

# Locomotor activity patterns of muskellunge (*Esox masquinongy*) assessed using tri-axial acceleration sensing acoustic transmitters

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**Abstract** The trade-off between remaining stationary and being active has consequences for the survival and growth of fishes. Recent advancements in telemetry tools have enabled researchers to assess activity patterns of free-swimming fishes using tri-axial acceleration-sensing acoustic transmitters. This study describes the summer activity patterns of muskellunge (*Esox masquinongy*) in an 8 km reach of the Rideau River, Ontario between 1 June and 20 August 2010. Acceleration measurements indicated that muskellunge

tended to remain inactive for much of the time. The effect of time of day (i.e., diel patterns), water temperature, and fish size were also examined. Activity was lowest at dawn, increased throughout the day, peaked at dusk, and declined at night. Activity also declined above temperatures of 25 °C and was lower for larger muskellunge. A comparison of fish captured with rod and reel versus boat electrofisher failed to reveal a significant difference in behaviour. The results of this study illustrate the utility of accelerometer transmitters for studying the behavioural ecology of free-swimming fishes. The results also confirm that muskellunge are generally sedentary during the summer period, but do exhibit reasonably pronounced diel activity patterns.

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## Introduction

Locomotor activity can account for a large component of the daily energy budget of fishes (Boisclair and Leggett 1989). When locomotor activity increases, encounters with food sources also increase (Werner and Anholt 1993), potentially leading to higher growth rates and survival (Grant and Noakes 1987). However, there is a well-known growth-mortality trade-off that drives behavioural decisions: increasing locomotor activity also exposes fishes to a greater risk of encountering predators (Werner and Anholt 1993; Biro et al. 2006; Stamps 2007). Several factors can influence locomotor activity

including hunger (Pettersson and Brönmark 1993), food availability (Metcalf et al. 2004; Orpwood et al. 2006), prey size (Kerr 1971), reproductive status (Abrams 1993), and various environmental factors that change daily and seasonally (Fry 1971). One of the more common drivers of locomotor activity is the diel (i.e., daily) pattern of light and dark (Helfman 1993; Reeb 2002). For example, brown trout (*Salmo trutta*) exhibited the highest movement rates during the nighttime (Young 1999), northern pike (*Esox lucius*) were most active during daytime (Diana 1980), and walleye (*Sander vitreus*) were most active between dusk and dawn (Kelso 1978). As fish are ectothermic, water temperature is one of the most important determinants of activity because changes in temperature directly affect biochemical reactions, which govern swimming capacity and performance (Fry 1971; Brett and Groves 1979; Bennett 1984). More specifically, as temperatures increase or decrease, generally, so does locomotor activity (Brett 1971), which is often demonstrated on a seasonal basis (e.g., Todd and Rabeni 1989; Hasler et al. 2009; Hanson et al. 2010).

In North America, muskellunge (*Esox masquinongy*) are apex freshwater predators and prized sport fish (Margenau and Petchenik 2004). As an esocid, muskellunge are considered mesothermal or ‘cool-water’ species (Casselman 1978), with a thermal preference of approximately 25 °C (Scott and Crossman 1973; Jobling 1981; Clapp and Wahl 1996). They are known to display strong spawning site fidelity (Jennings et al. 2011), reproductive homing (Crossman 1990), and a high association with vegetated littoral zones (Miller and Menzel 1986; Eilers 2008). Muskellunge often employ a sit-and-wait foraging tactic (New et al. 2001) and display a dietary preference for yellow perch (*Perca flavescens*) and catostomids where present (Bozek et al. 1999). Several radio tracking studies have demonstrated predictable seasonal movements that include the establishment of shallow summer home ranges following spring spawning and the breakdown of summer home ranges with movements toward deeper over-wintering areas during fall (Dombeck 1979; Younk et al. 1996; Weeks and Hansen 2009). Less, however, is known about their daily activity patterns.

Field-based biotelemetry has enabled researchers to obtain accurate measurements of the physiology and behaviour of wild, free-swimming fish for use in predictive modeling, to supplement our current understanding of organismal ecology, and to inform management (Lucas et al. 1991; Lucas and Baras 2000; Cooke et al. 2004a, b, 2013). A relatively new suite of sensors used with

biologging and biotelemetry devices are tri-axial accelerometers, which either log (Wilson et al. 2006; Broell et al. 2013) or transmit (O’Toole et al. 2010; Wilson et al. 2013) information regarding activity and fine-scale behaviour. Sampling rates for accelerometers range from 10 Hz for transmitters (Wilson et al. 2013) to  $\geq 100$  Hz for loggers (Broell et al. 2013). Data can be collected at much finer temporal scales compared to conventional non-sensor radio or acoustic tracking, enabling researchers to study fine-scale behavioural patterns of a target species. However, one disadvantage of logger or archival devices is that the unit must be retrieved from the study animal (Ropert-Coudert and Wilson 2005), whereas transmitters simply relay information to a nearby stationary receiver, allowing for easier retrieval of data (Lucas and Baras 2000; see also Table 4, Murchie et al. 2011).

Given the potential utility of accelerometer transmitters at helping researchers elucidate fine-scale behaviour of free-swimming fishes, our primary objective for this study was to evaluate the summer activity patterns of muskellunge using this relatively new type of acoustic transmitter. We were specifically interested in understanding patterns related to diel activity as well as how those patterns were influenced by water temperature and fish size. Moreover, given the interest in muskellunge as a recreationally targeted species, we had a secondary objective of determining whether there were differences in the behaviour of fish captured (and tagged) via angling relative to those captured by boat electrofisher.

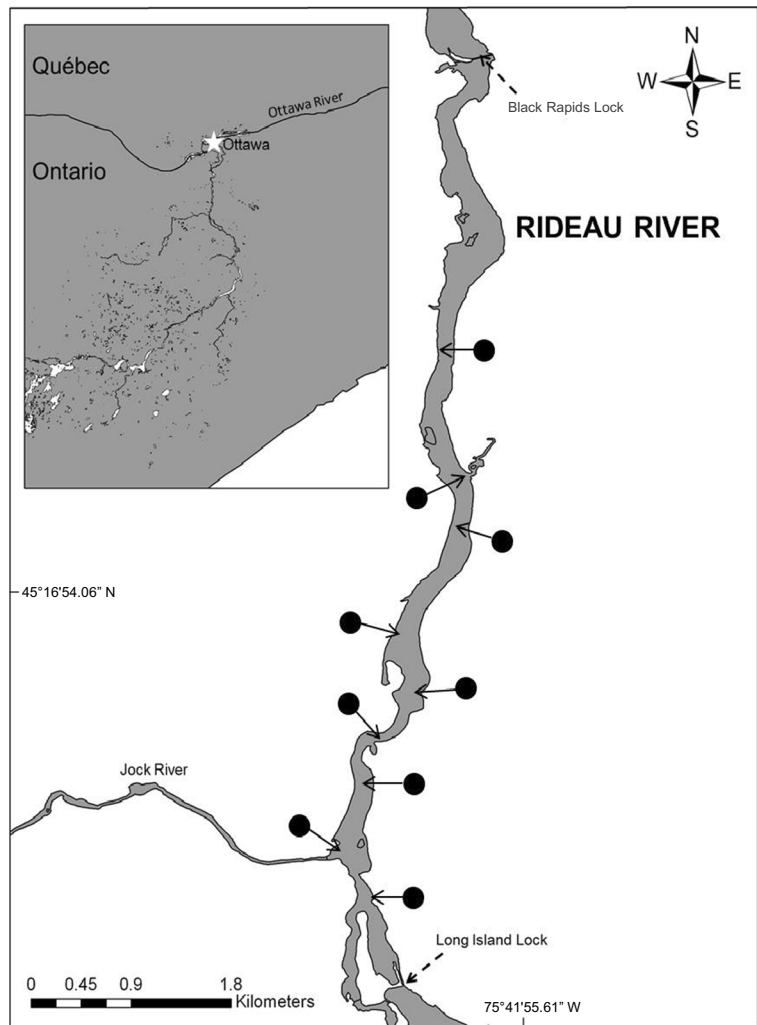
## Methods

### Study site

This study was conducted on a section of the Rideau River, Ontario, Canada between the Long Island and Black Rapids Locks (approximately 8 km in length; Fig. 1). Mean and maximum depth was 2.5 and 10 m, respectively. Much of the shallow, littoral zone is heavily vegetated. Habitats within the river include shallow flats with abundant macrophytes (primarily clasp pondweed *Potamogeton richardsonii*), creek mouths, shallow riffles, pools, deep river channels, and boulders.

Nine acoustic receivers (VR2W, Vemco/Amirix Systems, Shad Bay, Nova Scotia, Canada) were deployed to record transmitted data as tagged fish swam nearby (Fig. 1). Each receiver was either hung beneath navigational buoys, which were located on the deep

**Fig. 1** The Rideau River, Ontario, Canada between the Long Island and Black Rapids Locks. Solid circles represent approximate positions of acoustic receivers



ledge of the river channel, or attached to a short piece of angle iron, tied to three sandbags, and sunk to the bottom (a total of three receivers) so that each piece of angle iron stood upright. Receivers were placed in areas muskellunge were known or suspected to occupy to maximize detections.

Water temperature data were collected at hourly intervals from a temperature recording station approximately 60 km upstream of our study site at the Smiths Falls Water Treatment Plant (SFWTP). We used linear regression to validate these temperatures with data collected from a thermal logger (iButton DS1921Z; resolution  $\pm 0.1$  °C, accuracy  $\pm 1$  °C; Maxim Integrated Products, Inc., Sunnyvale, California) in the study site. The logger only recorded data up to 26.4 °C because a high water temperature alarm was inadvertently set

while deploying the unit. The SFWTP station collected data above these temperatures, making it a good alternative for use in our study. The correlation coefficient of our linear regression analysis indicated a strong relationship between the water temperatures obtained from the study site and those of the SFWTP and thus supported our approach (regression,  $r=0.96$ ). Water temperatures recorded by the SFWTP ranged from 18.7 to 29.9 °C during the study period.

#### Transmitters

We used individually coded acoustic transmitters containing an acceleration sensor, aptly dubbed ‘accelerometers’ (model V9AP, Vemco/Amirix Systems, Shad Bay, Nova Scotia, Canada). Each transmitter also had a

pressure sensor, but because receivers were largely placed in relatively shallow water pressure data were not used. Transmitter dimensions were 46×9 mm and weighed 3.3 g in water and 6.3 g in air. This model transmitter measures acceleration for a period of 20 s and at a sampling rate of five times per second. When transmitters were within range of an acoustic receiver, data were transmitted at a rate of once every 90 s. Battery life was approximately 90 days. All transmitters measured the acceleration of free-swimming fishes by calculating the root mean square of acceleration in three axes – X-, Y-, and Z-axis – to produce a single g-force value. Because acceleration is measured as the instantaneous change in velocity over time, each g-force value was then converted into m/s<sup>2</sup> (1 g-force is equal to 9.8 m/s<sup>2</sup>). Maximum acceleration values produced were 48.0 m/s<sup>2</sup> (4.9 g-forces). Acceleration is considered a proxy for swimming activity (i.e., locomotion) and therefore referred to as activity (Wilson et al. 2013). Fish were tracked until all transmitter batteries had ceased functioning on 20 August 2010.

#### Capture methods

Eight muskellunge were captured via electrofishing (for settings see Landsman et al. 2011) in late April 2010 and subsequently tagged (see below). However, one was found dead in July 2010 and because of concerns related to abnormal behavioural patterns of a potentially unhealthy fish, its data were excluded from analysis. Of the surviving seven muskies that were included in our

analysis, the mean total length (TL) of electrofished muskellunge was 80.6 cm±16.7 standard deviation (S.D.) and sizes ranged from 53.0 to 101.0 cm (Table 1). To explore potential differences between muskellunge captured by electrofishing and by angling, we added another six individuals caught by hook-and-line. Mean TL was 100.5 cm±8.3 standard deviation (S.D.), ranging from 87.0 to 109.8 cm (Table 1).

#### Tagging

Following electrofishing in late April 2010, most muskellunge entered a state of electronarcosis, which has been used as a form of electroanesthesia and has been shown to reduce handling time by several minutes (Madden and Houston 1976; Jennings and Looney 1998; Sattari et al. 2009), allowing us to surgically implant individually coded transmitters. All individuals were held in a 100 L cooler of water. Not all muskellunge, however, could be electroanesthetized properly and clove oil was used as an anesthetic for several fish (concentration: 15 ppm). Once anesthetized, either electro or chemical, an incision approximately 1.5 cm long was made with a size 15-blade scalpel along the ventral midline and the tag was gently inserted into the coelomic cavity. A reverse curved needle and two simple interrupted absorbable monofilament sutures were used to close the incision (PDS II 3/0, Ethicon Ltd., New Jersey; Cooke et al. 2003; Wagner et al. 2010). Electroanesthetized fish were revived alongside the boat and chemically anesthetized fish were flushed with fresh

**Table 1** Transmitter ID, biological data, and detection information of 13 muskellunge captured from the Rideau River, Ontario, Canada

ID#	Sex	Capture method	Total length (cm)	# Detections	# Days detected
2084	M	Electrofishing	67.5	14,065	79
2086	F	Electrofishing	101.0	5222	69
2088	M	Electrofishing	78.5	11,074	78
2090	M	Electrofishing	53.0	988	33
2092	F	Electrofishing	97.0	1564	26
2096	F	Electrofishing	88.0	5113	76
2098	M	Electrofishing	79.5	6814	66
2104	M	Angling	96.0	2945	40
2106a	F	Angling	99.9	645	5
2106b	F	Angling	109.8	893	11
2110	M	Angling	87.0	8518	36
2112	M	Angling	107	6086	58
2114	F	Angling	103.5	4318	35

river water to aid in recovery. Muskellunge were released when equilibrium was gained and strong swimming actions were observed. All muskellunge were released at the site of capture. This process took approximately 5 and 10 min for electroanesthetized and chemically anesthetized individuals, respectively. Fish captured via angling methods were not subjected to anesthesia in order to try and reduce stress associated with the capture and tagging process as angling has been shown to elicit a greater stress response in muskellunge compared to electrofishing (Landsman et al. 2011). Instead, they were fitted externally with transmitters similar to methods used in Landsman et al. (2011). Briefly, a wire harness was wrapped around the transmitter and secured using multiple layers of Plasti Dip (Plasti Dip International; Blaine, Minnesota) with the wires then passed through the dorsal musculature using two hypodermic needles (Bridger and Booth 2003). A thin strip of neoprene was also attached to the transmitter and placed between it and the fish to reduce abrasion. All surgeries and transmitter attachment procedures were conducted by the same trained individual using guidelines provided by the Canadian Council for Animal Care issued through Carleton University, Ottawa, Canada.

Statistical analysis

Data from the month of May was excluded from analysis to avoid confounding factors associated with any late spawning that may have taken place during that month. Data were aggregated by calculating the hourly median value of acceleration by Fish ID. Only median acceleration values computed using  $\geq$  four observations per hour were used. Doing so better represents average muskellunge activity and avoided extreme measurements that could complicate model validation.

Diel period (i.e., DN and TDN separated into two terms with and without inclusion of twilight periods, see Table 2), centered water temperature, and centered total length as well as two-way interactions between each set of variables were used to model activity with a linear mixed-effect model (Zuur et al. 2009). A bell-shaped relationship of acceleration and temperature was described by the terms  $\text{temp} + \text{temp}^2$ . Fish ID was included as a random effect. A set of candidate models representing all possible combinations of terms was constructed and the models were fitted with a transformed acceleration variable (response variable) of  $1/\text{acceleration}$  to reduce heteroscedasticity and normalize the residuals. An exponential correlation structure was used to account for temporal auto-correlation in the

**Table 2** Linear mixed model results of muskellunge activity as a function of diel period (TDN – dawn, dusk, day, night; DN – no twilight periods), fish size, and water temperature (“Temp + Temp<sup>2</sup>” terms) from 1 June to 20 August 2010.

Models	K	AICc	$\Delta$ AICc	Model likelihood	AICc weight	Log likelihood	Cumulative weight
TL * DielTDN + cTemp + cTemp <sup>2</sup>	13	1938.65	0.00	1.00	0.42	-956.27	0.42
cTL + DielTDN + cTemp + cTemp <sup>2</sup>	10	1939.71	1.06	0.59	0.25	-959.82	0.67
cTL * DielTDN + cTL * cTemp + cTL * cTemp <sup>2</sup>	15	1941.01	2.36	0.31	0.13	-955.43	0.80
DielTDN + cTemp + cTemp <sup>2</sup>	9	1941.98	3.32	0.19	0.080	-961.96	0.88
DielTDN + cTL * cTemp + cTL * cTemp <sup>2</sup>	12	1942.01	3.36	0.19	0.080	-958.95	0.96
cTL * DielTDN	11	1944.85	6.20	0.05	0.020	-961.38	0.98
cTL + DielTDN	8	1946.53	7.87	0.02	0.010	-965.24	0.99
cTL * DielTDN + DielTDN * cTemp + DielTDN * cTemp <sup>2</sup>	19	1948.26	9.60	0.01	0.00	-955.00	0.99
cTL + DielTDN * cTemp + DielTDN * cTemp <sup>2</sup>	16	1948.36	9.71	0.01	0.00	-958.09	0.99
DielTDN	7	1948.68	10.03	0.01	0.00	-967.32	1.00
DielTDN * cTemp + DielTDN * cTemp <sup>2</sup>	15	1950.55	11.90	0.00	0.00	-960.20	1.00
cTL * DielTDN + cTL * cTemp + cTL * cTemp <sup>2</sup> + DielTDN * cTemp + DielTDN * cTemp <sup>2</sup>	21	1950.66	12.00	0.00	0.00	-954.17	1.00
cTL * cTemp + cTL * cTemp <sup>2</sup> + DielTDN * cTemp + DielTDN * cTemp <sup>2</sup>	18	1950.67	12.02	0.00	0.00	-957.22	1.00

Centered terms are denoted with a lowercase “c” before the term. Models were ranked using Akaike’s Information Criterion (AICc) and only models up to a  $\Delta$ AICc value of 12.02 are shown



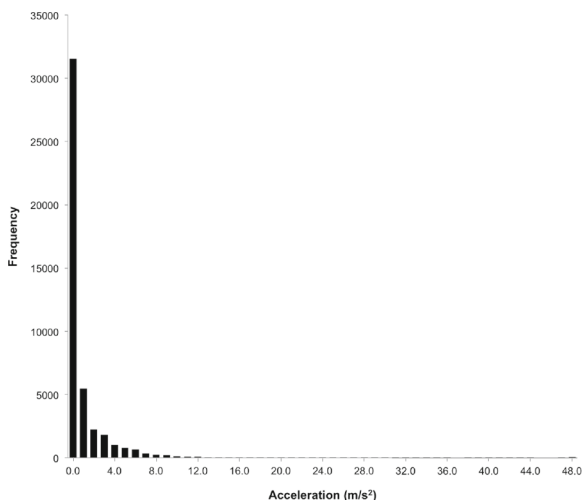
residuals. Models were ranked using their AICc values, with the best and equally supported models being those within 2.00 AICc units of the top ranked model (Burnham and Anderson 2002). Model averaged predictions were created based on the 95 % confidence set for the best model (Burnham and Anderson 2002).

We were also interested in determining whether any differences in activity were evident between muskellunge captured with different capture methods (i.e., electrofishing or angling). To explore this, we added data from six angled muskellunge and aggregated the data in the same manner as our analysis for the non-angled muskellunge. Then, using the top ranked AICc model derived from our data analysis for non-angled fish, we added capture method as an additional explanatory variable to test its effect on muskellunge activity and assessed its significance based on the associated  $P$ -value ( $\alpha \leq 0.05$ ). All analyses were carried out using the package nlme in R (Pinheiro et al. 2014).

## Results

### General activity

From 1 June to 20 August 2010, receivers logged 44,840 acceleration measurements. The vast majority (70.3 %) of detections were acceleration values  $\leq 1.0 \text{ m/s}^2$  (Fig. 2). Detection frequency steadily declined above readings of  $1.0 \text{ m/s}^2$  (Fig. 2). Transmitters were

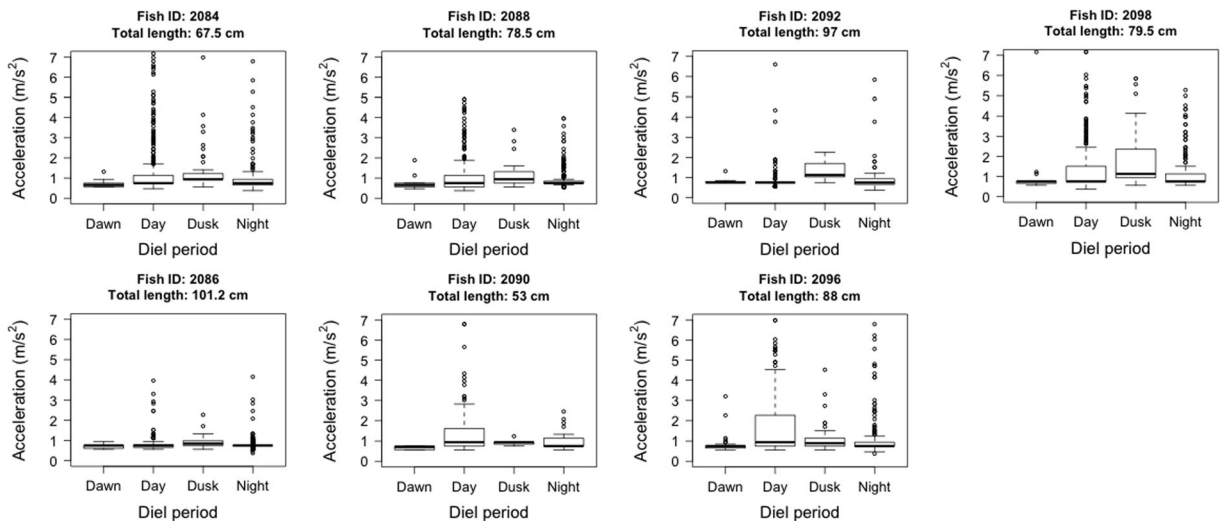


**Fig. 2** Frequency histogram of acceleration measurements for free-ranging, non-angled muskellunge during 1 June and 20 August 2010

capable of measuring maximum acceleration values of  $48.0 \text{ m/s}^2$ , of which 73 such detections were made. Most (53.4 %) of the  $48.0 \text{ m/s}^2$  burst events occurred during the daytime, followed by night (26.0 %), dusk (19.2 %), and dawn (1.4 %). Two fish (67.5 and 78.5 cm TL) accounted for over 75 % of  $48.0 \text{ m/s}^2$  burst events. Acceleration was variable among fish at different diel periods with some showing more activity at dusk and others during the day (Fig. 3). Variation in acceleration was low at dawn and the largest muskellunge tagged in the study displayed relatively similar acceleration measurements across all diel periods (Fig. 3).

### Correlates of activity

The top five models included in our 95 % confidence set contained the TDN (i.e., twilight-day-night) diel term and the temp + temp<sup>2</sup> terms that assumes a bell-shaped relationship between activity and water temperature. The TL factor was included in four of the five models. The top ranked model of our candidate set indicated that there was an interaction between muskellunge size and diel period (Table 2). Specifically, activity increased throughout the day, peaked at dusk, and declined at night to a low at dawn (Figs. 3 and 4), but the level of activity did not remain constant for each fish size. For example, activity was similar among sizes at dawn. However, activity during the day and dusk was higher for the smallest fish relative to the largest, with the difference between the smallest and largest fish being exacerbated at dusk. In addition, muskellunge activity indicated a bell-shaped relationship with water temperature where activity increased to a maximum at about  $25 \text{ }^\circ\text{C}$  and declined above (Fig. 3). One difference between the top ranked model and the second ranked model was the exclusion of the size-diel period interaction term in the latter (Table 2). Otherwise, all other variables showed consistent response directions (i.e., increasing/decreasing; Table 3) between the two top ranked models. The direction of the model coefficients for each diel period and for the relationship between activity and water temperature were also consistent across the top five models (data not shown). Each model showed activity increasing from a low at dawn to a peak at dusk and a decrease at night, and all models described a bell-shaped relationship between activity and water temperature. No differences in activity were found between muskellunge captured via angling or electrofishing ( $F_{1,10} = 0.0003$ ,  $P = 0.98$ ).



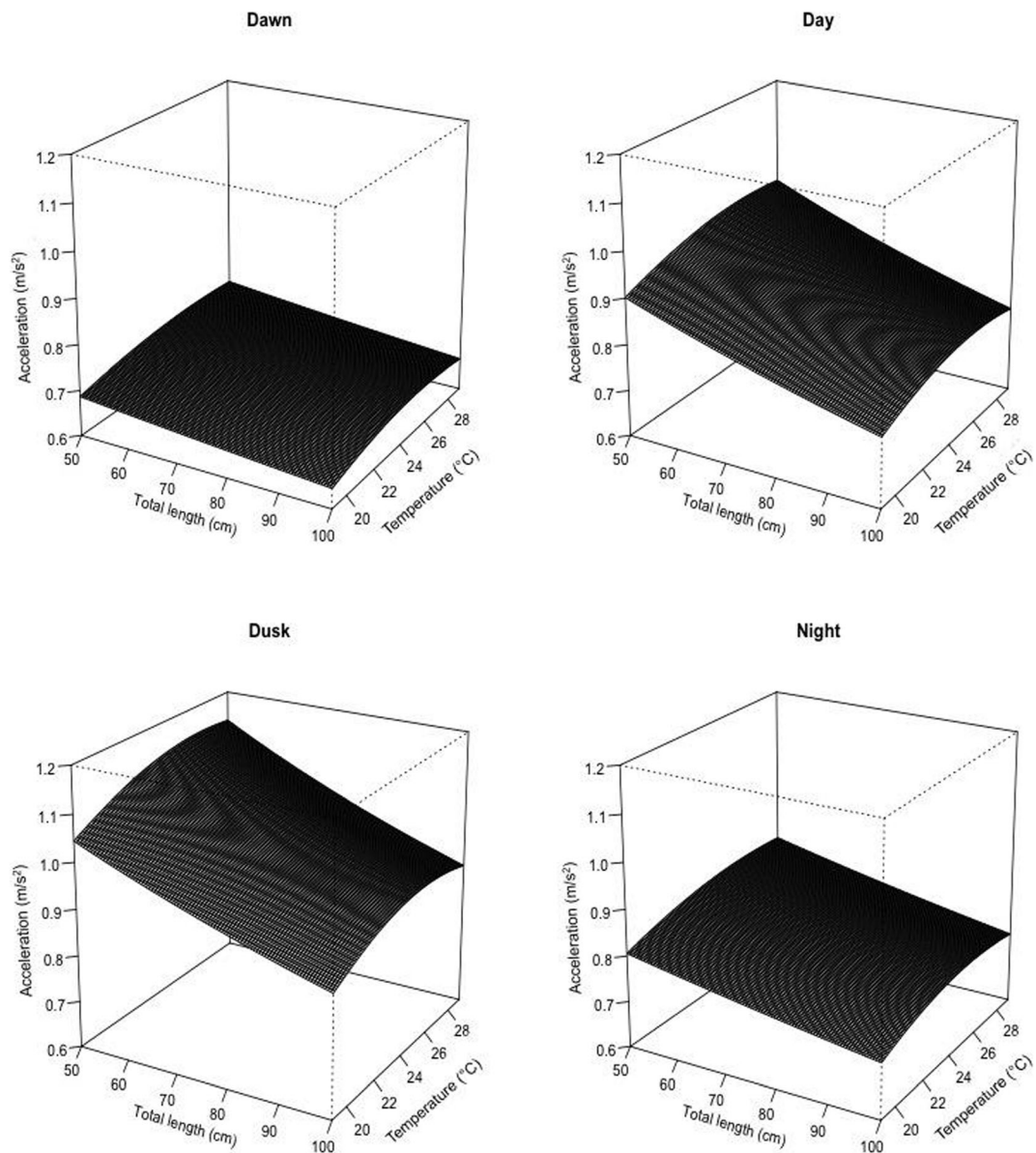
**Fig. 3** Boxplots showing variation in diel acceleration (i.e., activity) values for each free-ranging, non-angled muskellunge in our analysis. Only acceleration values up to 7 m/s<sup>2</sup> are shown. Total length is also noted for each individual fish

**Discussion**

Esocids are generally considered ambush or stalking predators (e.g., Scott and Crossman 1973; Diana 1980; Hart 1997; New et al. 2001; Juanes et al. 2002), sitting relatively still for periods of time before initiating a rapid strike at prey (New et al. 2001). The abundance of white muscle necessary for burst swimming (Altringham and Ellerby 1999), large caudal fin for creating powerful thrust (Webb 1994), and rearward fin placement make esocids well suited for engaging in ambushing or stalking behaviours. Our data further support research that suggests muskellunge are largely sedentary predators. Interpreting precisely what is occurring in terms of behaviour for a given acceleration measurement is difficult. While some studies suggest that increased activity reflects searching behaviour related to foraging (e.g., Werner and Anholt 1993), this might not be the case for ambush predators like esocids (Diana 1980). We posit that, for muskellunge in our study, it is likely many of the bursts in activity are foraging events because there is an abundance of cover in the study site from which to ambush prey. It is also likely that bursts are not anti-predatory responses because this species is the apex predator in the Rideau River. Alternatively, some of the measured bursts could be related to startle responses from passing boats or potential angling events. An ethogram conducted prior to the study (e.g., Murchie et al. 2011; Brownscombe et al. 2014) would have enabled us to more definitively relate certain behaviours

to measurements, but given logistical constraints, this was not feasible for the present study. There is also less known about muskellunge behaviour in relatively oligotrophic water. Both this study and Miller and Menzel (1986) examined muskellunge behaviour in systems with abundant vegetation, but in waterbodies with limited littoral cover, activity may be much higher as fish seek habitats to forage in. Indeed, Kobler et al. (2009) noted searching behaviours characterized by higher activity in northern pike inhabiting open water. This likely occurs in muskellunge, but has yet to be demonstrated in the literature.

Vision is a critical sensory system for muskellunge (New et al. 2001) and our results show that their activity increases throughout the day when light levels are strongest. However, vision is also a crucial predator-avoidance mechanism used by prey fishes. To compensate, predators may forage during crepuscular periods as these intermediate light levels maximize prey capture while minimizing the risk of being detected on approach (i.e., “Twilight Hypothesis”; Pitcher and Turner 1986). Indeed, Miller and Menzel (1986) demonstrated increased movement at crepuscular periods. Our work, however, only partially supports these findings. Instead, we recorded the lowest activity at dawn, an increase through the day, a peak at dusk, and a steady decrease at night. In contrast, smallmouth bass (*Micropterus dolomieu*) were shown to exhibit markedly crepuscular summer activity patterns (Todd and Rabeni 1989) while other centrarchids displayed lowest



**Fig. 4** Perspective plots of acceleration (i.e., activity) for free-ranging muskellunge as a function of diel period, total length, and water temperature during the period from 1 June to 20 August 2010

activity at night and highest at dusk (i.e., 16:00–22:00 h; Shoup et al. 2004). For the closely related northern pike, however, diel activity patterns vary. For example, Diana (1980) showed little activity at crepuscular periods with more activity during the day, while other researchers demonstrated higher crepuscular activity than at other times (Mackay and Craig 1983; Cook and Bergersen 1988; Baktoft et al. 2012). In general, northern pike researchers agree that activity decreases at night (Baktoft et al. 2012), which the present study shows is

also true for muskellunge. Taken together, our results indicate clear diel summer activity patterns for muskellunge, and differences between studies may be owed to interspecific (i.e., muskellunge versus northern pike) or site-specific/regional differences.

Larger size in fish is considered an asset and as increased activity exposes fish to a higher risk of predation (Stamps 2007), larger individuals should be less active to protect their assets (i.e., asset protection principal; Clark 1994). Indeed, activity of muskellunge in



**Table 3** Full linear mixed effect model output information for the top ranked models with  $\Delta AICc$  values <2.00

Model (Rank)	Variable	Value	Std. error	df	T-value	P-value
cTL * DielTDN + cTemp + cTemp2 (#1)	Intercept	1.45	0.040	4375	36.68	<0.0001
	cTL	-0.0019	0.0031	5	-0.61	0.57
	TDN(Day)	-0.31	0.028	4375	-10.85	<0.0001
	TDN(Dusk)	-0.48	0.038	4375	-12.64	<0.0001
	TDN(Night)	-0.20	0.029	4375	-7.03	<0.0001
	cTemp	-0.086	0.038	4375	-2.29	0.022
	cTemp <sup>2</sup>	0.0017	0.00078	4375	2.15	0.031
	cTL×TDN(Day)	0.0063	0.0025	4375	2.51	0.012
	cTL×TDN(Dusk)	0.0066	0.0033	4375	1.98	0.048
	cTL×TDN(Night)	0.0036	0.0026	4375	1.40	0.16
cTL + DielTDN + cTemp + cTemp2 (#2)	Intercept	1.45	0.034	4378	36.79	<0.0001
	cTL	0.0032	0.0019	5	1.67	0.16
	TDN(Day)	-0.31	0.028	4378	-10.00	<0.0001
	TDN(Dusk)	-0.48	0.038	4378	12.72	<0.0001
	TDN(Night)	-0.21	0.029	4378	-7.19	<0.0001
	cTemp	-0.087	0.038	4378	-2.31	0.021
	cTemp <sup>2</sup>	0.0017	0.00078	4378	2.17	0.030

The analysis was performed using the inverse of acceleration and coefficient estimates should be interpreted as increasing acceleration (i.e., activity) when a negative (-) sign is present and vice versa when estimates are positive. Lowercase “c” preceding variables indicates centered terms

Abbreviations: TL total length, TDN twilight-day-night diel periods, temp and temp<sup>2</sup> bell-shaped relationship with activity

the present study declined as body length increased, which may offer some support for the asset protection principle. Furthermore, larger fish were also shown to have decreased metabolisms and lowered digestive rates, smaller meal sizes relative to body size, and less ability to achieve a larger size (Brett and Groves 1979). There is also evidence that smaller fish have higher consumption rates (Buckel et al. 1995). In addition, spatial distribution has been shown to vary among size classes (Werner et al. 1977) potentially as a method of reducing resource competition (see Ross 1986). Therefore, it is plausible that differences in activity patterns may reflect smaller individuals moving more to search for habitat with fewer conspecifics.

Water temperature is one of the most influential factors governing fish behaviour (e.g., Fry 1971) given the dependence of enzymatic activity and muscle contraction on temperature (Brett 1971; Bennett 1984; Rall and Woledge 1990; Videler and Wardle 1991). Our results show that muskellunge activity increased up to 25 °C and declined at temperatures above this value. In fish, increasing water temperature increases metabolic

demand, and thus should result in higher activity needed to obtain food (Clarke and Johnston 1999; Metcalfe et al. 2004). Similar results to those demonstrated in this study have also been shown by Dombeck (1979) where muskellunge activity increased up to 27 °C, but declined at temperatures above. Other studies have shown comparable activity patterns in species such as northern pike (Casselman 1978) and sockeye salmon (*Oncorhynchus nerka*) (Brett 1971). The reduction in activity at high water temperatures may be a reflection of the great energetic cost to muskellunge of maintaining elevated activity at unfavorable water temperatures.

Maximum acceleration was measured at 48 m/s<sup>2</sup> (the transmitter’s highest measurement capability), a value within reason given maximum acceleration values of the related northern pike have been recorded as high as 130 m/s<sup>2</sup> during feeding strikes (Harper and Blake 1991) and 151 m/s<sup>2</sup> for escape responses (Frith and Blake 1991; see also Domenici and Blake 1997). The limitations of the transmitters used in the present study prevented us from recording true maximum acceleration because measurements were sampled every 5 s and

averaged over a 20 s period. Therefore, the V9AP transmitters may not be the best tool for measuring maximum acceleration or for calculating precise acceleration measurements given the averaging that has to occur for this type of device. Instead, researchers should consider accelerometer-logging devices that do not generate means and sample at a minimum rate of 30 Hz (Broell et al. 2013; Noda et al. 2014; D. Webber, personal communication). Yet, the resolution of accelerometer transmitters like the one used here continues to improve. For instance, prior versions of the Vemco V9AP recorded maximum accelerations of only 3.5 m/s<sup>2</sup> (O'Toole et al. 2010; Murchie et al. 2011) as opposed to 48.0 m/s<sup>2</sup> in the present study.

Given that muskellunge are a popular target of recreational anglers, we compared the behaviour of fish captured, tagged, and released using both rod and reel and boat electrofisher. This study design was somewhat imperfect because it is possible that different gear types select for different behaviour types (e.g., one could predict that angled fish are more bold and active than those caught by the less discriminatory electrofisher; e.g., Uusi-Heikkilä et al. 2008) and also result in different post-capture behavioural consequences (e.g., Klefoth et al. 2008). However, we failed to document significant differences in the behaviour of fish relative to capture gear suggesting that neither of those possibilities (i.e., gear selectivity or differential behavioural consequences of capture) were relevant drivers here. The little work that has been done on post-release behaviour of fish tends to identify very short duration (several days) alterations in behaviour (e.g., Klefoth et al. 2008) such that detecting effects across the longer study period used here might be unlikely. It is also worth noting that our sample sizes were reasonably small as this was not the primary objective of the study.

## Conclusion

In summary, the activity patterns presented here may serve as a foundation for future research questions, particularly with respect to what specific mechanisms drive muskellunge activity patterns. This is important if the goal is to better understand the community ecology of freshwater systems, particularly those containing apex predators. This study also supports several observations made in other muskellunge research projects with respect to diel and temperature-related activity

patterns. It is interesting to note the similarities between our results and those generated multiple decades ago, despite the use of vastly different technology. Our findings also support the utility of accelerometer transmitters as viable biotelemetry devices. Cooke et al. (2004a) discuss accelerometers and other biotelemetry as tools to delineate specific physiological and behavioural patterns in ecological research. This integrative approach represents a crucial step forward as we seek greater understanding of how organisms function in and interact with their environments, which will likely have a positive impact on conservation and management of fishes in the near future (Cooke et al. 2013). Although accelerometer acoustic transmitters can be expensive, we believe the benefits of remotely monitoring subjects, collecting data on short temporal scales, and the ease of data retrieval compared to biologging devices (see also Table 4, Murchie et al. 2011) outweigh the costs.

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## References

- Abrams MV (1993) The trade-off between foraging and courting in male guppies. *Anim Behav* 45:673–681
- Altringham JD, Ellerby DJ (1999) Fish swimming: patterns in muscle function. *J Exp Biol* 202:3397–3403
- Baktoft H, Aarestrup K, Berg S, Boel M, Jacobsen L, Jepsen N, Koed A, Svendsen JC, Skov C (2012) Seasonal and diel effects on the activity of northern pike studied by high-resolution positional telemetry. *Ecol Freshw Fish* 21:386–394
- Bennett AF (1984) Thermal dependence of muscle function. *Am J Physiol Regul Integr Comp Physiol* 16:217–229

- Biro PA, Abrahams MV, Post JR, Parkinson EA (2006) Behavioural trade-offs between growth and mortality explain evolution of submaximal growth rates. *J Anim Ecol* 75: 1165–1171
- Boisclair D, Leggett WC (1989) The importance of activity in bioenergetics models applied to actively foraging fishes. *Can J Fish Aquat Sci* 46:1859–1867
- Bozek MA, Burri TM, Frie RV (1999) Diets of muskellunge in northern Wisconsin lakes. *N Am J Fish Manag* 19:258–270
- Brett JR (1971) Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Am Zool* 11:99–113
- Brett JR, Groves TDD (1979) Physiological energetics. In: Hoar WS, Randall DJ, Brett JR (eds) *Fish Physiology*, vol 8. Academic, New York, pp 599–667
- Bridger CJ, Booth RK (2003) The effects of biotelemetry transmitter presence and attachment procedures on fish physiology and behavior. *Rev Fish Sci* 11:13–34
- Broell F, Noda T, Wright S, Domenici P, Steffensen JF, Auclair JP, Taggart CT (2013) Accelerometer tags: detecting and identifying activities in fish and the effect of sampling frequency. *J Exp Biol* 216:1255–1264
- Brownscombe JW, Gutowsky LFG, Danylchuk AJ, Cooke SJ (2014) Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. *Mar Ecol Prog Ser* 505:241–251
- Buckel JA, Steinberg ND, Conover DO (1995) Effects of salinity, salinity, and fish size on growth and consumption of juvenile bluefish. *J Fish Biol* 47:696–706
- Burnham KP, Anderson DR (2002) Multimodel inference: understanding AIC and BIC in model selection. *Sociol Methods Res* 33:261–304
- Casselmann JM (1978) Effects of environmental factors on growth, survival, activity, and exploitation of northern pike. *Am Fish Soc Spec Publ* 11:114–128
- Clapp DF, Wahl DH (1996) Comparison of food consumption, growth, and metabolism among muskellunge—an investigation of population differentiation. *Trans Am Fish Soc* 125: 402–410
- Clark CW (1994) Antipredator behaviour and the asset-protection principle. *Behav Ecol* 5:159–170
- Clarke A, Johnston NM (1999) Scaling of metabolic rate with body mass and temperature in teleost fish. *J Anim Ecol* 68: 893–905
- Cook MF, Bergersen EP (1988) Movements, habitat selection, and activity periods of northern pike in Eleven Mile Reservoir, Colorado. *Trans Am Fish Soc* 117:495–502
- Cooke SJ, Graeb BDS, Suski CD, Ostrand KG (2003) Effects of suture material on incision healing, growth and survival of juvenile largemouth bass implanted with miniature radio transmitters: case study of a novice and experienced fish surgeon. *J Fish Biol* 62:1366–1380
- Cooke SJ, Hinch SG, Wikelski M, Andrews RD, Kuchel LJ, Wolcott TG, Butler PJ (2004a) Biotelemetry: a mechanistic approach to ecology. *Trends Ecol Evol* 19:324–343
- Cooke SJ, Thorstad EB, Hinch SG (2004b) Activity and energetics of free-swimming fish: insights from electromyogram telemetry. *Fish Fish* 5:21–52
- Cooke SJ, Midwood JD, Thiem JD, Klimley P, Lucas MC, Thorstad EB, Eiler J, Holbrook C, Ebner BC (2013) Tracking animals in freshwater with electronic tags: past, present and future. *Anim Biotechnol* 1:5
- Crossman EJ (1990) Reproductive homing in muskellunge, *Esox masquinongy*. *Can J Fish Aquat Sci* 47:1803–1812
- Diana JS (1980) Diel activity pattern and swimming speeds of northern pike (*Esox lucius*) in Lac Ste. Anne, Alberta. *Can J Fish Aquat Sci* 37:1454–1458
- Dombek MP (1979) Movement and behavior of the muskellunge determined by radio-telemetry, Technical Bulletin 113. Wisconsin Department of Natural Resources Technical, Madison, pp 1–20
- Domenici P, Blake RW (1997) The kinematics and performance of fish fast-start swimming. *J Exp Biol* 200:1165–1178
- Eilers CD (2008) Movement, home-range, and habitat selection of muskellunge (*Esox masquinongy* Mitchell) in Thornapple Lake, Michigan. Master's thesis, Central Michigan University
- Frith HR, Blake RW (1991) Mechanics of the startle response in the northern pike, *Esox Lucius*. *Can J Zool* 69:2831–2839
- Fry FEJ (1971) The effect of environmental factors on the physiology of fish. In: Hoar WS, Randall DJ (eds) *Fish physiology*, vol 6. Academic, New York, pp 1–98
- Grant JWA, Noakes DLG (1987) Movers and stayers: foraging tactics of young-of-the-year brook charr, *Salvelinus fontinalis*. *J Anim Ecol* 56:1001–1013
- Hanson KC, Hasler CT, Donaldson MR, Cooke SJ (2010) Stability of swimming performance and activity hierarchies among wild largemouth bass at multiple temporal scales: evidence for context-dependent shuffling between seasons. *Can J Zool* 88:324–333
- Harper DG, Blake RW (1991) Prey capture and the fast-start performance of northern pike *Esox lucius*. *J Exp Biol* 155:175–192
- Hart PJB (1997) Foraging tactics. In: Godin JG (ed) *Behavioural ecology of teleost fishes*. Oxford University Press, United States, 400 pp
- Hasler CT, Suski CD, Hanson KC, Cooke SJ, Philipp DP, Tufts BL (2009) Effect of water temperature on laboratory swimming performance and natural activity levels of adult largemouth bass. *Can J Zool* 87:589–596
- Helfman GS (1993) Fish behaviour by day, night and twilight. In: Pitcher TJ (ed) *Behaviour of Teleost Fishes*, 2nd edn. Chapman and Hall, London, pp 479–512
- Jennings CA, Looney GL (1998) Evaluation of two types of anesthesia for performing surgery on striped bass. *N Am J Fish Manag* 18:187–190
- Jennings MJ, Hatzembeler GR, Kampa JM (2011) Spring capture site fidelity of adult muskellunge in inland lakes. *N Am J Fish Manag* 31:461–467
- Jobling M (1981) Temperature and final preferendum: rapid methods for the assessment of optimum growth temperatures. *J Fish Biol* 19:439–455
- Juanes F, Buckel JA, Scharf FS (2002) Feeding ecology of piscivorous fishes. In: Hart PJB, Reynolds JD (eds) *Handbook of fish biology and fisheries*, vol 1, Fish biology. Blackwell Publishing Ltd., Oxford, pp 267–283
- Kelso JRM (1978) Diel rhythm in activity of walleye, *Stizostedion vitreum vitreum*. *J Fish Biol* 12:593–599
- Kerr SR (1971) Prediction of fish growth efficiency in nature. *J Fish Res Board Can* 28:809–814

- Klefoth T, Kobler A, Arlinghaus R (2008) The impact of catch-and-release angling on short-term behaviour and habitat choice of northern pike (*Esox lucius* L.). *Hydrobiologia* 601:99–110
- Kobler A, Klefoth T, Mehner T, Arlinghaus R (2009) Coexistence of behavioural types in an aquatic top predator: a response to resource limitation? *Oecologia* 161:837–847
- Landsman SJ, Wachelka HJ, Suski CD, Cooke SJ (2011) Evaluation of the physiology, behaviour, and survival of adult muskellunge (*Esox masquinongy*) captured and released by specialized anglers. *Fish Res* 110:377–386
- Lucas MC, Baras E (2000) Methods for studying spatial behaviour of freshwater fishes in the natural environment. *Fish Fish* 1: 283–316
- Lucas MC, Priede IG, Armstrong JD, Gindy ANZ, deVera L (1991) Direct measurements of metabolism, activity and feeding behaviour of pike, *Esox lucius* L., in the wild, by the use of heart rate telemetry. *J Fish Biol* 39:325–345
- Mackay WC, Craig JF (1983) A comparison of four systems for studying the activity of pike, *Esox lucius* (L.), perch, *Perca fluviatilis* (L.) and *P. flavescens* (Mitchill). In: Pincock DG (ed) Proceedings of the Fourth International Conference of Wildlife Biotelemetry, August 22–24, 1983, Halifax, Nova Scotia, Canada. Applied Microelectronics Institute and Technical University of Nova Scotia, Halifax, pp 22–30
- Madden JA, Houston AH (1976) Use of electroanaesthesia with freshwater teleosts: physiological consequences in the rainbow trout *Salmo gairdneri* Richardson. *J Fish Biol* 9:457–462
- Margenau TL, Petchenik JB (2004) Social aspects of muskellunge management in Wisconsin. *N Am J Fish Manag* 24:82–93
- Metcalfe NB, Fraser NHC, Burns MD (2004) Food availability and the nocturnal vs. diurnal foraging trade-off in juvenile salmon. *J Anim Ecol* 68:371–381
- Miller ML, Menzel BW (1986) Movement, activity, and habitat use patterns of muskellunge in West Okoboji Lake, Iowa. In: Hall GE (ed) Managing muskies: a treatise on the biology and propagation of muskellunge in North America. American Fisheries Society, Special Publication 15, Bethesda, Maryland, pp 51–61
- Murchie KJ, Cooke SJ, Danylchuk AJ, Suski CD (2011) Estimates of field activity and metabolic rates of bonefish (*Albula vulpes*) in coastal marine habitats using acoustic tri-axial accelerometer transmitters and intermittent flow respirometry. *J Exp Mar Biol Ecol* 396:147–155
- New JG, Alborg Fewkes L, Khan AN (2001) Strike feeding behavior in the muskellunge, *Esox masquinongy*: contributions of the lateral line and visual sensory systems. *J Exp Biol* 204:1207–1221
- Noda T, Kawabata Y, Arai N, Mitamura H, Watanabe S (2014) Animal-mounted gyroscope/accelerometer/magnetometer: in-situ measurement of the movement performance of fast-start behaviour in fish. *J Exp Mar Biol Ecol* 451:55–68
- Orpwood JE, Griffiths SW, Armstrong JD (2006) Effects of food availability on temporal activity patterns and growth of Atlantic salmon. *J Anim Ecol* 75:677–685
- O'Toole AC, Murchie KJ, Pullen C, Hanson KC, Suski CD, Danylchuk AJ, Cooke SJ (2010) activity and depth distribution of adult great barracuda (*Sphyraena barracuda*) in Bahamian coastal habitats determined using acceleration and pressure biotelemetry transmitters. *Mar Freshw Res* 61: 1446–1456
- Pettersson LB, Brönmark C (1993) Trading off safety against food: state dependent habitat choice and foraging in crucian carp. *Oecologia* 95:353–357
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2014) nlme: linear and nonlinear mixed effects models. R package version 3.1–102
- Pitcher TJ, Turner JR (1986) Danger at dawn: experimental support for the twilight hypothesis in shoaling minnows. *J Fish Biol* 29:59–70
- Rall JA, Woledge RC (1990) Influence of temperature on mechanics and energetics of muscle contraction. *Am J Physiol* 259: 197–203
- Reebs SG (2002) Plasticity of diel and circadian activity rhythms in fishes. *Rev Fish Biol Fish* 12:349–371
- Ropert-Coudert Y, Wilson RP (2005) Trends and perspectives in animal-attached remote sensing. *Front Ecol Environ* 3:437–444
- Ross ST (1986) Resource partitioning in fish assemblages: a review of field studies. *Copeia* 2:352–388
- Sattari A, Mirzargar SS, Abrishamifard A, Lourakzadegan R, Bahonar A, Mousavi HE, Niasari A (2009) Comparison of electroanesthesia with chemical anesthesia (MS222 and clove oil) in rainbow trout (*Oncorhynchus mykiss*) using plasma cortisol and glucose responses as physiological stress indicators. *Asian J Anim Vet Adv* 4:306–313
- Scott WB, Crossman EJ (1973) Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa, p 966
- Shoup DE, Carlson RE, Heath RT (2004) Diel activity levels of centrarchid fishes in a small Ohio lake. *Trans Am Fish Soc* 133:1264–1269
- Stamps JA (2007) Growth-mortality tradeoffs and 'personality traits' in animals. *Ecol Lett* 10:355–363
- Todd BL, Rabeni CF (1989) Movement and habitat use by stream-dwelling smallmouth bass. *Trans Am Fish Soc* 118:229–242
- Uusi-Heikkilä S, Wolter C, Klefoth T, Arlinghaus R (2008) A behavioral perspective on fishing-induced evolution. *Trends Ecol Evol* 23:419–421
- Videler JJ, Wardle CS (1991) Fish swimming stride by stride: speed limits and endurance. *Rev Fish Biol Fisher* 1:23–40
- Wagner GN, Cooke SJ, Brown RS, Deters KA (2010) Incision closure and surgery. In: Brown RS, Cooke SJ, Wagner GN, Eppard MB (eds) Methods for surgical implantation of acoustic transmitters in juvenile salmonids: a review of literature and guidelines for technique. U.S. Army Corps of Engineers, pp 53–68
- Webb PW (1994) The biology of fish swimming. In: Maddock L, Bone Q, Rayner JMV (eds) Mechanics and physiology of animal swimming. Cambridge University Press, Cambridge, pp 45–62
- Weeks JG, Hansen MJ (2009) Walleye and Muskellunge movement in the Manitowish chain of Lakes, Vilas County, Wisconsin. *N Am J Fish Manag* 29:791–804
- Werner EE, Anholt BR (1993) Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *Am Nat* 142:242–272

- Werner EE, Hall DJ, Laughlin DR, Wagner DJ, Wilsmann LA, Funk FC (1977) Habitat partitioning in a freshwater fish community. *J Fish Res Board Can* 34:360–370
- Wilson RP, White CR, Quintana F, Halsey LG, Liebsch N, Martin GR, Butler PJ (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. *J Anim Ecol* 75:1081–1090
- Wilson SM, Hinch SG, Eliason EJ, Farrell AP, Cooke SJ (2013) Calibrating acoustic transmitters for estimating energy use by wild adult Pacific salmon. *Comp Biochem Physiol A* 164:491–498
- Young MK (1999) Summer diel activity and movement of adult brown trout in high-elevation streams in Wyoming, U.S.A. *J Fish Biol* 54:181–189
- Younk JA, Cook MF, Goeman TJ, Spencer PD (1996) Seasonal habitat use and movements of muskellunge in the Mississippi River. Minnesota Department of Natural Resources Investigational Report 449
- Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) *Mixed effects models and extensions in ecology with R*. Springer, New York