




## ORIGINAL RESEARCH

# Body condition metrics explain fish movement in experimental streams

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animal movement; body condition; Leuciscidae; passive integrated transponder tags; stream fish; *Semotilus atromaculatus*.

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Editor: Hazel Nichols

Associate Editor: Shannon Gerry

Received 7 August 2022; revised 21 November 2022; accepted 10 January 2023

doi:10.1111/jzo.13049

**Abstract**

Body condition refers to an array of physiological or nutritious states in animals, but body condition is typically measured using a single metric in animal behavior studies. In this paper, we conducted a three-day laboratory study to evaluate whether metrics of body condition affected movement of wild-caught creek chub (*Semotilus atromaculatus*) at 16 and 22°C. Movement was counted between two circular tanks connected by a straight corridor, which was equipped with a pair of passive integrated transponder antennas. Fish movement was most frequent during periods of darkness in a simulated photoperiod, and more mobile individuals consistently moved more frequently across the 3 days. In general, individuals in better body condition were more mobile than those in poorer condition, and different metrics of body condition affected movement to different degrees. Specifically, per cent weight loss and dry matter content (ratio of wet versus dehydrated weight) were better predictors of movement than weight-at-length, which is most typically used as a surrogate of body condition in animals. In addition, body condition and length interacted to affect fish movement, where body condition affected movement of smaller individuals more significantly than that of larger individuals. Body condition effects on activity were similar at 16 and 22°C. This study demonstrates that body condition metrics may not always affect certain behavior in a similar way. Body condition metrics need to be carefully selected when used in the context of animal behavior, and more than a single metric should be tested when feasible.

**Introduction**

Body condition refers to a physiological or nutritious state in animals, measured by an array of metrics such as weight at given body length, fat reserves, and stress levels. An individual's state is determined by a combination of extrinsic (e.g., food availability) and intrinsic factors (e.g., metabolic rates), which regulate the cost–benefit ratio associated with certain behaviors (Luttbeg & Sih, 2010; Näslund & Johnsson, 2016; Sih et al., 2015). States have been linked to consistent differences in behaviors among individuals including aggression (Hu et al., 2021; Näslund & Johnsson, 2016), boldness (Bjornson & Anderson, 2018), exploration (Brown & Braithwaite, 2004), and movement (Nilsson et al., 2014). These behaviors are often correlated with each other, referred to as animal personality or behavioral syndromes (Conrad et al., 2011; Kaiser & Müller, 2021). Therefore, understanding body condition as a determinant of behaviors is paramount in not only understanding proximate and ultimate explanations of individual behavioral differences (Bateson & Laland, 2013) but also predicting

how environmental changes shift behavioral norms in populations via impacts on the body condition of individuals that comprise the populations (Sih, 2013).

Individuals differ in their activity levels (Nilsson et al., 2014; Réale et al., 2007). There have been mixed results as to how this behavior is affected by body condition. In some studies, individuals in poorer body condition are more active than those in better condition (Sih et al., 2015). These results are attributed to a greater food demand by individuals in poorer condition, who need to forage more frequently even when risks such as predation are present (Dall et al., 2004). On the contrary, individuals in better body condition are more active in other cases (Bjornson & Anderson, 2018) because their superior physiological state provides them with advantages such as escaping from predation and outcompeting with other species (Luttbeg & Sih, 2010). Evidently, these mixed empirical results are at least partly due to experimental settings used in different studies. Mixed effects of body condition are also likely due to different characteristics of individuals such as age and body size because costs and benefits of certain

behaviors change through ontogeny (Brodersen *et al.*, 2008; Luttbeg & Sih, 2010). Thus, body condition effects on activity levels need to be investigated contextually.

Knowledge is also lacking as to whether different metrics of body condition explain behavior consistently. Fish are suitable to fill this knowledge gap because their body condition is routinely measured in different ways (Stevenson & Woods Jr., 2006). However, the majority of previous fish behavior studies have used weight-at-length indices as a body condition metric, where heavier individuals relative to body length are considered in better body condition (Bjornson & Anderson, 2018; Pellegrini *et al.*, 2010; Polverino, Cigliano, *et al.*, 2016). Dry matter content is an alternative metric that estimates energy density (Johnson *et al.*, 2017). This is a more direct measurement of body condition than weight-at-length, but individuals need to be sacrificed to obtain dehydrated weight. Another body condition metric is relative weight loss. Under food deprivation scenarios, this metric is used as a proxy for metabolic demand and available energy reserves, where relative weight loss is greater for individuals with higher metabolic demands or lower energy reserves (Krause *et al.*, 1998). Given that these metrics do not identically measure body condition, it is critical to evaluate and identify which metrics are most predictive of individual variation in behavior.

In this study, we conducted a three-day laboratory experiment to investigate whether three metrics of body condition affected movement of wild-caught individuals of stream fish. Our objectives were two-fold. First, we evaluated whether fish movement would be best explained by weight-at-length, weight loss, or dry matter content. Second, we tested for an interactive effect between body length and condition. This interactive effect has been reported in previous field studies of fish movement (Gowan & Fausch, 1996; Kanno *et al.*, 2022), suggesting that the importance of body condition on movement may shift with body length.

## Materials and methods

### Study species

Creek chub (*Semotilus atromaculatus*; Family Leuciscidae) are widely distributed east of the Rocky Mountains in North America and occur primarily in small creeks (Warren Jr. & Burr, 2014). They occupy cool water habitats, where summer water temperature approximates 17–22°C (Beauchene *et al.*, 2014; Lyons *et al.*, 2009). They often coexist with cold water species such as trout at colder temperatures (Beauchene *et al.*, 2014; Rahel & Hubert, 1991). We chose 16 and 22°C as tank temperatures in the current study based on the thermal habitat preferences of this species. Creek chub can reach 200 mm in body length, and their local abundance can be high; creek chub <100 mm targeted in the current study are often found in large numbers locally (Leonard & Orth, 1986). Creek chub are omnivorous (Champagne *et al.*, 2022; Leonard & Orth, 1986) and may compete for food resources via exploitation, but not via behavioral interference and aggression

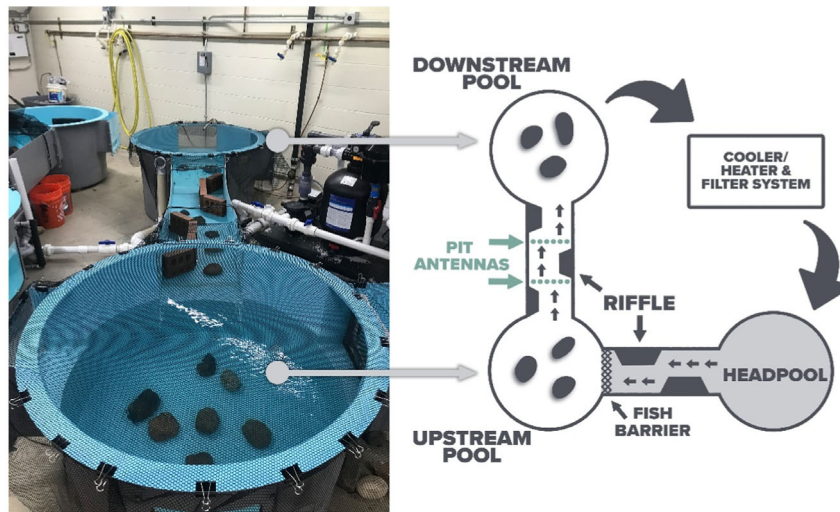
(Taniguchi *et al.*, 1998). In the current study, we did not observe any signs of aggression such as chasing, fin nipping, or bodily injuries. Thus, creek chub are a suitable species in a laboratory test of behavior, where individuals are housed together and subject to the same conditions.

Creek chub were collected from Spring Creek, Fort Collins, Colorado (40°33'55.9"N, 105°03'08.4"W) between 9:00 and noon on October 4, 2021. Water temperature in the creek ranged from 15 to 17°C during the period of fish collection. A backpack electrofishing unit was used to stun creek chub temporarily for netting (Model LR-24, Smith-Root Inc., Vancouver, WA, USA). Electrofishing was conducted with a pulsed direct current setting at 200 V, 45 Hz, and 20% duty cycle. Once captured, fish were anesthetized with an immersion in an AQUI-S (eugenol) solution, were measured for total length (mm) and weight (g), and were marked with 12-mm half duplex passive integrated transponder (PIT) tags for individual identification (Oregon RFID) in the field. PIT tags were inserted in the abdominal cavity by making a small incision using a No. 11 scalpel (Cary *et al.*, 2017). Fish were then allowed to recover in livewells placed in the creek. A total of 112 individuals were transported in oxygenated and insulated coolers to the experimental stream units on the Colorado State University main campus, where fish were exposed to a 1-h immersion in a 37% formaldehyde solution to treat parasites.

### Experimental stream units

We constructed two replicates of recirculating experimental stream units (Matthews *et al.*, 2006) to evaluate body condition effects on fish movement at 16 and 22°C in the Anatomy/Zoology Building on the Colorado State University main campus, Fort Collins, Colorado. One experimental stream was randomly assigned to 16°C and the other assigned to 22°C. An experimental stream unit consisted of three fiberglass circular tanks (“pools”, Model FCT-235) and two straight corridors (“riffles”; Red Ewald LLC, Karnes City, TX, USA), a bead filtration system equipped with UV sterilizers (Model 930 084; Pentair Aquatic Eco-Systems Inc., Apopka, FL, USA), and an air-cooled heat pump for water temperature control (Model Titan HP-2; Aqua Logic Inc., San Diego, CA, USA; Fig. 1). Pools were 122 cm in diameter, with water filled up to approximately 56 cm deep. Riffles were 180 cm long, 43 cm wide, and water depth was 15 cm. Each experimental stream unit recirculated approximately 2300 L of water.

In each experimental stream, fish could not access the head pool due to a physical barrier so that fish were limited to using the two downstream pools connected by the riffle located between them (Fig. 1). A pair of PIT antennas were deployed in the riffle perpendicular to flow and recorded the movement of creek chub between the two pools. A pair of antennas was operated by a multi-antenna reader (Oregon RFID, Portland, OR, USA). Antennas made of 5.26-mm<sup>2</sup> wires were looped four times outside the fiberglass riffle (Fig. 1). Read range of the antennas extended up to 25 cm along the riffle and the reader recorded time and individuals that passed through the antennas. Each antenna was placed approximately 33 cm from



**Figure 1** Schematic diagram and photo of a recirculating experimental stream unit used to monitor fish movement between two pools via a riffle, which was equipped with a pair of passive integrated transponder antennas. The pools were 122 cm deep and 76 cm in diameter, and riffles were 180 cm long, 43 cm wide, and 38 cm deep (water depth was 15 cm). The unit recirculated approximately 2300 L of water. Water recirculated through the filtration system and then heater/chiller unit to maintain the desired water temperature; arrows indicate flow direction. Black nylon nets were placed above pools to prevent fish from jumping out of the pools.

the edge of the pools so that individuals were detected by the antenna only if they entered the riffle. Antenna performance was checked twice daily, and data were downloaded daily. We did not locate any sign of intermittency in antenna operations during the 3-day study period. Each pool contained six to nine boulders and cobbles (30–80 cm long) to provide cover for fish. Pools were covered by nylon nets to prevent fish from jumping out of the pools. Bricks were placed in the riffles to redirect flow of water and constrain the width of the waterway. This was designed to maximize tag detections by preventing multiple individuals from passing through the antennas precisely side-by-side. An antenna was programmed to scan for PIT tags 10 times per second.

Lights in the room were automated to characterize diurnal patterns of movement. The sunrise started at 6 am daily at the lowest color temperature (2700 K) and brightness (1%), and color and brightness increased by approximately 10% in 5-minute increments until they reached maximum color temperature (6500 K) and brightness (100%, or 538 lux) at 7 am. The maximum color temperature and brightness were maintained from 7 am until 9 pm. The sunset started at 9 pm and lasted until 10 pm by decreasing the color and brightness by approximately 10% every 5 min. The room was completely dark between 10 pm and 6 am.

## Data collection

The 112 wild-caught creek chub were randomly assigned to one of the two experimental stream units by 16:00 on October 4, 2021, the same day when they were collected, and their inter-pool movement was monitored until 13:00 on October 8, 2021. Movement data in the first 24 h were treated as an

acclimation period and thus were not included in the data analysis. Movement was limited in this period, and count of movement would have been just 1% of the total count if this period had been included in the data analysis. A total of 10 individuals suffered mortality during transportation from the field (one individual) or in the first 24 h in the experimental stream units (two individuals at 16°C and seven at 22°C). These 10 individuals were not included in any analysis. As a result, movement data were available on 52 individuals at 16°C and 50 individuals at 22°C at the end of the 3-day study period. Total length ranged from 74–94 mm (mean = 85 mm) at 16°C and 74–97 mm (mean = 84 mm) at 22°C, and weight ranged from 3.79–8.63 g (mean = 5.89 g) at 16°C and 3.64–8.71 g (mean = 5.66 mg) at 22°C. There was no statistically significant difference between the two experimental stream units in fish total length (*t*-test:  $t = -0.75$ , d.f. = 98.9,  $P = 0.46$ ) or weight (*t*-test:  $t = -0.94$ , d.f. = 97.7,  $P = 0.35$ ). During the 3-day study period, creek chub were fed once daily between 16:00 and 19:00 with thawed bloodworms at 3% of total weight of all individuals in each experimental stream unit to induce some degree of weight loss. Food was distributed between the two pools in each unit to avoid providing a spatial cue on food availability and affecting fish movement. Water temperature remained  $\pm 0.7^\circ\text{C}$  of the target temperature in each unit; pH stayed at 7.6; and ammonia, nitrate and nitrite were  $\sim 0$  ppm.

At the completion of the 3-day movement study period, each individual was measured for weight (g) to estimate % weight loss between the beginning and completion of the study. Creek chub were then sacrificed and immediately dried at 60°C until their dehydrated weight measurements stabilized to ensure evaporation of water. Before dehydrating, creek chub were

wiped of water on their skin using a towel and were weighed again. Dry matter content was estimated as percentage of post-dehydrated weight relative to this pre-dehydrated weight.

## Statistical analysis

The main goal was to evaluate whether fish movement was explained by body condition metrics represented by weight-at-length, weight loss, and dry matter content. To address this question, we used total count of inter-pool movement over 3 days for each individual as the response variable and tested whether it was linked to the body condition metrics in Poisson generalized linear models (GLM). Total count of inter-pool movement was quantified using two different approaches based on detections by two PIT antennas deployed in the riffle. We considered inter-pool movement to have occurred when an individual was detected sequentially by both antennas, and we organized PIT antenna detection data chronologically for each individual to identify such sequences. One approach was to count the number of inter-pool movement irrespective of time gap in detections between the two antennas. We supposed that prolonged gaps in detections between the two antennas could occur when fish did not traverse the riffle swiftly but stayed there during inter-pool movement, or when one of the antennas failed detecting fish. A second approach was to define inter-pool movement as a sequence of detections between the two antennas that occurred  $\leq 60$  s. Total count of movement defined by the two approaches was highly correlated with each other (Spearman's  $r = 0.97$ ), indicating that fish movement was measured nearly identically using both approaches. As a result, we used the second approach to count the total number of inter-pool movement over 3 days in Poisson GLM. Movement count was aggregated across 3 days because daily count of movement was correlated between each other (see Results), indicative of consistent variation in behavior among individuals over time. We also counted hourly total numbers of inter-pool movement across individuals to characterize diurnal patterns of movement.

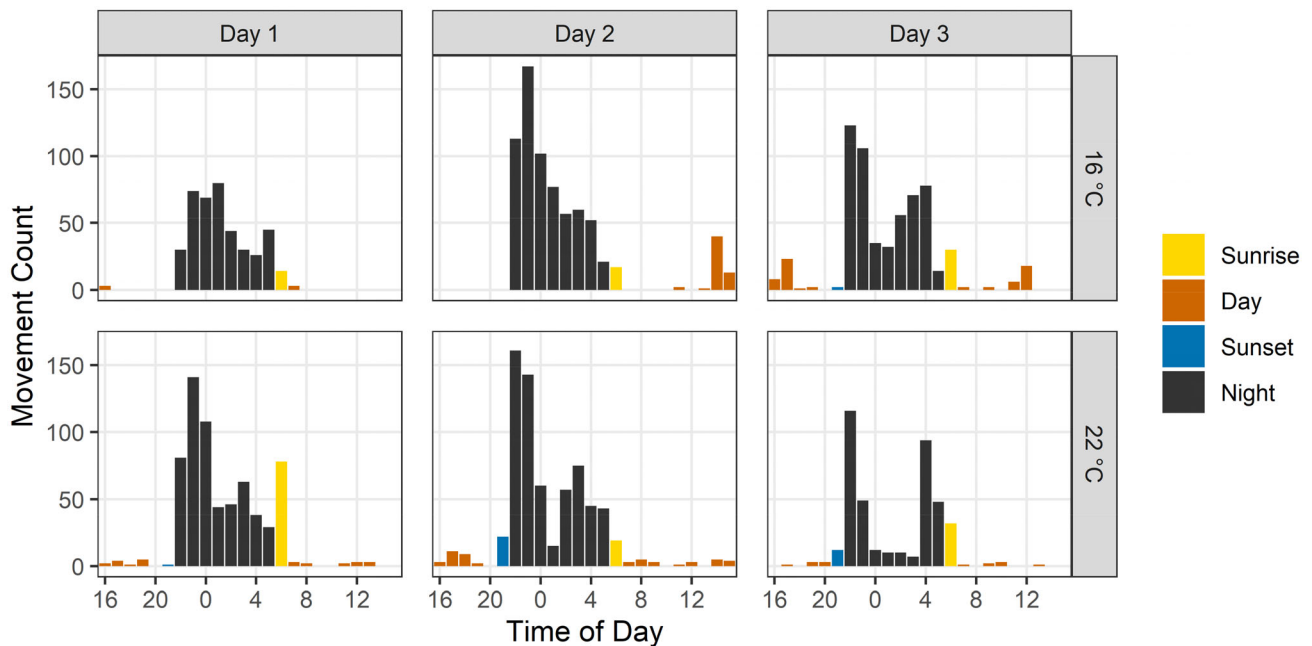
Four explanatory variables were used in Poisson GLM, and they were weight-at-length, weight loss, dry matter content, and total length. Although our main focus was to evaluate body condition effects on movement, we included total length as an explanatory variable because stream fish movement often depends on body size, and body size and condition interact to affect movement in the wild (Gowan & Fausch, 1996; Terui *et al.*, 2021). Weight-at-length was characterized by comparing the weight of fish to the predicted weight of fish at the same total length (TL) based on field measurements of the 102 individuals that survived the 3-day study period. The logarithmic conversion is typically used to characterize relationships between weight and total length, but the relationship was evidently linear in this study because of the narrow ranges of total length and weight. The relationship between weight (g) and TL (mm) of creek chub in this study was  $\text{Weight} = -12.69 + 0.22 \times \text{TL}$  ( $r^2 = 0.91$ ). Weight-at-length was calculated as  $\frac{\text{measured weight}}{\text{predicted weight}} - 1$ , so that its mean is centered at 0, with negative values indicative of lighter fish (poorer body condition) and

positive values indicative of heavier fish (better body condition) at that total length (Al-Chokhachy *et al.*, 2019; Kanno *et al.*, 2022). Weight loss was quantified as percentage difference in weight measured in the field and that measured in the laboratory at the completion of the 3-day movement study period. Finally, dry matter content was percentage of dehydrated weight relative to pre-dehydrated weight and was used as an indicator of energy density (Johnson *et al.*, 2017).

Poisson GLMs were constructed and analyzed at 16 and 22°C individually in two steps. The first step was to compare and rank models with main effects only, and the second step was to evaluate interactions between body condition and length. In the first step, we compared a total of 15 models using all possible combinations of the four explanatory variables as main effects, including weight-at-length, weight loss, dry matter content, and total length. Explanatory variables were centered by mean and then divided by standard deviation to allow comparisons of their effect sizes on movement, and no pair of the explanatory variables was highly correlated with each other (Spearman's  $|r| \leq 0.36$ ). Models were compared using Akaike's information criteria corrected for small sample size ( $AIC_c$ ), and models with  $AIC_c$  values less than 2 of the most supported model were considered competing models and retained (Burnham & Anderson, 2002). Total length was included in all competing models at each temperature. In the second step, we added an interaction term between total length and an explanatory variable of body condition in a model, and a set of models were once again compared using  $AIC_c$ . The most supported model had an  $AIC_c$  value greater than 2 at 22°C, and two competing models were identified at 16°C ( $\Delta AIC_c = 0.34$ ; see Results). At 16°C, the inferences on explanatory variable effects on movement were averaged between the two competing models based on Akaike's weight. The models were conditionally averaged, meaning that effects of explanatory variables were averaged if they were included in both models, but otherwise we report effect sizes in either of the two models in which explanatory variables were included. To visualize the interactive effects of body condition metrics and body size, we plotted model-predicted total count of movement as a function of body condition metrics for three sizes of fish (mean and mean  $\pm 1.5$  SD) at each temperature. All data management and statistical analysis were conducted using Program R (R Core Team, 2022).

## Results

Fish movement between the two pools differed greatly among individuals. Total count of inter-pool movement per individual ranged from 0 to 120 at 16°C (mean = 34, SD = 25,  $n = 52$  individuals) and 0–110 at 22°C (mean = 34, SD = 26,  $n = 50$  individuals) over the three-day study period, and total count of movement did not differ between 16 and 22°C (Poisson  $t$ -test,  $p = 0.59$ ). All individuals except four fish (16°C) and two fish (22°C) moved at least once between the two pools. Of a total count of 1765 movements summed across individuals and days, 89% occurred in darkness (10 pm–6 pm) at 16°C (Fig. 2). Similarly, 85% of a total of 1768 movements were



**Figure 2** Total count of inter-pool fish movement summed across individuals by hour over the 3-day study period at 16 and 22°C. Hours were grouped by sunrise (6–7 am), day (7 am–9 pm), sunset (9–10 pm), and night (10 pm–6 am). Each day starts at 16:00, when monitoring of movement started on October 5, 2021.

recorded in darkness at 22°C (Fig. 2). Comparisons of daily movement count showed that individuals moving between the pools more frequently on one day were consistently more mobile on the other days at 16°C (Kendall's  $W = 0.67$ ,  $p < 0.001$ ) and 22°C (Kendall's  $W = 0.66$ ,  $p < 0.001$ ).

Poisson GLM demonstrated that metrics of body condition explained variation in fish movement. At 16°C, total count of movement was best explained by dry matter content, weight loss, weight-at-length, and total length, and there was no competing model when only main effects were evaluated (Table 1). When interaction terms were considered, two competing models were identified ( $\Delta AIC_c = 0.34$ ; Table 1). One model included all main effects and an interaction between weight loss and total length and a second model with all the main effects and an interaction between weight-at-length and total length. Accordingly, we report statistical inferences by conditionally averaging these two models at 16°C below. At 22°C, two competing models with main effects were identified (Table 1). The best supported model contained dry matter, weight loss, and total length, and the second-ranked model included weight-at-length additionally. Interaction terms were considered for these two models, and the best supported model with an interaction included dry matter content, weight loss, total length, and an interaction between dry matter content and total length. No competing interaction model was identified (Table 1), and we report inferences on the top-ranked interaction model at 22°C below.

Individuals in better body condition moved more frequently than those in poorer condition at 16 and 22°C (Fig. 3).

Individuals with higher dry matter content, an indicator of energy density, were more mobile than those with lower dry matter content at 16°C (mean coefficient = 0.15,  $SE = 0.03$ ,  $P < 0.001$ ) and 22°C (mean coefficient = 0.23,  $SE = 0.02$ ,  $P < 0.001$ ). Similarly, individuals that lost less weight moved more frequently at 16°C (mean coefficient =  $-0.36$ ,  $SE = 0.05$ ,  $P < 0.001$ ) and 22°C (mean coefficient =  $-0.21$ ,  $SE = 0.02$ ,  $P < 0.001$ ). Weight-at-length was the least predictive body condition metric of movement and was included in the best supported model at only 16°C (mean coefficient = 0.11,  $SE = 0.04$ ,  $P = 0.002$ ). Total length was the most predictive variable of movement at 16°C (mean coefficient = 0.44,  $SE = 0.04$ ,  $P < 0.001$ ) and 22°C (mean coefficient = 0.24,  $SE = 0.02$ ,  $P < 0.001$ ). These results showed that individual traits affecting fish movement were similar between 16 and 22°C.

Finally, variation in body condition had greater effects on movement of smaller individuals than on larger individuals (Fig. 4). At 16°C, the weight loss effect on movement was more pronounced among smaller individuals, compared to larger individuals (Fig. 4a). On the contrary, weight-at-length affected movement of larger individuals more significantly than smaller individuals at 16°C, but weight-at-length explained less variation in movement than other body condition metrics (Figs 3 and 4b). At 22°C, dry matter content explained variation in movement among smaller individuals, but not among larger individuals (Fig. 4c). Taken together, movement of smaller individuals was more responsive to body condition metrics at 16 and 22°C.

**Table 1** List of Poisson generalized linear models that explain individual variation in fish movement count

	Model	AIC <sub>c</sub>	ΔAIC <sub>c</sub>	Weight	
16°C	Step 2 (With an interaction)	Dry Matter Content, Weight Loss, Weight-at-Length, Total Length, Weight Loss × TL	992.1	0.00	0.51
		Dry Matter Content, Weight Loss, Weight-at-Length, Total Length, Weight-at-Length × TL	992.5	0.34	0.43
		Dry Matter Content, Weight Loss, Weight-at-Length, Total Length, Dry Content Matter × TL	996.7	4.53	0.05
	Step 1 (Main effects only)	Dry Matter Content, Weight Loss, Weight-at-Length, Total Length	994.4	0.00	1.00
		Dry Matter Content, Weight Loss, Total Length	1016.4	22.01	0.00
		Weight Loss, Weight-at-Length, Total Length	1018.6	24.27	0.00
22°C	Step 2 (With an interaction)	Dry Matter Content, Weight Loss, Total Length, Dry Content Matter × TL	1154.1	0.00	0.75
		Dry Matter Content, Weight Loss, Weight-at-Length, Total Length, Dry Content Matter × TL	1156.3	2.19	0.25
		Dry Matter Content, Weight Loss, Weight-at-Length, Total Length, Weight Loss × TL	1179.3	25.14	0.00
	Step 1 (Main effects only)	Dry Matter Content, Weight Loss, Total length	1181.6	0.00	0.69
		Dry Matter Content, Weight Loss, Weight-at-Length, Total Length	1183.2	1.56	0.31
		Dry Matter Content, Weight-at-Length, Total Length	1224.5	42.94	0.00

Models are ranked by Akaike's information criterion corrected for small sample size (AIC<sub>c</sub>), with ΔAIC<sub>c</sub> values showing differences in AIC between the given model and the best supported model at each temperature and step and Akaike's weight (Weight) for model averaging. In the first step, all unique combinations of four explanatory variables as main effects were compared and ranked at each temperature (15 models). Competing models (ΔAIC<sub>c</sub> < 2) were then retained in Step 2 to test an interactive effect between total length (TL) and each of body condition variable (three models at 16°C and 5 models at 22°C). The top three models are shown at each temperature and step, and crosses (x) denote interactions.

## Discussion

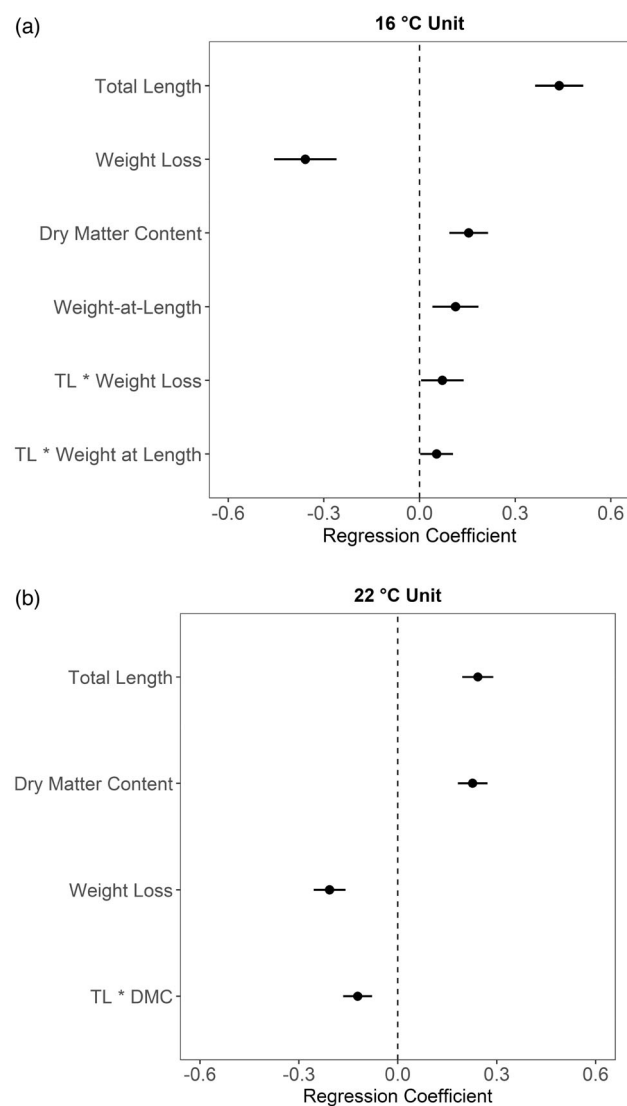
Propensity to move between experimental pools varied greatly among creek chub individuals. But individuals showed consistent movement behavior over the course of this three-day study. The movement of creek chub was explained by body length and three body condition metrics. Previous studies evaluated whether movement is linked to a single body condition metric (Baines *et al.*, 2015; Cote *et al.*, 2010), but our study showed that different condition metrics may affect movement differently. Body length and condition, and their interactions, affected inter-pool movement of creek chub similarly at 16 and 22°C, indicating that determinants of movement did not depend on temperature in this ectothermic animal, at least for the range of temperature tested in this study.

Body condition metrics affected fish movement to different degrees, and the three metrics were not correlated with each other. These results indicate that each of the metrics uniquely measured body condition. In our study, weight-at-length was the least predictive metric of fish movement among the three body condition metrics and was not included in the top predictive model of fish movement at 22°C, although it is the most common metric of body condition in animal behavior studies given its relative ease and non-lethal measurement (Bjornson & Anderson, 2018; Pellegrini *et al.*, 2010). However, weight-at-length is not necessarily indicative of lipid reserves or energy density, which likely measures physiological states more accurately (Johnson *et al.*, 2017; Wilder *et al.*, 2016). Indeed, weight-at-length has had mixed effects on animal behavior (Carvalho *et al.*, 2021; David *et al.*, 2012; Polverino, Bierbach, *et al.*, 2016). Body condition metrics are not limited

to those tested in this study (Stevenson & Woods Jr., 2006). Our study highlights the importance of defining and selecting body condition metrics carefully and the need for testing more than a single metric, when possible (Wilder *et al.*, 2016). For example, dry matter content measurements require lethal sampling, which is not always feasible in some settings.

We found that body condition and length interacted to affect fish movement, where smaller individuals in better body condition were more mobile than those in poorer condition, but body condition was less predictive of movement among larger individuals. This interactive effect suggests that state-dependency of behavior varies by fish body size and through ontogeny (Luttbeg & Sih, 2010; Näslund & Johnsson, 2016; Polverino, Cigliano, *et al.*, 2016). Smaller individuals of fish have higher relative metabolic demands due to lower absolute lipid reserves than larger individuals (Brown & Braithwaite, 2004; Krause *et al.*, 1998). Because feeding was restricted once daily to induce some degree of weight loss in this study, we reason that body condition influenced movement of smaller creek chub in particular. The restricted feeding schedule may be partly responsible for the higher movement levels of creek chub in better condition, particularly in smaller individuals. In our experiment, individuals in poorer body condition could not have satisfied their metabolic demands and improved condition by foraging for food actively. Instead, superior physiological state of fish in better body condition may have afforded them to be more mobile (Bjornson & Anderson, 2018; Luttbeg & Sih, 2010).

Individuals showed consistent movement levels across the three-day study period. Inter-pool movement by creek chub was infrequent in the first 24 hours (*i.e.*, acclimation period),



**Figure 3** Regression coefficient (effect size) of the explanatory variables of fish movement in the Poisson generalized linear models with an interactive term at 16°C (a) and 22°C (b). Regression coefficient estimates were averaged between two competing models at 16°C, and the single best model was identified at 22°C (i.e., no model averaging). Points represent mean estimates and error bars are 95% confidence intervals. The explanatory variables were mean-centered divided by standard deviation; thus, regression coefficient quantified the magnitude of how their changes in one standard deviation unit affected total count of inter-pool movement on the logarithmic scale. The explanatory variables are ordered by their absolute effect size from top to down; DMC, dry matter content; TL, total length.

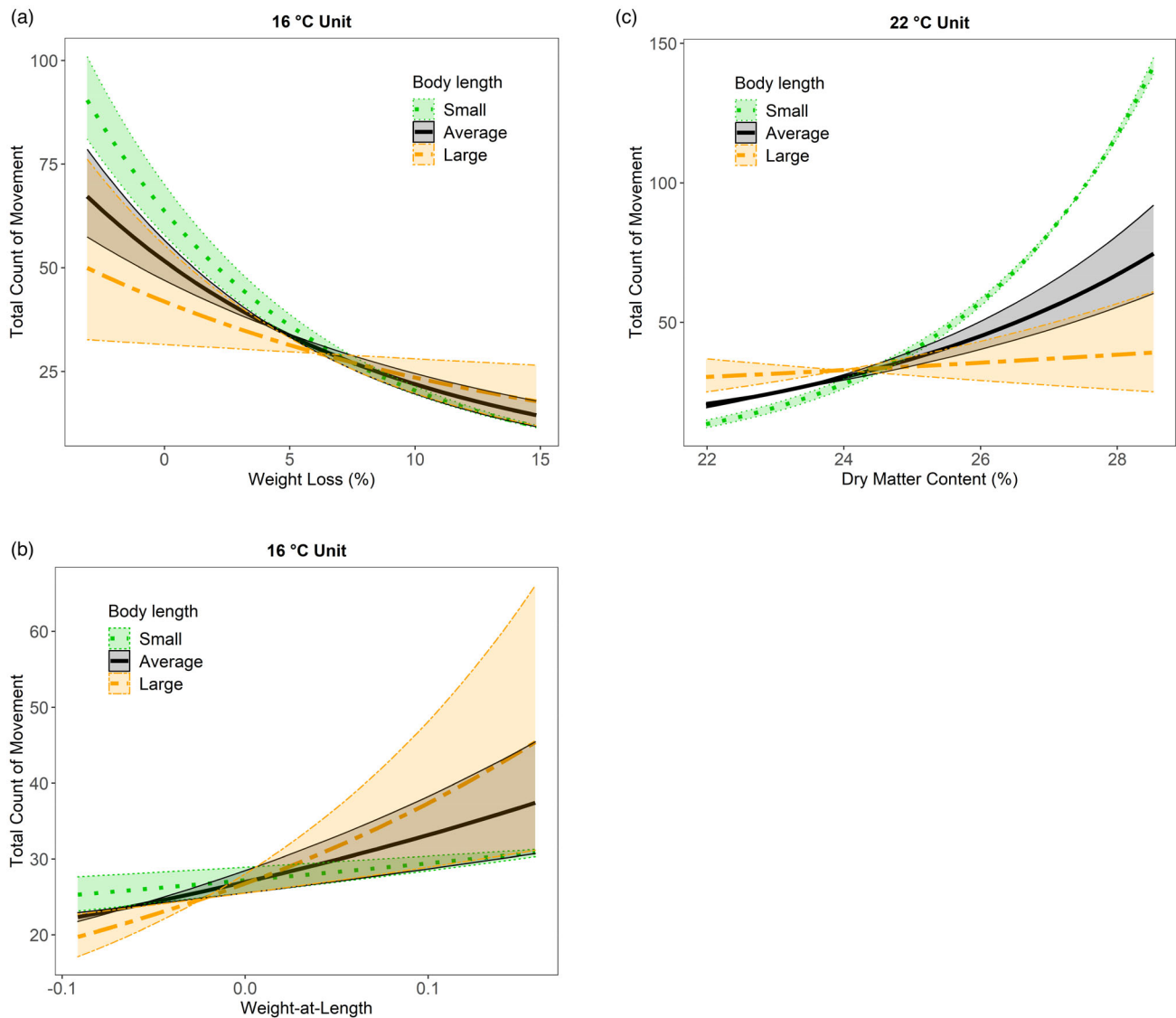
followed by much more frequent movement over the 3-day data collection period, which typifies habituation phases of animals to the new environment (Matsunaga & Watanabe, 2010; Mikheev & Andreev, 1993). We conducted this study over 3 days to align the temporal coverage of movement data with body condition, in which fish needed to be sacrificed for dry

matter content measurements. Consistency in behavior over a longer period and across contexts is a prerequisite to characterizing behaviors as animal personalities (Conrad *et al.*, 2011; Kaiser & Müller, 2021), and body condition has been identified as a driver of animal personalities (Luttbeg & Sih, 2010; Näslund & Johnsson, 2016). Certain physiological traits that affect body condition, such as metabolic rates, are intrinsically different among individuals (Biro & Stamps, 2010; Metcalfe *et al.*, 2016), but body condition changes over time in the wild due to extrinsic factors such as food availability (Sih, 2013). Thus, consistency in state-dependent behavior across environmental contexts should be determined by the relative influences of intrinsic and extrinsic factors that affect body condition.

Movement between the experimental pools was clearly nocturnal in creek chub, where inter-pool movement was most frequent after the simulated sunset during the hours when the lights were off. In the laboratory, stream fishes display nocturnal movement behaviors in some studies (Keep *et al.*, 2021; Magnan & FitzGerald, 1984) but not in others (Keep *et al.*, 2021; Nagrodski *et al.*, 2013). In the wild, some stream fishes are most active and exploratory at night, while others are active during the day (Baker & Ross, 1981; Greenberg, 1991; Reeb *et al.*, 1995). Nocturnal movement is often attributed to anti-predator behavior, food availability, and temperature-mediated metabolic demand in freshwater fishes (Magnan & FitzGerald, 1984; Metcalfe & Steel, 2001). Because predators were absent, food was provided once daily in the daytime, and temperature was constant over time in our study, these factors cannot be directly linked to nocturnal movement patterns. Intriguingly, movement was more frequent during sunrise than during sunset. The simulated photoperiod in this study provides strong evidence that fish responded behaviorally to light, a finding which is challenging to disentangle in the wild where water temperature and oxygen levels fluctuate diurnally in addition to light (Ferencz & Cardenas, 2017; Guasch *et al.*, 1998).

A limitation of this study was that we used a body size range (74–97 mm TL) of a single species; thus, the generality of our findings to other fish species is not known. Creek chub are omnivorous, consuming detritus, algae, and aquatic and terrestrial invertebrates (Champagne *et al.*, 2022; Leonard & Orth, 1986). They eat drifting food in the water column (Taniguchi *et al.*, 1998) and forage on the stream bottom (Quist *et al.*, 2006). Therefore, our findings may best represent body condition effects on movement for opportunistic general feeders. Diet and feeding ecology also shift through ontogeny in fishes (Sánchez-Hernández *et al.*, 2019). Replicating similar investigations across more species and life stages is necessary for more fully understanding the relationships between body condition metrics and fish movement.

In summary, our laboratory study demonstrated that three metrics of body condition affected fish movement to different degrees, and more direct measures of condition (i.e., dry matter content and weight loss) were more predictive of individual variation in movement than a commonly used but less direct measure (i.e., weight-at-length). Movement often comprises an axis of personality, which is consistent and repeatable variation in behavior among individuals across contexts (Nilsson



**Figure 4** Body length–dependent effects of weight loss (a) and weight-at-length (b) at 16°C and dry matter content at 22°C (c) on total count of inter-pool fish movement, predicted by Poisson generalized linear models with an interactive term. Mean predictions are shown in thick lines with bands indicating 95% confidence intervals. Small fish were mean  $-1.5$  sd (77 mm at 16°C and 75 mm at 22°C) and large fish were mean  $+1.5$  sd (93 mm at 16 and 22°C) in total length. Mean total length was 85 mm at 16°C and 84 mm at 22°C. Positive values of weight-at-length are individuals that weigh more than the average weight of the fish at the same total length and negative values are those that weigh less.

*et al.*, 2014; Réale *et al.*, 2007). Given the short duration of this study, it is premature to make definitive statements on body condition effects on personality, although individual consistency in movement was clear across 3 days. Testing an array of body condition metrics as a determinant of movement and other behavioral traits should be warranted across a broader range of contexts, including a combination of laboratory and field settings (Fraser *et al.*, 2001). Stream fish in the wild change their movement behavior in response to food availability (Hansen & Closs, 2009), conspecific density (Olsson *et al.*, 2006), and the presence of predators (Gilliam & Fraser, 2001), which were controlled for in our study. A greater

understanding of body condition effects on animal personality will reveal adaptive significance of individual behavioral variation (Dall *et al.*, 2004; Dingemanse & Wolf, 2010; Sih *et al.*, 2015) and individuals' behavioral plasticity in a changing and increasingly stochastic environment (Wood *et al.*, 2021).

## Acknowledgements

This study was financially supported by the Warner College of Natural Resources at Colorado State University. We thank Audrey Harris, George Valentine, Bailey Carey, Cole Carpenter,



Dallas Lokey, and Ryan Mellin for their field assistance. Cole Campbell, Jason Hanlon, and Matt O'Neill assisted with setting up experimental streams.

## Conflict of interest

The authors declare that they have no conflicts of interest.

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