

# Does thermal plasticity affect susceptibility to capture in fish? Insights from a simulated trap and trawl fishery

J. Hollins, B. Koeck, A. Crespel, D.M. Bailey, and S.S. Killen

**Abstract:** In fishes, physiological and behavioural traits can correlate with vulnerability to capture with fishing gears, highlighting the capacity of fisheries selection to drive phenotypic change in exploited populations. There remains a paucity of information regarding how different fishing gears may select on phenotypic traits and how relationships between individual traits and capture vulnerability change across environmental gradients. By simulating the capture process in a trawl and trap using wild minnows (*Phoxinus phoxinus*) acclimated to different temperatures, we investigated how contrasting fishing gears select on behavioural and physiological traits and how this selection is modulated by temperature. Despite similar risk of capture in each gear, selection differed between traps and trawls. Fish exhibiting low spontaneous activity were at greater capture risk in the trawl across all temperatures, while traps showed no selection except at 24 °C. No relationships between physiological traits and capture vulnerability were found, except between swim performance and trap capture vulnerability at 24 °C. This study demonstrates that fisheries selection on individual traits is likely context-specific, depending on both fishing gear type and environment.

**Résumé :** Chez les poissons, des caractères physiologiques et comportementaux peuvent être corrélés à la vulnérabilité à la capture par des engins de pêche, ce qui souligne la capacité de la sélection par la pêche d'entraîner des modifications phénotypiques dans les populations exploitées. Peu d'information est toutefois disponible sur la sélection de différents caractères phénotypiques pouvant découler de différents engins de pêche et sur les variations des relations entre des caractères précis et la vulnérabilité à la capture le long de gradients de conditions ambiantes. En simulant le processus de capture dans un chalut et un casier de ménés sauvages (*Phoxinus phoxinus*) acclimatés à différents températures, nous avons examiné la sélection de caractères comportementaux et physiologiques par différents engins de pêche, et comment la température module cette sélection. Malgré le fait que le risque de capture est semblable pour les différents engins, la sélection varie entre les casiers et les chaluts. Les poissons présentant une faible activité spontanée ont un plus grand risque de capture dans un chalut à toutes les températures étudiées, alors que les casiers ne font pas preuve de sélection, saduf à 24 °C. Aucune relation entre des caractères physiologiques et la vulnérabilité à la capture na peche de caractères précis dépend probablement du contexte, notamment du type d'engin de pêche et du milieu ambiant. [Traduit par la Rédaction]

# Introduction

In fishes, physiological and behavioural traits often correlate with an individual's vulnerability to capture by fishing gears (Diaz Pauli et al. 2015; Killen et al. 2015a; Koeck et al. 2019; Monk and Arlinghaus 2017a; Redpath et al. 2010). 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. 2017; Diaz Pauli and Sih 2017), but may also influence evolutionary responses if traits under selection are heritable (Arnold 2010; Diaz Pauli and Sih 2017; 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. 2014; 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. 2015; Hollins et al. 2018; Horodysky et al. 2015).

Fishing gears can be categorized 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 that 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. 2015). For active gears, physiological traits linked to individual swim performance may be particularly relevant in terms of determining capture vulnerability (Killen et al. 2015b; Kim and Wardle 2003; Marras et al. 2010). 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

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underlying this behaviour are unclear. Individual burst-swimming performance is linked with anaerobic metabolic capacity (Killen et al. 2015a; 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. 2015a). 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. 2015a), 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 that can influence individual fish's susceptibility to capture in passive fishing gears (Andersen et al. 2016; Arlinghaus et al. 2017; Diaz Pauli and Sih 2017; Metcalfe et al. 2016). SMR is a physiological trait that shows wide intraspecific variation (Burton et al. 2011; Metcalfe et al. 2016) 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, 2012a). 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 2008; Hessenauer et al. 2015; Hollins et al. 2018; Klefoth et al. 2017; 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. 2012b, 2014; Redpath et al. 2010). 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 (Diaz Pauli et al. 2015; Koeck et al. 2019; Monk and Arlinghaus 2017a; Redpath et al. 2010; 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 fluviatalis) 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 that 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 empirical work is needed to improve our understanding of how environmental factors alter correlations among labile traits and to inform us on which traits are available as targets for direct or correlated selection in the context of fisheries.

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. This constrained aerobic capacity may limit the phenotypic expression of fish, 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 that exhibit the greatest vulnerability to capture.

Experimental lab-based approaches to studying fisheries selection permit precise control over the myriad factors that 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 study fisheries selection (Conover and Baumann 2009; Reznick and Ghalambor 2005) and provide several advantages when compared studying wild, commercial species already exposed to fisheries selection for decades. 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 aimed 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? The results here will further our understanding of how environmental factors modulate trait-based selectivity by fishing, a topic that to date has been largely overlooked.

### Methods

All experimental procedures were conducted within the Graham Kerr building, College of Medical, Veterinary & Life Sciences, University of Glasgow, Glasgow. All minnows were initially held at 16 °C, at which point baseline measurements of physiological and behavioural traits were taken (Fig. 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, to act as a temporal control, while the remaining half were sequentially acclimated to 20 and 24 °C. European minnow occupy freshwater environments at temporal of 2-20 °C. Both the control and first acclimation temperatures therefore represent conditions likely experienced by wild fish, while 24 °C was anticipated to constrain the aerobic metabolic capacity of experimental fish and roughly corresponds to projections of maximum temperature increases in freshwater systems in the UK by the year 2100 (Robins et al. 2016), in accordance with Intergovernmental Panel on Climate Change (IPCC) high emissions scenario projections. After each acclimation period, both the warm acclimated and control fish had all physiological and behavioural measurements repeated, in addition to being subjected to both a simulated trawl and trap fishery (Fig. 1).

**Fig. 1.** Timeline (day.month.year) 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 nine fish died before respirometry or capture vulnerability assays could be performed at 24 °C.

	Time		
	T1	T2	Т3
Tank ID	11.05.2017-02.06.2017	06.07.2017-04.08.2017	07.10.2017-28.10.2017
1	16°C Swim Performance Metabolic Phenotype	16°C Swim Performance Metabolic Phenotype Activity	16°C Swim Performance Metabolic Phenotype
3	Activity	Trap/Trawl Vulnerability	Trap/Trawl Vulnerability
4 5	16°C Swim Performance Metabolic Phenotype	20°C Swim Performance Metabolic Phenotype	24°C Swim Performance Metabolic Phenotype
6	Activity	Trap/Trawl Vulnerability	Trap/Trawl Vulnerability

# 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, Glasgow, Scotland. Fish were then kept in aerated tanks (100 cm  $\times$  40 cm  $\times$  40 cm) 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  $\pm$  0.56 cm and 4.84  $\pm$  0.64 g, mean length (and mass)  $\pm$ SD) were subsequently split across six aerated tanks (50 cm  $\times$ 40 cm  $\times$  40 cm) so that each tank housed 12 individuals. Each tank received identical water and contained a shelter, gravel substrate, and plastic plants, and all fish were kept on a 12 h light : 12 h dark 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 anaesthetized using benzocaine and implanted with individually coded passive integrated transponder (PIT) tags to allow identification. Fish were then allowed 1 week to recover before experimental procedures began.

# 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. 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 (Fig. 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 remeasured, alongside trap and trawl vulnerability (Fig. 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. After a recovery period of at least 3 days, all fish were then profiled for vulnerability to capture in whichever gear they had not yet faced. Once all assays were complete, fish were maintained at their acclimated temperatures for 2 months (16 and 20 °C), before a final temperature increase could begin (Fig. 1). Again, tanks 1–3 remained at 16 °C, while tanks 4–6 were incrementally warmed from 20 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 time period T2 (Fig. 1).

### Swim performance

Individual swim performance was determined for each fish using a constant acceleration test (CAT; Killen et al. 2015a). CATs were performed after each acclimation temperature had been reached over the course or 14 days at each of T1, T2, and T3. For each CAT, fish were placed into the working section (45 cm  $\times$ 14 cm  $\times$  14 cm) of a 30 L Steffensen-type swim tunnel (Loligo systems, Tjele, Denmark), designed to exercise fish at controlled speeds in nonturbulent 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 was left to acclimate for 30 min at a water velocity of 5 cm·s<sup>-1</sup> (approximately one body length per second, BL·s<sup>-1</sup>). Once acclimation was complete, water velocity was then increased by 2.5 cm·s<sup>-1</sup> every minute. 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 swim performance, fuelled through both aerobic and anaerobic metabolism.

#### Behaviour

Once all fish had been assessed for swim performance, fish were then assessed for behavioural traits at each of T1, T2, and T3. All fish were left to recover in their tanks after swim trials for at least 10 days before behavioural trials began. Individual fish activity was determined using an open field assay using an 80 cm  $\times$  20 cm behavioural arena divided into two sections separated by a removable plastic divider. All activity assays were conducted within a metal scaffold covered with opaque curtains, which minimized 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. Four arenas were placed side-by-side within the frame so four fish could be profiled simultaneously. Fish activity throughout these trials was recorded using two

cameras (Logitech, C920 HD Pro Webcam) fixed to the top of the frame so that each camera had two tanks in frame. The first section of the behavioural arena consisted of a small acclimation area (10 cm  $\times$  20 cm), with gravel substrate, where fish were placed at the beginning of the trial. Here, fish were allowed to acclimate for 10 min, before the first plastic divider was withdrawn and the second section of the arena became visible to fish. This second 70 cm  $\times$  20 cm section consisted of an open field, with no substrate or shelter present. Fish were then allowed to swim freely about the arena for 20 min. 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 min portion of the activity trial. A fish was defined as "active" once it had moved one 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 s. The middle 10 min section of the video was used to quantify activity to minimize the potential impact of removing or replacing the arena dividers on fish behaviour, and the 5 min either side of this period were not used.

#### Respirometry

Immediately 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 MMR were achieved by manually chasing individual fish to exhaustion for a period of 2 min 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 et al. 2017). Once exhausted, fish were quickly transferred to individual cylindrical glass respirometry chambers (75 mL volume) attached to an intermittent flow respirometry system (Killen et al. 2015a; Thambithurai et al. 2018). Oxygen content of the water within the closed respirometry circuit was quantified once every 2 s using a Firesting four-channel oxygen meter and associated sensors (PyroScience GmbH, Aschen, Germany). The circuit itself comprised 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  $\pm$  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 min to flush chambers with fresh oxygenated water and then switch 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 min time interval throughout the first 30 min of recovery immediately following exhaustive exercise. MMR  $(mg O_2 \cdot h^{-1})$  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  $\sim$ 17 h total. Once retrieved from the respirometry chambers, fish were measured for wet mass and standard length, so that effects of fish size on metabolic traits could accurately be accounted for. Background bacterial respiration was accounted for by measuring rates of oxygen depletion in each respirometry chamber three times each before fish entered the chamber and after they were removed. The relationship between these start and end points were then used to interpolate estimates of background respiration during each closed cycle for the duration of the time fish were held in the chambers and

subtracted from estimates of fish oxygen consumption. Whole animal SMR (mg  $O_2 \cdot h^{-1}$ ) was estimated as the lowest 20th percentile of measurements taken throughout the measurement period (Chabot et al. 2016). Absolute AS was calculated as the difference between MMR and SMR.

#### **Fishery simulations**

All fish were individually subjected to a simulated trawl and trap fishery. All simulations were designed to replicate the capture process, after fish had already encountered fishing gears (Hollins et al. 2018) and were all conducted at the fish's respective acclimation temperatures. 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. Fishery simulations were conducted at T2 and T3, over a period of 5 days in each instance, at least 2 weeks after the cessation of respirometry.

#### Trap

Trapping simulations were performed in a rectangular 120 cm  $\times$ 60 cm  $\times$  60 cm arena filled to a depth of 14 cm, housed within a frame covered with opaque curtains to minimize 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 12 cm  $\times$  12 cm  $\times$  17 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<sup>3</sup> 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 was allowed to explore the arena and interact with the trap. The fish was given a maximum of 30 min to enter the trap, at which point the trial was stopped and the fish recorded as "caught" and the time until capture noted, while if the fish did not enter the trap it was recorded as an "escape". Once the trial was complete, the fish were returned to their holding tanks and fed, and the water in the arena was completely drained and replaced.

#### Trawl

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 and thermoregulated at each tested fish's acclimation temperature  $\pm$  0.1 °C. The working section of the tunnel was 70 cm long  $\times$  20 cm  $\times$  20 cm wide and with a 3 cm 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 30 cm 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 Can. J. Fish. Aquat. Sci. Downloaded from cdnsciencepub.com by UNIVERSITY OF GLASGOW on 01/20/21 For personal use only.



Fig. 2. Kaplan Meier survival curves of minnows within simulated trawl (top) and trap (bottom) fisheries tested at different temperatures.

(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 min at a speed approximating 0.5  $BL \cdot s^{-1}$ . Following this acclimation period, water velocity was gradually increased to 58.25 cm·s<sup>-1</sup> over a period of ~30 s, 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 3 cm  $\times$  3 cm. The trawl included escape routes to allow fish to avoid spending time in the net by passing 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 ~2 cm 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<sup>-1</sup> in front of the trawl against the net mesh and did not resume swimming for 5 s, the trial was stopped and the fish recorded as "caught", alongside the time until capture, 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".

## Statistical analyses

All statistical analyses were performed in R.3.5.1 (R Development Core Team) using the survival (Therneau 2020), lme4 (Bates et al. 2015), MuMIn (Barton 2009), and rptR (Stoffel et al. 2017) packages. To investigate how temperature affects overall capture vulnerability in each gear (question (i) in Introduction), we compared survival curves for trawls and traps across acclimation temperatures for each round of fishing simulations individually. Comparisons of survival curves for each gear across temperatures were made using Cox proportional hazard models (Cox PH) using both time until capture (continuous variable) and whether or not the fish was caught (binary variable) as response variables and acclimation temperature as the single predictor variable. The role of individual traits in determining vulnerability to capture (question (ii)) was also assessed using Cox PH models fitted to each fishery simulation individually. All behavioural data used for Cox PH models were first log(n + 1)-transformed, while maximum swim speed was log-transformed. Metabolic traits (SMR, AS, and MMR) used in Cox PH models 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 to the mean mass of all fish. The inverse log of these values was then taken and used to account for confounding effects of body mass and growth on metabolic rates between successive measurements (McLean et al. 2018). Cox PH models addressing question (ii) used  $\log(n + 1)$ -transformed behavioural traits and adjusted metabolic traits as predictor variables, alongside log-transformed absolute maximum swim speed (cm·s<sup>-1</sup>). Models of best fit were determined using maximum likelihood estimation, with nonsignificant interactions dropped sequentially, starting with those with the smallest  $\beta$  values, but were retained if their removal resulted in higher AIC values ( $\Delta AIC > 2$ ; Arnold 2010), with assumptions of proportional hazards assessed using the cox.zph function within the survival package in R. Cox PH models can be used to determine temperature-mediated change in both overall capture vulnerability and patterns of selection in the simulated fisheries conducted here; however, Cox PH models cannot describe the degree to which these patterns are driven by changes in the trait composition of the experimental fish populations. As a mechanistic approach linking individual traits to capture vulnerability in fish is an important aspect of understanding how patterns observed in experimental conditions may manifest under real fisheries scenarios, linear mixed effects models (LMEs) were used to investigate responses of individual fish traits to increasing acclimation temperature. LMEs investigating the role of temperature on the distributions of individual fish traits used "Treatment" (a categorical variable with two levels: control and warmed) and "Time" (a categorical variable with three levels: T1, T2, and T3) as fixed effects and Fish ID as a random effect, predicting each individually measured fish trait. Each trait used had been transformed as described

**Table 1.** Results of Cox proportional hazards models examining the role of temperature in determining overall probability of capture in trap and trawl fishing gears.

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Gear type	Temperature comparison (°C)	β	Z	р
Trawl	16 vs 20	-0.07716	-0.215	0.830
	16 vs 24	0.9850	2.524	0.0116
Trap	16 vs 20	0.3433	1.292	0.196
	16 vs 24	0.4073	1.335	0.182

**Note:** Comparisons are made within each gear type at each stage of the experiment.

above, with the exception of swim speed, which was instead normalized to  $BL \cdot s^{-1}$  to account for fish growth between trials. 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).

Finally, the adjusted repeatability of each individually measured behavioural and physiological trait was also investigated using  $\log(n + 1)$ -transformed behavioural traits, adjusted metabolic traits, and swim performance (BL·s<sup>-1</sup>) as response variables. Adjusted repeatability of each trait was calculated as described by Stoffel et al. (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 or uncaught data, using fish ID as a random effect. The repeatability of both individual traits and capture vulnerability provides further context on the consistency and strength of patterns of fisheries selection on individual traits and whether it is the same individual fish being caught by fishing gears under different scenarios.

#### Results

# 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 (Fig. 2; Table 1). Probability of capture did not differ between fish trialled at 16 and 20 °C in the trawl (p = 0.83) or in the trap (p = 0.20; Table 1). Trawls conducted at T2 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; Fig. 2). In contrast, fish probability of capture in the trawl was higher at 24 °C than at 16 °C (p = 0.012; Table 1), where 66.6% of fish were caught (median chase time = 38 s; Fig. 2) compared with 37.5% of fish caught at 16 °C (median chase time = 159 s). Risk of capture in the trap was similar between both 16 versus 20 °C (p = 0.20) and 16 versus 24 °C (hazards ratio (HR) = 0.41, p = 0.18; Table 1). Trapping at 16 and 20 °C caught 77.1% and 93.8% of fish (median capture times = 61 and 71 s, respectively), while trapping trials conducted at T3 caught 81.2% of fish at 16 °C (median capture time = 26 s) and 80% of fish at 24 °C (median capture time = 280 s).

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

Fish that spent more time moving in the open field assay (i.e., were more active) were less likely to be caught in the trawl at all temperatures, (p = 0.04 and p = 0.025 for both trawl trials conducted at 16 °C and p = 0.005 and p = 0.03 for trials conducted at



**Table 2.** Results of Cox proportional hazards models examining the role of individual behavioural traits in determining probability of capture in trap and trawl fishing gears.

Model	Term	β	Z	р
Trawl 16T2	Adj.(AS)	4.510	1.829	0.067
	Adj.(MMR)	-4.360	-1.823	0.068
	SGR	-4.030	-1.244	0.213
	Log(activity)	-0.371	-2.049	0.040
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
Trap 16T3	SGR	4.335	1.674	0.079
Trawl 20T2	Log(activity)	-0.946	-2.340	0.005
Trap 20T2	Null model	NA	NA	NA
Trawl 24T3	Log(activity)	-0.358	-2.164	0.030
Trap 24T3	$\log(U_{\max})$	-0.040	-2.680	0.008

20 and 24 °C, respectively; Fig. 3; Table 2), but there were no relationships between trawl vulnerability and any other trait. This selectivity regime was maintained across temperatures despite significantly higher fish activities found at 20 °C (refer to online

**Table 3.** Across context repeatabilities of individual behavioural and physiological traits assessed with LMEs using the trait of interest as a response variable and acclimation temperature and fish ID as fixed and random effects, respectively.

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Trait	Adj. R	SE	CI	р
Activity	0.462	0.078	0.296, 0.621	< 0.001
$U_{\max} (BL \cdot s^{-1})$	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	0.080	0.147, 0.456	< 0.001

Supplementary Table S1<sup>1</sup>; Supplementary Fig. S1<sup>1</sup>). Activity increased with temperature up until 20 °C, before decreasing at 24 °C. Although activity was consistently associated with capture vulnerability in the trawl and was found to be a repeatable trait (Table 3), trawl capture vulnerability itself was not repeatable across or within temperatures (Table 4). This indicates that while selection on activity was consistent, capture vulnerability was not. 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; Fig. 4; Table 2). This relationship between swimming performance

<sup>&</sup>lt;sup>1</sup>Supplementary data are available with the article at https://doi.org/10.1139/cjfas-2020-0125.

Table 4. Agreement repeatabilities of capture in each fishing gear.

Trait	Agreement R	SE	CI	р
Trawl capture	0.190	0.148	0, 0.525	0.129
Trap capture	0	1.760	0, 7.117	0.500
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

**Note:** Binary caught or uncaught data for each gear type were used for the response variable in each case, using individual fish ID as a random effect.

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 and 20 °C (Supplementary Table S1<sup>1</sup>; Supplementary Fig. S2<sup>1</sup>). Vulnerability to trap capture was not found to be repeatable across temperatures (Table 4). 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 (Table 2).

### Discussion

These results 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 (Fig. 2). Specifically, there was an increase in the proportion of fish captured by trawling but 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. 2017; Diaz Pauli et al. 2015; Uusi-Heikkilä et al. 2008; Figs. 3 and 4). While metabolic 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 (Fig. 3), and fish with a higher swimming capacity were less likely to be caught by trap at the warmest temperature (Fig. 4). The relationship between swimming capacity and trap capture vulnerability at 24 °C coincided with an overall reduction in swim performance and adjusted aerobic scope in 24 °C acclimated fish (Supplementary Fig. S3<sup>1</sup>), suggesting that at this temperature, fish were beyond their thermal optimum. Establishing the capacity for fishing gears to select on physiological and behavioural traits in fish populations, and how this is modulated by the environment could have important implications for sustainable fisheries management (Horodysky et al. 2015; Laugen et al. 2014; 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.

In contrast with previous experiments investigating links between individual traits and capture vulnerability (Diaz Pauli et al. 2015; Hollins et al. 2019; Killen et al. 2015*a*), capture vulnerability across temperatures was not found to be a repeatable trait in its own right in either the trap or trawl (Table 4). Repeatability would likely have been reduced in the current study because we were measuring repeatability across temperature contexts (Stoffel et al. 2017). However, repeatability was also low for repeated measurements of fish from the control treatment conducted at 16 °C only. Previous experiments have tested trawl capture vulnerability in several fish simultaneously (Hollins et al. 2019; Killen et al. 2015*a*), which may have dampened any stochastic effects on capture probability, increasing repeatability of capture vulnerability. 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 was likely a major cause of reduced repeatability in this study, this suggests that depending on acclimation temperature, different individuals are 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.

We found no relationship between any of SMR, MMR, or AS and risk of capture by either gear at any acclimation temperature (Table 2). 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. 2010; 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. (2015a). 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 correlated 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. (2015a) 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. (2015a) 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 2; Fig. 3), 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 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 utilizing 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 (Table 1; Fig. 2), coinciding with a reduction in swim performance seen in fish acclimated at 24 °C (Supplementary Table S1<sup>1</sup>; Supplementary Fig. S2<sup>1</sup>). This reduction in overall swimming performance may have driven the high capture rate in the trawl at 24 °C (Table 1; Fig. 2; Supplementary Fig. S1<sup>1</sup>), potentially masking any selection on individual swimming performance that may 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 Fig. 4. Comparison of uncaught (blue) and caught (orange) fish swim speeds in the trap at 16 versus 20 °C (top) and 16 versus 24 °C (bottom).



become less likely to locate and make use of available escape routes.

While population-level increases in activity found at 20 °C could have driven high overall levels of capture risk in the trap, individual-level activity was not associated with trap capture vulnerability in any instance (Table 2). 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. 2015). Alternatively, selection on individual minnow's spontaneous activity may have been weakened by the design of the fisheries simulations, which replicated the later stages of fisheries capture, after the fishing gear had already been encountered by fish (Hollins et al. 2018). This may have decreased the capacity for individual fish's activity to influence susceptibility to capture, as this trait may have been more relevant in determining capture vulnerability during earlier stages in the capture process not examined in the present study (by determining encounter rate with gears, 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 where spontaneous activity is maximized, 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 fishing 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 (e.g., tendency for individual fish to approach a novel object; Klefoth et al. 2017) may have been more relevant in determining susceptibility. 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 4). This is despite traits related to foraging and exploration being thought to be particularly relevant in determining vulnerability to capture by passive gears (Hessenauer et al. 2015; Hollins et al. 2018; Klefoth et al. 2017; Koeck et al. 2019; Monk and Arlinghaus 2017a, 2017b). The negative relationship between swim performance and capture vulnerability in the trap found at 24 °C is difficult to explain, as there is no clear mechanism by which poor-swimming fish would be more likely to be caught by a trap. 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. It is possible that individual fish exhibiting the lowest swim performance at 24 °C were those experiencing the most severe effects of warm temperature acclimation and that these individuals were the furthest beyond their thermal optimum of the warm-acclimated fish. These particularly affected fish may have begun to exhibit behaviours that subsequently increased their likelihood of capture, for example by increasing the perceived benefit of food or shelter provided by the trap compared with less stressed fish.

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 a 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 maneuvering outside of the path of a pursuing trawl, the fish that 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 maneuvering outside of the path of the trawl more difficult.

To summarize, 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 nonselective 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.

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