, during which time their behaviours were recorded using a high definition video camera (GoPro Hero 4 16:9 Full HD, 720p; GoPro, San Mateo, California, USA) mounted directly overhead of the arena. Footage of the assay was then reviewed by eye to record the time until fish first began to explore the arena once the trial began, and the amount of time spent moving during the trial itself. A fish was defined as ‘moving’ once it had moved more than 1 body length (BL) from its starting position, and as ‘stationary’ once it had been static for at least 3 s. Fish moving their tail or pectoral fins but not travelling were classified as ‘stationary’.

4.2.4 Tag Implantation and Telemetry

Once behavioural and physiological assays were complete, fish were them surgically implanted with acoustic transmitters (V9-HR, 170+180 kHz, VEMCO Ltd, maximum transmission frequency = 2s, 9mm diameter, 24mm length, 2.1g in water) to allow their behaviour and patterns of movement to be quantified in the field. Each fish was first sedated using benzocaine and then restrained between two damp sponges to hold the fish in place, and also restrict and fish movement during the surgery. Once sedated, a small incision was made along the midline of the fish, and the acoustic transmitter implanted within the fish's peritoneal cavity. The incision was then closed using an interrupted stitch, and the sedated fish transferred to a designated tank where they could be monitored. All fish showed good signs of recovery, (regaining equilibrium, directed swimming, etc), and all sutures were inspected by a veterinarian 3 days after the procedure. Fish were subsequently released back into the Dubh Lochan on 06.09.16, and their movements monitored until the data was retrieved from receivers on 29.11.16.

The telemetry array consisted of 13 omnidirectional HR acoustic receivers (High Residence 2 receiver, 170/180 kHz, VEMCO, Nova Scotia, Canada) arranged in interlocking, equilateral triangles with overlapping detection ranges (see Guzzo et al. 2018 for range testing information). Internal clocks of the receivers were synchronised using acoustic transmitters integrated within the receivers themselves, and also using 6 stationary V5 sync tags arranged in a line along the centre of the lake. These static tags also allowed for the calibration of transmitter error during data processing. Receivers were mounted upright attached to vertical aluminium rods fixed within 20kg buckets of concrete, and further stabilised by two crossing sections of rebar at the bucket base. A length of rope was attached to the top of each aluminium bar at one end, and to a large yellow buoy at the other. For each receiver, the length of rope was measured to ensure that even in the event of increases in water depth, for example from heavy rainfall, the rope would remain slack, and not shift the position of the receiver it was attached to. Static sync tags were stabilised in a similar way to the receivers, attached to an aluminium rod, except with a 5kg concrete anchor.

Following receiver recovery and data download, raw data were sent to Vemco where transmitter detections were processed to 2D positions for each implanted acoustic transmitter, and each static transmitter, using hyperbolic positioning algorithms based on time difference of arrival for each transmission detected by three or more receivers in the array. Once data were received from

Vemco, we processed the data further by excluding relocations determined to have a horizontal positioning error (HPE) of 2, based on recommendations from VEMCO. After filtering, relocations of each fish were reduced by 2.07-77.7%, and the total number of relocations for each fish ranged from 155,451 – 1,638,255 while mean time between relocations (dt) ranged from 4.42 – 34.23s (Table 4.1). By excluding these data points, we were able to constrain position error of relocations within a mean range of 0.4-1.09m, as determined from error calibration using static tags. After this filtering step, fish trajectories were smoothed using a Savitzky-Golay (SG) filter (McLean and Skowron Volponi 2018) to eliminate noise from movement data. Metrics of movement and behaviour were produced from a subset of the data collected from the first receiver download, encompassing the time period 13.09.16 – 31.10.16:

4.2.4.1 *Movement Speed and Distance Travelled*

In order to account for potentially confounding effects of data quality on movement metrics between fish, trajectories were rediscretised in time using a constant step duration of 30s. Portions of fish telemetry tracks characterised by dT>30s (as determined from pre-filtered data) were not used for the quantification of movement speed, and distance travelled, to avoid generating behavioural metrics from trajectories produced solely through interpolation of the SG filter, and only movements speeds above 0.5 body lengths s^{-1} were used (using each fish's own length as a criterion). Distance travelled was then calculated as the sum of the Euclidean distances between successive relocations within 24 hours. Movement speed between successive relocations was calculated as the Euclidean distances between locations, divided by the time difference between those same positions. Only estimates of movement speed made between 10:00-14:00 were used in the characterisation of individual speed, as this was when fish tended to be in an active state.

4.2.4.2 *Habitat Utilisation Distributions, and Distance from Shore*

In order to reduce computation time, 50% and 95% habitat utilisation distributions of each fish were calculated using the 30s rediscretised fish trajectories. From these movement models, 50% and 95%

kernel utilisation distributions were calculated as the smallest area containing 50% and 95% of fish locations, respectively. Distance from shore was calculated as the Euclidean distance of each fish position from the nearest shoreline, using relocations between 10:00 and 14:00 each day, as this was when fish were most active, and so was representative of habitat use during fish's routine behaviours. Shoreline position was determined by following the shoreline in the same boat fishing was conducted from, and taking a GPS position and depth estimate every ~5s using a vessel mounted echosounder (Humminbird helix 9, Johnson Outdoors ltd, USA) Utilisation distributions were generated using dynamic Brownian bridge movement models (DBBMMs), using a window size of 61 relocations, or approximately 30 minutes of fish tracking. This window was chosen as it is narrow enough to permit the fastest possible computation time, while also wide enough so as to not erroneously identify behavioural change points caused by outlying movement speeds or travelling distances, which are difficult to distinguish from telemetry error (Kranstauber *et al.* 2012). 30 minutes is also well within the time window at which fish relocations were autocorrelated with one another (approximately 24 hours), meaning that the possibility of smoothing over several successive behavioural changes is very unlikely

4.2.4.3 *Trajectory Straightness*

As a measure of movement linearity, all SG-filtered, un-rediscretised fish trajectories were divided into 30 minute blocks, and maximum expected displacement (E_{max}) calculated for each block. E_{max} is a single value measure of straightness independent of scale, and so robust to differences in movement distance between fish. It is dimensionless, with values close to 0 being more sinuous, while larger values are straighter (McLean and Skowron Volponi 2018; Raoult *et al.* 2018). Only trajectory blocks between 10:00 and 14:00 each day were used in the calculation of E_{max}.

4.2.4.4 *Statistical Analysis*

All statistical analyses were performed in R.3.6.1 (R development Core Team). In all cases, metabolic traits (SMR, AS, and MMR) were adjusted for mass by calculating the residuals from the linear regression of each metabolic trait (SMR, AS and MMR) against log transformed mass, and adding calculated residuals to the predicted value of that metabolic trait at the mean mass of all fish. The inverse log of these values was then taken and used to remove the confounding effects of fish mass on metabolic traits (McLean et al. 2018). Individual boldness was log(+1) transformed, and individual E_{max} log transformed to meet assumptions of normality for parametric linear model and ANOVA analyses. The relationship between metabolic traits and behavioural traits derived from both behavioural assay and acoustic telemetry was investigated using GLMs via the function lm (stats package, base R). In each case, adjusted SMR, AS and MMR were used as explanatory variables for each of assay-derived boldness, and telemetry derived 50 and 95% utilisation distributions, trajectory straightness, mean daily movement speed, mean daily distance travelled, and mean daily distance from shore as responses. Models of best fit were determined using maximum likelihood estimation. Non-significant terms were dropped sequentially, starting with those with the smallest t-values, but were retained if their removal resulted in higher AIC values ($\Delta AIC > 2$ (Arnold 2010). Significance testing was used to indicate the strength of observed patterns between physiological traits and metrics of behaviour and space use. To investigate differences in traits between rod and reel susceptible and gill net susceptible perch, ANOVAs were performed on each measured trait using ‘capture method’ as a predictor variable. All behavioural traits derived from acoustic telemetry and laboratory assay were tested for repeatability as described by Stoffel et al., (2017) using variances in each trait calculated via LMEs including fish ID as a random effect. For traits derived from acoustic telemetry, repeatabilities were calculated using mean values calculated daily. Visual inspection of semi variograms fitted to each fish’s relocation data individually indicated that after 24 hours, no autocorrelation structure remains within any fish trajectories, and so assumptions of independent measures required for estimation of repeatabilities are met.

4.3 RESULTS

4.3.1 Captured Fish

A total of 25 fish were caught using a combination of rod and reel and gill nets, with 12 caught on rod and reel, and 13 in gill nets. All fish had their metabolic phenotypes quantified using respirometry, and their boldness determined using an open field behavioural assay. Once implanted with V9 acoustic transmitters, all fish were released in the centre of the Dubh Lochan. Of these 25 fish, 24 survived for the duration of this tracking study, while one fish caught by gill-net apparently died shortly after release, as no movement from the release point was observed. As a result, no analyses of fish behaviour in the wild includes data collected from this individual. No significant differences in fish mass or length was found between fish caught in the different gears.

4.3.2 Patterns of Habitat Use and Behaviour

There was marked inter-individual variation in patterns of space use and behaviour among the wild perch captured via either method. 95% utilisation distributions, representing the total area of habitat regularly exploited by fish (*i.e.* its 'home range'), varied among individuals by several orders of magnitude, with the largest utilisation distribution expressed by a 26.4cm individual, encompassing an area of 2.4 Ha (approximately 24% of the total area of the lake). In contrast, the smallest 95% utilisation distribution was exhibited by a 17.5 cm individual, whose 95% UD extended to just 0.0027 Ha. This high degree of variation is also found within 50% UDs, which represent individual fish's core region of intensive habitat use. The fish exhibiting the most restricted 95% UD also exhibited the smallest 50% UD, encompassing just 0.0007 Ha, while the largest 50% UD was exhibited by a 26.9cm individual, and covered an area of 0.35 Ha. Both daily 95% and 50% UDs showed significant within individual repeatability during the study period, (R=0.253, 95%CI: 0.118, 0.383, p=<0.001; R=0.306, 95%CI: 0.145,0.453, p=<0.001, respectively, Table 4.2).

Fish	Proportion of HPE >2	Mean dt (filtered)	Total Detections (filtered)	First Detection	Last Detection
43231	29.31	25.2	287292	06/09/2016	29/11/2016
43232	13.49	11	265288	06/09/2016	15/10/2016
43233	2.07	4.5	1585902	06/09/2016	29/11/2016
43235	4.29	5	1383391	06/09/2016	29/11/2016
43237	6.48	4.6	1417759	06/09/2016	29/11/2016
43238	68.53	26	206727	06/09/2016	29/11/2016
43239	8.03	5	1356206	06/09/2016	29/11/2016
43240	77.70	23.9	155451	06/09/2016	29/11/2016
43241	8.16	5.07	1378513	06/09/2016	29/11/2016
43242	14.35	6.04	1145723	06/09/2016	29/11/2016
43243	14.38	34.23	213284	06/09/2016	29/11/2016
43244	52.04	15.1	404506	06/09/2016	26/11/2016
43245	7.13	5.3	1252584	06/09/2016	29/11/2016
43246	14.21	6.7	872976	06/09/2016	29/11/2016
43247	4.47	5.2	1353826	06/09/2016	29/11/2016
43248	32.19	11.3	587026	06/09/2016	29/11/2016
43249	61.73	7.9	524584	06/09/2016	29/11/2016
43250	5.53	4.96	1419976	06/09/2016	29/11/2016
43251	1.98	4.5	1596455	06/09/2016	29/11/2016
43252	1.22	4.42	1638255	06/09/2016	29/11/2016
43253	30.15	9.8	671140	06/09/2016	29/11/2016
43254	21.80	5.9	1004234	06/09/2016	29/11/2016
43255	5.40	4.9	1455208	06/09/2016	29/11/2016
43256	45.62	24.84	205085	06/09/2016	29/11/2016
43257	24.60	4.59	849567	06/09/2016	29/11/2016

Table 4.1: Data profiles of perch relocations during the study period. Number of relocations and mean time between positions (dt) are calculated after filtering based on data quality

Trait	*R*	*SE*	*CI*	*p*	*Time Frame*
50% UD	0.306	0.078	0.145,0.453	<0.001	Daily
95% UD	0.253	0.069	0.118, 0.383	<0.001	Daily
Daily Distance Travelled	0.583	0.076	0.141, 0.701	<0.001	Daily
Mean Daily Speed	0.255	0.056	0.148, 0.357	<0.001	Daily
E_{max}	0.221	0.054	0.118, 0.324	<0.001	Daily
Mean Daily Distance from Shore	0.629	0.069	0.47,0.737	<0.001	Daily
Assay Boldness Score	0.333	0.163	0, 0.62	0.034	Per Trial

Table 4.2: Repeatabilities of individual behavioural assessed using LMEs. Repeatability was calculated for each individual trait using the trait of interest as a response variable and fish ID as a random effect

Trait	Term	Estimate	SE	df	*t*	*P*
95% UD	Intercept	3.174	0.128	23	24.73	<0.0001
50% UD	Intercept	2.29	0.12	23	18.99	<0.0001
Distance from Shore	Intercept	27.695	3.001	23	9.227	<0.0001
Mean Daily Distance Travelled	Intercept	1650.1	233.4	23	7.07	<0.0001
Mean Daily Speed	Intercept	0.072	0.0154	23	4.689	0.0001
Mean E_{max}	Intercept	0.973	0.241	23	4.025	0.0006
	adj.SMR	-0.145	0.087	23	-1.669	0.11
Time Spent moving in Assay	Intercept	-2.382	1.558	23	-1.529	0.141
	adj.SMR	1.838	0.531	23	3.458	0.002
	adj.AS	-0.54	0.278	23	-1.945	0.064

Table 4.3: Results of linear models examining the effect of metabolic phenotype on behavioural traits measured using acoustic telemetry and during behavioural assays

Trait	df	F	p
adj.SMR	24	0.004	0.953
adj.AS	24	7.978	0.01*
adj.MMR	24	5.48	0.028*
log 50% UD	24	3.233	0.09
log 95% UD	24	4.483	0.046*
log E_{max}	24	0.913	0.35
Mean Daily Distance from Shore	24	1.339	0.26
Assay Activity	24	7.083	0.014*
Mean Daily Distance Travelled	24	0.111	0.742
Length	24	0.605	0.445
Mass	24	1.337	0.259
Mean Travelling Speed	24	3.233	0.086

Table 4.4: Results of ANOVAs comparing the traits of angled and gill netted perch to one another

Daily distance travelled showed similar degrees of variation and strong repeatability (R=0.583, CI: 0.141, 0.701, p<0.001, Table 4.2). Patterns of distance from shore showed contrasting patterns between individuals, with some fish moving further offshore during more 'active' periods (*i.e.* from 10:00-14:00), before returning in shore, and vice versa. This trait also showed the highest repeatability of all measured traits (R=0.629, CI:0.47,0.737, p<0.001, table 4.2). Both mean daily active speeds and E_{max} values showed high degrees of within and between individual variation. Mean daily active speeds ranged from 0.011 m s^{-1} (SD ±0.0005) for the slowest fish, to 2.218 m s^{-1} (0.587). E_{max} values produced from discretised fish trajectories also showed high degrees of within and between individual variation, with the most sinuous movement generating an E_{max} value of 0.295 (SD ±0.504) exhibited by a 16.0 cm individual, while the most linear movement was displayed by a 19.8cm fish with a mean E_{max} value of 0.792 (SD ± 0.518). Repeatabilities for mean daily active speed and trajectory sinuosity were among the lowest for all telemetered traits, but were still significant, with repeatability values of R=0.255 p<0.001 and R=0.211, p=0.001, respectively (Table 4.2).

4.3.3 Do metabolic traits predict behavioural traits measured in the lab, or field?

There was no relationship between metabolic traits and any metric of space use or behaviour derived from acoustic telemetry (Table 4.3). In almost every case the null model was the most parsimonious, with only the GLM investigating relationships between E_{max} and physiological traits retaining a physiological term, adj.SMR, and even then, the relationship was non-significant. However, a significant positive relationship between adj.SMR and individual boldness in the laboratory assay was found (p=0.002).

4.3.4 Do the phenotypic traits of rod and reel and gill net vulnerable fish differ from one another?

Significant differences in mean trait values were found between fish caught in each gear type in terms of physiological, behavioural, and space use traits. Gill-netted fish were found to have lower aerobic scopes than angled fish (F(1,23)=7.98, p=0.01, figure 4.2), a pattern driven by their lower adj.MMRs (F(1,23) = 5.48, p=0.03, figure 4.2), and were also found to exhibit higher 95% UDs, (F(1,22)=4.48, p = 0.046), than their angled conspecifics (Figure 4.4). The lowest 95% UD was exhibited by a rod and reel caught fish, and 7 of 10 lowest 95% UD values were also found in fish caught by the same gear. A similar pattern was seen in the lab-derived boldness scores. Time spent moving in the behavioural assay was more variable among the angled caught perch, with several fish remaining immobile for the duration of the assay, while gill-netted fish were more active (F(1,23)=7.083, p = 0.014, figure 4,3). While gill netted fish were found to exhibit lower AS, higher 95% UDs, and be more active in behavioural assays, adj.AS showed no relationship with either of these traits, and no relationship was found between 95% UD and time spent active during the behavioural assay. Both mean daily active swim speed, and mean E_{max} of fish were slightly higher in gillnetted fish than in angled fish, although these differences were not statistically significant (p=0.182 and p=0.35). No other differences in physiological or behavioural traits were found between rod and reel caught and gillnetted fish (table 4.3).

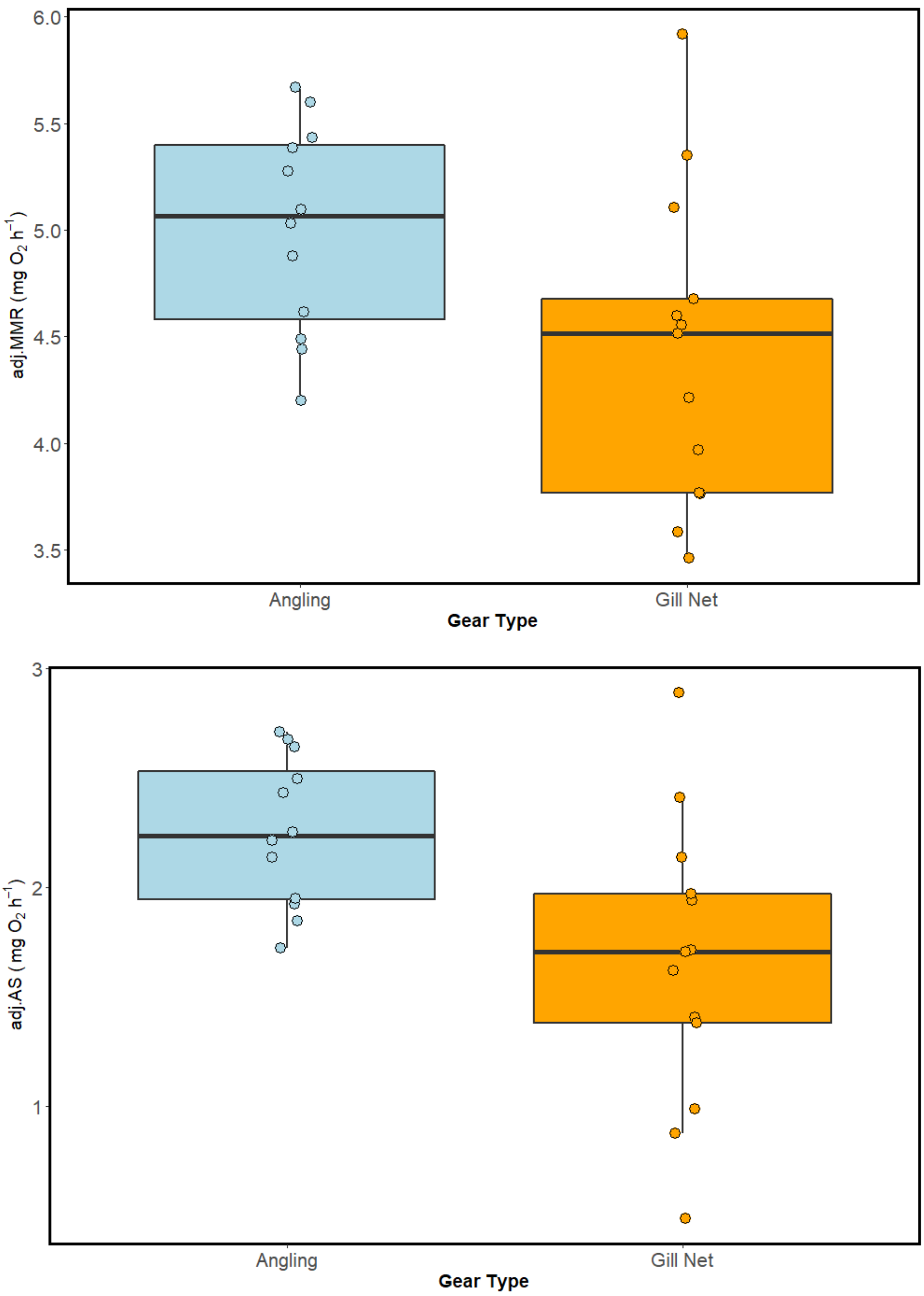

Figure 4.2: Comparison of adjusted AS and MMRs of perch caught via angling and gill netting. Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of datapoints between each hinge

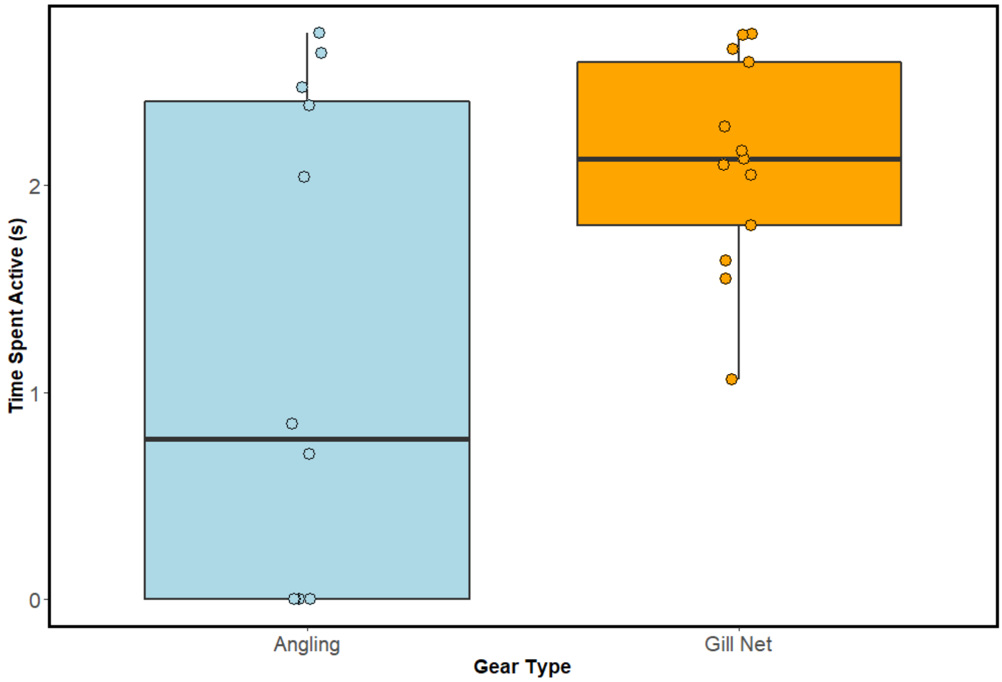

Figure 4.3: Comparison of time spent active during lab-based behavioural assays between angled and gill-netted fish. Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of datapoints between each hinge

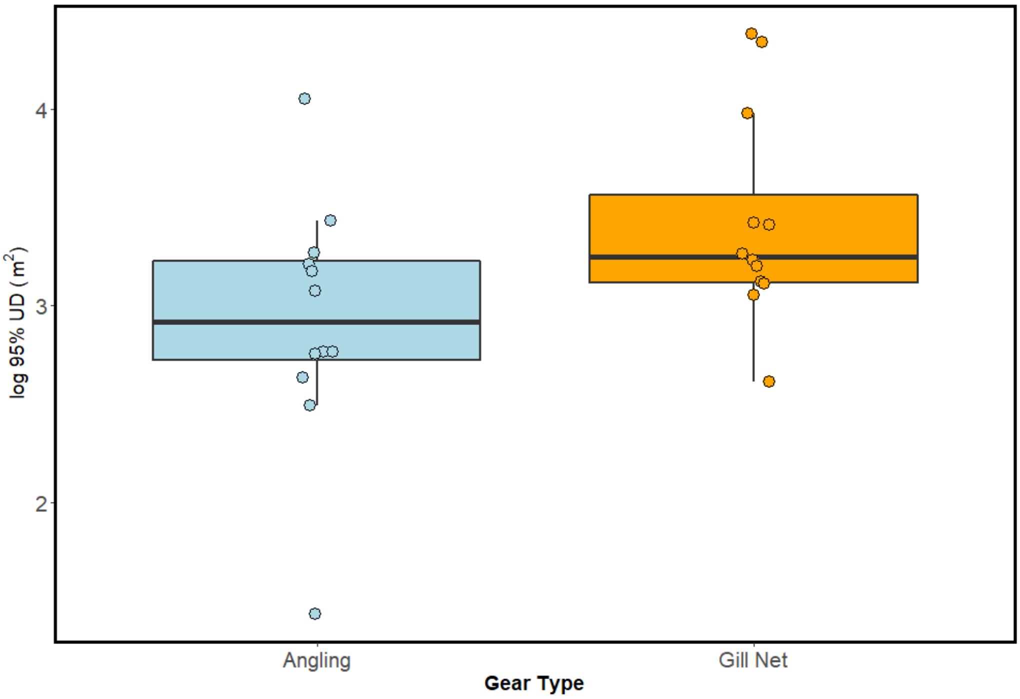

Figure 4.4: Comparison of 95% utilisation distributions between angled and gill-netted fish. Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of datapoints between each hinge

4.4 DISCUSSION

Using a combination of lab-based respirometry and behavioural assays alongside acoustic telemetry to determine patterns of habitat use and behaviour of fish in the wild, we investigated the capacity of angling and gillnetting to select on individual behavioural and metabolic traits. We found that perch caught in gill nets routinely utilised a greater proportion of the lake, exhibited lower AS, and were more active in behavioural assays than their angled conspecifics. However, no correlations between traits related to metabolism, and telemetered traits related to space use and behaviour in the wild was found (Table 4.3). This suggests that if these between gear differences in trait values are a result of gear selectivity, that selection was operating on these traits independently. No component of metabolic phenotype was correlated with any behavioural or movement metric of fish in the wild, as has been reported in previous studies (Baktoft *et al.* 2016; Laskowski *et al.* 2016), although a positive relationship between perch SMR and time spent moving during an open field behavioural assay was observed (table 4.3). This is the first study demonstrating that angled and gill net susceptible fish can differ in traits related to metabolism, behaviour, and patterns of space use, demonstrating that even within active or passive fishing gear categories, different gear types can exert selective pressure on distinct groups of individual traits, and that these traits may be under selection in passive fisheries.

Gill netted perch exhibited significantly larger 95% UDs than their angled conspecifics (Figure 4.4), and also had larger 50% UDs, higher active swim speeds, and greater daily mean distances from shore, however, only their 95% UDs were statistically significant. Cumulatively, these trends suggest that gill nets selectively remove active individuals with broad patterns of habitat use, likely through a mechanism of increased encounter rates, while angling does not. These different patterns of selection are likely driven by the contrasting mechanisms of capture employed by each gear, with gill nets relying on fish becoming entangled incidentally during routine active behaviours, whereas angling lures must be detected and consciously attacked by fish to capture them. While encounter rates may be insufficient to lead to capture on rod and reel (Klefoth *et al.* 2017b; Monk and

Arlinghaus 2017a; Monk and Arlinghaus 2017b), it may be sufficient to explain capture vulnerability in gill nets (Biro and Post 2008a). Despite correlations between 95% and 50% UDs, and that 95% UDs had comparatively lower repeatability, only differences in 95% UDs were statistically significant between angled and gillnetted fish. This is likely because 50% UDs represent core habitat use (Crook 2004; Kirby *et al.* 2017), and so represent habitat use of the fish when it is not engaged in active behaviours. As such, the fish is unlikely to have been engaged in 'catchable' behaviours when occupying the area represented by this core home range, and so not be relevant in determining capture vulnerability in either gear. Furthermore, the area encompassed by 50% UDs were typically located closer to the shoreline, and extended into macrophyte dominated habitat, where gill nets could not be deployed, and so is a trait unlikely to be relevant in determining gill-net capture vulnerability.

This study found that angled and gillnetted fish exhibited different metabolic traits in terms of MMR and, consequently, AS although no differences in SMRs were found between the two groups of fish. Individual metabolic rate has been implicated in determining capture vulnerability by passive gears as it underlies baseline levels of energetic demand and potentially feeding motivation and risk-prone behaviours (Hollins *et al.* 2018; Killen *et al.* 2011; Killen *et al.* 2012b; Metcalfe *et al.* 2016b). Fish with a high SMR may therefore be expected to be more vulnerable to capture by gears mimicking prey (Hollins *et al.* 2018; Lennox *et al.* 2017b). Results of the current study are in contrast to lower SMRs in largemouth bass (*Micropterus salmoides)* from low-angling vulnerability breeding lines (Redpath *et al.* 2010b), and lower baseline energetic demands of exploited wild bass populations as compared to non-fished conspecifics (Hessenauer *et al.* 2015). However, our findings agree with more empirical investigations investigating direct links between SMR and angling vulnerability in bluegill sunfish (*Lepomis macrochirus*) (Louison *et al.* 2018b) and European perch(Väätäinen *et al.* 2018), which found no relationships between the two traits. AS and MMRs were lower in gill netted fish as compared to angled fish, in contrast to the findings of Biro and Post (2008).Considering that gill netted fish also exhibited significantly greater 95% UDs this is contrary to what was expected. As metabolic traits were not correlated with any movement metric telemetered from free swimming fish, the mechanism driving this selection remains unclear. Perch can show intraspecific variation in diet (Nakayama *et al.* 2017), which has been shown experimentally to influence SMRs in brown trout (*Salmo trutta*) (Auer *et al.* 2016). As intraspecific variation in prey selection could explain why certain perch were more likely to be caught via angling, indirect selection on metabolic traits as a result of selection on diet is possible, but seems unlikely to be the mechanism here. Auer *et al.* (2016) found that dietary differences changed only values of SMR, while MMRs were unchanged, and this study found no differences in the SMRs of angled and gillnetted fish. An alternative mechanism may be that fish with high AS are more likely to attack a fishing lure as they can accommodate greater metabolic costs incurred through feeding (McLean *et al.* 2018), and so fish exhibiting lower AS may be less likely to respond if they had fed recently.

We found that individual SMR showed a significant positive relationship with activity during an open-field behavioural assay in tested perch, in contrast to the findings of previous studies (Väätäinen *et al.* 2018).However, angled perch showed significantly lower time spent active during the behavioural assay compared to their gill-netted counterparts While this is the opposite pattern than what was expected, angling has been demonstrated to selectively remove timid individuals from fish populations in previous studies (Wilson *et al.* 2011). Any fishing gear has the potential to select timid individuals if it is deployed near available shelter, or a habitat more likely to be used less-risk prone individuals. As both rod and reel and gill nets were deployed in identical habitats (*i.e.,* the interface between the macrophyte boundary and open water) selection on fish habitat use via gear overlap in this way would not have been possible. As such, the differences in boldness between gill netted and angled fish in this study are not attributable to the different gears targeting distinct habitats. One possibility is that the more timid fish were only available to capture via angling, as they would only leave the comparative safety of the macrophyte boundary in response to a potential food item, for example the lures used in angling in this study. As it is not possible to deploy gill nets within the macrophyte boundary itself, and the nets cannot lure fish out of the shelter by mimicking a prey item, fish which were less willing to cross the macrophyte boundary would be underrepresented in the catch of the gill nets (figure 4.3).

No differences in mean E_{max} and active swim speeds were found between angled and gillnetted fish (table 4.3). E_{max} values telemetered from angled fish encompassed a broader range of values, but were generally lower than those telemetered from gill netted fish, while the active swim speeds of gill netted fish were generally higher than those of angled fish. This indicates that gill netted fish spent more time engaged in behaviours involving tortuous movement, such as exploration or foraging, when the did engage in linear, directed swimming, they travelled at greater speeds when they did. As more tortuous, active behaviours are often associated with fish being more catchable in general (Arlinghaus *et al.* 2017a; Conrad *et al.* 2011; Hollins *et al.* 2018), it is interesting that E_{max} values showed no significant differences between rod and reel and gill netted fish. This is likely attributable to the large standard variation around E_{max} values , decreasing repeatability, and thus limiting the potential for fisheries selection. Trajectory sinuosity and the behavioural states underlying it, also showed strong diurnal patterns, and are more strongly influenced by environmental parameters than areas of habitat utilisation (Baktoft *et al.* 2012; Nakayama *et al.* 2016). Selection on these behaviours may therefore be weakened by timing mis-matches between gear deployments and when fish are engaged in catchable behaviour, in addition to requiring the fishing gear be deployed within the utilised habitat of the fish.

While gill netted and angled fish exhibited significantly different metabolic, behavioural, and space use traits, no correlations among these traits were detected. The controlled conditions that behaviour was assayed under in the laboratory obviously do not replicate those experienced by fish in the Dubh Lochan, however several studies have found that fish performance during lab-based behavioural assays can predict aspects of observed behaviour in the field (Klaminder *et al.* 2016; Laskowski *et al.* 2016; Závorka *et al.* 2015; Závorka *et al.* 2016). It is unclear why this study did not find this to be the case. While expression of behavioural traits by fish is strongly influenced by environmental conditions (Killen *et al.* 2013; Nakayama *et al.* 2016; Stehfest *et al.* 2015), and so while it is possible that behaviour of fish during this assay is not representative of that same fish's behaviour in the wild, it seems likely that performance of perch during this behavioural assay is representative of some behaviour in the field not adequately described by any one of the metrics quantified through telemetry. Further analysis using these metrics to infer underlying behavioural states (e.g. Hidden Markov models, or multi-state correlated random walk models) may address this shortcoming in future (Baktoft *et al.* 2016; Nakayama *et al.* 2017).

Metabolic traits have yet to be shown to predict behaviour or performance of fish in the wild (Baktoft *et al.* 2016; Laskowski *et al.* 2016), including in this study. Considering the number of studies reporting correlations between metabolic and behavioural traits in fish (see Metcalfe *et al.* 2016 for review), the fact that no relationship between metabolic traits and behaviour in the field was found by this study is surprising. Although SMR has shows evidence of repeatability (Norin and Malte 2011a), and is therefore likely representative of inherent traits of the fishthe degree to which this repeatability is maintained in the wild fish is poorly understood. The metabolic traits measured in this study represent a snapshot of a highly dynamic process, and so it is perhaps not surprising that relationships between physiological traits taken at a single temperature under controlled conditions do not predict fish performance and behaviour in field, where conditions are that much more dynamic. While not possible in this study, quantifying reaction norms of fish's physiological traits across a range of environmental conditions may more effectively predict fish patterns of habitat use and behaviour in the wild.

This study highlights the capacity for different fishing gears to select on distinct groups of physiological and behavioural traits, despite both gill nets and angling both being passive fishing methods. In this study, selection on 95% UDs by gill nets appears to be driven by encounter rates between fish and fishing gear, while angling may select against timid fish by luring fish unavailable to gill nets out of the shelter provided by macrophytes. Differences in metabolic traits were also found in angled and gillnetted fish, potentially driven through an indirect mechanism of feeding motivation, although selection on these traits was independent of selection on traits related to space use and behaviour. Spatial traits determined by habitat selection (e.g. 50 and 95% UD, distance from shore and distance travelled) showed greater repeatability than those determined by behavioural state, and so may be more likely candidate traits for fisheries selection to act upon. this study successfully demonstrates that fishing gears relying on contrasting mechanisms of capture can exert distinct selectivity regimes on wild fish populations, with respect to traits related to physiology, behaviour, and patterns of habitat use and selection. Furthermore, the large degree of repeatable, intraspecific variation present in patterns of habitat use in these wild fish highlights these traits as likely candidates determining capture vulnerability in different gears, and warrant further study.

5. DOES CAPTURE METHOD PREDICT ECOLOGICAL NICHE OF SKAGERRAK ATLANTIC COD?

5.1 INTRODUCTION

The impacts of fisheries induced evolution (FIE) and fisheries driven phenotypic change on fish stocks is typically considered in terms of alterations to growth, fecundity, and other life history and developmental traits (Enberg *et al.* 2009a; Enberg *et al.* 2012; Heino *et al.* 2015; Richard 2007). Life history traits are comparatively simple to quantify, hold direct relevance for assessing the capacity of exploited fish stocks to recover from harvest (Enberg *et al.* 2009b; Kuparinen and Hutchings 2012; Rijnsdorp *et al.* 2010; Walsh *et al.* 2006), and also provide useful indicators when assessing the current health of a given fish stock (Heino *et al.* 2013a; Olsen *et al.* 2004). More recently, the capacity for fisheries selection to elicit phenotypic change in exploited fish stocks has begun to be considered in terms of both behavioural (Arlinghaus *et al.* 2017a; Claireaux *et al.* 2018; Diaz Pauli and Sih 2017a; Klefoth *et al.* 2017b) and physiological traits (Hollins *et al.* 2018; Killen *et al.* 2015c; Koeck *et al.* 2018). Intraspecific variation in both behavioural and physiological traits is widespread in fish (Burton *et al.* 2011a; Metcalfe *et al.* 2016b) and can determine the likelihood of a fish encountering and interacting with a fishing gear (Biro and Post 2008a; Monk and Arlinghaus 2017a; Monk and Arlinghaus 2017b; Redpath *et al.* 2010b), or the capacity of fish to escape from fishing gear once it has been encountered (Diaz Pauli *et al.* 2015a; Hollins *et al.* 2019; Killen *et al.* 2015b). Fisheries selection therefore has the potential to induce behavioural and physiological phenotypic change in exploited fish stocks beyond those associated with changes in life history traits. Altering the phenotypic composition of fish populations in terms of their behavioural and physiological traits has the potential to drive major shifts in the ecological niche occupied by exploited fish species, with consequences for food-web dynamics (Claireaux *et al.* 2018), resilience to environmental change (Farrell 2016), and the sustainability of existing fisheries (Heino *et al.* 2013a; Laugen *et al.* 2014b).

Accounting for the evolutionary impacts of fishing is now recognised as an important component of sustainable ecosystem-based fisheries management (Garcia and Cochrane 2005; Laugen *et al.* 2014b), however this requires thorough knowledge on the capacity of different fishing gears to select on individual fish traits, and how this may alter the ecological niche of targeted species. Fishing gears consist of both active and passive types, and are distinguished by their mechanism of capture (Hollins *et al.* 2018; Sampson 2014), with active gears pursuing or encircling target fish with nets (e.g. trawls, seine netting, etc), while passive gears are static, and rely on fish to approach and interact with the gear to be caught (e.g. traps, baited hooks, etc). These contrasting mechanisms of capture mean that traits determining capture vulnerability in one gear may not be relevant in another (Diaz Pauli *et al.* 2015), resulting in differences in the trait changes which may be expected as a result of fisheries selection. Experimental approaches have shown that individual fish's swim performance can influence capture vulnerability in a trawls (Hollins *et al.* 2019; Killen *et al.* 2015b), with fish that exhibit greater swim performance having a lower risk of capture. In contrast, traits related to space use and risk perception may be more likely to be under selection in fisheries employing passive gears (Biro and Post 2008a; Monk and Arlinghaus 2017a; Monk and Arlinghaus 2017b), with fish exhibiting large home ranges, or that are more prone to engage in riskier behaviours more likely to be caught. It may therefore be expected that a fish population which has been subjected to trawling will be disproportionately comprised of high-performance swimmers, compared to a population which has been fished using passive gears, such as baited hooks, which may be comprised of largely more 'timid' individuals, with more restricted home ranges (Arlinghaus *et al.* 2017a; Monk and Arlinghaus 2017a). However, despite a growing body of literature investigating relationships between individual physiological and behavioural traits and capture vulnerability in different gear types, almost nothing is known about whether this selectivity alters the ecological niche collectively occupied by target fish stocks (Ljungberg *et al.* 2019).

The Atlantic cod (*Gadus morhua*) is a commercially important fish species, whose stocks have undergone phenotypic changes in response to commercial fishing pressure throughout their range (Olsen *et al.* 2004; Olsen *et al.* 2012; Swain *et al.* 2007). Atlantic cod also shows intraspecific variation in a number of traits with potential relevance for determining capture vulnerability, including vertical habitat use (Olsen *et al.* 2012) and swim performance (Reidy *et al.* 2000).

Intraspecific variation in diet has also been found in Atlantic cod (Sherwood and Grabowski 2010), with certain cod consuming more fish, while others relied more on crustacean prey. Hooks and traps often make use of either crustacean or fish-based bait, potentially selecting against individuals whose diet more closely represents the bait used in each case. Traits related to habitat use, swim performance and diet preference may each have the capacity to influence capture vulnerability in active, passive, or both categories of fishing gears in individual cod, and drive differences in ecological traits among individuals. For example, intraspecific variation in swim performance may determine both the accessibility of faster moving fish prey items to individual cod (Kaufman *et al.* 2011; Langerhans 2009), and influence their capacity to escape a pursuing trawl (Hollins *et al.* 2019; Killen *et al.* 2015b; Kim and Wardle 2003).

Previous studies on fishing gear selection have recorded differences in the traits of Atlantic cod susceptible to capture in different gear types, particularly with respect to body condition (Huse *et al.* 2000; Ovegård *et al.* 2012). While any selection on fish condition is likely partially caused by mechanical effects of the mesh sizes of gill nets or trawls more effectively retaining fish in better condition (Kuparinen *et al.* 2009), large cod can be underrepresented in trawl catches, which has been attributed to their greater swim performance (Huse *et al.* 2000; Kuparinen *et al.* 2009), while poor condition cod are generally over-represented in the catch of baited gears, and is thought to be driven by differences in feeding motivation (Ljungberg *et al.* 2019; Ovegård *et al.* 2012). Despite these differences in traits between gill net, trap, longline and trawl vulnerable cod, the degree to which selection on these traits may also drive selection on the ecological niche of cod has only been assessed in one study to date (Ljungberg *et al.* 2019). Ljungberg e*t al.* (2019) compared the condition, stomach contents, and stable isotope derived-ecological niche (Jackson *et al.* 2011; Layman *et al.* 2012) of trap and gill net caught Atlantic cod, and found that while differences in condition factor between gill netted and trapped cod throughout the study sites, ecological niche of captured cod only varied between gear types at one gear deployment site. That differences in ecological niche were only found between gill nets and traps at specific sites (Ljungberg *et al.* 2019) suggests that the capacity of fisheries selection to alter the ecological niche of exploited fish species is limited, only arising where specific criteria are met. However, as both gill nets and traps are passive gears, differences in each gears’ mechanisms of capture are comparatively subtle, and so may have had more limited capacity to select on distinct groups of ecological traits. The degree to which fishing gears relying on more disparate mechanisms of capture (e.g. static passive gears vs mobile active gears) may select on cod exhibiting different ecological traits is currently unknown.

This study investigates the capacity of active and passive gears to select on contrasting ecological traits of Atlantic Cod in the Skagerrak strait in a real fisheries context. We targeted the same population of Atlantic cod using both a commercial trawl (active gear) and rod-and-reel based jigging (passive gears) off the coast of Hirtshals, Denmark, and then compared the ecological niche of trawled and jigged cod using stable isotope analysis. As both the trawl and jigging targeted the same underlying cod population, any differences in trait compositions between the catches of the two gears can be inferred to be driven by a mechanism of fisheries selection. Using this approach, we aimed to determine the degree to which different fishing gears can select on the ecological traits of wild Atlantic cod by i) directly comparing the stable isotope signatures of trawled and jigged cod and ii) determining the degree of ecological overlap between trawled and jigged cod using measures of isotopic derived niche space.

5.2 MATERIALS AND METHODS

5.2.1 Study site

All fishing was conducted during summer within a confined area of the Skagerrak off the coast of Hirtshals, Denmark at a depth of 60-80m (figure 5.1), between 16.5.2017-25.6.2017. Sea surface temperatures during this time ranged from 12.8°C-16°C, with a summer thermocline and halocline likely present at a depth of 10-40m and 10-22m, respectively (Jackson, 2004)(Richardson 1985). The Skagerrak is typically characterised by salinities typical of brackish waters, driven by outflow from the Baltic sea, however salinities of the study site are generally higher, and more typical of marine environments (Albretsen *et al.* 2011; Kristiansen and Aas 2015). The benthic environment of the study site is comprised of rocky reefs with attached macrophyte, characterised by overhangsand isolated gullies where Atlantic cod often aggregate. These reef areas are interspersed among larger areas of sandy sea floor, more accessible to trawls. During summer, cod typically inhabit depths 5-30m making use of progressively deeper, cooler waters as surface temperatures increase (Freitas *et al.* 2015), and exhibit diel vertical migration, inhabiting deeper waters during the day and moving up in the water column to shallower waters at night (Freitas *et al.* 2015; Olsen *et al.* 2012). Skagerrak cod are omnivorous, consuming a mixture of shrimp, crabs, and fish, but show seasonal changes in diet, with a greater proportion of brachyuran crabs consumed by cod during summer (Hop *et al.* 1992).

5.2.2 Fishing

Fishing was conducted within an approximately 20x20 km area, 15km off the coast of Hirtshals. Jigging was conducted on 16.5.2017 and 22.5.2017 from a 10m research vessel. All fishing was conducted during daylight hours (04:20 - 22:22) between approximately 06:00 and 14:00, using a Svenskepilken lure with multiple hooks attached with snoods using shrimp (*Pandalus borealis*) as bait. Jigging targeted the portion of the water column just above, but not directly on, the seafloor to prevent the entanglement of gear on the substrate. Trawling was opportunistic and conducted from a commercial fishing vessel on 25.06.17, using a single demersal trawl of ~8m total stretched length, with a mouth width of ~5m, fixed with rockhopper gear along the footrope. Trawls were towed at an average of 3 knots for approximately 2.5 hours with each deployment, with a total of 4 trawl deployments conducted throughout the day’s fishing. A total of 59 cod were collected from the trawl for sampling, and 49 from jigging. In order to control for differences in growth and life history stage between cod, and the potential confounding effects that would have on stable isotope signatures (Trueman *et al.* 2005), only cod between 30-50cm were used for sampling.

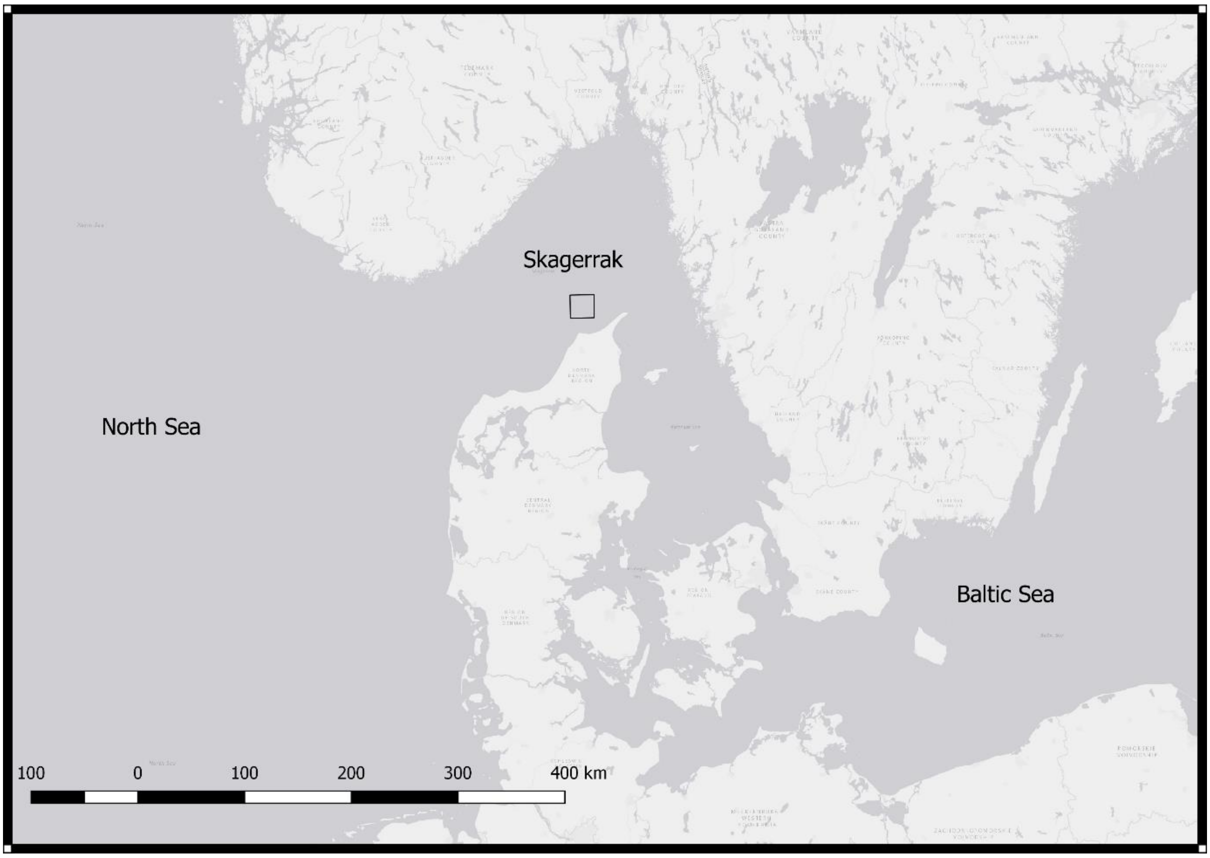

Figure 5.1 Location of the study site and fishing area. Trawls and jigs were both deployed within the area demarcated by the black box.

5.2.3 Sample Collection and Preparation

Fin clips from cod pectoral fins were the tissue type chosen for stable isotope analysis, as they permitted non-lethal sampling of caught cod, and provide a tissue turnover time comparable to that of white muscle, *i.e.* on the scale of months (Busst and Britton 2018; Hanisch *et al.* 2010; Jackson *et al.* 2011; Sanderson *et al.* 2009). The isotopic composition of fin clip tissue therefore provides an integrative indicator of the ecological traits exhibited by each sampled cod, incorporating components of spatial ecology and diet, over a scale of months. Stable isotope signatures of the cod in this study are therefore representative of broad scale ecological patterns, as opposed to switches in diet or habitat use occurring over smaller spatiotemporal scales (MacNeil *et al.* 2005). Fin clips were collected along the inner margin of the pectoral fin closest to the body of the fish and placed in labelled Eppendorf tubes before being dried for 48hr at 60°C. Fin clips were then homogenised in their Eppendorf tubes by grinding the dried tissue with a ceramic rod. Once fin clips were homogenised, the powdered homogenates were then weighed out to mean weight of 0.7mg, and transferred to 3x5mm tin capsules, which were then held in a well plate, ready for analysis.

5.2.4 Stable Isotope Analysis

Stable isotope analysis was conducted at the Life Sciences Mass Spectrometry Facility, East Kilbride, UK. The isotopic composition of carbon (C) and nitrogen (N) present in each fin slip samples were then quantified using continuous flow isotope ratio mass spectrometry (Thermo Fisher Delta Plus XP, interfaced with a Costech ECS 4010 elemental analyser). During sample runs, laboratory standards of alanine and gelatine were run in the mass spectrometer after every 7 fin-clip samples, and checked against international isotope standards (provided by the International Atomic Energy Agency and the National Institute of Standards and Technology), to correct for drift and linearity. Once the isotopic compositions of C and N in fin clips were quantified, ratios of heavy (^{13}C, ^{15}N) to light (^{12}C, ^{14}N) isotopes in each sample were then calculated. These values are expressed using δ notation as deviations from the ratio of heavy to light isotopes present in internationally agreed standards for each element in parts per thousand (‰), and calculated using the following equation:

$$\delta(‰) = \left(\frac{R_{Sample}}{R_{Standard}} - 1\right) * 1000 \quad (Eq. 1)$$

Δ values of tissues can therefore be either positive or negative with respect to each element, with positive and negative values indicating that the tissue is either enriched in the heavier or lighter isotope compared to the standard, respectively. Generally, the isotopic composition of carbon in cod fin clips will largely be determined by source of carbon at the base of each food web the cod is a part of (Trueman *et al.* 2012). Higher δ^{13}C values are to be expected from organisms in more benthic or littoral habitats, where a greater proportion of available C is provided from terrestrial sources, while pelagic and deep water habitats, where the majority of available C is derived from the photosynthesis of phytoplankton, will have lower δ^{13}C. Patterns of δ^{15}N are primarily driven by diet, becoming ~3.4‰ higher in animal tissues for each successive trophic level the animal occupies, although several deviations from this enrichment factor have been found (Hussey *et al.* 2014) . Determination of the specific trophic level occupied by an organism requires estimates of $\delta^{15}N$ at the base of the food web it occupies, which was not done here. Rather, in this study, isotopic signatures of cod fin clips are used to evaluate whether jigged and trawled cod exhibit distinct ecological traits from one another, as opposed to assigning specific ecological traits to either group.

5.2.5 Statistical Analyses

All statistical analyses were performed in R.3.6.1 (R development Core Team). Comparisons of $\delta^{13}C$ and $\delta^{15}N$ values of jigged and trawled cod were made using general linear models via the function lm (stats package, Base R), using fish length and capture method as continuous and categorical predictor variables, respectively. As both trophic level and space use traits of fish can show strong relationships with fish length, each with the capacity to influence both $\delta^{15}N$ and $\delta^{13}C$ values of cod tissues, (Freitas *et al.* 2015; Jennings *et al.* 2001; Romanuk *et al.* 2011), individual fish length was included as a covariate in GLMs for both isotopes. Models of best fit were determined using maximum likelihood estimation. Non-significant terms were dropped sequentially, starting with those with the smallest t-values, but were retained if their removal resulted in higher AIC values (ΔAIC > 2 (Arnold 2010). Significance testing was used to indicate the strength of observed patterns between $\delta^{15}N$ and $\delta^{13}C$ and capture method and fish length. Comparisons of total occupied niche space between jigged and trawled fish were made using standard Bayesian ellipses in the R package SIBER (Jackson *et al.* 2011) . Standard ellipse area (SEA) is calculated from the bivariate isotopic space constructed by plotting values of $\delta^{15}N$ and $\delta^{13}C$ against one another, with the resulting 2-dimensional output analogous to an estimate of mean niche width and position alongside a 95% standard deviation. Bayesian standard ellipse areas (SEA_B) are robust to differences in sample size, compared to alternative SEA methods, such as convex hulls.

5.3 RESULTS

5.3.1 Are there differences in the stable isotope signatures of tissues between jig and trawl-vulnerable Atlantic cod?

Cod collected via trawling and jigging showed no significant differences in length (F(1,105)=0.745, p=0.39), between the two gear types, but between gear differences in δ^{15}N were detected. Δ^{15}N values showed a significant relationship with fish length (p=0.011, table 5.1), but this differed between gear types, highlighted by a significant interaction between gear type and length present in the glm (p=0.016, table 5.1). Δ^{15}N values of trawled cod were higher (p=0.006) and encompassed a narrower range of values (figure 5.2) than in jigged cod. In contrast, δ ^{13}C values were slightly higher and showed greater variation in trawled fish than the values of jigged fish (figure 5.2), although no relationships were found between δ^{13}C and either fish length, or capture method.

5.3.2 Do the ecological niches of jigged and trawled Atlantic cod overlap?

The SEA$_B$ of trawled cod was larger than that of jigged cod (99.925% of 10,000 iterations), but also showed evidence of overlap in niche space. 36.7% of the total niche occupied by the SEA$_B$ of trawled and jigged cod was identical, indicating that the ecological niche of each group was not totally distinct (figure 5.3). However, as the total occupied niche space of jigged cod was comparatively small, 75.3% of the jigged SEA$_B$ is encompassed by the niche area of trawled cod.

Isotope	*Term*	*Estimate*	*SE*	*df*	*t*	*p*
δ15N	Intercept	11.347	1.92	103	5.909	<0.001
	Fish Length	0.011	0.005	103	2.56	0.012
	Gear Type	5.666	2.017	103	2.809	0.006
	Fish Length*Gear Type	-0.012	0.0048	103	-2.44	0.016
δ13C	Intercept	-18.206	0.049	103	-374.1	<0.001

Table 5.1 Results from GLMs comparing the δ13C and δ15N values of trawled and jigged cod.

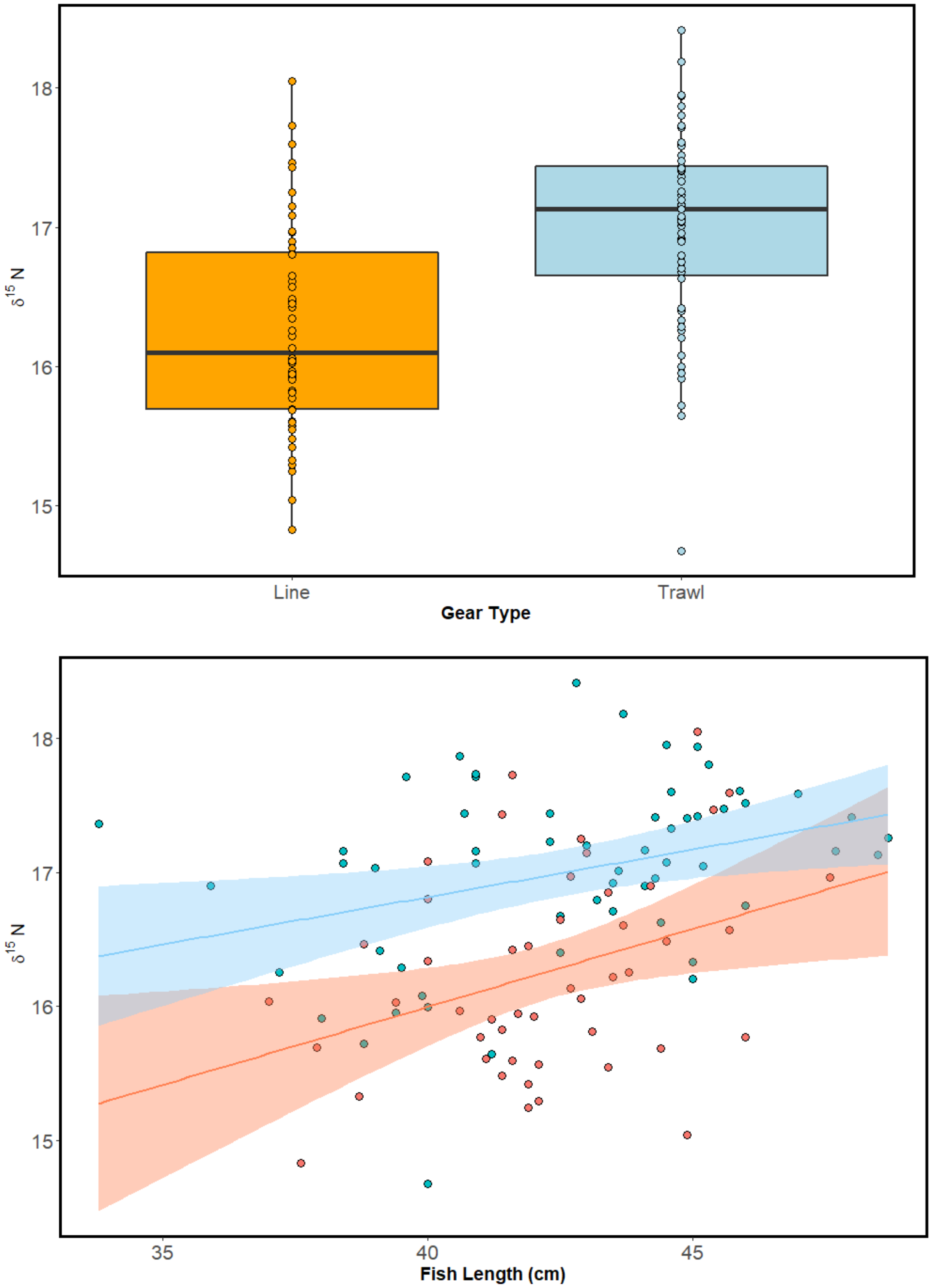

Figure 5.2: Differences in δ^{15}N between jigged and trawled Atlantic cod, line caught are orange, trawled are blue. Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of datapoints between each hinge. Trendlines are linear regressions between δ^{15}N values and fish length for each gear type. Shaded areas around trendlines indicate 95% confidence intervals

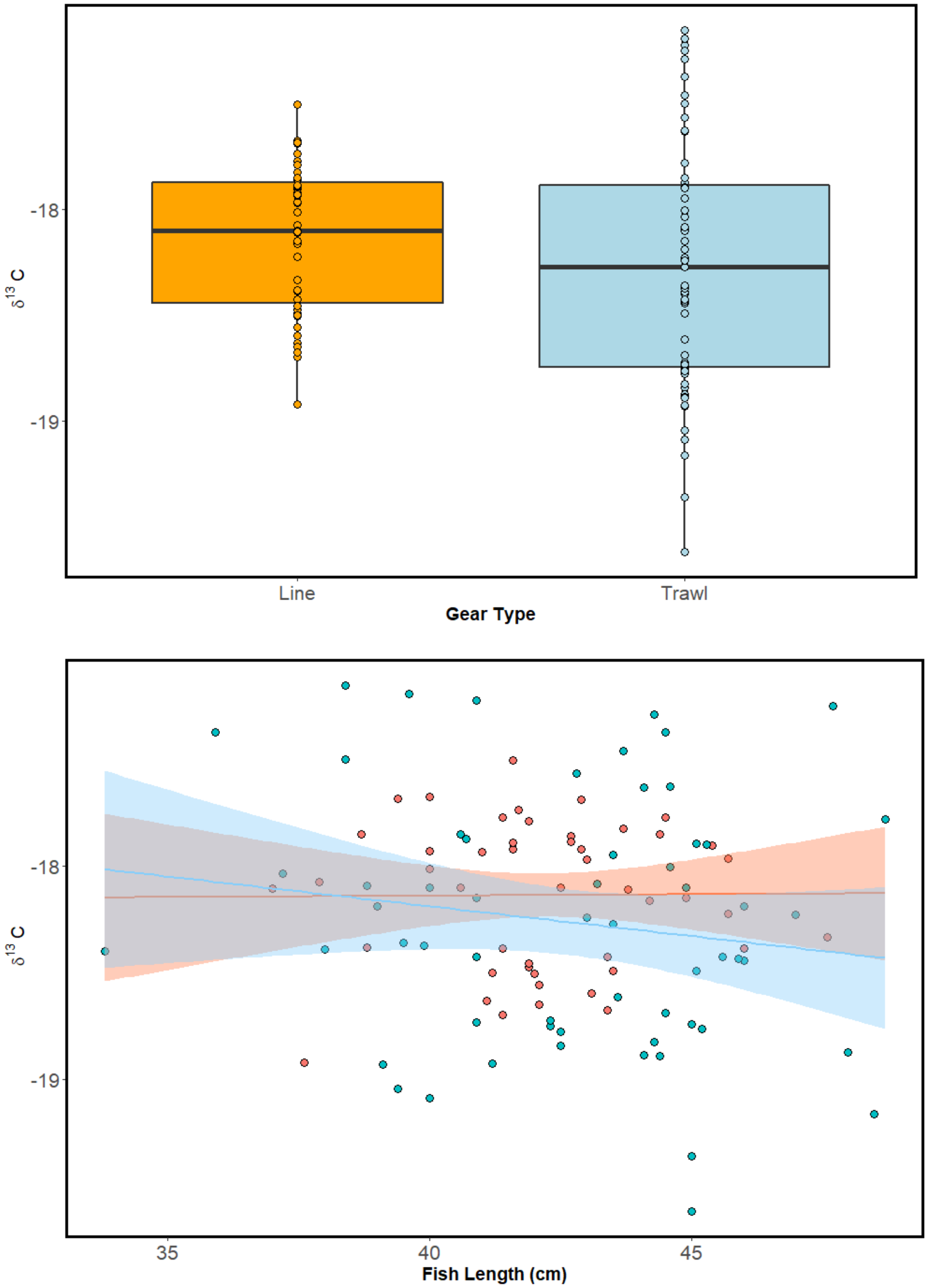

Figure 5.3: Differences in δ^{13}C between jigged and trawled Atlantic cod . Boxplot upper and lower hinges represent the 25th and 75th percentiles, respectively, while the horizontal line within the box represents the median. Length of the whiskers represents the range of datapoints between each hinge. Trendlines are linear regressions between δ^{13}C values and fish length for each gear type. Shaded areas around trendlines indicate 95% confidence intervals

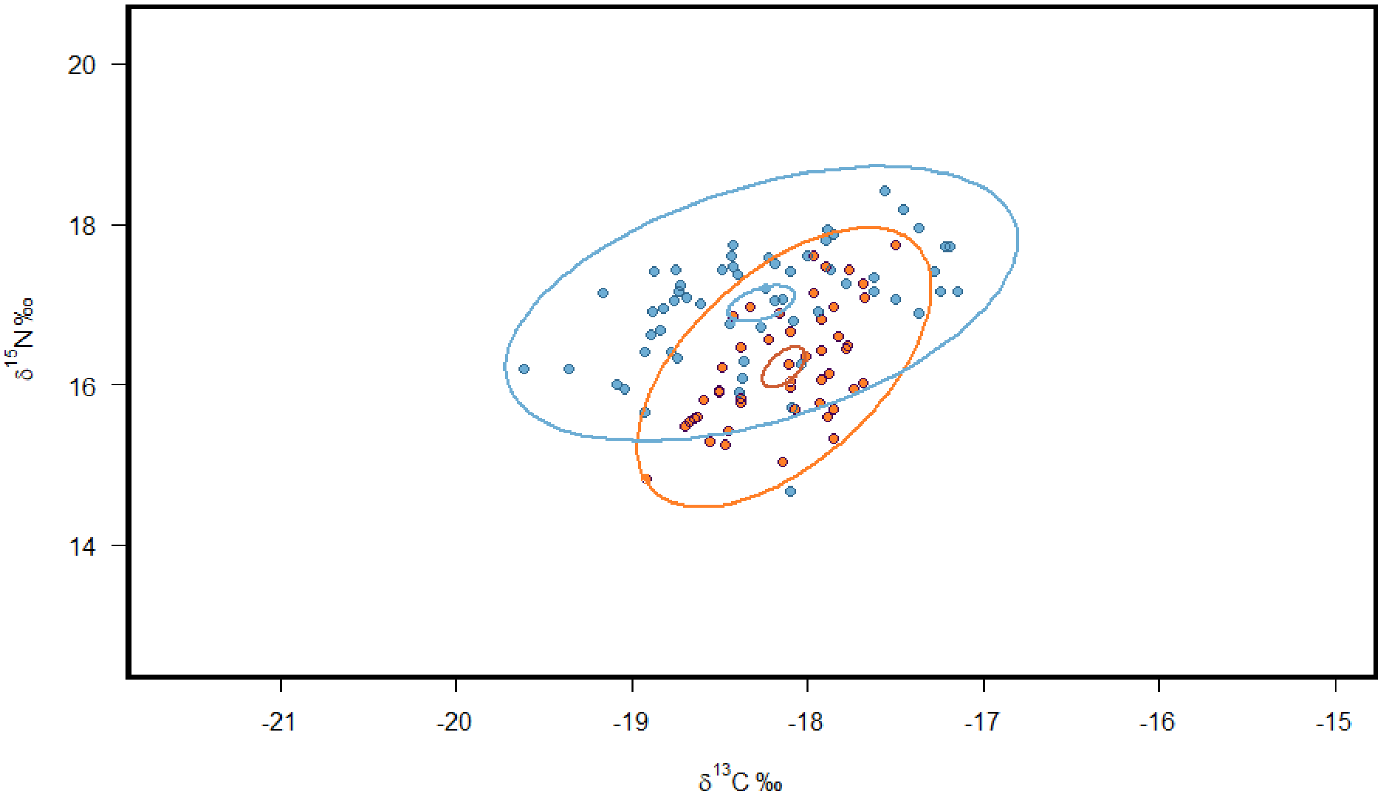

Figure 5.5: Standard Bayesian Ellipses representing the 2D isotopic niche occupied by trawled (blue) and jigged (orange) cod. Smaller ellipses represent mean niche space occupied by each fish group, and are encompassed by larger ellipses representing 95% credible intervals generated from posterior Bayesian model estimates.

5.4 DISCUSSION

By comparing the stable isotope signatures of Atlantic cod collected at the same location in the Skagerrak strait, but using contrasting fishing techniques, we investigated the capacity of rod and reel jigging and commercial trawling to select on the ecological traits of wild cod. We found that cod caught in the commercial trawl collectively occupied a broader niche space than their jigged conspecifics, and also exhibited greater δ^{15}N values (Figures 5.2 and 5.3), independently of effects of fish size. This is in contrast to previous studies, which only found limited evidence for gear specific selection on the ecological traits of cod by traps and gillnets (Ljungberg *et al.* 2019). This disparity in results may be attributable to the comparisons between gears made in each study, as the mechanisms of capture are more similar between traps and gill nets than they are between jigging and trawling (Hollins *et al.* 2018). Traps and gill nets may therefore have had limited scope to select on contrasting ecological traits. This study is the first to demonstrate active and passive gears have the capacity to select on the ecological traits of wild fish, providing evidence that fisheries selection can alter the ecological niche occupied by exploited fish populations beyond effects of selection on life history and developmental traits.

Δ^{15}N values of trawled cod were higher than that of cod caught by jigging, suggesting that they occupied an ecological niche at a slightly higher trophic level. In contrast, no differences in δ^{13}C values were found between jigged and trawled fish, although a much broader range of values was present in trawled fish, as indicated by their larger SEA_B value.

As no baseline isotope samples were taken as part of this study, it is not possible to assign a trophic level to fish from the δ^{15}N values of their tissues (Hussey *et al.* 2014). Variation in δ^{15}N is generally attributed to differences in diet, and the trophic level occupied by the sampled organism, while δ^{13}C variation is considered more strongly driven by differences in where the organism forages or hunts (MacKenzie *et al.* 2011; Trueman *et al.* 2012). It is now known that this is not always the case, and δ^{15}N values of fish tissues can also be influenced by patterns of habitat use (Chouvelon *et al.* 2012; Hansen *et al.* 2012). However, it seems likely that the differences in δ^{15}N observed in this study are driven by dietary differences between trawled and jigged cod, as opposed to differences in space use. One potential way jigging may have selected against low δ^{15}N is through a mechanism of differences in feeding motivation. Several studies have found that Atlantic cod in poorer condition are over-represented in the catches of baited, compared to un-baited passive gears (Huse *et al.* 2000; Ljungberg *et al.* 2019; Ovegård *et al.* 2012). These differences have been attributed to differences in feeding motivation between fish, with lower-condition fish more likely to respond to a potential food source upon its detection, and so are also more likely to attack a baited hook or enter a baited trap, than high-condition fish (Kuparinen *et al.* 2009). The results of this study indirectly support this mechanism, as lower condition cod typically have lower proportions of fish in their diets

(Sherwood *et al.* 2007), which would in turn decrease the δ^{15}N values of their tissues. Unfortunately, in this study, comparisons of fish condition between gear types was not possible, due to trawled fish being weighed/measured immediately upon capture, whereas for jigged fish mass not measured until some days after the capture event, as they were to be used in a separate experiment. Furthermore, several of the cod collected via trawling had clearly consumed other fish caught alongside themselves in the trawl-net. As time constraints did not allow for procedures such as gastric lavage or removal of the stomach to be done on board the trawler, it was not possible to control for this confounding effect on fish mass.

While differences in δ^{15}N values between trawled and jigged cod are likely driven by differences in trophic traits between the two groups, other potential causes of these differences need to be considered. Habitat driven δ^{15}N values in fish tissues have been found in previous studies, (Chouvelon *et al.* 2012; Hansen *et al.* 2012; Sherwood and Rose 2005), but generally over mesoscale gradients, in contrast to the limited area where fishing was conducted here. Therefore, any small differences in where fishing gears were deployed within the defined fishing area of this study are unlikely to have manifested in stable isotope signatures of δ^{15}N. However, turnover times of the fin-clip tissues used in this study mean that that isotope signatures of cod could have incorporated ecological information from before the fish had entered the Skagerrak (Busst and Britton 2018; Hanisch *et al.* 2010; Jackson *et al.* 2011; Sanderson *et al.* 2009). Despite this, differences in δ^{15}N values between trawled and jigged fish being driven by dietary differences, as opposed to differences in broad scale oceanic habitat use (Chouvelon *et al.* 2012; Hansen *et al.* 2012; Sherwood and Rose 2005), still seems more likely. If trawling and jigging were selecting on different use of oceanic habitat by cod, then differences in δ^{15}N present between the two gear types would also be expected in δ^{13}C, as they are more strongly driven by onshore/offshore gradients than δ^{15}N (Trueman *et al.* 2012).

No differences in δ^{13}C were found between trawled and jigged cod. While both δ^{13}C and δ^{15}N values of fish tissues can be determined by diet, δ^{15}N values are more representative of the trophic level of a given organism, whereas δ^{13}C are more strongly driven by differences in foraging location. It is likely that the restricted area where fishing was conducted in this study limited the capacity for horizontal patterns δ13C values to drive stable isotope signatures of studied cod beyond those attributable differences in past use of oceanic habitat (Svedäng *et al.* 2007). However, inter-individual differences in vertical habitat use in Skagerrak cod (Freitas *et al.* 2015; Olsen *et al.* 2012) had the potential to drive inter-individual differences in δ^{13}C values of caught fish (Woodland and Secor 2013), and also determine availability to the fishing gears in this study (Olsen *et al.* 2012). These results therefore indicate that there are no differences in selection on spatial traits between trawling and jigging. As mentioned previously, it is difficult to exclude the possibility of a false-negative when conducting SIA, however, a lack of differences in selection on spatial traits between jigging and trawling remains a likely explanation for the lack of differences in δ^{13}C between gears observed here (Figure 5.3). As the vertical position of cod will be strongly determined by time of day due to patterns of diel vertical migration (DVM)(Freitas *et al.* 2015; Olsen *et al.* 2012), the time at which fishing was conducted will determine the scope for any fishing gear to select on the vertical habitat use of cod. While the magnitude of DVM is reduced during the summer months when the water column is more stratified (Freitas *et al.* 2015; Olsen *et al.* 2012), cod generally occupy a broader range of depths during the day before converging closer to the surface during the night (Freitas *et al.* 2015; Olsen *et al.* 2012). As fishing was conducted during daylight hours for both gear types, it therefore seems unlikely that the lack of differences in δ^{13}C between gears are an artefact of deploying gears when intraspecific variation in space use was reduced among targeted fish. While the fact that no differences in δ^{13}C values were found between trawled and jigged cod indicate that there were no differences in selection on individual cod's spatial traits by the two gears, it is important to note that this does not necessarily suggest that selection on vertical habitat use does not occur in either gear. As this study compares the traits of cod vulnerable to trawling and jigging to one another, as opposed to comparing the traits of captured to un-captured fish, this study does not allow us to infer the strength of selection on individual traits in absolute terms for either gear. Therefore, if vertical habitat use is selected upon by both trawling and jigging to a similar extent, then differences in δ^{13}C values between trawled and jigged god will not be present between the two gears.

Although δ^{15}N values of trawled cod were higher and encompassed a narrower range of values than those of jigged cod, the total occupied niche size of trawled cod was larger (Figure 5.5), driven by greater variation in δ^{13}C. This implies that in terms of selection on ecological niche in absolute terms, the trawl was less selective than jigging. This certainly seems to be the case for selection on traits related to space use, as the range of δ^{13}C values present in jigged fish is completely encompassed by that of trawled fish, which exhibited both the highest and lowest δ^{13}C values recorded in this study (Figure 5.3). It is interesting to note that while the comparatively restricted range of δ^{13}C values of fish caught by jigging suggests that this fishing method exerts more selection on space use than trawling, jigging seemed to select against fish exhibiting intermediate δ^{13}C values (Figures 5.3 and 5.5). This suggests that fish with more generalist space-use and forging traits were at the greatest risk of capture in jigging, as opposed to specialists which might be expected to exhibit more extreme values of δ^{13}C, in either direction. The mechanism behind this selection is unclear, but may be attributable to more opportunistic, generalist cod which forage in a range of environments also being more likely to investigate the potential prey item of a jigging lure, alongside fish which may have had greater feeding motivation due to lower condition (Huse *et al.* 2000; Kuparinen *et al.* 2009; Ljungberg *et al.* 2019; Ovegård *et al.* 2012). Selective removal of opportunistic and low condition cod by jigging would cumulatively result in an underrepresentation of specialist feeders and high-trophic level individuals in jigged cod, and so explain why δ^{15}N values of trawled cod were comparatively high, while also displaying a broader range of δ^{13}C values. This would also suggest that while low condition fish with high feeding motivation are vulnerable to capture via jigging in particular, generally trawls are less selective on ecological traits, with only low trophic level cod underrepresented in the total trawl catch (Figure 5.5).

As this study compares the traits of trawl-vulnerable and jig-vulnerable fish to one another, as opposed to comparing traits of caught and uncaught fish, predicting how fisheries employing these gears may alter the ecological niche occupied by targeted fish stocks using these results should be done with caution. Without knowing the stable isotope signatures of uncaught cod, we can only ascertain the degree to which selection on ecological traits is different between the two gears, and it is not possible to determine the degree to which similarities in the catch compositions of both gears are driven by an absence of selection in either gear, or both gears selecting upon ecological traits in an identical way. Furthermore, the study site is subjected to frequent commercial trawl deployments, while cod are less frequently targeted using rod and line in this area (Stock Annex: Cod (*Gadus morhua*) in Subarea 4 and divisions 7.d and 20 (North Sea, eastern English Channel, Skagerrak)). This means that it is likely that the study population here could have already experienced phenotypic change as a result of fisheries harvest. Furthermore, as most fish in this study were likely 2 years old+, there has been ample opportunity for these cod to have experienced trawling events before. The degree to which these factors may have influenced the results reported here is not known. However, with those caveats in mind, the results of this study indicate that selection on ecological traits by the trawl is comparatively weak compared to that of rod and reel based jigging, which seemed to select against low trophic level cod, likely through a mechanism of feeding motivation (Huse *et al.* 2000; Kuparinen *et al.* 2009; Ljungberg *et al.* 2019; Ovegård *et al.* 2012). Selection against fish with high feeding motivation may indirectly select against individuals with greater energetic demand, as they are at greater risk of experiencing fitness consequences in the event that food becomes limiting (Killen *et al.* 2012b; Killen 2014). Jigging may therefore have the capacity to alter the phenotypic composition of fish populations with respect to their underlying physiological traits, particularly with respect to energetic demand and metabolism (Burton *et al.* 2011a; Hessenauer *et al.* 2015; Hollins *et al.* 2018; Metcalfe *et al.* 2016b). The degree to which intraspecific variation in metabolic traits predicts individual fitness in the wild is a contentious issue (Farrell 2016; Giomi *et al.* 2019), and so how indirect selection on physiological traits would alter the ecological niche of exploited cod is difficult to predict. However, it may be expected that removal of cod with high feeding motivation and associated energetic demand could relax competition for resources among individual cod. This decreased competition could be further driven by jigging selectivity through the removal of generalist cod showing 'intermediate' ecological traits (Figure 5.5), leaving a population largely comprised of specialist individuals which can more effectively partition available resources between one another. However, the removal of more generalist or opportunistic cod from the population will also likely reduce the resilience of a given cod population to future environmental disturbances (Davies *et al.* 2004; Graham 2007).

This study is the first attempt to investigate the degree to which active and passive gear types may select on the ecological traits of Atlantic cod in a real fisheries scenario. We found that although $\delta^{15}N$ values of trawled cod were higher than that of jigged cod, trawled cod occupied a broader ecological niche, driven by the presence of extreme high and low values of $\delta^{13}C$ in the trawl catch. This was interpreted as rod and reel-based jigging selectively removing low condition, generalist foragers through a mechanism of feeding motivation. However, this study has two main limitations, which suggest that these results should be interpreted with caution. Firstly, while it appears that the trawl is comparatively non-selective with respect to ecological traits, and thus likely represents the composition of the underlying cod population of the Skagerrak fairly well, without knowing the ecological traits of fish which were caught by neither gear it is not possible to infer the strength of selection in either gear in absolute terms. Secondly, while both jigging and trawling was conducted in a similar location during the same time of year, stable isotope signatures of fish tissues are dynamic, and the possibility of a false positive result driven by changes in the ecological traits of Skagerrak cod between gear deployments cannot be completely excluded. However, this seems unlikely to be the case. As the stable isotope signatures of fin clips represent an integrative chemical signal accumulated over months (Busst and Britton 2018; Hanisch *et al.* 2010; Sanderson *et al.* 2009), there is limited scope for a dietary switch between gear deployments to have influenced the stable isotope signatures in this study. While differences in selection on ecological traits by trawls and jigging, driven through a mechanism of feeding motivation, seems the most parsimonious explanation for the results presented here, future studies would be strengthened by minimising elapsed time between gear deployments, and also increasing sampling effort to try to investigate the ecological traits of fish not susceptible to capture in conventional gear types. This was not logistically possible here, but future work of this type should aim for as close to simultaneous gear deployments as possible. This would allow stronger conclusions to be made with regard to both the capacity for gears to select on ecological traits, and how this selection may alter the ecological niche of exploited cod populations.

6. GENERAL DISCUSSION

This thesis utilised a holistic approach to investigate the capacity of fishing gears to select on the physiological traits of fish. Conducted work encompassed experiments using small scale replicated fisheries in the laboratory, to data collected from commercially important fish species in a real-world fisheries scenario. This work addresses existing knowledge gaps by providing empirical demonstrations of mechanistic links between individual fish physiological traits and capture vulnerability across contexts, assessing the capacity for selection on physiological traits to occur in the field, and finally investigating how fisheries selection may alter the ecological niche of exploited species. In general, the results presented in this thesis provide mixed evidence for the capacity of fishing gears to select on the physiological traits of fish but highlights several exciting avenues for future work to be conducted. In this final chapter, I discuss the implications of these results, and highlight priorities for future work investigating fisheries selection on physiological traits.

The results of Chapter 2 showed that relationships between anaerobic metabolic capacity and capture vulnerability were only apparent when tested minnows faced the trawl alongside familiar conspecifics, in accordance with a previous study using a similar experimental design (Killen *et al.* 2015b). Alongside familiar fish, individuals with high anaerobic metabolic capacity spent less time in the net than low anaerobic capacity fish. However, when fish faced the trawl alongside shoalmates which had not been encountered before, capture vulnerability became unrelated to any measured physiological traits, and seemed more strongly determined by stochastic processes. Furthermore, the inclusion of escape routes around the trawl weakened the relationship between anaerobic metabolic traits and capture vulnerability compared to previous work (Killen *et al.* 2015b), by providing a way for fish to avoid spending any time in the pursuing net, independently of their swimming ability. Considering that no relationship between swim performance and capture vulnerability was recorded in Chapter 3, where fish faced the trawl individually, the results of this thesis highlight the degree to which selection on physiological traits may be disrupted even by comparatively subtle changes to social context. When comparing the results of Killen *et al.* (2015) to those of Chapters 2 and 3 of this thesis, it is interesting to note that while the addition of escape routes weakened physiological selection in the trawl, selection did not become decoupled from swimming capacity until fish either faced the trawl alongside unfamiliar fish (Chapter 2) or individually (Chapter 3). This implies that in these experimental contexts, social cues and behavioural interactions among fish may have a greater effect on influencing physiological selection than physical modifications to the gear itself.

Despite most evidence for the capacity for fisheries to select on physiological traits being provided by studies investigating selection by passive gears (Prokkola *et al.* 2019; Redpath *et al.* 2010b; Steven J. Cooke *et al.* 2007), the results of Chapter 3 found no evidence for traps could select on any components of metabolic phenotype. While this is in accordance with more empirical studies investigating links among metabolic traits and capture vulnerability via angling (Louison *et al.* 2018b; Väätäinen *et al.* 2018), considering that selection on minnow activity was found to be so consistent in the trawl within the same experiment, the absence of any trap selection in Chapter 3 was surprising. While the small scale of the fisheries recreations in Chapter 3 may have contributed to this lack of selection by the trap, experimental minnows were frequently observed attempting to access the bait being used as an attractant but were unable to locate the entry to the trap. In this way, the trap may have been selecting on both feeding motivation, and some element of cognitive capacity of individual minnow. If this is the case, then the lack of selection found by the trap in Chapter 3 may be a false negative, as no measures of cognitive capacity was measured in experimental minnows.

The results presented in Chapters 2 and 3, alongside the results of previous work (Killen *et al.* 2015b; Louison *et al.* 2018b; Väätäinen *et al.* 2018) seem to suggest that trawls have greater capacity to select on individual physiological and behavioural traits than passive gears. While this may be true within the experimental context that this work has been conducted, I would not necessarily expect this to be the case in fisheries in the wild. Although physiological and behavioural traits were related to capture vulnerability in the trawl in Chapters 2 and 3 respectively, what is perhaps as interesting as the relationships themselves is the degree to which they indirectly demonstrate how, during the final stages of selection, capture vulnerability can become easily detached from individual traits by overriding stochastic factors. For example, Chapters 2 and 3 both suggest that factors such as fish position relative to the trawl can be a strong determinant of whether or not that fish is actually caught, showing interesting parallels with how different behavioural responses to an approaching trawl can influence the probability of fish capture in the wild (Rose 1995; Underwood *et al.* 2015; Winger 2010). The effect of fish position and space use on capture vulnerability is particularly apparent in Chapter 3, where minnows with high spontaneous activity were found to be at consistently lower risk of capture in the trawl by increasing the likelihood of them encountering a potential escape route by chance. While individual spontaneous activity was found to be a repeatable behavioural trait, trawl capture vulnerability was not found to be repeatable, further suggesting that this mechanism of escape may be essentially random. A similar effect might have been in play in the simulated trap fishery. While the starting position of the minnow relative to the trap was the same for each trial, fish often explored the behavioural arena to differing extents before approaching the trap. This meant that certain fish will have approached the trap ‘head on’, and so have been immediately presented with the trap entrance upon approach. Fish approaching the trap entrance directly in this way may have been easier to catch than those which approached from the sides, again presenting a potential mechanism where capture vulnerability was more strongly determined by fish behaviour immediately before capture, as opposed to by any physiological or behavioural trait. While analysing the space use of minnows around the trap in such detail was beyond the scope of the experiment conducted in Chapter 3, comparing the relative importance of individual physiological traits vs stochastic processes in determining capture vulnerability in this way may be a useful avenue for future research.

As stated in Chapter 1, the capture success for any type of gear is determined by the cumulative probability of outcomes along a set sequence of decision points, which occur at increasingly fine spatiotemporal scales. As the scale of fisheries selection shifts throughout the capture process, so do the traits relevant for determining capture vulnerability. For example, physiological traits determining patterns of habitat use will be relevant in determining the overlap between fish and deployed fishing gears, but perhaps less relevant in determining the capacity for a fish to escape a pursuing trawl once it has been encountered. Furthermore, as the capture process proceeds, each stage of capture reduces phenotypic diversity of fish available for the subsequent stage to select upon, limiting the capacity for further selection to occur. As experimental approaches to fisheries selection often focus on these final stages of selection, (*i.e*. those occurring after fish have encountered the gear) an emphasis has been placed on the importance of traits related to fine scale behaviours (*e.g.* boldness, aggression, escape responses (Arlinghaus *et al.* 2017a; Conrad *et al.* 2011)) in determining capture vulnerability in fishing gears. However, as described previously, the plasticity of these behaviours (Killen *et al.* 2016a; Killen *et al.* 2011; Killen *et al.* 2013; Stoner 2004; Stoner and Ottmar 2004; Stoner *et al.* 2006), and the modulation of their relationship with physiological traits by the external environment (Killen *et al.* 2011; Killen *et al.* 2013; Killen *et al.* 2012b), weakens the potential for fisheries selection to operate on them. This is also a likely explanation for why experimental evidence for the capacity of fisheries selection to operate on behavioural and physiological traits remains mixed (Thambithurai *et al.* 2018; Väätäinen *et al.* 2018; Vainikka *et al.* 2016; Wilson *et al.* 2011), despite compelling evidence provided by selection line (Redpath *et al.* 2010b) and field experiments (Hessenauer *et al.* 2015; Monk and Arlinghaus 2017a). Furthermore, it is important to note that by the time these fine scale behavioural responses become relevant in determining whether a fish is caught, much of any potential fisheries selection will have already occurred. Experimental approaches which facilitate encounters between fish and fishing gears may therefore lose much of their potential to detect relationships between individual fish traits and capture vulnerability, as there is no scope for traits related to broader scale patterns of behaviour, and the underlying physiological traits which may determine them, to influence capture vulnerability. This is not to say that selection during these final stages of capture does not occur, rather that the strength of selection at this point will likely be comparatively weak compared to at earlier stages in the capture process. Further research into how physiological traits correlate with broad scale patterns of habitat use and behaviour, or mesoscale experimental approaches investigating the comparative strength of selection on different traits at different stages of the capture process could begin to address these knowledge-gaps.

The relevance of broad scale patterns of habitat-use in determining vulnerability to capture was highlighted in Chapter 4, where European perch with larger home-range sizes were found to be at greater risk of capture by gill net. The results of Chapter 4 also show that in the wild, traits related to patterns of space use and habitat selection were highly repeatable and showed little within-individual variation when compared to metrics describing movement at finer scales, such as sinuosity, or movement speed. Patterns of habitat use of wild fish have been found to influence capture vulnerability in other passive fisheries (Monk and Arlinghaus 2017b; Olsen *et al.* 2012), and the results of Chapter 4, alongside the huge variation in habitat selection found between perch within the same study, support the idea these traits may be extremely relevant in determining which fish are available for capture by a fishery, and thus be under selection. Telemetry data not reported in this thesis due to time and length constraints show that several of the tracked perch showed zero overlap in 95% utilisation distributions. As such, if fishing had been intensively focussed on one area, as opposed to conducted rotationally as in Chapter 4, then several fish would have had no chance of being captured as they never overlapped with deployed gear.

As intraspecific variation in patterns of space use seems a likely trait influencing capture vulnerability in wild fish, the question then becomes whether these patterns of space use are related to individual physiological traits. Addressing this question requires overcoming many logistic challenges, but recent advances in biologging and biotelemetry allow us to better understand the ecological relevance of intraspecific variation in physiological traits (Farrell 2016), and even measure them in free swimming fish (Cooke *et al.* 2016; Metcalfe *et al.* 2016a; Treberg *et al.* 2016). Currently, evidence for intraspecific variation in physiological traits driving within-species differences in patterns of space use in the wild is limited (Villegas-Ríos *et al.* 2018), and no evidence has been found supporting a relationship between metabolic phenotype and spatial behaviour so far (Baktoft *et al.* 2016; Laskowski *et al.* 2016). As metabolic phenotype must be defined under controlled, standard conditions, and much of the intraspecific variation which could be driven by physiological traits may be caused be differences in physiological responses to environmental gradients (Teal *et al.* 2018; Whitlock *et al.* 2015), future work investigating links among metabolic traits and patterns of space use in the wild may benefit from quantifying fish's metabolic traits using a reaction norm approach. Considering the important role that intraspecific variation in habitat use likely has on determining overlap between fish and fishing gears, studies integrating physiological measures into investigations of fish movement and behaviour will provide further understanding on the capacity for fisheries to select on physiological traits.

One of the most interesting findings of the thesis is presented in Chapter 5, where stable isotope signatures of trawled and jigged Atlantic cod indicated that active and passive gears may select on the ecological niche of wild fish to different extents. These differences were attributed to differences in feeding motivation between trawled and jigged cod, providing evidence that commercial fishing gears have the capacity to select fine scale behaviours, in addition to broader patterns of habitat use (Olsen *et al.* 2012). However, as Chapter 5 compared the ecological traits of trawled vs jigged fish, as opposed to caught vs uncaught fish in either gear, determining the degree to which either gear selected on individual fish traits in absolute terms is difficult. As both gears targeted similar habitats, it is possible that both trawling and jigging selected on habitat use of wild cod to similar extents, causing trawled and jigged cods to have similar δ^{13}C. Therefore this study does not necessarily imply that fishing gears do not select on spatial traits, but that if selection on spatial traits of wild cod occurs, it is to a similar extent by both trawling and jigging. The possibility of a false negative result in $\delta^{13}C$ values of caught cod is discussed in more detail in Chapter 5. While this result is interesting and provides evidence that selection on individual fish traits will have ecological consequences beyond the effects of altering life-history traits of exploited fish, whether or not the ecological niche of cod is determined by their underlying physiological traits remains to be seen. Therefore, the data presented in Chapter 5 currently present no direct evidence for the capacity of fishing gears to select on physiological traits either way.

While the findings presented in this thesis further our understanding of how intraspecific variation in physiological traits can influence the capture vulnerability of individual fish, clearly further research is required to accurately assess whether or not fisheries selection on physiological traits occurs in the wild, and what its consequences for the ecological traits of exploited fish stocks, and viability of commercial fishing activities may be. Fisheries selection on life history traits has been directly implicated in the collapse of exploited fish populations (Olsen et al. 2004), as well as their failure to recover where moratoriums on fishing activities have been put in place (Swain et al. 2007). These impacts highlight the importance of considering the impact of fishing activities in terms of directly driving population declines of target and non-target species, but also in terms of the impact fisheries induced phenotypic change may have on targeted species themselves, and the cascading effects these changes may have throughout ecosystems (Kuparinen and Merilä 2007;Swain, 2011). However, how comparable the impacts of fisheries selection on physiological traits may be to that of selection on life history traits remains unclear. As highlighted within this thesis, experimental evidence has shown that physiological traits can correlate with a range of behaviours which may be relevant in determining fish's vulnerability to capture (Hollins et al. 2018; Metcalfe et al. 2016). Accordingly, where specific behaviours correlate with capture vulnerability, exploited fish populations may exhibit eroded diversity in terms of present behavioural traits (Arlinghaus et al. 2017). While the consequences of intraspecific variation in behavioural traits remain poorly understood in fish, it is possible that reduced behavioural diversity in exploited fish populations may alter the ecological niche collectively occupied by fish populations exposed to fishing pressure

(Ljungberg *et al.* 2019), with knock-on consequences for predator-prey interactions, connectivity among fish populations, mortality rates, and other ecological processes (Claireaux et al. 2018). Fisheries selection on physiological traits, either directly or through correlational selection on behavioural traits, may also erode the diversity of physiological phenotypes present in wild fish populations. While altering the distribution of physiological traits of fish populations may also have consequences for the food web dynamics and demand for energetic resources of exploited ecosystems (Burton et al. 2011; Killen et al. 2011; Metcalfe et al. 2016), impacts may extend further to fish growth rates (McKenzie et al. 2012; Reid et al. 2011;2012; Robertson et al 2015), environmental preferences and tolerance of environmental change (Farrel, 2016; Killen, 2014), and other measures of fish performance (Killen et al. 2015). In addition to altering the dynamics of ecosystems subjected to fisheries exploitation, reductions in the diversity of physiological and behavioural traits represented in wild fish populations caused through directional fisheries selection may lead wild fish populations into an ‘evolutionary trap’, wherein the capacity for fish to adapt to environmental change, or scenarios of reduced fishing pressure is narrowed as a resulted of eroded genetic diversity. Altering the physiological phenotypic composition of wild fish populations through fisheries selection may therefore limit the efficacy of conservation measures such as reductions in or cessation of fishing activity. Future scenarios of climate change and the expansion of ocean hypoxic zones are predicted to alter the geographic distributions of fish species, likely through a mechanism of sublethal effects on physiology (Marras et al. 2015), and so may interact with fisheries selection on physiological traits to produce synergistic effects on exploited fish distributions and abundances (Hollins et al. 2018).

It is clear that accounting for capacity for fisheries to elicit phenotypic change in exploited fish populations is an important component of fisheries management (Laugen et al. 2014). When mitigating the evolutionary impacts of fishing activity on life history traits, management practices such as setting minimum landing sizes of targeted fish to help ensure immature fish remain below size limits (Ernande et al. 2004), or restricting fishing activity to isolated spawning grounds to release proportions of the population from the selective pressures of fishing (Andersen et al. 2007) are likely to be effective (Kuparinen and Merilä 2007). However, employing selection criteria on fish catches, such as the minimum size limits used to mitigate selection on life history traits, in order to minimise fisheries selection on physiological traits would likely be extremely challenging, owing to these traits' plasticity and the potential overriding influence of external factors such as temperature, or social environment on fish behaviour and performance. Furthermore, while gear modifications which exploit behavioural differences between fish species to exclude non-target catch from capture exist, within-species differences in behavioural responses to fishing gears will be less distinct, and so gear modifications potentially not as effective.

In contrast, investigating how physiological traits determine patterns of habitat use in wild fish, and in turn how this could affect fisheries selection via overlap between fish and deployed gears may help develop strategies to mitigate fisheries selection on physiological traits. Selection on individual traits via habitat overlap is less likely to be influenced by extraneous factors than selection on finer scale behaviours further along in the capture process and will also play a role in determining the vulnerability of fish to capture in all gear types, at a point in the capture process where the potential scope for selection is greatest. As such, selection on individual spatial traits could be much stronger than selection on finer scale behaviours, which may be expected to be more strongly influenced by differences in gear type and environmental conditions. From a management perspective, focussing research efforts to investigate selection at this earlier stage also makes sense. Phenotypic change in spatial traits, such as dispersal distances and home range, will have knock-on effects for efficacy of current fisheries management techniques such as spatial closures to fishing. If management efforts in future seek to reduce the potential for fisheries to elicit phenotypic change in fish populations, this may be accomplished by altering where and when fishing gears are deployed so that fishing effort does not target fish with specific patterns of habitat use disproportionately. However, while the strategies outlined here may act to reduce selection on physiological traits in exploited fish populations, they will not mitigate evolutionary responses to the elevated mortality imposed by fishing activity in their own right. Evolutionary responses of exploited fish stocks are driven by both the strength of selection on individual fish traits, and also the intensity of fisheries harvest. As modifying existing fishing practices to reduce selectivity on physiological traits must be done in such a way so as to also mitigate (or at least not worsen) selectivity on behavioural and life history traits, while also maintaining sufficient selectivity to minimise bycatch, by far the most parsimonious solution appears to be to reduce the intensity of fisheries harvest. This will act to reduce strength of selection across all phenotypes present in exploited populations, in terms of life history, behavioural, and physiological traits, while also helping mitigate population declines in wild fish stocks, which are much more likely to directly lead to the collapse of wild fish populations than fisheries induced phenotypic change. The role of intraspecific variation in physiology in determining individual fish capture vulnerability presents opportunity for many new avenues of research in both laboratory and field settings, and is an important topic to consider when assessing the impacts of intensive fisheries harvest. Relevant approaches encompass telemetry, respirometry, enzyme analysis, fisheries simulations, genetics and stable isotope analysis among many others. Holistic approaches applying several of these techniques to include aspects of physiology and whole organism behaviour in the wild would be particularly powerful approaches, and are made all the more feasible by advances in biologging and biotelemetry, (Cooke *et al.* 2016; Guzzo *et al.* 2018; Metcalfe *et al.* 2016a; Treberg *et al.* 2016) and other approaches to investigating physiology in the field (Chung *et al.* 2019). There are several avenues by which individual physiological traits may affect which fish are captured by recreational or commercial fisheries and those that are not. Fisheries selection on physiological traits may elicit changes in traits associated with metabolic demand, locomotor performance, neuroendocrine function, and/or sensory physiology or produce correlated responses in behavioural or life-history traits. The consequences of these effects will be important to consider how fisheries selection may interact with other phenomena such as climate change to exert synergistic effects on wild fish populations, and I hope that this thesis encourages further research in this area.

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