The Role of Metabolic Phenotype in the Capacity to Balance Competing Energetic Demands

Michael J. Lawrence[1,2,*]
Hanna Scheuffele[3]
Stephen B. Beever[3]
Peter E. Holder[2]
Colin J. Garroway[1]
Steven J. Cooke[2]
Timothy D. Clark[3]
[1]Department of Biology, University of Manitoba, Winnipeg, Manitoba R3T 2N2, Canada; [2]Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada; [3]School of Life and Environmental Sciences, Deakin University, Geelong, Victoria 3216, Australia

Accepted 8/23/2022; Electronically Published 1/12/2023

ABSTRACT

Given the critical role of metabolism in the life history of all organisms, there is particular interest in understanding the relationship between individual metabolic phenotypes and the capacity to partition energy into competing life history traits. Such relationships could be predictive of individual phenotypic performances throughout life. Here, we were specifically interested in whether an individual fish's metabolic phenotype can shape its propensity to feed following a significant stressor (2-min exhaustive exercise challenge). Such a relationship would provide insight into previous intraspecific observations linking high metabolism with faster growth. Using a teleost fish, the barramundi (*Lates calcarifer*), we predicted that individuals with high standard metabolic rates (SMRs) and maximal metabolic rates (MMRs) would be faster to recover and resume feeding after exercise. Contrary to our prediction, neither SMR nor MMR was correlated with latency to feed after exercise (food was offered at 0.5, 1.5, 3, and 18 h after exercise). Only time after exercise and individual fish ID were significant predictors of latency to feed. Measurements of MMR from the same individuals (three measurements spaced 8–12 d apart) revealed a moderate degree of repeatability ($R = 0.319$). We propose that interindividual differences in biochemical and endocrine processes may be more influential than whole-organism metabolic phenotype in mediating feeding latency after exercise.

*Corresponding author; email: m_lawrence27@live.ca.

Keywords: barramundi, teleost, stress, exhaustive exercise, specific dynamic action, bold-shy continuum, individual variation.

Introduction

As anthropogenic influences continue to impact the natural world (Vitousek et al. 1997), a primary challenge for scientists is to understand the phenotypic traits of organisms that may provide resilience to environmental change (Mori et al. 2013). Because of its fundamental role in determining the performance of animals, metabolic rate has attracted much attention as a potentially holistic physiological metric for providing insight into lifetime fitness (Pettersen et al. 2016). Indeed, intraspecific metabolic phenotypes have been linked to various important life history traits, including predator avoidance capacities (Brodin 2001; Millidine et al. 2006; Krams et al. 2013; Killen et al. 2015), reproductive characteristics (Blackmer et al. 2005; Careau et al. 2009; Schradin et al. 2009; Sloat and Reeves 2014; Algera et al. 2017; Prystay et al. 2019), and bold-shy personality types (Ros et al. 2006; Careau et al. 2009, 2019; Redpath et al. 2010; Rosengren et al. 2017; reviewed in Careau et al. 2008).

Fishes have emerged as popular model organisms for examining interactions between metabolic phenotypes and performance in challenging environments and situations (e.g., hypoxia, exhaustive exercise, salinity changes, etc.; Hettler 1976; Schurmann and Steffensen 1997; Norin et al. 2016; Lawrence et al. 2019). For example, individual variation in the metabolic phenotype of juvenile barramundi (*Lates calcarifer*) conferred a differential ability among individuals to respond to various environmental challenges (Norin et al. 2016). In tilapia (*Oreochromis mossambicus*), metabolic rate played a predictive role in aggression scores and swimming activities of individuals (Ros et al. 2006). While our knowledge of these topics is improving, much work remains to understand the interrelationships between metabolic, behavioral, and ecological traits (reviewed in Metcalfe et al. 2016).

Intraspecific variation in standard (resting) metabolic rate (SMR), maximum metabolic rate (MMR), and aerobic scope (MMR − SMR) can be high in fishes after accounting for body size (e.g., Febry and Lutz 1987; Nelson and Claireaux 2005; Marras et al. 2010; Norin and Malte 2012; Norin et al. 2016). In a study of barramundi, for example, the interindividual variability in these traits was reported as 2.3-, 1.7-, and 2.2-fold, respectively (Norin et al. 2016). This suggests that there may be behavioral and ecological trait delineation in fish populations that stems from differences in metabolic phenotype

Physiological and Biochemical Zoology, volume 96, number 2, March/April 2023. https://doi.org/10.1086/722478

at the level of the individual (see Guderley and Pörtner 2010; Metcalfe et al. 2016; Ward et al. 2016). Having said that, individual metabolic traits must be consistent (repeatable) through time if metabolic phenotypes are to have an enduring influence. While the repeatability (Pearson product-moment correlation coefficient [r]) of SMR has been examined in individual fish to some degree and has shown a level of consistency ($r = 0.264–0.680$; McCarthy 2000; O'Connor et al. 2000; Cutts et al. 2001; Norin and Malte 2011; Norin et al. 2016; Reemeyer and Rees 2020), data on the repeatability of MMR and aerobic scope are scant (see Svendsen et al. 2014; Metcalfe et al. 2016; Reemeyer and Rees 2020). This knowledge gap must be filled if we are to obtain an understanding of the predictive power of using metabolic phenotypes to inform lifetime performance and resilience.

Appropriate allocation of metabolic resources toward competing demands is key to lifetime fitness (Stearns 2000). For example, exercise (and subsequent recovery) is critical in most animals for tasks such as prey capture and predator avoidance, yet it may trade off with other important energy-demanding processes, such as digestion and reproductive maturation (Scarabello et al. 1991; Jourdan-Pineau et al. 2010; Jackson et al. 2017). Indeed, meal consumption before exercise can result in decreased swimming performance in fishes, presumably as a result of blood flow and energy resources (e.g., oxygen, ATP) being diverted toward the process of specific dynamic action (the energy used during meal consumption, digestion, and assimilation; Alsop and Wood 1997; Jourdan-Pineau et al. 2010; Li et al. 2018). Theory predicts that metabolic phenotype (i.e., the magnitude of SMR, MMR, and/or aerobic scope) should govern the capacity of individuals to allocate resources to simultaneous energy-demanding processes. Given that some metabolic phenotypes have been reported to recover faster than others (Marras et al. 2010; Killen et al. 2014, 2015; Ozolina et al. 2016; Pang et al. 2020), it follows that individual metabolic phenotypes should differentially juggle the competing demands of exercise recovery and other energy-demanding processes, such as the resumption of feeding. As such, the latency of individuals to eat following exercise may be influential in setting lifetime growth rates of different metabolic phenotypes. Such energetic trade-offs among critical life history traits have rarely been examined at the individual level, but they are necessary to understand if we seek to link physiological phenotypes with life history traits and fitness.

Here, we sought to elucidate the role of metabolic phenotype in determining the capacity of individuals to accomplish two competing energy-demanding processes. Specifically, using the culturally and economically important tropical barramundi (Harrison et al. 2014), we aimed to identify which metabolic phenotypes may possess an advantage when faced with a feeding opportunity shortly after exhaustive exercise. We hypothesized that an individual's propensity to feed following exercise should be positively tied to its MMR phenotype, whereby a higher MMR should improve the capacity for simultaneous resource supply to the two demanding processes. Given the general knowledge gap concerning the repeatability of MMR in fishes (Svendsen et al. 2014; Metcalfe et al. 2016), we assessed the MMR of each individual on three occasions over a 6-wk period to determine the consistency of this phenotypic trait.

Material and Methods

Animal Care and Holding Conditions

Juvenile barramundi (*Lates calcarifer*, Bloch 1790; mean body mass ± SEM = 21.98 ± 0.53 g) were obtained from a commercial aquaculture facility (MainStream Aquaculture, Werribee, Australia) and shipped ~1 h by road to Deakin University's Queenscliff Marine Science Centre (also known as Queenscliff Marine Lab; Queenscliff, Australia, 38°16′13.5″S, 144°38′04.2″E). Fish were reared at the aquaculture facility in freshwater at 29°C and were the progeny of several adult brood stock. Fish were obtained in two cohorts (separated by 2 wk), comprising 142 animals in total, during January and February 2019. Upon arrival, each cohort of fish was divided evenly among two large freshwater tanks, each containing a static volume of water (~250 L) thermostated at 29°C (TECO TK-500, TECO US) and with vigorous aeration. Fish were allowed to settle for approximately 4 h before the seawater transition, achieved by adding a small flow through of oceanic seawater (~0.4 L min^{-1}; pumped from the mouth of Port Phillip Bay, 38°15′31.2″S, 144°38′41.9″E), commenced. Salinity increased by ~15 ppt d^{-1}, and the fish were given at least 3 d to acclimate to full-strength seawater (35 ppt) before any further handling (temperature remained at 29°C). There were no mortalities associated with the seawater transition. Fish were kept under a 12L : 12D cycle (7:00 a.m.–7:00 p.m., daylight hours) and fed ad lib. with commercial pellet food (3-mm floating barramundi pellets, Skretting Australia, Cambridge, Australia) every other day unless otherwise noted.

Following seawater acclimation, each barramundi was injected intraperitoneally with an 8-mm passive integrated transponder tag for individual identification by first lightly anesthetizing the animal (0.03 mL AQUI-S L^{-1} water) and then injecting the tag ventrally into the peritoneal cavity using a custom syringe and 16-gauge needle (Biomark, Boise, ID). Such tags have been shown to have a negligible influence on a fish's SMR 7 d after implantation (Reemeyer et al. 2019). Fish were then distributed haphazardly among nine smaller holding tanks (29 cm width × 39 cm length; ~22.5 L) in groups of ≤9 individual fish and given 6 d to recover and to continue seawater acclimation before the experiments. The tanks were part of a larger rack system, which consisted of 15 tanks in total, that shared a ~400-L sump (total system: ~750 L; held at 29°C). The sump contained a protein skimmer, a 1-kW immersion heater, and a biofilter with aeration, and all water passed through a UV sterilizer in transit to the tanks and through a particle filter immediately before returning to the sump. Each holding tank received additional aeration.

Respirometry and Maximum Metabolic Rate

The respirometry system was custom built using 15 plastic tanks (29 cm width × 39 cm length; 14.2 L; water depth: ~12 cm) covered with a buoyant and gas-impermeable liner floating on the surface (e.g., Clark et al. 2009; see fig. 1). The system was checked to ensure no oxygen exchange with the atmosphere before the experiments. This setup was selected over more traditional respirometers (e.g., Clark et al. 2013; Svendsen et al. 2016), as it allowed the fish to

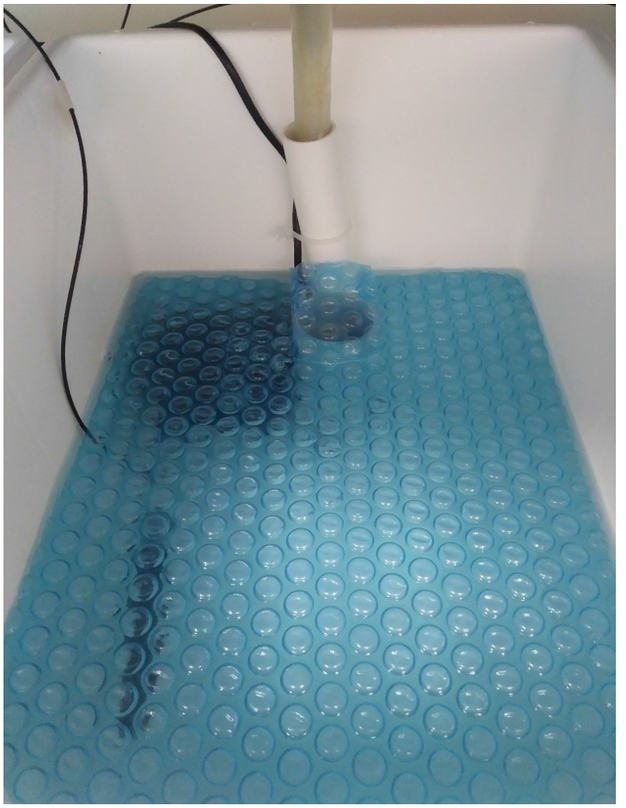

Figure 1. Image showing the respirometer setup used in experiments. The respirometer consisted of an opaque plastic container with an inflow from the reservoir system (back clear tube), an outflow (just in front of inflow), and a small circulation pump (back left). A FireSting sensor spot (PyroScience) was attached to the inside of a small piece of tubing connected to the circulation pump to ensure that oxygen levels were constantly measured. The fish was allowed to swim freely within the respirometer during the trial. A floating gas-impermeable lining was used to prevent atmospheric diffusion of oxygen into the chamber.

swim freely within the respirometer and to exhibit normal feeding behaviors. Each respirometer contained a recirculation pump with an integrated oxygen sensor (FireSting, PyroScience, Aachen, Germany). The recirculation pump with the oxygen sensor was contained entirely within the respirometer and helped to ensure sufficient water mixing during the experiments. Oxygen data were recorded from each tank every 5 s to a laptop computer running Oxygen Logger software (PyroScience). The 15-tank system was supplied by a flush pump (UNO magnetic drive pump, HCM-135LXP), which drew water from a sump tank (~400 L, 29°C) at ~45 L min^{-1} (~3 L min^{-1} per respirometer). The flush pump was manually switched off throughout the MMR screening process (see below) but, at other times, was set on a 15:30 min flush:seal cycle. Respirometer oxygen levels never dropped below 85% during the sealed cycle to avoid any confounds associated with methodically induced hypoxia. For ~0.5 h before and after each trial, the flush to each of the fish-free respirometers was ceased to determine rates of background (microbial) oxygen consumption ($\dot{M}O_2$). As in Lawrence et al. (2019), the regression between these two time points was used to correct fish $\dot{M}O_2$ values for microbial respiration through time (see Killen et al. 2021). The displacement volume of all components within the respirometer was accounted for during all $\dot{M}O_2$ calculations.

MMR was elicited using a standardized chase protocol (reviewed in Norin and Clark 2016). Individuals were chased one at a time in a circular exercise arena (~19 L, 29°C) for a total of 2 min (as per Norin et al. 2016) in five batches of ≤15 fish per day. While a 3-min chase duration has been used previously for barramundi (Norin and Clark 2016), we elected to use a 2-min duration, as preliminary trials showed that fish were largely unresponsive by the end of this time period. All fish were visibly exhausted at the conclusion of the 2-min protocol (confirmed by failure of fish to burst when their tail was gently pinched; Raby et al. 2012), at which point they were taken from the arena, weighed (in air), scanned for their passive integrated transponder tags, and then placed immediately into a respirometer. Longer air exposures were not used because we wanted to avoid possible long-term effects of bradycardia on recovery processes (e.g., Cooke et al. 2001). $\dot{M}O_2$ measurements commenced within 15 s after exercise and continued for ~30 min to ensure that MMR was recorded. Then the fish were removed, and the respirometer systems were flushed before the next batch of 15 fish. Typically, the last batch of fish for the day was left in the respirometers overnight to calculate SMR (details below).

All fish from each of the two cohorts were analyzed for their MMRs (mg O_2 min^{-1} kg^{-1}) and ranked from highest to lowest. For the first cohort of fish ($n = 70$), we selected eight fish with the highest MMR and seven fish with the lowest MMR for use in subsequent experiments. The same process was followed for the second cohort of fish ($n = 72$) 2 wk later, except we selected seven fish with the highest MMR and eight fish with the lowest MMR. We also included a group of 15 fish haphazardly selected from the middle of the high/low distribution to get a continuum of metabolic phenotypes in the feeding trials (see below).

To determine the repeatability (R) of an individual's MMR through time, we placed all 142 fish through another two of the same MMR screening protocols (as described above) at subsequent time points to give three MMR measurements per fish (technical issues resulted in some fish receiving only one [3 of 142 fish] or two [17 of 142 fish] MMR measurements). Measurement periods were separated by 8–12 d to allow fish to recover from the chasing events, with the exception of fish used in the latency to feed experiment (see below). Repeatability was then estimated using generalized linear mixed models, as described below.

Latency to Feed Following Exercise

The latency to feed trials were conducted on a total of 45 barramundi consisting of the high/low MMR and on haphazardly selected fish. Before conducting the latency to feed trials, we allowed all fish at least 6 d to recover following the preceding MMR trial. During this time, fish were fed every other day but were fasted 48 h in advance of the feeding trials. On the morning of the feeding

experiments, the focal fish were caught individually and placed in the circular exercise arena to undergo an exercise protocol, as detailed above. Following chasing, fish were weighed and quickly transferred to one of the respirometers, where MMR was immediately measured over a 30-min closed cycle, and then the flush pump was adjusted to maintain a 15 : 30 min flush : seal cycle over the rest of the experiment (18 h total). Following the chase, a single floating food pellet was added to the respirometer underneath the surface liner at discrete time intervals (0.5, 1.5, 3, and 18 h after the chase). Once the pellet was in the tank, each fish was given 5 min to consume the pellet, which was recorded as a binary response (pellet eaten? yes/no). All observations were made visually by the experimenter in proximity to the tank. This likely had no effect on feeding behaviors, as this exact procedure was used to feed the fish in their holding tanks and the animals were often waiting to accept the pellet as soon as the corner of the plastic surface liner was lifted. If the pellet was not eaten in the allotted time, it was removed from the tank using fine forceps. Our goal was to determine whether MMR phenotype played a role in metabolic recovery rate and latency to feed following exercise. All 15 fish were removed from the respirometers the following morning and returned to their holding tanks, where feed was supplied ad lib. every other day. Both the high- and low-MMR groups of fish were tested for feeding latency immediately following the second MMR determination, whereas the trial on the haphazardly selected fish occurred 10 d following the third MMR trial as a result of time constraints. Metabolic parameters were determined on this day for the haphazardly selected fish to be linked with latency to feed data, but they were not included in the repeatability assessments because we had already obtained three MMR measurements for these fish.

Data Analysis and Statistics

The last batch of (fasted) fish used for MMR screening each day was left in the respirometers overnight to obtain SMR measurements ($n = 45$), where SMR was taken as the mean of the lowest three $\dot{M}O_2$ values. Additionally, SMR was calculated overnight for individuals that did not eat any pellets in the first 3 h of the latency to feed experiments ($n = 9$; SMR calculated between 3 and 18 h after exercise). Thus, we obtained a smaller data set of SMR values to examine in parallel with the large data set of MMR values. MMR for each individual was taken as the highest $\dot{M}O_2$ value occurring over any 5-min period after exercise (which nearly always occurred during the first 5 min after exercise). In all analyses after the MMR ranking procedure, SMR and MMR were expressed in absolute terms (i.e., milligrams O_2 per minute), and mass was included as a fixed effect in statistical modeling (see below). Aerobic scope was determined for individuals for which both SMR measurements and MMR measurements existed ($n = 24$), and it was calculated as an individual's MMR minus its SMR (Clark et al. 2013; Lawrence et al. 2019). To assess the relationship between MMR and latency to feed, we used the MMR measured just before the introduction of the food pellet (e.g., at $t = 0$ h following the second MMR exercise protocol for the high- and low-MMR phenotypes). Recovery rate was also calculated just before the introduction of the food pellet as the rate of decline in $\dot{M}O_2$ over the first 15 min after exercise (i.e., linear regression of the first three $\dot{M}O_2$ measurements over time, reported as milligrams O_2 per minute per hour). We iteratively chose 15 min, as most individuals remained inactive during this time, such that $\dot{M}O_2$ tended to decline linearly rather than rise spontaneously as fish became active.

All statistical analyses were handled using R (ver. 3.5.1) and R Studio (ver. 1.3.1093). Determinations of feeding latency were fit to generalized linear mixed models using the R package brms (Bürkner 2017, 2018), an R-based interface with the programming language Stan (Stan Development Team 2020). All models used binary data (i.e., yes/no) as the response variable when assessing latency to feed at each time point. We treated individual fish ID (repeated measures of the same fish) and respirometer ID as random effects allowing intercepts to vary, with fixed effects of the model being the metabolic trait of interest (MMR, SMR, aerobic scope, or recovery rate), the amount of time that had passed following the exhaustive exercise event (i.e., 0.5, 1.5, 3, or 18 h), and the fish's body mass. We first tested for an interaction between the metabolic parameter of interest (e.g., SMR, MMR, aerobic scope) and the time after exercise and found no evidence for one. As latency to feed data were binomial, we fitted logistic regression models. R package brms fits models with Markov chains Monte Carlo. We ran four Markov chains Monte Carlo to check for model convergence and ran chains for 10,000 iterations, with a warm-up length of 5,000 iterations. The breadth and position of 95% credible intervals were used to determine whether any of the model parameters for population-level effects had a detectable influence on the fish's tendency to feed after exercise. Relationships between the various metabolic parameters were assessed using the same approach as outlined above, albeit using a Gaussian distribution; we examined the relationships between recovery rate and MMR, between recovery rate and SMR, and between MMR and SMR. SMR was always treated as the independent variable, and the fish's body mass was included in the MMR-SMR comparison as a fixed effect.

Repeatability analyses were performed using the R package brms (Bürkner 2017, 2018). Repeatability was determined by first fitting a generalized linear model to our data with the response variable of MMR, the random effects of fish ID and respirometer ID, and the fixed effect of the fish's body mass. Models were fit to a Gaussian distribution and followed the same model parameters as outlined above. Repeatability was then estimated by dividing the proportion of variance explained by fish ID by the total variance explained by the model (see Dingemanse and Dochtermann 2013).

Results

As a preface, units for 95% credible intervals for all feeding data are expressed as an increase in the probability of eating a pellet per parameter unit, which is grams for body mass; milligrams O_2 per minute for MMR, SMR, and aerobic scope; milligrams O_2 per minute per hour for recovery rate; and hours for time. Remaining parameters are unitless. For the metabolism correlations, units are expressed as the rate of increase in the dependent metabolic parameter (i.e., recovery rate or MMR) as a result of a change in the independent parameter (i.e., SMR or MMR). Parameter estimates'

95% credible intervals encompassing zero indicate a nonsignificant relationship.

Metabolic Phenotype and Latency to Feed after Exercise

The tendency of juvenile barramundi to feed following exhaustive exercise was influenced by time, whereby 15 of 42 fish consumed food 0.5 h after exercise, and this increased to 32 of 42 fish by 18 h after exercise (fig. 2). Specific parameters for all models are given in table 1. Fish ID was important in driving whether a fish fed (95% credible interval 2.75 to 9.25; fig. 3*A*), but this was not driven by MMR (95% credible interval −74.92 to 40.08; fig. 3*A*) or body mass (95% credible interval −0.10 to 1.06; fig. 3*A*). Respirometer ID had a minor impact on the tendency of fish to feed (95% credible interval 0.16 to 5.74; fig. 3*A*).

Findings were essentially identical when including SMR (fig. 3*B*) or recovery rate (fig. 3*C*), rather than MMR, in the model. For example, for the model containing SMR, the variation in propensity to feed was influenced by individual ID (95% credible interval 2.34 to 8.81; fig. 3*B*) but not by SMR (95% credible interval −350.48 to 261.78; fig. 3*B*) or body mass (95% credible interval −0.02 to 1.30; fig. 3*B*). Again, there was a minor effect of respirometer ID on the tendency of fish to feed (95% credible interval 0.10 to 5.98; fig. 3*B*). There was also no effect of aerobic scope on propensity to feed (table 1), so we limited our data presentation to SMR and MMR for simplicity.

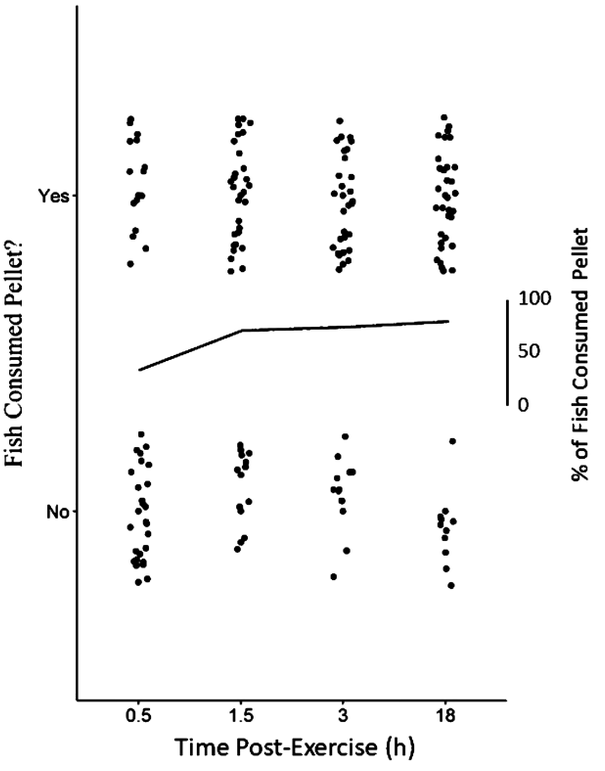

Figure 2. Depiction of the propensity of individual barramundi to feed in the first 18 h following an exhaustive exercise event. Fish were fed a single food pellet at discrete time intervals (0.5, 1.5, 3, and 18 h) after being chased to exhaustion and were observed as to whether they voluntarily consumed the pellet (yes/no). The data showed that as the fish were allowed to recover, a greater percentage of individuals elected to feed.

Interestingly, some of the variance in recovery rate could be explained by MMR (95% credible interval 1.67 to 6.00; fig. 4*A*), which positively correlated with recovery rate (MMR model estimate = 3.84). In contrast, SMR did not play a significant role in predicting recovery rate (95% credible interval −9.38 to 10.60; fig. 4*B*). Despite a visual tendency, SMR was not significantly correlated with MMR (95% credible interval −0.30 to 2.69; fig. 5). Body mass was a significant predictor of recovery rate in both the SMR–recovery rate comparison (95% credible interval 0.004 to 0.045; fig. 4*B*) and the MMR-SMR comparison (95% credible interval 0.004 to 0.010; fig. 5). Model estimates for correlative data are given in table 2.

Repeatability of Maximal Metabolic Rate

Individual-level repeatability of MMR was found to be moderate, as our repeatability estimate was 0.319 (see table 3 for model estimates). That is, there was a degree of consistency in MMR through time. Given that our models used the MMR measured from each individual immediately before the feeding latency trials, we assumed that we maximized our potential to detect a correlation between MMR and latency to feed.

Discussion

Feeding Responses after Exercise

In contrast to our predictions, MMR did not affect the likelihood of an individual fish to feed during the postexercise recovery phase. While studies have largely focused on the relationship between MMR and performance metrics, such as activity/locomotion and growth (Downs et al. 2016; reviewed in Biro and Stamps 2010; Metcalfe et al. 2016), with mixed results (Hayes et al. 1992; Ozolina et al. 2016), we are not aware of any previous attempts to link MMR to feeding behaviors. Our results highlight the complexities that exist in the relationships between metabolic traits and behavior, adding to prior work suggesting that metabolism-behavior interactions may be modulated by environmental circumstances (Killen et al. 2011, 2012).

Similarly, interindividual differences in SMR were not predictive of latency to feed after exercise in juvenile barramundi. Interestingly, it has previously been shown that juvenile barramundi with a high SMR eat more and grow faster than lower-SMR conspecifics when left undisturbed in holding tanks (Norin et al. 2016). Studies of a range of vertebrates have similarly reported that high-SMR individuals often demonstrate higher rates of risk-taking and foraging activities (Møller 2009; Huntingford et al. 2010; Killen et al. 2011; Reid et al. 2011; reviewed in Biro and Stamps 2010), yet this relationship does not always exist (e.g., Auer et al. 2015). Higher SMR is believed to necessitate a greater intake of food resources to sustain basal demands, which may impart riskier behaviors (reviewed in Metcalfe et al. 2016). The present study adds another dimension to this literature, suggesting that the positive SMR–food consumption relationship may weaken if animals encounter routine disturbances like the exercise protocol outlined here.

Table 1: Parameter estimates from modeling the likelihood of feeding following exhaustive exercise with individual metabolic phenotypes of juvenile barramundi

Parameter	Estimate	Estimate error	Lower 95% credible limit	Upper 95% credible limit
MMR:				
Group-level effects:				
Respirometer ID	2.5389	1.4605	.1567	5.7442
Fish ID	5.2579	1.6660	2.7486	9.2475
Population-level effects:				
Intercept	−8.2746	5.2736	−19.9300	.8373
Time 1.5 h	4.8861	1.2663	**2.6854**	**7.6215**
Time 3 h	5.4428	1.3878	**3.0526**	**8.4840**
Time 18 h	6.8008	1.7286	**3.9249**	**10.6653**
MMR	−16.7135	28.8402	−74.9248	40.0768
Body mass	.4175	.2930	−.0981	1.0625
SMR:				
Group-level effects:				
Respirometer ID	2.2573	1.5799	.1029	5.9828
Fish ID	4.8085	1.6863	2.3377	8.8088
Population-level effects:				
Intercept	−14.8054	6.5727	**−29.6042**	**−3.7952**
Time 1.5 h	4.2542	1.3499	**1.8520**	**7.1246**
Time 3 h	4.9358	1.4815	**2.3414**	**8.1884**
Time 18 h	6.5759	1.8895	**3.4706**	**10.8560**
SMR	−37.7872	151.8912	−350.4769	261.7816
Body mass	.5506	.3307	−.0174	1.3027
Aerobic scope:				
Group-level effects:				
Respirometer ID	2.1880	1.5448	.1024	5.8531
Fish ID	4.8617	1.7141	2.3662	9.0294
Population-level effects:				
Intercept	−14.7726	6.1898	**−28.7773**	**−4.4726**
Time 1.5 h	4.2975	1.3576	**1.8978**	**7.2140**
Time 3 h	4.9658	1.4681	**2.3870**	**8.1553**
Time 18 h	6.6066	1.8685	**3.4862**	**10.7780**
Aerobic scope	−26.6824	44.1025	−123.1606	55.4778
Body mass	.6894	.4238	−.0284	1.6514
Recovery rate:				
Group-level effects:				
Respirometer ID	2.5563	1.4734	.1741	5.7927
Fish ID	5.2861	1.7015	2.7503	9.3163
Population-level effects:				
Intercept	−8.7085	5.2069	−20.3488	.4686
Time 1.5 h	4.8854	1.2668	**2.6666**	**7.6346**
Time 3 h	5.4391	1.3746	**3.0710**	**8.4613**
Time 18 h	6.8044	1.7331	**3.9252**	**10.7148**
Recovery rate	−1.9718	5.2815	−12.8802	8.3263
Body mass	.3271	.2209	−.0587	.8192

Note. Modeling was conducted using a Bayesian approach with a Markov chain Monte Carlo. Statistically significant effects of population-level effects were determined from nonzero 95% credible intervals, and they are shown in bold. Units for credible intervals are expressed as an increase in the probability of eating a pellet per parameter unit, which is grams for body mass; milligrams O_2 per minute for standard metabolic rate (SMR), maximal metabolic rate (MMR), and aerobic scope; milligrams O_2 per minute per hour for recovery rate; and hours for time. Remaining parameters are unitless.

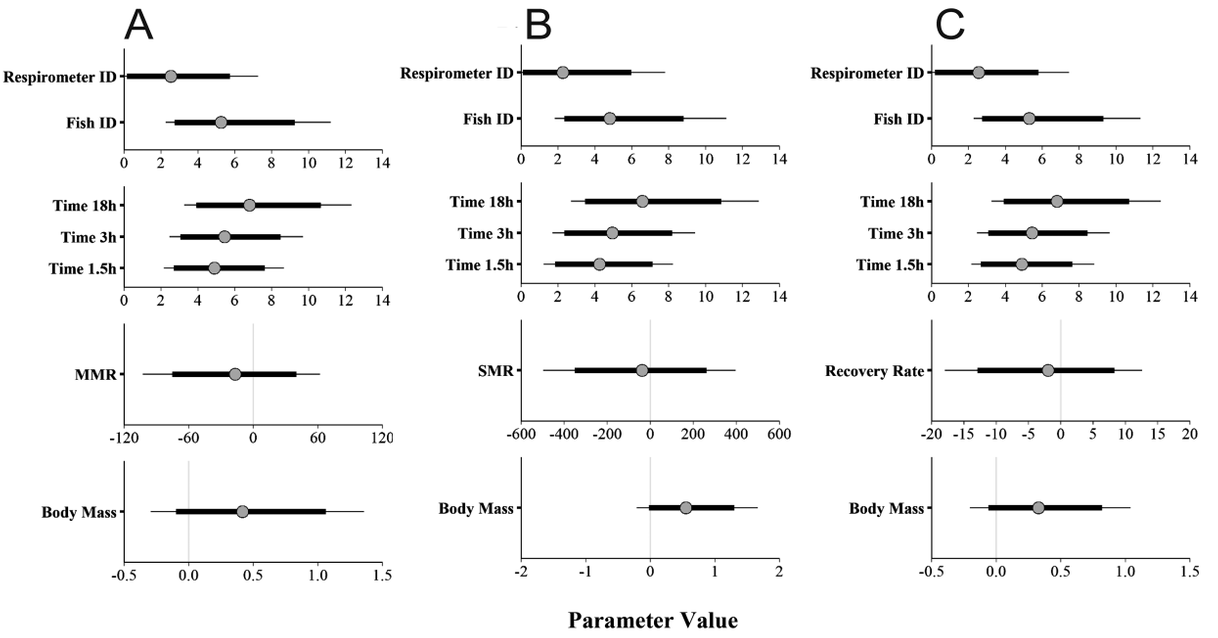

Figure 3. Visualization of the parameter estimates for the Markov chain Monte Carlo model looking at the relationship between an individual's absolute maximal metabolic rate (MMR; *A*), standard metabolic rate (SMR; *B*), or recovery rate (*C*) and the propensity to feed following exhaustive exercise at three distinct time points (1.5, 3, and 18 h). Parameter estimates include group-level effects of individual fish ID and respirometer ID as well as population-level effects, including the time after exercise; the individual's MMR, SMR, or recovery rate; and the fish's body mass. The circles represent the posterior mean value for the given parameter, while the thick and thin lines represent the 95% and 99% credible intervals of the model, respectively. For population-level effects (i.e., time, body mass, and metabolic parameter), 95% credible intervals of parameter estimates overlapping zero represent nonsignificance of that parameter in the model. Units for parameter values are expressed as an increase in the probability of eating a pellet per parameter unit, which is grams for body mass, milligrams O_2 per minute for SMR and MMR, milligrams O_2 per minute per hour for recovery rate, and hours for time. Remaining parameters are unitless.

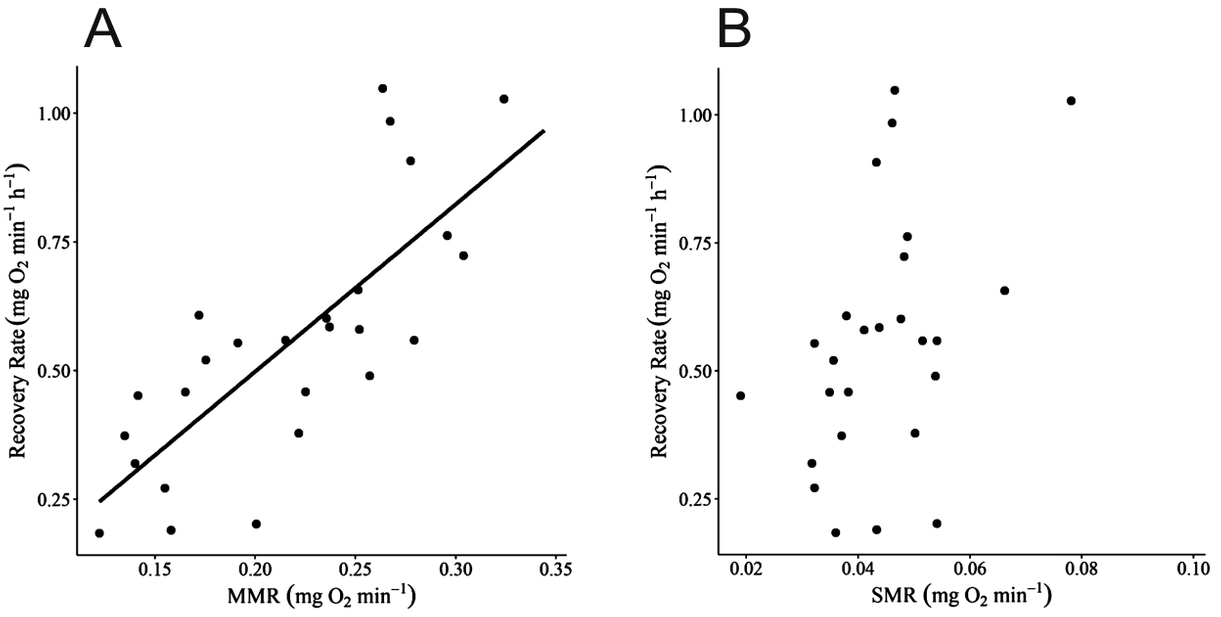

Figure 4. Linear relationships between a barramundi's maximal metabolic rate (MMR) and its recovery rate following a bout of exhaustive exercise (i.e., 2-min chase; *A*) and between a barramundi's standard metabolic rate (SMR) and its recovery rate (*B*). Each point represents an individual fish. The linear relationship between the two parameters is represented by the line. A significant relationship exists between MMR and recovery rate (Bayesian model 95% credible interval: 1.67 to 6.00 increase in MMR per change in recovery rate). Body mass was a significant predictor of recovery rate in the SMR versus recovery rate model (Bayesian model 95% credible interval: 0.004 to 0.045 increase in recovery rate per change in body mass).

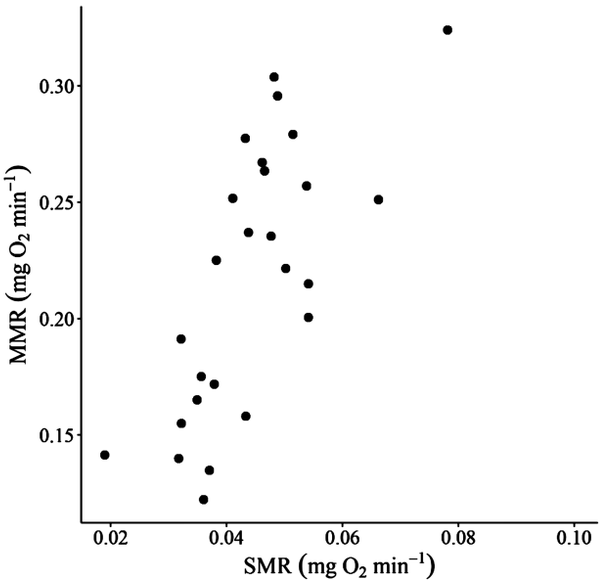

Figure 5. Linear relationship between a barramundi's standard metabolic rate (SMR) and maximal metabolic rate (MMR). Each point represents an individual fish. No significant relationship was found between the two parameters (Bayesian model 95% credible interval: −0.30 to 2.69 increase in MMR per change in SMR). Body mass was a significant predictor of SMR in the model (Bayesian model 95% credible interval: 0.004 to 0.010 increase in recovery rate per change in body mass).

Indeed, periods of stress are thought to add further complexity to physiology-behavior interactions (e.g., Johnstone et al. 2012; Sopinka et al. 2015).

As specific dynamic action requires a large metabolic/oxygen allocation (Alsop and Wood 1997; Jordan and Steffensen 2007; Sandblom et al. 2014; Tuong et al. 2018; reviewed in Secor 2009), an expedited recovery from exercise would presumably help to free up metabolic resources for feeding/digestion activities. Theoretically, slower recovery following exhaustive exercise could be associated with negative fitness consequences (Priede 1977). While information on individual MMR- and SMR-recovery dynamics is scant, higher resting metabolic rates are thought to be associated with a quicker recovery from exercise (Hochachka 1961; Cooke et al. 2007; Marras et al. 2010) and with faster meal processing (Millidine et al. 2009). The mechanisms underlying these effects are unknown (Cooke et al. 2007), but they likely result from having an inherently higher basal capacity to deal with perturbations (e.g., higher basal expression of enzymes and transporters, overall reaction rates, better cardiovascular function; see Killen et al. 2016). Our results show that metabolic recovery dynamics did not play a role in altering feeding latency in juvenile barramundi, although we did find that higher-MMR fish had faster recovery rates even once body mass was accounted for in the model (fig. 4*A*). Future work should aim to address the specific physiological mechanism(s) linking an individual's metabolic rate with its recovery processes to elucidate the role of metabolic phenotype in modulating behavioral responses after a stressor.

As expected, time was a significant factor affecting feeding likelihood in all our models, whereby more fish fed as the recovery period progressed (fig. 2). Recovery from an exhaustive exercise event involves a prolonged elevation in oxygen uptake rates (i.e., excess postexercise oxygen consumption [EPOC]; Scarabello et al. 1991), with available metabolic resources being allocated toward the reestablishment of internal homeostasis and steady-state conditions (reviewed in Wood 1991; Milligan 1996). Indeed, recovery from such events generally takes the form of an exponential decay and can take several hours or days to fully complete (Scarabello et al. 1991; Raby et al. 2015; Clark et al. 2017; Lawrence et al. 2019). As recovery proceeds, a greater proportion of an animal's metabolic scope is made available for activities such as feeding. This likely explains at least part of the time-course effect

Table 2: Parameter estimates from modeling the relationships between recovery rate, maximal metabolic rate (MMR), and standard metabolic rate (SMR) in juvenile barramundi

Relationship, parameter	Estimate	Estimate error	Lower 95% credible limit	Upper 95% credible limit
Recovery rate vs. MMR:				
Intercept	−.1320	.1364	−.4053	.1393
MMR	3.8367	1.0973	**1.6688**	**6.0026**
Body mass	−.0070	.0110	−.0288	.0147
Recovery rate vs. SMR:				
Intercept	.0000	.1831	−.3639	.3600
SMR	.6687	5.0810	−9.3844	10.6001
Body mass	.0249	.0104	**.0044**	**.0452**
MMR vs. SMR:				
Intercept	.0200	.0273	−.0340	.0736
SMR	1.2101	.7630	−.2965	2.6927
Body mass	.0068	.0016	**.0037**	**.0100**

Note. Modeling was conducted using a Bayesian approach with a Markov chain Monte Carlo. Statistically significant effects of population-level effects were determined from nonzero 95% credible intervals, and they are shown in bold. Units for 95% credible intervals are expressed as an increase in recovery rate or in MMR per unit of MMR or SMR, where units for MMR and SMR are expressed in milligrams O_2 per minute and recovery rate is expressed in milligrams O_2 per minute per hour. In the case of MMR modeling versus SMR modeling, this included body mass as a fixed effect.

Table 3: Parameter estimates from modeling the repeatability of maximal metabolic rate (MMR) of juvenile barramundi

Parameter	Estimate	Estimate error	Lower 95% credible limit	Upper 95% credible limit
Group-level effects:				
Fish ID	.0042	.0028	.0002	.0101
Respirometer ID	.0089	.0029	.0041	.0154
Population-level effects:				
Intercept	.0332	.0062	**.0210**	**.0453**
Body mass	.0087	.0002	**.0082**	**.0091**

Note. Modeling was conducted using a Bayesian approach with a Markov chain Monte Carlo. Statistically significant effects of population-level effects were determined from nonzero 95% credible intervals, and they are shown in bold. Units for 95% credible intervals are expressed as a change in MMR (mg O_2 min^{-1}) explained by fish ID (unitless), respirometer ID (unitless), and body mass (g). Repeatability of MMR was calculated as 0.319 (see "Results").

on feeding responses seen in the present study. Comparable studies are lacking, but stress can result in a cessation of feeding activities in vertebrates (reviewed in Carr 2002; Bazhan and Zelena 2013). In fishes, specifically, this has been well documented in salmonids (Wedemeyer 1976; Pickering et al. 1982; Mesa and Schreck 1989; McCormick et al. 1998). In largemouth bass (*Micropterus salmoides*), there was a significantly longer time to resume feeding after angling (~8–15 h) when compared to nonangling controls (~0.3 h; Siepker et al. 2007). Moreover, shoaling confers an antipredator and risk-dilution benefit (Queiroz and Magurran 2005; Lawrence et al. 2018; reviewed in Pitcher 1986), and prior work has shown that latencies to feed in several species of teleosts are markedly higher in isolated fish than in groups of fish (Saxby et al. 2010). Neuroendocrine secretions from the hypothalamus-pituitary-interrenal/adrenal axis have been found to be anorexigenic, thereby suppressing appetite in vertebrates and suggesting that hormonal changes may be an important regulator of feeding responses (Gregory and Wood 1999; Bernier and Peter 2001; Carr 2002; Bernier et al. 2004; Tanaka et al. 2009; reviewed in Bernier 2006; Maniam and Morris 2012). Some of these processes may have mediated feeding latency in the present study as well as contributed to the lack of feeding of a minority of barramundi even at 18 h after exercise (fig. 2).

Repeatability of Maximal Metabolic Rate

The values of MMR (and SMR) measured in the present study align well with those reported previously for juvenile barramundi (Norin et al. 2016). MMR in the present study showed a moderate level of repeatability. While repeatability of MMR has been reported to at least a low level in teleosts (McCarthy 2000; O'Connor et al. 2000; Cutts et al. 2001; Norin and Malte 2011; Svendsen et al. 2014; Norin et al. 2016) and vertebrates at large (reviewed in Nespolo and Franco 2007), consistency in MMR can degrade through time (Seppänen et al. 2010; Norin and Malte 2011; White et al. 2012) and in response to environmental challenges (O'Connor et al. 2000; Norin et al. 2016; Reemeyer and Rees 2020). A previous study on juvenile barramundi showed that repeatability in MMR was detectable but not as strong as repeatability in SMR (Norin et al. 2016). As in our work, Norin et al. (2016) found a moderate level of repeatability in the MMR of juvenile barramundi (Kendall's concordance coefficient = 0.361). This MMR repeatability appeared to break down under the addition of various environmental stressors, suggesting that environmental factors are likely important in altering MMR repeatability in fishes. Our results suggest that while there may be a degree of temporal repeatability in MMR, care must be taken when attributing a single metabolic measurement to other physiological or behavioral metrics, especially if these measurements are temporally separated or occur while animals are experiencing additional stressors. In general, there are many performance metrics measured in biology that require further validation of their repeatability through time (e.g., Roche et al. 2020), especially when the goal is to link interindividual physiological/behavioral parameters with fitness.

Acknowledgments

We would like to thank the researchers and staff at the Queenscliff Marine Lab for the support they provided in making this project possible. Funding for this project was provided by Deakin University, an Australian Research Council Future Fellowship to T.D.C. (FT180100154), Mitacs through the Mitacs Globalink Research Award (application IT12763), and a Carleton University Student Travel/Research Bursary awarded to M.J.L. M.J.L. was also supported by a Government of Ontario Queen Elizabeth II Graduate Scholarship in Science and Technology, and S.J.C. and M.J.L. were further supported by the Natural Sciences and Engineering Research Council.

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