

Does shelter influence the metabolic traits of a teleost fish?

Emmanuelle Chrétien¹  | Steven J. Cooke²  | Daniel Boisclair¹ 

¹Département de Sciences Biologiques, Université de Montréal, Montréal, Québec, Canada

²Fish Ecology and Conservation Physiology Laboratory, Department of Biology and Institute of Environmental and Interdisciplinary Science, Carleton University, Ottawa, Ontario, Canada

Correspondence

Emmanuelle Chrétien, Département de Sciences Biologiques, Université de Montréal, Campus MIL, 1375 Avenue. Thérèse-Lavoie-Roux, Montréal, QC H2V 0B3, Canada.
Email: emmanuelle.chretien@umontreal.ca

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Abstract

Availability of shelter is an important component of habitat selection for animals as it can influence survival (protection against harsh physical conditions and predation) and growth (energy acquisition and expenditure). Few studies address the effect of shelter on metabolic expenditures associated with non-mechanical tasks (excluding station holding or movement). The main goal of this study was to investigate the influence of shelter use on metabolic traits of smallmouth bass (*Micropterus dolomieu*) from two populations (Kiamika River and Lake Long). Respirometry experiments on smallmouth bass were conducted to measure standard metabolic rate (SMR), resting metabolic rate (RMR), aerobic scope (AS), recovery time (RT) and excess post-exercise oxygen consumption (EPOC) in the presence or absence of shelter. The presence of shelter did not affect most metabolic traits, except for RMR, which was reduced in the presence of shelter for Lake Long fish. The results of this study also show that larger fish had lower SMR in the presence of shelter than when it was absent. When accounting for social hierarchy, there were no differences in most metabolic traits in dominant or subordinate fish in the presence or absence of shelter, except for RT, which was significantly lower in the presence of shelter for dominant fish. These results do not support the existence of an unequivocal relationship between individual metabolic traits and the presence of shelter. If physiological motives may influence the use of shelter, sheltering in itself might not have important consequences on energy expenditures required for non-mechanical tasks.

KEYWORDS

energy expenditure, freshwater fish, habitat selection, recovery time, refuge

1 | INTRODUCTION

The presence of shelter at a location has important implications for fitness and is therefore a key determinant of habitat selection for animals (Fukui, 2001; Michaels & Preziosi, 2015). Shelter use improves survival by providing protection from harsh physical conditions and predators (Hughes & Ward, 1993; Millidine *et al.*, 2006; Moreno *et al.*, 1996; Pollard, 2006; Tufto *et al.*, 1996) and augments reproductive success by increasing progeny survival (Narvarte *et al.*, 2013; Parsons & Chao, 1983). Shelter use also has consequences for growth (Finstad *et al.*, 2007; Walsh & Downie, 2005), but its net effect

depends on the balance between energy acquisition and expenditure (Brownscombe *et al.*, 2017; Lind & Cresswell, 2005).

Sheltering is generally thought to reduce energy acquisition because of a “hide and seek trade-off” between curtailed foraging when hiding from harsh physical conditions and predators, and improved foraging when seeking prey (Krause *et al.*, 2000; Lind & Cresswell, 2005). Some animals may incur starvation risks if sheltering limits time spent foraging (Hughes & Ward, 1993; Krause *et al.*, 2000; Lind & Cresswell, 2005). Yet, other animals may augment their foraging efficiency by sheltering (*e.g.*, ambush predators: Kevan & Greco, 2001; Tsairi & Bouskila, 2006). Some animals try to maximize

energy acquisition resulting from the hide and seek trade-off using habitat edges (Fagan *et al.*, 1999). The consequences of sheltering on energy acquisition may depend on animal life stage, feeding strategy and food availability (Ahrenstorff *et al.*, 2009; Hafs *et al.*, 2014; Krause *et al.*, 1998; Krause *et al.*, 2000).

Sheltering is also expected to reduce energy expenditure (Lind & Cresswell, 2005). In particular, sheltering may reduce an animal's energy expenditure associated with conducting mechanical tasks (station holding or movement; *e.g.*, swimming) in a fluid environment. In energetically costly landscapes like rivers, drift-feeding fish do station holding on coarse substrate relative to their size to minimize costs of locomotion and maximize food intake (Fausch, 1984; Hafs *et al.*, 2014). Sheltering may also reduce energy expenditure incurred by non-mechanical tasks such as maintaining the physiological integrity of animals (*e.g.*, thermoregulation: Beck & Jennings, 2003; Seebacher & Alford, 2002) or replacing otherwise energetically demanding activities (*e.g.*, camouflage, vigilance, alertness: Lind & Cresswell, 2005; Millidine *et al.*, 2006). No matter if animals seek shelter to lower energy expenditures (*e.g.*, station holding or movement) or if sheltering has consequences on their physiology (*e.g.*, reduce metabolic costs), this relationship between energy expenditure and sheltering merits further investigation.

Energy expenditures incurred by non-mechanical tasks are largely studied by estimating standard metabolic rate (SMR), the minimal energy expenditure required to sustain the life of a post-absorptive ectotherm, like a fish, at a given temperature (Chabot *et al.*, 2016; Clark *et al.*, 2013; Fry, 1971). Resting metabolic rate (RMR) is another baseline measure of metabolism that may include low levels of spontaneous activity (Burton *et al.*, 2011; Jobling, 1994). A number of studies have identified that, for given physical and chemical conditions, shelter may reduce SMR or RMR of fish by 8–30% (Finstad *et al.*, 2004; Fischer, 2000; Millidine *et al.*, 2006; Norin *et al.*, 2018) even when mechanical tasks and intraspecific and interspecific interactions are absent. Shelters may replace the need for camouflage or vigilance, which may have associated metabolic costs, to remain undetected (Millidine *et al.*, 2006). Relatedly, in the absence of shelter, an increase in metabolic costs could be expected because of increased vigilance rates and mental alertness (Lind & Cresswell, 2005). This further emphasizes the importance of shelter for fish fitness as, everything else being similar, a reduction in SMR or RMR increases energy availability for growth and reproduction. Yet, it may be hypothesized that other physiological traits may improve our understanding of the importance of shelter on animal fitness.

Aerobic scope (AS) is the difference between maximum metabolic rate (MMR: the maximum energy expenditure that can be incurred by an animal; Fry, 1971; Norin & Clark, 2016) and SMR. AS corresponds to the animal's metabolic range for aerobic activities (Fry, 1971). Thus, AS may have long-term consequences on growth and reproduction. This perspective is consistent with the suggestion that AS may be a useful fitness indicator for fish (Claireaux & Lefrançois, 2007; Farrell *et al.*, 2008). High MMR and/or low SMR may allow fish to have a larger scope for aerobic activity above

maintenance levels, depending if this fish's AS is more driven by MMR or SMR (Clark *et al.*, 2013). The potential for shelter to increase AS through its effect on SMR has important implications for our understanding of the determinants of habitat selection, especially for fish.

Recovery time (RT) represents the delay for metabolic rates to return to SMR from exhaustive exercise, and excess post-exercise oxygen consumption (EPOC) is the amount of oxygen required to recover from MMR (Hancock & Gleeson, 2008). Long RT and high EPOC constitute metabolic traits that can limit an animal's capacity to resume or perform repeated mechanical tasks and thus have important fitness consequences (Zeng *et al.*, 2010). It has been shown that RT correlates positively with vigilance in fish, suggesting that energy expenditure incurred by vigilance increases RT after exercise (Killen *et al.*, 2015). Because sheltering may replace the need for vigilance, it might be hypothesized that shelter use may reduce RT. In an experiment on lizard metabolic recovery, Hailey *et al.* (1987) observed that lizards (*Podarcis* spp.) recovering from exercise used shelters for longer durations than unexercised lizards. It is unclear if exhausted lizards used shelter longer because they did not recover enough to engage in new activity or if sheltering was beneficial for their recovery. These studies nevertheless lead to the hypotheses that shelter use may affect RT and EPOC.

The main objective of this study was to quantify the effects of the presence of shelter on five metabolic traits in fish: SMR, RMR, AS, RT and EPOC. Because metabolic traits may vary within species because of population-level physiological adaptations to local environmental conditions (Burton *et al.*, 2011; Eliason *et al.*, 2011; Metcalfe *et al.*, 2016), we quantified the effects of the presence of shelter on metabolic traits of smallmouth bass (*Micropterus dolomieu*, Lacépède) collected from two populations with contrasting ecosystems (*i.e.*, a river and lake). We hypothesized that: (a) SMR and RMR would be lower in the presence of shelter, (b) AS would be higher in the presence of shelter, (c) RT and EPOC would be reduced in the presence of shelter and (d) the effects of shelter on metabolic traits of fish from the two populations would be similar.

2 | MATERIALS AND METHODS

2.1 | Study species

We studied the effects of the presence of shelter on metabolic traits of smallmouth bass from a river (Kiamika River; 46.61631, –75.21021) and a lake (Lake Long; 45.99755, –74.00023) situated in the Laurentians region (Quebec, Canada). Smallmouth bass naturally dwell in rivers and lakes, which provides the opportunity to test individuals of the same species that differ in the energetic challenges they face in their natural habitat. These fish are also known to use submerged structures (*e.g.*, sunken logs, big rocky substrate, macrophytes) that serve as shelter in rivers, lakes and reservoirs (Coble, 1975; Warren, 2009), but the effect of such structures on SMR, RMR, AS, RT and EPOC remains to be tested.

2.2 | Fish capture and holding

Smallmouth bass from the Kiamika River and Lake Long were captured by angling using barbless circle hooks to minimize injuries (Cooke & Suski, 2005) between 25 June and 3 August 2018. All fish (except one individual from Lake Long) were captured within 5 m of structures that could be used as shelter (e.g., logs, emergent plants and rocks; Figure 1). We transported the fish captured from the Kiamika River by truck to Station de biologie des Laurentides (SBL) affiliated to Université de Montréal in insulated containers filled with oxygenated river water (175 km, c. 2.5 h drive). The use of insulated containers ensured water temperature did not vary during transport, and dissolved oxygen was maintained at air saturation (>95%) with air-bubblers connected to a deep cycle battery. Lake Long is on SBL territory, and thus we transported the fish captured in that lake by boat to the laboratory in the same type of containers (c. 500 m, 15 min ride). All fish were given a tag with visual implant elastomer (Northwest Marine Technology, Anacortes, WA, USA) for later identification of individuals for respirometry experiments.

Holding conditions consisted in two large opaque flow-through tanks ($2.1 \times 0.6 \times 0.6$ m, 0.7 m^3 total, 0.6 m^3 of water) that could be separated in three sections with dark mesh dividers. A maximum of eight fish were held in each tank at the same time, and dividers were added to separate fish by size and population. Holding tanks were continuously supplied with filtered and UV-treated fresh water pumped from Lake Croche (adjacent to the laboratory on SBL territory), at a rate of $0.14 \text{ m}^3 \text{ h}^{-1}$, which allowed complete water replacement every 4 h. Dissolved oxygen was maintained at air saturation (>95%) with a recirculating pump and air-bubblers. Acclimation temperature was set at 20°C , which corresponds to the average

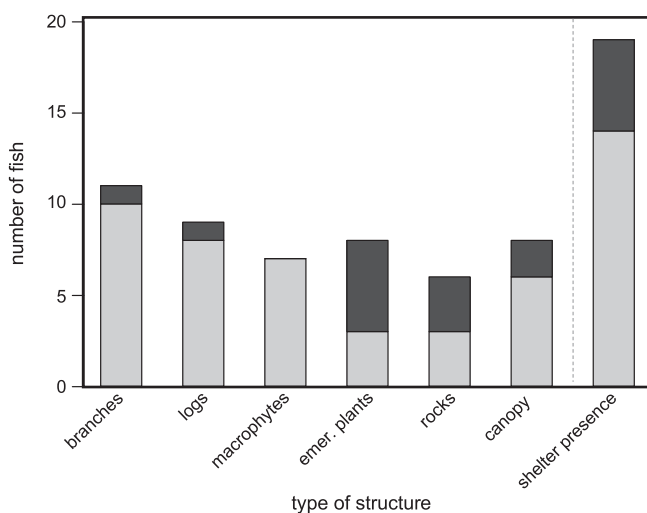


FIGURE 1 Type of sheltering structures found near smallmouth bass *Micropterus dolomieu* capture locations in the Kiamika River (grey) and Lake Long (black). Each bar represents the number of fish captured near each type of structure, and the far right bar shows the total number of fish captured near any sheltering structure (□) Kiamika and (■) Long

temperature measured in smallmouth bass locations in the Kiamika River for a separate telemetry study (unpublished data), and is comprised within the summer thermal regime of both populations. Water temperature was maintained at 20°C by adjusting the water intake level in the lake (Table 1). Fish were held at an ambient light regime (14 h day/10 h night). Large opaque plastic tubes (30 cm long, 10 cm in diameter) were available for fish to hide in holding tanks (one tube per fish). Fish were fed small minnows daily, but were starved for 48 h before respirometry experiments. All fish were held for 3 or 4 days before the first respirometry experiment was conducted.

2.3 | Respirometry experiments

Fish metabolic rates were calculated using estimates of oxygen consumption rates, which are taken to represent accurate measures of overall aerobic metabolism (Cech, 1990; Fry & Hart, 1948). Oxygen consumption rates ($\dot{M}\text{O}_2$: $\text{mg O}_2 \text{ h}^{-1}$) were estimated using intermittent flow-through respirometry equipment and software (Loligo Systems, Tjele, Denmark). The respirometry set-up comprised four rectangular chambers ($37.5 \times 14.7 \times 12.7$ cm; chamber + tubing volume: 5.45 l) submerged in large coolers (hereafter water basin) ($78 \times 33 \times 36$ cm, 80 l of water) supplied constantly with filtered and UV-treated fresh water. Each chamber was fitted with two sets of air-tight tubing and water pumps, the first forming a closed circulation loop on which an oxygen probe was connected, and the second allowing a complete flushing and refreshing of water inside the chambers. Flush pumps were automated to run for 7 min of every 12 min loop. Dissolved-oxygen levels were maintained above 80% at all times with the constant supply of fresh water and air-bubblers in the water basin. Temperature in the water basin was controlled with a Pt100 temperature probe and TMP-REG instrument (Loligo Systems, Tjele, Denmark) relayed to a hot and a cold water bath. Water temperature was held at 20°C during all respirometry experiments.

The effect of shelter on SMR, RMR, AS, RT and EPOC was tested by conducting respirometry experiments while any given fish was held in a chamber covered (treatment “with shelter”) or not covered (treatment “without shelter”) with the same type of plastic tube as available in holding tank. We assigned treatment order randomly, and respirometry experiments conducted for a given fish under different treatments were separated by 3 days, during which fish were returned to their holding tank. All but four fish (two from each population) were tested in both conditions (presence or absence of shelter). One trial

TABLE 1 Holding conditions of smallmouth bass *Micropterus dolomieu* at Station de biologie des Laurentides (Quebec, Canada)

Variable	Basin 1	Basin 2
Water temperature ($^\circ\text{C}$)	19.8 ± 0.5	19.7 ± 0.5
Dissolved oxygen (mg l^{-1})	8.7 ± 0.3	8.7 ± 0.2
Dissolved oxygen (% air saturation)	98.8 ± 2.3	99.0 ± 2.0

Note. Water temperature and dissolved oxygen were measured twice daily during summer 2018. For each variable, values presented are mean \pm S.D.

involving two fish was interrupted by a power outage because of a storm. Two fish also had to be removed because they were fed by mistake before the trial. The final data set of this study comprises 36 observations on 14 and 6 smallmouth bass from the Kiamika River and Lake Long, respectively.

Each respirometry experiment started mid-day (c. between noon and 3 pm) with a 3:30 min chase +1 min air exposure protocol to induce fish exhaustion following the method described in Roche *et al.* (2013). Chase duration was set to 3:30 min after a pilot experiment on a different sample of smallmouth bass from the two study populations. Recording of oxygen consumption started immediately after transferring the fish into the chambers and continued until oxygen consumption stabilized. Respirometry experiments lasted 21 ± 2 h (mean \pm S.D.). Within an hour before the onset – and after the termination – of each respirometry experiment, background oxygen consumption ($\dot{V}O_2$) was recorded in the empty chamber by a single 20 min long measurement. During the experiments, fish were exposed to the same ambient light regime (14 h day/10 h night) as during holding. After experiments, fish were euthanized with clove oil. This research was conducted with the approval of Université de Montréal's animal care committee (CDEA 18-032) and Canadian Council on Animal Care.

2.4 | Calculations of metabolic traits

$\dot{V}O_2$ was subtracted from $\dot{M}O_2$ measurements, assuming a linear change in $\dot{V}O_2$ over time. We adjusted metabolic rates ($\dot{M}O_{2adj}$) to the mean body mass of our sample (0.152 kg) using the slope b of the log–log relationship between $\dot{M}O_2$ and mass (Equation 1, Steffensen *et al.*, 1994; Ultsch, 1995). There was no interacting effect of population on the log–log relationship between $\dot{M}O_2$ and mass ($p_{pop} \times mass = 0.829$ and $p_{pop} \times mass = 0.293$ for SMR and MMR, respectively); thus the Kiamika River and Lake Long fish shared the same slopes b of increase in $\dot{M}O_2$ with mass (SMR: $b = 0.810$, $R^2_a = 0.958$; MMR: $b = 0.785$, $R^2_a = 0.857$).

$$O_{2adj} = (\text{mean fish mass})^{b-1} \times (\text{individual fish mass})^{1-b} \times \text{individual fish } O_2 \quad (1)$$

We estimated SMR ($\text{mg } O_2 \text{ kg}^{-1} \text{ h}^{-1}$) using the 0.2 quantile of the $\dot{M}O_2$ data with the package *fishMO2* in R (Chabot, 2016; Chabot *et al.*, 2016; R Foundation for Statistical Computing, 2018). SMR was estimated over a distribution of, on average, 47 $\dot{M}O_2$ values (from 21 to 73 $\dot{M}O_2$ values). The range of data used for its calculation started when $\dot{M}O_2$ stabilized to a minimum level. In this study, this minimum level generally occurred during the night and ended at sunrise, the moment at which fish activity and respiration started to rise. If the effect of shelter on metabolism requires that an individual be visually hidden, it may be hypothesized that the effect of shelter on SMR estimated during the night (when it is dark) may be difficult to assess. We estimated RMR as the minimum metabolic rate during daytime (after 07.30 hours until the end of the experiment)

using the same 0.2 quantile method. RMR was determined over a distribution of, on average, 13 $\dot{M}O_2$ values (from 4 to 33 $\dot{M}O_2$ values). MMR ($\text{mg } O_2 \text{ kg}^{-1} \text{ h}^{-1}$) was estimated as the highest rate of oxygen consumption recorded over any 12 min loop. We calculated AS ($\text{mg } O_2 \text{ kg}^{-1} \text{ h}^{-1}$) as the difference between MMR and SMR. RT was the duration (in minutes) required until $\dot{M}O_2$ levels stabilized to SMR. EPOC ($\text{mg } O_2 \text{ kg}^{-1}$) is the amount of oxygen required to recover from MMR and was calculated as the area under the $\dot{M}O_2$ curve estimated by the sixth-order polynomial recovery function, until the values of the curve were equal to SMR (Killen *et al.*, 2014).

2.5 | Statistical analyses

All data analyses were computed in R v. 3.5.1 (R Foundation for Statistical Computing, 2018). We used linear mixed models (LMMs) with the package *lme4* (Bates *et al.*, 2014) to test the effects of shelter and population on all metabolic traits. LMMs are appropriate tools to deal with non-independence in data such as repeated measures on the same individual (Zuur *et al.*, 2009). Fish ID and chamber number were included as potential random effects. Fish body mass, experimental order and all two-way interaction terms were included as fixed effects in case they contributed to variation in metabolic traits, but dropped from models if non-significant. For each metabolic trait, we created a full model with all descriptors and their interaction, as well as both random effects. First, the best random structure was selected based on the smallest AIC, then the fixed effects component was simplified by backward elimination (Zuur *et al.*, 2009). In all cases, the only random effect retained in models was fish ID. For each model, marginal R^2 (R^2_m : variance explained by fixed effects) and conditional R^2 (R^2_c : variance explained by fixed and random effects) were obtained from the models fitted through restricted maximum likelihood analysis. The difference between R^2_c and R^2_m for each model represents variability among individual fish. Model assumptions were confirmed by a visual inspection of residual-fits plots.

3 | RESULTS

Metabolic traits varied by 10% (EPOC) to 38% (AS) among combinations of treatments and populations (Table 2). SMR of smallmouth bass from Lake Long was 20% higher than that of Kiamika River fish ($P < 0.001$; Figure 2) but did not vary with the presence of shelter ($P = 0.709$; Table 3). Despite metabolic rates being adjusted to fish mass, SMR was significantly affected by the interaction between fish mass and treatment ($P = 0.021$; Table 3): there was no relationship between SMR and mass in the treatment with shelter, whereas SMR increased with fish mass in the absence of shelter (Supporting Information Table S1; Supporting Information Figure S1 in Appendix S1). SMR was negatively related to experiment order ($P = 0.034$; Table 3; Supporting Information Table S1): rates were on average 6% lower during the second experiment. RMR was 18% higher for fish from Lake Long than for fish from the Kiamika River ($P < 0.001$;

TABLE 2 Metabolic traits of smallmouth bass *Micropterus dolomieu* estimated by respirometry experiments for each combination of treatments and populations (mean \pm standard error)

Response Variable	Kiamika		Long	
	With shelter	Without shelter	With shelter	Without shelter
SMR (mg O ₂ kg ⁻¹ h ⁻¹)	98.43 \pm 9.83	94.43 \pm 9.95	115.68 \pm 14.00	116.00 \pm 10.81
RMR (mg O ₂ kg ⁻¹ h ⁻¹)	101.63 \pm 10.02	98.98 \pm 12.64	114.12 \pm 13.57	124.15 \pm 14.52
MMR (mg O ₂ kg ⁻¹ h ⁻¹)	285.27 \pm 48.90	296.83 \pm 48.70	242.01 \pm 57.75	260.35 \pm 40.39
AS (mg O ₂ kg ⁻¹ h ⁻¹)	186.84 \pm 46.53	202.40 \pm 47.77	126.33 \pm 48.90	144.36 \pm 39.61
RT (min)	402.00 \pm 123.12	447.31 \pm 132.39	529.20 \pm 128.75	503.80 \pm 232.93
EPOC (mg O ₂ kg ⁻¹)	379.90 \pm 141.11	415.37 \pm 162.87	424.83 \pm 72.93	389.08 \pm 156.31

Note. SMR, RMR, MMR and AS are adjusted to the mean body mass of this study's sample (0.152 kg).

AS: aerobic scope; MMR: maximum metabolic rate; RMR: resting metabolic rate; SMR: standard metabolic rate.

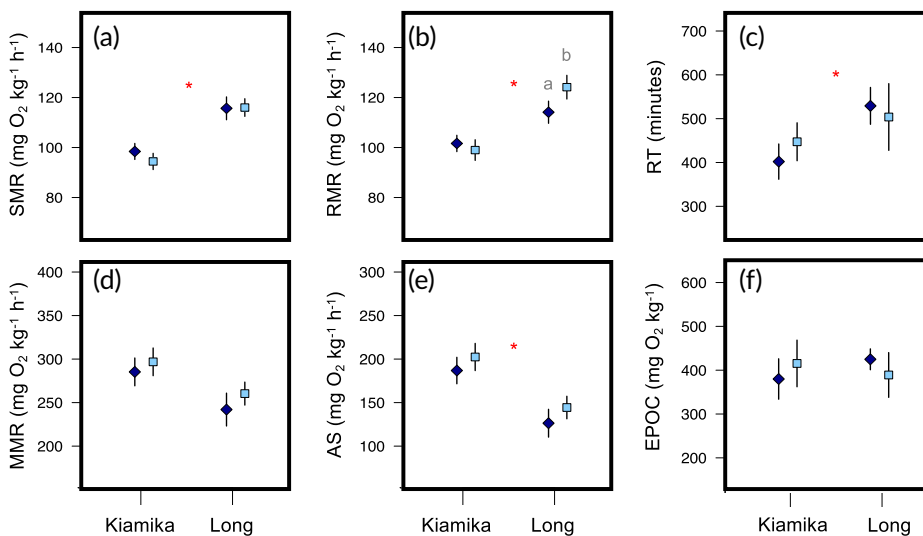
**FIGURE 2** Mean \pm standard error values of (a) standard metabolic rate (SMR), (b) resting metabolic rate (RMR), (c) maximum metabolic rate (MMR), (d) aerobic scope (AS), (e) recovery time (RT) and (f) excess post-exercise oxygen consumption (EPOC) of smallmouth bass *Micropterus dolomieu* from the Kiamika River and Lake Long during respirometry experiments in the presence (dark diamonds) or absence (light squares) of shelter. Red asterisks and grey letters indicate significant differences between populations and treatments, respectively (◆) with shelter and (□) without shelter

Figure 2). There was an interacting effect of treatment and population on RMR ($P = 0.044$; Table 3): RMR was 9% higher for Lake Long fish in the absence of shelter than in its presence, but treatment had no significant effect on RMR for Kiamika River fish (Figure 2). RMR was negatively related to experiment order ($P = 0.043$; Table 3; Supporting Information Table S1). The estimates were 5% lower during the second experiment. LMMs explained a total of 75.3% and 59.3% of SMR and RMR variation, respectively, and most of it was associated with fixed effects (50.3% and 44.1% for SMR and RMR, respectively; Table 3).

MMR was on average 16% higher in Kiamika River fish than in fish from Lake Long (Table 2; Figure 2), but this difference was not significant ($P = 0.057$; Table 3). MMR did not vary with the presence or absence of shelter ($P = 0.320$). AS of smallmouth bass from Lake Long was 30% lower than that of Kiamika fish ($P = 0.004$; Table 3; Figure 2) but did not vary with the presence of shelter ($P = 0.212$; Table 3). LMMs explained a total of 61.7% and 69.6% of MMR and AS variation, respectively, and most of it was associated with the random effect (47.9% and 40.1%, respectively; Table 3).

RT varied among populations, fish from Lake Long showing on average 18% longer RT than fish from the Kiamika River ($P = 0.048$; Table 3; Figure 2). RT did not vary with treatment ($P = 0.121$; Table 3; Figure 2) but was negatively related to fish mass ($P < 0.001$; Table 3; Supporting Information Table S1). RT was influenced by the interaction between population and experiment order ($P = 0.021$; Table 3): RT was 17% shorter for all fish on the second experiment compared to the first, but during the second experiment, fish from Lake Long recovered 5% faster than fish from the Kiamika River (Supporting Information Table S1). EPOC did not vary between populations nor across treatment (Table 3), but was negatively related to fish mass ($P < 0.001$; Table 3; Supporting Information Table S1). EPOC was also influenced by the interaction between experiment order and fish mass: slope of decrease in EPOC with fish mass was steeper during the second experiment ($P = 0.009$; Table 3; Supporting Information Table S1). Most of the variations in RT and EPOC were explained by fixed effects of the LMMs (47.5% and 46.7%, respectively), and total variation explained was of 58% and 68.9%, respectively (Table 3).

TABLE 3 Results of linear mixed models relating metabolic traits of smallmouth bass *Micropterus dolomieu* to mass, treatment, population, experiment order and interactions between these variables

Response	Effect	Chi-square	df	P-value	R ² _m	R ² _c
SMR	Mass	1.7361	1	0.1876	0.503	0.753
	Treatment	0.1389	1	0.7094		
	Population*	19.0737	1	0.0001		
	Order*	4.4994	1	0.0339		
	Treatment × mass*	5.3495	1	0.0207		
RMR	Mass	1.0831	1	0.2980	0.441	0.593
	Treatment	0.6140	1	0.4333		
	Population*	14.2823	1	0.0002		
	Order*	4.1087	1	0.0427		
	Treatment × mass	3.5399	1	0.0599		
MMR	Treatment	0.9872	1	0.3204	0.138	0.617
	Population	3.6159	1	0.0572		
AS	Mass	0.0592	1	0.8078	0.295	0.696
	Treatment	1.5567	1	0.2121		
	Population*	8.4447	1	0.0037		
RT	Treatment × mass	2.7546	1	0.0970	0.475	0.58
	Mass*	11.9141	1	0.0006		
	Treatment	2.3985	1	0.1214		
	Population*	3.9285	1	0.0475		
	Order*	5.3229	1	0.0210		
EPOC	Population × order*	5.3196	1	0.0211	0.467	0.689
	Mass*	17.809	1	<0.0001		
	Treatment	1.1704	1	0.2793		
	Population	0.0599	1	0.8066		
	Order	1.1205	1	0.2898		
	Order × mass*	6.7581	1	0.0093		

Note. Random effect of fish ID was included in models. R²_m is the marginal R² (variance explained by the fixed effects) and R²_c is the conditional R² (variance explained by the fixed and the random effects). AS: aerobic scope; EPOC: excess post-exercise oxygen consumption; MMR: maximum metabolic rate; RMR: resting metabolic rate; RT: recovery time; SMR: standard metabolic rate. *Significant effects.

3.1 | Dominance

The experimental and statistical designs used in this study were based on the assumption that all experimental fish were similar except for their mass and population. Nonetheless, observations in the holding tanks suggest that some fish may have potentially been characterized as subordinate or dominant. Dominance in a fish was determined as exhibition of aggressive behaviour (e.g., pecking and chasing) towards other fish. A fish was identified as “subordinate” if it was subjected to pecking, chasing and so on. When aggressive behaviour was not witnessed in a group of fish, each fish dominance was defined as “unknown.” We acknowledge that these characterizations of dominance are simplistic, as they did not design this study to measure dominance ranks. We decided nonetheless to test if the effect of shelter on metabolic traits would be influenced by dominance status identified in the sample of this study. No dominant behaviour could be identified for any fish from Lake Long, and it could not be assessed

for two fish of the Kiamika River. Therefore, the data set for dominance comprises 12 fish only from the Kiamika River (five dominants and seven subordinates).

Dominant (0.08–0.23 kg) and subordinate (0.05–0.25 kg) fish were of similar size range. Dominance had no significant effect on metabolic traits (Supporting Information Table S2; Figure 3). Metabolic traits did not vary in the presence or absence of shelter for either dominant or subordinate fish, except for RT. Dominant fish had 26% shorter RT in the presence of shelter than in its absence ($P = 0.050$; Supporting Information Table S2; Figure 3). Comparison of R²_c and R²_m for each model using this dominant-subordinate sub-set of data reveals different trends than that of models created with the full data set for SMR and RMR (Supporting Information Table S2). For this sub-set, individual fish accounted for 52.7% and 31.1% of explained variation in SMR and RMR, respectively. In comparison, 25% and 15.2% of explained variation in SMR and RMR were attributable to individual fish in the full data set (Table 3).

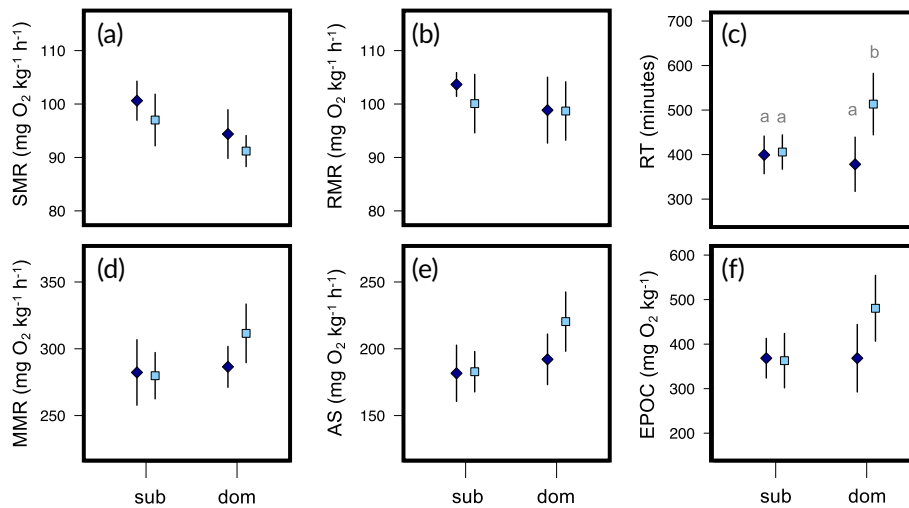


FIGURE 3 Mean \pm standard error values of (a) standard metabolic rate (SMR), (b) resting metabolic rate (RMR), (c) maximum metabolic rate (MMR), (d) aerobic scope (AS), (e) recovery time (RT) and (f) excess post-exercise oxygen consumption (EPOC) of subordinate (sub) or dominant (dom) smallmouth bass *Micropterus dolomieu* measured by respirometry experiments in the presence (dark diamonds) or absence (light squares) of shelter. Grey letters indicate significant differences between dominance status (\blacklozenge) with shelter and (\square) without shelter

4 | DISCUSSION

4.1 | Metabolic traits and the presence of shelter

This study revealed no reduction in SMR of smallmouth bass with the presence of shelter. Nonetheless, the presence of shelter had a significant effect in reducing RMR for Lake Long fish. It may be expected that the presence of shelter would have no effect on metabolic rates estimated during the night (in the dark) if the main goal of sheltering is for the fish to be visually hidden. It is therefore important to account for light levels when comparing the results of this study to that of other studies. Orange-fin anemonefish *Amphiprion chrysopterus* showed 8% lower SMR, measured in the dark during the night, in the presence of healthy anemones compared to bleached anemones, while daytime metabolic rates did not differ (Norin *et al.*, 2018). In contrast, no differences in SMR or RMR were observed when shelter was present or absent in a closely related species of clown fish *Amphiprion ozellaris* (Kegler *et al.*, 2013). In Atlantic salmon *Salmo salar*, RMR measured during the day were 30% lower when shelter was available (Millidine *et al.*, 2006) or under simulated ice cover (Finstad *et al.*, 2004). The presence of shelter also resulted in 30% lower RMR measured during the day in burbot *Lota lota*, but had no effect on that of stone loach *Barbatula barbatula* (Fischer, 2000). A comparison of results on two *Amphiprion* spp. – and that of the other studies listed earlier – highlights that there is no consistent lowering effect of shelter presence on SMR or RMR, nor any trend to be drawn by the light level at which measurements were made.

The presence or absence of shelter did not affect AS. This metabolic trait is the difference between MMR and SMR, and both traits did not vary with the presence of shelter. We were not expecting MMR to change with the presence of shelter. The chase and air exposure protocol used in our study simulates fisheries stress (Cooke *et al.*, 2013, 2014) and is effective to induce maximal fish exhaustion, and thus to measure MMR (Roche *et al.*, 2013). If the fish is

completely exhausted, and has reached MMR, there should be no change in MMR with the presence of shelter.

The presence of shelter did not reduce RT (except in dominant individuals, discussed later) and EPOC of smallmouth bass. To the best of our knowledge, no other study has investigated the potential for shelter to reduce RT or EPOC, and therefore, direct comparisons with the results of this study are not possible. Nonetheless, a previous study showed that latency to fast start escape response (a proxy for vigilance) was negatively related to RT (Killen *et al.*, 2015). In other words, more vigilant individuals had longer RT. Vigilance is thought to be energetically costly because of higher brain activity (Moss *et al.*, 1998). As sheltering can be a cost-effective strategy to replace vigilance (Millidine *et al.*, 2006), we were expecting that RT would be faster and that EPOC would be reduced in the presence of shelter. Animals often seek shelter after intense activity to recover and tend to stay hidden longer after being active than resting (Hailey *et al.*, 1987; Krause *et al.*, 1998), although there is some evidence that finding shelter may be more difficult for exhausted organisms (Brownscombe *et al.*, 2014). Despite this apparent need for sheltering for recovery, “forced” shelter presence vs. absence during the respirometry experiments in this study did not unequivocally affect RT or EPOC. Physiological motive may lead an animal to use shelter, but the hypothesis that shelter use may have consequences on energy expenditures required for non-mechanical tasks is not supported by our results.

It is also important to note that fish may have a different conception of what a shelter is than what we expected. A respirometry chamber is a confined space placed in a water basin in which there are other chambers and obstacles (pumps and tubing). Fish may feel there is high structural complexity in their surroundings that may act as shelters. In fact, Millidine *et al.* (2006) found that use of shelter was not necessary for Atlantic salmon to lower their metabolic rates, and only the availability of the shelter in the chamber was important: fish rested near the shelter and not inside it during most of the experiments. Moreover, the shelter used in Millidine *et al.* (2006) study was

made from clear material, which means that sheltering did not provide different light level to the fish, but its presence still resulted in 30% lower RMR in Atlantic salmon. It is possible that smallmouth bass considered their surroundings in the respirometry experiment (pumps, tubings and so on) as available shelters, even if not placed over the chamber. Nonetheless, none of these provided the shade and direct overhead shelter common in a field setting (e.g., under a log). If the main goal of sheltering is for the fish to be visually hidden, no effect on SMR measured in the dark should be expected. Nonetheless, fish had on average 6 ± 1.5 h to acclimate to the presence of shelter over the respirometry chamber from the onset of the respirometry experiment until lights were turned off, and had knowledge of being hidden. The extent at which this knowledge may indeed affect fish respiration remains to be fully assessed.

The interaction between body mass and treatment had a significant effect on SMR. Larger fish had lower SMR in the presence of shelter than when it was absent. The same trend was also observed in RMR, but the effect was not significant (Supporting Information - Figure S1). This could indicate that shelter had a more calming effect on larger fish than on smaller ones, or that sheltering is more common in larger individuals. The presence of shelter is the most reported habitat association for adult smallmouth bass, whereas juveniles are more associated with large substrate relative to their size (Edwards *et al.*, 1983; Todd & Rabeni, 1989; Warren, 2009). Male and female smallmouth bass mature minimally at >20 and >22 cm, respectively (Warren, 2009), which indicates that the data set of our study comprises sub-adults and adults. It is possible that the interacting effects of body mass and treatment on SMR reflect different habitat associations within the size range of individuals in this study's sample as the shelter provided during the experiment (similar to a log) is more in line with the type of shelter used preferentially by larger individuals in nature (in contrast to macrophytes or rocks). However, this is not supported by our data. We saw no relationship between body mass and the type of physical structure in proximity of capture areas. We also observed that RT and EPOC were negatively related to body mass. The opposite trend was observed in other studies on freshwater fish (Zhang *et al.*, 2014), whereas no relationship between body mass and recovery was found in reptiles or amphibians (Gleeson, 1991).

The experiment order had a significant effect on SMR and RMR, and its interaction with population or fish mass affected RT and EPOC, respectively. The time that fish were held in captivity represented a compromise between the minimum time necessary to recover from capture and transport to the field station, and the maximum time to avoid stress from prolonged captivity in wild-caught fish. Previous work showed that no differences were observed in the performance of wild-caught smallmouth bass measured within 1 and 7 days in captivity (Peake, 2004). Fish were kept in captivity for 3 or 4 days before the first experiment, and another 3 day period separated the first and second experiments. Despite short captivity duration, habituation to husbandry conditions and respirometry chamber may explain the lower rates measured during the second experiment.

4.2 | Lentic vs. lotic smallmouth bass

There were significant differences in SMR, RMR, AS and RT between the two smallmouth bass populations. Fish from the Kiamika River had a 20% lower SMR, a 30% higher AS and a 22% shorter RT than lake fish, in line with our predictions. These differences may be inherent to the type of natural environment these fish usually dwell in. It may be more important for river fish to have a low SMR and a higher AS because of the high costs of swimming in moving water. Relatedly, shorter RT after intense activities may be necessary to river dwelling fish. There was an interaction between population and treatment for RMR; Lake Long fish have lower RMR in the presence of shelter, whereas there were no differences in Kiamika fish. We were expecting that the presence of shelter would lower SMR/RMR of all fish, regardless of population. For the river population, however, benefits of sheltering may be more related to protection from the physical environment than to reduce energy expenditures for non-mechanical tasks. We cannot rule out that benefits associated with shelter use by these fish were not detected in this study because we did not manipulate flow velocities, restrict food consumption or simulate predator presence (although the chase protocol used to induce MMR simulates a fishing stress; Cooke *et al.*, 2013). Although the results of this study are consistent with expected differences in metabolic traits between fish inhabiting rivers and lakes, this study compares a small number of fish from one river and one lake. Experiments involving fish from a large number of rivers and lakes are needed before drawing any formal conclusion.

4.3 | Dominance

Metabolic rates (SMR, RMR, MMR and AS) did not vary in the presence or absence of shelter for either dominant or subordinate fish. Dominance can facilitate access to shelter if that important resource is limited. In crayfish *Orconectes rusticus*, even when shelters are in abundance, dominant individuals generally occupy the preferred shelters and are less likely to be evicted from them than subordinates (Martin & Moore, 2008). A dominant smallmouth bass would even prevent subordinates from using shelters in holding (pers. obs.). It is possible that subordinate smallmouth bass did not feel less vulnerable in the presence of shelter by fear of dominant individuals, even if they were not harassed by an aggressive conspecific during the respirometry experiment. Jolles *et al.* (2016) observed that recent social conditions could affect repeatability of behaviour or expression of personality in three-spined sticklebacks *Gasterosteus aculeatus*. One could expect that recent social conditions could also affect physiological responses. This is in line with the hypothesis that the presence of highly dominant individuals or hierarchy could mask variations in physiological traits among subordinates (Killen *et al.*, 2013). Although we did not see differences in metabolic rates in the presence or absence of shelter in subordinate fish, we did not observe significant differences with treatment among dominant fish either. We cannot conclude that dominance status had a modulating effect on metabolic rates estimated in the presence or absence of

shelter. We did observe that dominant smallmouth bass had 26% shorter RT in the presence of shelter than when it was absent, whereas no difference was observed between treatments in subordinate fish. This result may be related to the cost of vigilance or other metabolic costs to maintain the hierarchy when shelter is absent (Castro *et al.*, 2006; Millidine *et al.*, 2006). The presence of shelter (e.g., dense canopy cover) has been associated with reduced vigilance rates (Griesser & Nystrand, 2009) in the Siberian jay *Perisoreus infaustus*. Killen *et al.* (2015) observed that RT after exercise was positively correlated with vigilance. Our results might then suggest that dominant fish were more vigilant than subordinates. Additional work on smallmouth bass dominance structures is necessary to confirm this trend and could reveal other relationship between dominance and metabolic traits not detectable in the exploratory analysis.

4.4 | Individual variability

We observed interindividual variability in responses, expressed by the difference between R^2_m and R^2_c in models, regardless of population and treatment. For MMR and AS, variance explained by the random effects exceeded that of the fixed effects. This could indicate that MMR and AS are more plastic than SMR, RMR, RT and EPOC. Nonetheless, SMR and MMR have been reported to vary similarly between individuals of the same species (by about three-fold: Burton *et al.*, 2011; Norin & Clark, 2016; Norin & Malte, 2011). This could also indicate that the chase and air exposure protocol may not have always successfully achieved complete exhaustion. Nonetheless, we are confident that the method used in this study was robust as the chase duration was determined after a pilot experiment on smallmouth bass from the same populations as that of the present study, and that the air exposure after the chase is thought to be an effective way to ensure complete fish exhaustion (Norin & Clark, 2016; Roche *et al.*, 2013). Interindividual variability could be related to genotypes, maternal effects, early developmental conditions, social environment in holding or personality (Burton *et al.*, 2011; Killen *et al.*, 2013). We have no pedigree on the wild-caught smallmouth bass, and therefore, we cannot explore the potential effects of genetics, maternal effects or early developmental conditions. In addition, no differences in metabolic rates with treatment were revealed when accounting for the social environment in holding (i.e., dominance), except for RT, which was lower for dominant fish in the presence of shelter. Nonetheless, a more formal quantification of dominance status would be necessary to generalize the results of this study. Although it is possible that some interindividual variability could be attributable to personality in the present study, our design does not allow to estimate repeatability of responses adequately, as it would have required multiple measures in both treatments (with or without shelter; Roche *et al.*, 2016).

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AUTHOR CONTRIBUTIONS

Emmanuelle Chrétien, Steven J. Cooke and Daniel Boisclair designed the experiments. Emmanuelle Chrétien performed the experiments, analysed the data and wrote the manuscript. All authors contributed critically to the manuscript.

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ORCID

Emmanuelle Chrétien  <https://orcid.org/0000-0003-3798-7139>

Steven J. Cooke  <https://orcid.org/0000-0002-5407-0659>

Daniel Boisclair  <https://orcid.org/0000-0002-4353-9597>

REFERENCES

- Ahrenstorff, T. D., Sass, G. G., & Helmus, M. R. (2009). The influence of littoral zone coarse woody habitat on home range size, spatial distribution, and feeding ecology of largemouth bass (*Micropterus salmoides*). *Hydrobiologia*, 623, 223–233.
- Bates, D., Maechler, M., Bolker, B., & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. Available online at: <http://cran.r-project.org/web/packages/lme4/index.html>.
- Beck, D. D., & Jennings, R. D. (2003). Habitat use by Gila monsters: The importance of shelters. *Herpetological Monographs*, 17, 111.
- Brownscombe, J. W., Nowell, L., Samson, E., Danylchuk, A. J., & Cooke, S. J. (2014). Fishing-related stressors inhibit refuge-seeking behavior in released subadult great barracuda. *Transactions of the American Fisheries Society*, 143, 613–617.
- Brownscombe, J. W., Cooke, S. J., & Danylchuk, A. J. (2017). Spatiotemporal drivers of energy expenditure in a coastal marine fish. *Oecologia*, 183, 689–699.
- Burton, T., Killen, S. S., Armstrong, J. D., & Metcalfe, N. B. (2011). What causes intraspecific variation in resting metabolic rate and what are its ecological consequences? *Proceedings of the Royal Society B: Biological Sciences*, 278, 3465–3473.
- Castro, N., Ross, A. F. H., Becker, K., & Oliveira, R. F. (2006). Metabolic costs of aggressive behaviour in the Siamese fighting fish, *Betta splendens*. *Aggressive Behaviour*, 32, 474–480.
- Cech, J. J. (1990). Respirometry. In C. B. Schreck & P. B. Moyle (Eds.), *Methods for fish biology* (pp. 335–362). Bethesda, MD: American Fisheries Society.
- Chabot, D. (2016). FishMO2: Calculate and plot the standard metabolic rate (SMR), the critical oxygen level (O2crit) and the specific dynamic action (SDA) and related variables in fishes and crustaceans. Available online at: https://www.researchgate.net/profile/Denis_Chabot/project/fishMO2-a-R-package-to-calculate-and-plot-SMR-O2crit-and-SDA/attachment/5b9257c63843b006753838c6/AS:668177684000774@1536317382325/download/fishMO2_0.43.tar.gz?context=ProjectUpdatesLog.
- Chabot, D., Steffensen, J. F., & Farrell, A. P. (2016). The determination of standard metabolic rate in fishes. *Journal of Fish Biology*, 88, 81–121.
- Claireaux, G., & Lefrançois, C. (2007). Linking environmental variability and fish performance: Integration through the concept of scope for activity. *Philosophical Transactions of the Royal Society B, Biological sciences*, 362, 2031–2041.
- Clark, T. D., Sandblom, E., & Jutfelt, F. (2013). Aerobic scope measurements of fishes in an era of climate change: Respirometry, relevance and recommendations. *Journal of Experimental Biology*, 216, 2771–2782.

- Coble, D. W. (1975). Smallmouth bass. In H. Clepper (Ed.), *Black bass biology and management* (pp. 21–33). Washington, DC: Sport Fishing Institute.
- Cooke, S. J., Messmer, V., Tobin, A. J., Pratchett, M. S., & Clark, T. D. (2014). Refuge-seeking impairments mirror metabolic recovery following fisheries-related stressors in the Spanish flag snapper (*Lutjanus carponotatus*) on the great barrier reef. *Physiological and Biochemical Zoology*, 87, 136–147.
- Cooke, S. J., & Suski, C. D. (2005). Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? *Biodiversity and Conservation*, 14, 1195–1209.
- Cooke, S. J., Donaldson, M. R., O'Connor, C. M., Raby, G. D., Arlinghaus, R., Danylchuk, A. J., ... Suski, C. D. (2013). The physiological consequences of catch-and-release angling: Perspectives on experimental design, interpretation, extrapolation and relevance to stakeholders. *Fisheries Management and Ecology*, 20, 268–287.
- Edwards, E. A., Gebhart, G., & Maughan, O. E. (1983). *Habitat suitability information: Smallmouth bass*. U.S. Fish and Wildlife Service FWS/OBS-82/10.36.
- Eliason, E. J., Clark, T. D., Hague, M. J., Hanson, L. M., Gallagher, Z. S., Jeffries, K. M., ... Farrell, A. P. (2011). Differences in thermal tolerance among sockeye salmon populations. *Science*, 332, 109–112.
- Fagan, W. F., Cantrell, R. S., & Cosner, C. (1999). How habitat edges change species interactions. *American Naturalist*, 153, 165–182.
- Farrell, A. P., Hinch, S. G., Cooke, S. J., Patterson, D. A., Crossin, G. T., Lapointe, M., & Mathes, M. T. (2008). Pacific salmon in hot water: Applying aerobic scope models and nitelemetry to predict the success of spawning migrations. *Physiological and Biochemical Zoology*, 81, 697–708.
- Fausch, K. D. (1984). Profitable stream positions for salmonids: Relating specific growth rate to net energy gain. *Canadian Journal of Zoology*, 62, 441–451.
- Finstad, A. G., Forseth, T., Næsje, T. F., & Ugedal, O. (2004). The importance of ice cover for energy turnover in juvenile Atlantic salmon. *Journal of Animal Ecology*, 73, 959–966.
- Finstad, A. G., Einum, S., Forseth, T., & Ugedal, O. (2007). Shelter availability affects behaviour, size-dependent and mean growth of juvenile Atlantic salmon. *Freshwater Biology*, 52, 1710–1718.
- Fischer, P. (2000). An experimental test of metabolic and behavioural responses of benthic fish species to different types of substrate. *Canadian Journal of Fisheries & Aquatic Sciences*, 57, 2336–2344.
- Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. In W. S. Hoar & D. J. Randall (Eds.), *Fish physiology* (pp. 1–98). New York, NY: Academic Press.
- Fry, F. E. J., & Hart, J. S. (1948). The relation of temperature to oxygen consumption in the goldfish. *Biological Bulletin*, 94(1), 66–77.
- Fukui, A. (2001). Indirect interactions mediated by leaf shelters in animal-plant communities. *Population Ecology*, 43, 31–40.
- Gleeson, B. Y. T. T. (1991). Patterns of metabolic recovery from exercise in amphibians and reptiles. *Journal of Experimental Biology*, 160, 187–207.
- Griesser, M., & Nystrand, M. (2009). Vigilance and predation of a forest-living bird species depend on large-scale habitat structure. *Behavioral Ecology*, 20, 709–715.
- Hafs, A. W., Harrison, L. R., Utz, R. M., & Dunne, T. (2014). Quantifying the role of woody debris in providing bioenergetically favorable habitat for juvenile salmon. *Ecological Modelling*, 285, 30–38.
- Hailey, A., Gaitanaki, C., & Loubourdis, N. S. (1987). Metabolic recovery from exhaustive activity by a small lizard. *Comparative Biochemistry and Physiology A*, 88, 683–689.
- Hancock, T. V., & Gleeson, T. T. (2008). Contributions to elevated metabolism during recovery: Dissecting the excess postexercise oxygen consumption (EPOC) in the desert iguana (*Dipsosaurus dorsalis*). *Physiological and Biochemical Zoology*, 81, 1–13.
- Hughes, J. J., & Ward, D. (1993). Predation risk and distance to cover affect foraging behaviour in Namib desert gerbils. *Animal Behaviour*, 46, 1243–1245.
- Jobling, M. (1994). *Fish bioenergetics* (1st ed.). London, England: Chapman & Hall.
- Jolles, J. W., Aaron Taylor, B., & Manica, A. (2016). Recent social conditions affect boldness repeatability in individual sticklebacks. *Animal Behaviour*, 112, 139–145.
- Kegler, P., Kunzmann, A., Bröhl, S., & Herbert, N. A. (2013). No evidence of shelter providing a metabolic advantage to the false clown anemonefish *Amphiprion ocellaris*. *Journal of Fish Biology*, 82, 708–713.
- Kevan, P. G., & Greco, C. F. (2001). Contrasting patch choice behaviour by immature ambush predators, a spider (*Misumena vatia*) and an insect (*Phymata americana*). *Ecological Entomology*, 26, 148–153.
- Killen, S. S., Marras, S., Metcalfe, N. B., McKenzie, D. J., & Domenici, P. (2013). Environmental stressors alter relationships between physiology and behaviour. *Trends in Ecology and Evolution*, 28, 651–658.
- Killen, S. S., Reid, D., Marras, S., & Domenici, P. (2015). The interplay between aerobic metabolism and antipredator performance: Vigilance is related to recovery rate after exercise. *Frontiers in Physiology*, 6, 1–8.
- Killen, S. S., Mitchell, M. D., Rummer, J. L., Chivers, D. P., Ferrari, M. C. O., Meekan, M. G., & McCormick, M. I. (2014). Aerobic scope predicts dominance during early life in a tropical damselfish. *Functional Ecology*, 28, 1367–1376.
- Krause, J., Loader, S. P., McDermott, J., & Ruxton, G. D. (1998). Refuge use by fish as a function of body length-related metabolic expenditure and predation risks. *Proceedings of the Royal Society B: Biological Sciences*, 265, 2373–2379.
- Krause, J., Cheng, D. J.-S., Kirkman, E., & Ruxton, G. D. (2000). Species-specific patterns of refuge use in fish: The role of metabolic expenditure and body length. *Behaviour*, 137, 1113–1127.
- Lind, J., & Cresswell, W. (2005). Determining the fitness consequences of antipredation behavior. *Behavioral Ecology*, 16, 945–956.
- Martin, A. L., & Moore, P. A. (2008). The influence of dominance on shelter preference and eviction rates in the crayfish, *Orconectes rusticus*. *Ethology*, 114, 351–360.
- Metcalfe, N. B., Van Leeuwen, T. E., & Killen, S. S. (2016). Does individual variation in metabolic phenotype predict fish behaviour and performance? *Journal of Fish Biology*, 88, 298–321.
- Michaels, C. J., & Preziosi, R. F. (2015). Fitness effects of shelter provision for captive amphibian tadpoles. *Herpetological Journal*, 25, 7–12.
- Millidine, K. J., Armstrong, J. D., & Metcalfe, N. B. (2006). Presence of shelter reduces maintenance metabolism of juvenile salmon. *Functional Ecology*, 20, 839–845.
- Moreno, S., Delibes, M., & Villafuerte, R. (1996). Cover is safe during the day but dangerous at night: The use of vegetation by European wild rabbits. *Canadian Journal of Zoology*, 74, 1656–1660.
- Moss, M. C., Scholey, A. B., & Wesnes, K. (1998). Oxygen administration selectively enhances cognitive performance in healthy young adults: A placebo-controlled double-blind crossover study. *Psychopharmacology*, 138, 27–33.
- Narvarte, M., González, R. A., Storero, L., & Fernández, M. (2013). Effects of competition and egg predation on shelter use by *Octopus tehuelchus* females. *Marine Ecology Progress Series*, 482, 141–151.
- Norin, T., Mills, S. C., Crespel, A., Cortese, D., Killen, S. S., & Beldade, R. (2018). Anemone bleaching increases the metabolic demands of symbiont anemonefish. *Proceedings of the Royal Society B*, 285, 7–12.
- Norin, T., & Clark, T. D. (2016). Measurement and relevance of maximum metabolic rate in fishes. *Journal of Fish Biology*, 88, 122–151.
- Norin, T., & Malte, H. (2011). Repeatability of standard metabolic rate, active metabolic rate and aerobic scope in young brown trout during a period of moderate food availability. *Journal of Experimental Biology*, 214, 1668–1675.
- Parsons, K. C., & Chao, J. (1983). Nest cover and chick survival in herring gulls. *Colonial Waterbirds*, 6, 154–159.

- Peake, S. (2004). An evaluation of the use of critical swimming speed for determination of culvert water velocity criteria for smallmouth bass. *Transactions of the American Fisheries Society*, 133(6), 1472–1479.
- Pollard, J. C. (2006). Shelter for lambing sheep in New Zealand: A review. *New Zealand Journal of Agricultural Research*, 49, 395–404.
- R Foundation for Statistical Computing. (2018). *R: A language and environment for statistical computing*, Vienna, Austria: R Foundation for Statistical Computing.
- Roche, D. G., Careau, V., & Binning, S. A. (2016). Demystifying animal 'personality' (or not): Why individual variation matters to experimental biologists. *Journal of Experimental Biology*, 219, 3832–3843.
- Roche, D. G., Binning, S. A., Bosiger, Y., Johansen, J. L., & Rummer, J. L. (2013). Finding the best estimates of metabolic rates in a coral reef fish. *Journal of Experimental Biology*, 216, 2103–2110.
- Seebacher, F., & Alford, R. A. (2002). Shelter microhabitats determine body temperature and dehydration rates of a terrestrial amphibian (*Bufo marinus*). *Journal of Herpetology*, 36, 69–75.
- Steffensen, J. F., Bushnell, P. G., & Schurmann, H. (1994). Oxygen consumption in four species of teleosts from Greenland: No evidence of metabolic cold adaptation. *Polar Biology*, 14, 49–54.
- Todd, B. L., & Rabeni, C. F. (1989). Movement and habitat use by stream-dwelling smallmouth bass. *Transactions of the American Fisheries Society*, 118, 229–242.
- Tsairi, H., & Bouskila, A. (2006). Ambush site selection of a desert snake (*Echis coloratus*) at an oasis. *Herpetologica*, 60, 13–23.
- Tufto, J., Andersen, R., & Linnell, J. (1996). Habitat use and ecological correlates of home range size in a small cervid: The roe deer. *Journal of Animal Ecology*, 65, 715–724.
- Ultsch, G. R. (1995). On adjusting metabolic rates for body size. *Florida Scientist*, 58, 270–273.
- Walsh, P. T., & Downie, J. R. (2005). The effects of shelter availability and substrate quality on behaviour and post-metamorphic growth in three species of anurans: Implications for captive breeding. *Herpetological Journal*, 15, 245–255.
- Warren, M. L. J. (2009). Centrarchid identification and natural history. In S. J. Cooke & D. P. Philipp (Eds.), *Centrarchid fishes - Diversity, biology, and conservation* (p. 566). West Sussex, England: Wiley-Blackwell.
- Zeng, L. Q., Zhang, Y. G., Cao, Z. D., & Fu, S. J. (2010). Effect of temperature on excess post-exercise oxygen consumption in juvenile southern catfish (*Silurus meridionalis* Chen) following exhaustive exercise. *Fish Physiology and Biochemistry*, 36, 1243–1252.
- Zhang, Y., Huang, Q., Liu, S., He, D., Wei, G., & Luo, Y. (2014). Intraspecific mass scaling of metabolic rates in grass carp (*Ctenopharyngodon idellus*). *Journal of Comparative Physiology B*, 184, 347–354.
- Zuur, A. F., Ieno, E. N., Walker, N., Saveliev, A. A., & Smith, G. M. (2009). *Mixed effects models and extensions in ecology with R. statistics for biology and health*. New York, NY: Springer New York.

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