Diel patterns of hooking depth for active and passive angling methods for two freshwater teleost fishes

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ABSTRACT.—The increasing popularity of catch-and-release angling indicates a need to identify best practices that minimize sublethal injuries, impairments, and mortality. One factor impacting the viability of catch and release is the risk of hooking injury, which can impact survival in released fishes. In particular, deep hooking is known to increase post-release mortality in numerous species. As such, best practices include the use of equipment and promotion of angler behaviors that reduce incidences of deep hooking. In some areas, angling at night is restricted because of concerns that deep hooking is elevated relative to angling during the day. However, there has been little empirical research investigating whether deep hooking is influenced by the time of day (light levels). In the present study, we captured bluegill (*Lepomis macrochirus* Rafinesque, 1810) and pumpkinseed (*Lepomis gibbosus* Linnaeus, 1758) using active angling (cast and retrieve) and passive angling (with a bobber) throughout the 24-hr period, and recorded hook depth and hook location for each fish. We found that passive angling methods resulted in deeper hooking than active angling methods for both bluegill and pumpkinseed across all time periods. Although few pumpkinseed were caught at night, we found that the pumpkinseed caught were hooked more deeply and in more damaging hooking locations at night relative to the day. Hooking injury was independent of diel period for the more frequently landed species, bluegill. These findings emphasize the species-specific nature of catch-and-release outcomes, and suggest that further research is warranted to adequately quantify the impacts of recreational fishing at night.

Catch-and-release (C&R) angling, a practice where landed fish are returned to the water, is common in recreational fisheries (Muoneke and Childress 1994, Arlinghaus et al. 2007), with some fisheries reporting release rates >90% [e.g., common snook, *Centropomus undecimalis* (Bloch, 1792); Muller and Taylor 2006; muskellunge, *Esox masquinongy* (Mitchill, 1824); Brownscombe et al. 2014]. Although the premise of C&R is that fish survive with negligible injury, fitness impairments, or alterations in behavior or physiology (Wydoski 1977, Cooke and Schramm 2007), outcomes vary widely (Arlinghaus et al. 2007). Mortality rates can be high for some species (reviewed in Muoneke and Childress 1994, Bartholomew and Bohnsack 2005), while in others, sublethal impairments may reduce organismal fitness (Arlinghaus et al. 2007, Cooke et al. 2013). To ensure the sustainability of recreational C&R fisheries and to maintain optimal conditions for released fishes, significant research efforts have been devoted to characterizing negative C&R outcomes and identifying the factors that contribute to them such that best practices can be identified and shared with the angling community (Cooke and Suski 2005, Pelletier et al. 2007).

A main issue pertaining to the viability of C&R is the risk of hooking injury, as the location of hook penetration can directly impact the survivability of fish (reviewed in Muoneke and Childress 1994, Bartholomew and Bohnsack 2005). Indeed, anatomical hooking location is regarded as the single biggest factor influencing the outcome of a C&R event (Bartholomew and Bohnsack 2005, Hühn and Arlinghaus 2011, Cooke et al. 2013). Post-release mortality rates are often elevated when fish are "foul-hooked" or hooked in critical locations, such as the esophagus, gill, brain, or eye (Taylor and White 1992, Malchoff and MacNeill 1995, Gutowsky et al. 2011). Bartholomew and Bohnsack (2005) identified some of the main factors influencing hooking location including the type of bait, terminal gear (tackle at the end of the line, typically a hook or lure), fishing technique, and angler expertise. Efforts to further understand the factors that influence deep hooking would be valuable for identifying strategies to promote "shallow hooking."

In some marine and freshwater systems, recreational anglers target certain species at night to avoid crowded angling areas and improve catch rates (Cooke et al. 2017), taking advantage of presumed diel patterns of species-specific vulnerability to capture. Indeed, different fish species exhibit diverse behavioral, physiological, and morphological adaptations that enable them to exploit different environmental conditions (Horodysky et al. 2008, Chapman and Mckenzie 2009). Given the importance of diel rhythms in the biology and ecology of fish (Reebs 2002), it is reasonable to question whether outcomes for fish that are exposed to C&R would vary on a diel basis. Indeed, basic biological processes such as endocrine status, feed intake, locomotory activity, metabolic rate, and visual acuity vary among species on a diel basis (e.g., Thorpe 1978, Ali 1992, Boujard and Leatherland 1992, Houlihan et al. 2008), which all have the potential to be related to aspects of fish capture. Despite potential for diel variation in C&R outcomes on a diel basis, there is currently little research on this topic. Of particular concern is the potential for higher levels of deep hooking during the night, which might be exacerbated by use of passive angling methods (e.g., using a bobber, a float attached to a stationary line) that may make hooking events more difficult to detect (Lennox et al. 2015).

Here, we sought to determine whether diel patterns in deep hooking were evident and whether they varied significantly according to passive and active angling techniques. Bluegill (*Lepomis macrochirus* Rafinesque, 1810) and pumpkinseed (*Lepomis*

gibbosus Linnaeus, 1758) are common targets for C&R due to their high catchability relative to other species, and are also frequently caught as bycatch by anglers targeting other warm-water species (Quinn and Paukert 2009). Anglers commonly target these species using a bobber, and cast-and-retrieve angling (referred to herein as passive and active angling, respectively). Though not known to be commonly targeted at night, this tendency to be targeted successfully using these two disparate techniques makes *Lepomis* spp. a suitable model for studying diel differences in deep hooking, as this provides an effective way to disentangle potential factors driving deep hooking at night. Moreover, both species have been the subject of extensive research on C&R (e.g., Siewert and Cave 1990, Cooke et al. 2003), as well as diel activity and feeding behavior (e.g., Keast and Welsh 1968, Keast 1978, Wainwright 1996), which provides relevant context for interpreting findings.

Methods

Field Site.—Research was conducted at the Queen's University Biology Station on Lake Opinicon, Ontario (44°33′55.37″N, 76°19′23.26″W). Lake Opinicon is a mesotrophic lake (i.e., has a typical clarity measured with a Secchi disc between 3–5 m), with a maximum depth of 11 m. Angling was conducted by the researchers in 4-hr blocks between April 30 and May 6, 2015. The entire 24-hr cycle was covered during this time period, with each light level category (dark, low light, bright light; see section below on data management and statistical analyses) represented on at least four separate occasions. Light levels were inferred by time period, with no additional measurements taken to assess light levels. The water temperature at the time of the experiment (measured at a depth of 0.8 m) ranged between 10 and 18 °C throughout the study, while air temperature ranged from 8 to 24 °C. Weather over the study period was mostly clear, with some periods of light cloud cover, and no precipitation. Moon phases during the study period ranged from waxing gibbous (April 30–May 2) to waning gibbous (May 4–May 6), with the full moon occurring on May 3 (Government of Canada 2016).

Experimental Protocol.—Bluegill and pumpkinseed were angled using rod and reel from a dock or fishing boat using small barbed J hooks (Mustad, Gjovik, Norway N-2801, baitholder style, size 8). All anglers used the same organic bait (small worm pieces), measured to 1 cm in length, and two split shots (Gremlin Green, White Bear Lake, MN, USA, 55110, tin sinkers, unleaded, removable) were placed 5–6 cm above the hook. Fishing took place using both active and passive angling methods, with passive angling involving the use of spring oval bobbers placed 0.8 m above the hook. Passive anglers were instructed to wait until the bobber moved to reel the line in, and the same bobber type was used throughout the 24-hr period, (i.e., no photoluminescent bobbers were used at night). Active anglers did not make use of bobbers, but casted and jigged the lure while reeling in. Anglers attempted to standardize angling effort between the two methods as evenly as possible across the 24-hr period and between the two methods.

On landing, the anatomical location of the hook was recorded as: upper lip, lower lip, corner of mouth, upper palate, distal pharynx or esophagus, or gill. No instances of hooking in the tongue were observed, and only one instance of hooking in another location occurred in the study (one fish was hooked in the eye). This event, and any

hook that penetrated the tissue of the distal pharynx, esophagus, or any part of the gill lamellae, were referred to as a "foul hooking event." Hooking depth (mm) was measured from the outermost edge of the upper lip to the site of hook penetration. Finally, fish were measured in mm for both total length (TL, the length from the front of the lip to the end of the straightened caudal fin) and standard length (SL, the length from the front of the lip to the end of the caudal peduncle). On release, each fish was given a dorsal fin clip to ensure any recaptured fish were not included in further analysis.

Data Management and Statistical Analyses.—To assess diel patterns of deep hooking, we categorized light levels throughout the 24-hr period as "dark," "low light," or "bright light." These time periods were based on the start of civil twilight (i.e., first light in the morning), sunrise, sunset, and the end of civil twilight (i.e., the end of the last light at night): "dark" period (end of civil twilight to the beginning of civil twilight, 20:45–5:20); and, the "low light" period (start of civil twilight to an hour after sunrise, and an hour before sunset to the end of civil twilight, 5:20–6:50 and 19:15–20:45); "bright light" period (an hour after sunrise to an hour after sunset, 6:50–19:15).

Generalized linear mixed effects models were used to examine the effect of species (bluegill, pumpkinseed), angling method (active, passive), and light level (dark, low light, bright light) on relative hooking depth (i.e., hooking depth as a proportion of overall fish SL), and hooking location (i.e., hooked in the mouth, or foul hooked). A beta distribution, appropriate for proportion data, was used for the model assessing the effects of species, angling method, and light level on relative hooking depth. A logistic distribution, appropriate for binary data, was used for the model assessing the effects of species, angling method, and light level on hooking location. For all models, all two-way interaction effects were included, and angler identity was included as a random effect. The glmmADMB package (Bolker et al. 2012) within R version 3.2.1 (R Core Team 2015) was used for all generalized linear mixed models. Unless otherwise indicated, all results are presented using standard error of the mean.

Results

Fish Captured and Angling Method.—There was an uneven number of fish caught per species during the study period. Anglers caught a total of 469 fish over 7 d, including 330 bluegill and 139 pumpkinseed. The ratio of fish caught by angling method was even for pumpkinseed, but less so for bluegill (Table 1). Landed bluegill ranged in size from 65–170 mm SL and 85–216 mm TL, with average sizes of 126 (SE 1) mm (SL) and 155 (SE 2) mm (TL). Landed pumpkinseed ranged in size from 82 to 211 mm SL and 100 to 246 mm TL, with average sizes of 137 (SE 2) mm (SL) and 166 (SE 3) mm (TL; see Table 1). Angling method had a significant effect on hooking depth, with passive angling being more likely to result in deeper hooking relative to active angling (Table 2, Fig. 1). Angling method did not have a significant effect on incidence of foul hooking (Table 2).

Diel Patterns in Hooking Depth and Hooking Location.—Fish were captured unevenly across light levels and between species, with far more fish caught during bright periods than during dark periods and low light periods (Table 1). There was a significant interaction between species and light levels on hooking depth, such

Table 1. Number of bluegill and pumpkinseed fish caught using passive and angling methods at various light levels, standard length (SL) and total length (TL) of each group of fish (mean with standard error in parentheses), and the number of fish foul-hooked per species, light level, and angling method.

Angling method	n	Light level	Fish caught	SL (mm)	TL (mm)	Fish foul-hooked
Bluegill						
Active	130	Dark	13	129 (6)	161 (7)	0
		Low	21	121 (5)	157 (6)	1
		Bright	96	124 (3)	151 (3)	7
Passive	200	Dark	19	123 (6)	152 (7)	6
		Low	36	125 (3)	153 (4)	10
		Bright	145	129 (2)	158 (2)	28
Pumpkinseed						
Active	69	Dark	3	121 (16)	154 (20)	2
		Low	6	137 (13)	164 (16)	0
		Bright	60	136 (4)	165 (4)	3
Passive	70	Dark	1	152	185	1
		Low	13	145 (6)	179 (7)	5
		Bright	56	137 (3)	167 (4)	13

Table 2. Results of generalized linear mixed effects models that examined the effect of categorical data: species [bluegill (considered "baseline" for the statistical comparisons); pumpkinseed], angling method [active (baseline); passive], and light level [bright light (baseline); low light; dark]; on relative hooking depth (i.e., hooking depth as a proportion of overall fish SL), and hooking location (i.e., hooked in the mouth, or foul hooked). For hooking depth, a beta distribution for proportion data was used. For hooking location, a logistic distribution for binary data was used. For all models, angler identity was included as a random effect. See Methods for full statistical details. Significant factors are in bold ($P < 0.05$).

| Fixed effects	Estimate	SE	z value	P value
Hooking depth				
Light level (low)	0.09	0.18	0.51	0.610
Light level (dark)	−0.13	0.24	−0.53	0.600
Species	−0.10	0.13	−0.78	0.440
Angling type	**0.22**	**0.01**	**2.14**	**0.030**
Light level (low) × Species	−0.14	0.23	−0.59	0.550
Light level (dark) × Species	**0.94**	**0.39**	**2.43**	**0.020**
Light level (low) × Angling type	0.06	0.21	0.27	0.790
Light level (dark) × Angling type	0.32	0.29	1.11	0.270
Species × Angling type	0.17	0.17	0.99	0.320
Hooking location				
Light level (low)	−0.04	0.05	−0.70	0.490
Light level (dark)	−0.01	0.07	−0.06	0.960
Species	−0.02	0.04	−0.42	0.670
Angling type	0.05	0.03	1.44	0.150
Light level (low) × Species	0.04	0.08	0.51	0.610
Light level (dark) × Species	**0.82**	**0.15**	**5.38**	**<0.001**
Light level (low) × Angling type	0.10	0.07	1.48	0.140
Light level (dark) × Angling type	0.08	0.10	0.90	0.370
Species × Angling type	0.04	0.05	0.80	0.420
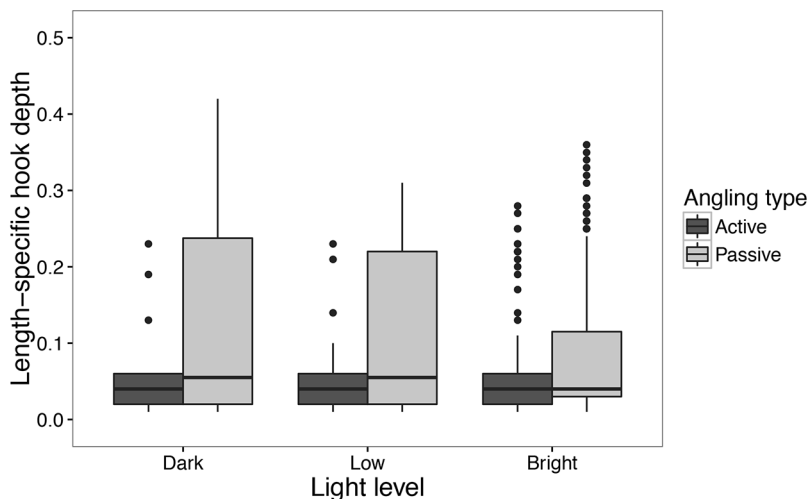
Figure 1. Length-specific hook depth (i.e., hooking depth as a proportion of fish standard length) for active vs passive angling. Error bars represent SE, and horizontal bars and vertical dots describe the group means and outliers, respectively. Passive angling resulted in deeper hooking for both species across the 24-hr period. See Methods and Table 2 for full statistical details.

that pumpkinseed were more likely to be deeply hooked in the dark and during low light conditions, relative to bright light conditions (Table 2; Fig. 2A). However, there was no effect of light level on bluegill relative hooking depth (Table 2, Fig. 2A). There was also a significant interaction between species and light levels on hooking location, such that pumpkinseed were hooked in unfavorable hooking locations more often in the dark, and during low light conditions, relative to bright light conditions (Table 2, Fig. 2B). There was no effect of light level on bluegill hooking location (Table 2, Fig. 2B).

Discussion

The present study aimed to investigate the effects of diel period and anatomical hooking location in bluegill and pumpkinseed, and we hypothesized that low light levels might make anglers less able to detect strikes. To investigate this possibility, we used both passive and active angling methods across a 24-hr period. Deep hooking is an important factor driving post-release survival in C&R fisheries, and many fisheries are regulated to reduce deep hooking. The results of the analyses indicated that diel patterns (associated with different light levels) influence the depth of hooking and likelihood of foul hooking in pumpkinseed, and that passive angling was significantly more likely to result in foul hooking of both species than active angling methods, regardless of light levels.

The effect of the passive angling method may be a result of the dampened amount of feedback an angler receives when using a bobber as opposed to active angling. Due to the increased reaction time associated with passive angling, fish are able to fully ingest the baited hook without being detected by the angler unless the fish strikes aggressively (Lennox et al. 2015). Conversely, when fish are actively angled, the hook is immediately set once a fish strikes the bait, leading to reduced incidences of deep hooking damage (Schisler et al. 1996). It is also possible that there is less angler
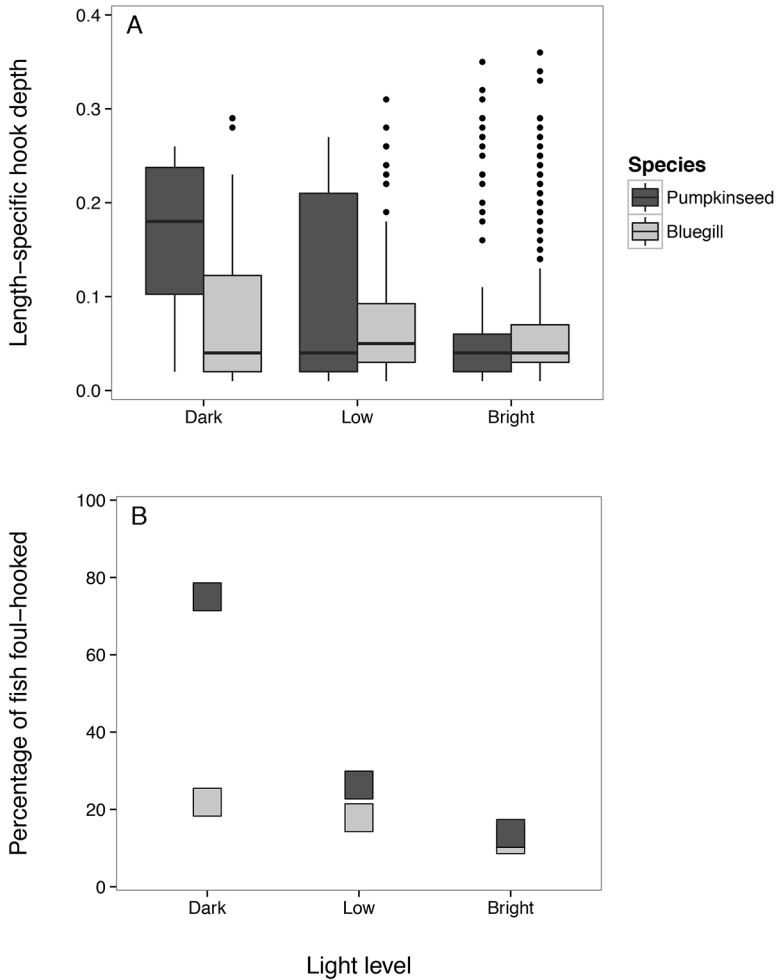
Figure 2. (A) Length-specific hook depth (i.e., hooking depth as a proportion of fish standard length), where error bars represent SE, and horizontal bars and vertical dots describe the group means and outliers, respectively. Panel (B) represents the percentage (including range of error) of fish that were foul hooked (i.e., hooked in a location other than the mouth) for bluegill (light gray boxes) and pumpkinseed (dark gray boxes) caught using active vs passive angling across the 24-hr period. Pumpkinseed were (A) more deeply hooked and (B) had higher incidences of foul hooking in the dark and low light conditions relative to bright light, while bluegill demonstrated no differences in (A) depth of hooking or (B) hooking location based on light level. See Methods and Table 2 for full statistical details.

engagement when passively angling, and as a result their attention maybe diverted from their bobber, increasing reaction time and thereby hooking depth. Our findings support previous research indicating that passive angling is more likely to result in deep hooking than active angling (Sullivan et al. 2013). However, we found no evidence that reduced angler response using either method contributes to deep hooking more at night relative to the day.

We did find a significant difference between the two species, with pumpkinseed being more likely to be foul hooked, and hooked more deeply, than bluegill at night.

First, we note that we had a relatively low sample size of both species caught at night, and particularly low numbers of pumpkinseed caught at night. Therefore, these results should be interpreted with caution, and further study with larger sample sizes, or targeting species more likely to be captured in the dark, would be helpful. However, these preliminary results indicate that there may be important species differences in incidence of deep hooking at night. For example, physiological and behavioral differences between the two species may have contributed to these disparities. Pharyngeal teeth structure differs between bluegill and pumpkinseed; the pharyngeal pads of bluegill are covered with fine needle-like teeth (Keast and Webb 1966), while pumpkinseed have pharyngeal pads covered with large molariform teeth (Hubbs and Lagler 1964). Cooke et al. (2003) suggested that this difference in mouth structure may lead to greater incidences of hooking through the roof of the mouth in bluegill, as occurred in the present study relative to foul-hooking incidents in pumpkinseed. Differences in feeding ecology between the two species may have contributed to outcomes. The above-stated morphological differences arise from pumpkinseed preference for snails as prey, while bluegill prefer zooplankton, leading to distinct habitat preferences between the two species (Wainwright 1996). Findings from a study of the feeding ecology of both species on Lake Opinicon supported this preference for hard-bodied prey among pumpkinseed (Keast 1978), which suggests that the significant differences in relative hooking depth between pumpkinseed and bluegill found here were not likely a result of low catch rate. Pumpkinseed demonstrate less feeding activity during the night compared to bluegill (Keast and Welsh 1968). This may serve to explain the differences in relative catch rates between the two species during dark periods, and offer rationale for why the pumpkinseed that were landed were comparably more deeply hooked, i.e., those that were hooked may have been feeding more aggressively. However, Reynolds and Casterlin (1976) demonstrated that these diel patterns in feeding are not regulated by temperature or light patterns in a laboratory setting, suggesting that these feeding patterns may be distinct from these stimuli. Feeding ecology of the two *Lepomis* spp. studied is not static. Keast (1978) found that dietary overlap and habitat preferences between the two species exhibited moderate variation monthly and across age classes (see also Keast and Welsh 1968). Finally, it should also be noted that sunfishes exhibit plasticity in both feeding behaviors and jaw morphology (Robinson et al. 1993, Mittelbach et al. 1999). This variation, between two similar species, serves to demonstrate that best practices pertaining to C&R may be distinct among species according to numerous subtleties in feeding, habitat use, and behavior. As such, any future study seeking to clarify correlations between deep hooking and feeding ecology in sunfishes should include both considerations in a single study.

Increased post-release mortality (such as that caused by deep hooking), has the potential to alter fish population dynamics (Post et al. 2002, Lewin et al. 2006, Coggins et al. 2007). To reduce incidences of fish injury and post release mortality, it is essential to add to the growing body of literature on best practices for recreational fisheries. Here, we have established that active angling significantly reduces the average hook depth in *Lepomis* spp., and its use over passive angling is therefore advised when these species are targeted or commonly caught as bycatch. If passive angling is used, anglers should ensure their view of their bobber is unhindered, thus future research examining the impacts of fishing at night may benefit from an examination

as to whether photoluminescent bobbers may be useful for reducing angler reaction time by optimizing visibility.

Bluegill and pumpkinseed are not known to be commonly fished at night; however, they are a popular target among recreational fishers (Cooke et al. 2005, Quinn and Paukert 2009), raising the question as to whether these species would be successfully angled at night, and if so, whether changes in light level would lead to different rates of deep hooking. We recommend researchers include consideration of diel patterns in appropriate studies, particularly in species commonly targeted at night, such as walleye (*Sander vitreus* Mitchill, 1818), striped bass [*Morone saxatilis* (Walbaum, 1792)], and some billfishes, to better understand the full range of potential impacts of recreational fishing activity.

Acknowledgments

Literature Cited

Ali MA, editor. 1992. Rhythms in fishes. New York, NY: Plenum Press.

Arlinghaus R, Cooke SJ, Lyman J, Policansky D, Schwab A, Suski C, Sutton SG, Thorstad EB. 2007. Understanding the complexity of catch-and-release in recreational fishing: an integrative synthesis of global knowledge from historical, ethical, social, and biological perspectives. Rev Fish Sci. 15:75–167. http://dx.doi.org/10.1080/10641260601149432

Bartholomew A, Bohnsack JA. 2005. A review of catch- and-release angling mortality with implications for no-take reserves. Rev Fish Biol Fish. 15:129–154. http://dx.doi.org/10.1007/s11160-005-2175-1

Bolker B, Skaug H, Magnusson A, Nielsen A. 2012. Getting started with the glmmADMB package. Available from: http://glmmadmb.r-forge.r-project.org/glmmADMB.pdf

Boujard T, Leatherland JF. 1992. Circadian rhythms and feeding time in fishes. Environ Biol Fish. 35(2):109–131. http://dx.doi.org/10.1007/BF00002186

Brownscombe JW, Bower SD, Bowden W, Nowell L, Midwood JD, Johnson N, Cooke SJ. 2014. Canadian recreational fisheries: 35 years of social, biological, and economic dynamics from a national survey. Fisheries. 39:251–260. http://dx.doi.org/10.1080/03632415.2014.915811

Chapman LJ, Mckenzie DJ. 2009. Behavioral responses and ecological consequences. Fish Physiol. 27:25–77. http://dx.doi.org/10.1016/S1546-5098(08)00002-2

Coggins LG, Catalano MJ, Allen MS, Pine WE 3rd, Walters CJ. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish Fish. 8:196–210. http://dx.doi.org/10.1111/j.1467-2679.2007.00247.x

Cooke SJ, Suski CD, Barthel BL, Ostrand KG, Tufts BL, Philipp DP. 2003. Injury and mortality induced by four hook types on bluegill and pumpkinseed. N Am J Fish Manage. 23(3):883–893. http://dx.doi.org/10.1577/M02-096

Cooke SJ, Suski CD. 2005. Do we need species-specific guidelines for catch-and-release recreational angling to effectively conserve diverse fishery resources? Biodivers Conserv. 14:1195–1209. http://dx.doi.org/10.1007/s10531-004-7845-0

Cooke SJ, Barthel BL, Suski CD, Siepker MJ, Philipp DP. 2005. Influence of circle hook size on hooking efficiency, injury, and size selectivity of bluegill with comments on circle hook

conservation benefits in recreational fisheries. N Am J Fish Manage. 25(1):211–219. http://dx.doi.org/10.1577/M04-056.1

Cooke SJ, Schramm HL. 2007. Catch-and-release science and its application to conservation and management of recreational fisheries. Fish Manag Ecol. 14(2):73–79. http://dx.doi.org/10.1111/j.1365-2400.2007.00527.x

Cooke SJ, Donaldson MR, O'connor CM, Raby GD, Arlinghaus R, Danylchuk AJ, Hanson KC, Hinch SG, Clark TD, Patterson DA, et al. 2013. The physiological consequences of catch-and-release angling: perspectives on experimental design, interpretation, extrapolation and relevance to stakeholders. Fish Manag Ecol. 20(2–3):268–287. http://dx.doi.org/10.1111/j.1365-2400.2012.00867.x

Cooke SJ, Lennox RL, Bower SD, Horodysky A, Danylchuk AJ. 2017. Fishing in the dark: the science and management of recreational fishing at night. Bull Mar Sci. 93(2):519–538. http://dx.doi.org/10.5343/bms.2015.1103

Government of Canada. 2016. Data Services Section, Meteorological Service of Canada, Environment Canada. Accessed March 18, 2016. Available from: http://climate.weather.gc.ca/data_index_e.html

Gutowsky LF, Harrison PM, Landsman SJ, Power M, Cooke SJ. 2011. Injury and immediate mortality associated with recreational troll capture of bull trout (*Salvelinus confluentus*) in a reservoir in the Kootenay-Rocky Mountain region of British Columbia. Fish Res. 109(2–3):379–383. http://dx.doi.org/10.1016/j.fishres.2011.02.022

Horodysky AZ, Brill RW, Warrant EJ, Musick JA, Latour RJ. 2008. Comparative visual function in five sciaenid fishes. J Exp Biol. 211:3601–3612. http://dx.doi.org/10.1242/jeb.023358

Houlihan D, Boujard T, Jobling M, editors. 2008. Food intake in fish. Oxford, UK: Wiley & Sons.

Hubbs CL, Lagler KF, editors. 1964. Fishes of the Great Lakes region. Ann Arbor, MI, USA: University of Michigan Press.

Hühn D, Arlinghaus R. 2011. Determinants of hooking mortality in freshwater recreational fisheries: a quantitative meta-analysis. *In:* Beard Jr TD, Arlinghaus R, Sutton SG, editors. The angler in the environment: social, economic, biological and ethical dimensions. Proceedings from the fifth world recreational fishing conference. Bethesda: American Fisheries Society, Symposium 75. p. 141–170.

Keast A, Webb D. 1966. Mouth and body form relative to feeding ecology in the fish fauna of a small lake, Lake Opinicon, Ontario. J Fish Res Board Can. 23(12):1845–1874. http://dx.doi.org/10.1139/f66-175

Keast A, Welsh L. 1968. Daily feeding periodicities, food uptake rates, and dietary changes with hour of day in some lake fishes. J Fish Res Board Can. 25:1133–1144. http://dx.doi.org/10.1139/f68-099

Keast A. 1978. Feeding interrelations between age-groups of pumpkinseed (*Lepomis gibbosus*) and comparisons with bluegill (*L. macrochirus*). J Fish Res Board Can. 35(1):12–27. http://dx.doi.org/10.1139/f78-003

Lennox RJ, Whoriskey K, Crossin GT, Cooke SJ. 2015. Influence of angler hook-set behaviour relative to hook type on capture success and incidences of deep hooking and injury in a teleost fish. Fish Res. 164:201–205. http://dx.doi.org/10.1016/j.fishres.2014.11.015

Lewin WC, Arlinghaus R, Mehner T. 2006. Documented and potential biological impacts of recreational fishing: insights for management and conservation. Rev Fish Sci. 14(4):305–367. http://dx.doi.org/10.1080/10641260600886455

Malchoff MH, MacNeill DB. 1995. Guidelines to increase survival of released sport fish, released fish survival sport fish fact sheet. Ithaca, NY: Cornell cooperative extension, Sea Grant.

Mittelbach GG, Osenberg CW, Wainwright PC. 1999. Variation in feeding morphology between pumpkinseed populations: phenotypic plasticity or evolution? Evol Ecol Res. 1(1):111–128.

Muller RG, Taylor RG. 2006. The 2005 stock assessment update of common snook, *Centropomus undecimalis*. St. Petersburg, Florida: Florida Marine Research Institute, Fish and Wildlife Conservation Commission, *IHR*, 20006-003.

Muoneke MI, Childress WM. 1994. Hooking mortality: a review for recreational fisheries. Rev Fish Sci. 2:123–156. http://dx.doi.org/10.1080/10641269409388555

Pelletier C, Hanson KC, Cooke SJ. 2007. Do catch-and-release guidelines from state and provincial fisheries agencies in North America conform to scientifically-based best practices? Environ Manage. 39(6):760–773. http://dx.doi.org/10.1007/s00267-006-0173-2

Post JR, Sullivan M, Cox S, Lester NP, Walters CJ, Parkinson EA, Paul AJ, Jackson L, Shuter BJ. 2002. Canada's recreational fisheries: the invisible collapse? Fisheries. 27(1):6–17. http://dx.doi.org/10.1577/1548-8446(2002)027<0006:CRF>2.0.CO;2

Quinn S, Paukert C. 2009. Centrarchid fisheries. *In:* Cooke SJ, Phillip DP, editors. Centrarchid fishes: diversity, biology and conservation. West Sussex: Blackwell Publishing. p. 312–339.

R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: https://www.R-project.org/

Reebs SG. 2002. Plasticity of diel and circadian activity rhythms in fishes. Rev Fish Biol Fish. 12(4):349–371. http://dx.doi.org/10.1023/A:1025371804611

Reynolds WW, Casterlin ME. 1976. Locomotor activity rhythms in the bluegill sunfish, *Lepomis macrochirus.* Am Midl Nat. 96(1):221–225. http://dx.doi.org/10.2307/2424581

Robinson BW, Wilson DS, Margosian AS, Lotito PT. 1993. Ecological and morphological differentiation of pumpkinseed sunfish in lakes without bluegill sunfish. Evol Ecol. 7(5):451–464. http://dx.doi.org/10.1007/BF01237641

Schisler GJ, Bergersen EP, Schisler GL. 1996. Post release hooking mortality of rainbow trout caught on scented artificial baits. N Am J Fish Manage. 16:570–578. http://dx.doi.org/10.1577/1548-8675(1996)016<0570:PHMORT>2.3.CO;2

Siewert HF, Cave JB. 1990. Survival of released bluegill, *Lepomis macrochirus*, caught on artificial flies, worms, and spinner lures. J Freshwat Ecol. 5:407–411. http://dx.doi.org/10.1080/02705060.1990.9665256

Sullivan CL, Meyer KA, Schill DJ. 2013. Deep hooking and angling success when passively and actively fishing for stream-dwelling trout with baited J and circle hooks. N Am J Fish Manage. 33(1):1–6. http://dx.doi.org/10.1080/02755947.2012.732670

Taylor MJ, White KR. 1992. A meta-analysis of hooking mortality of non-anadromous trout. N Am J Fish Manage. 12:760–767. http://dx.doi.org/10.1577/1548-8675(1992)012<0760:AMAOHM>2.3.CO;2

Thorpe JE. 1978. Rhythmic activity of fishes. London: Academic Press.

Wainwright PC. 1996. Ecological explanation through functional morphology: the feeding biology of sunfishes. Ecology. 77(5):1336–1343. http://dx.doi.org/10.2307/2265531

Wydoski RS. 1977. Relation of hooking mortality and sublethal hooking stress to quality fishery management. *In:* Catch-and-release fishing as a management tool. Arcata: Humboldt State University. p. 43–87.