Animal Behaviour 86 (2013) 365–373

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Diel vertical migration hypotheses explain size-dependent behaviour in a freshwater piscivore

L. F. G. Gutowsky [a,*], P. M. Harrison [b], E. G. Martins [a], A. Leake [c], D. A. Patterson [d], M. Power [b], S. J. Cooke [a,e]

[a] Fish Ecology and Conservation Physiology Laboratory, Ottawa-Carleton Institute for Biology, Carleton University, Ottawa, ON, Canada
[b] Department of Biology, University of Waterloo, Waterloo, ON, Canada
[c] Environmental Risk Management, Burnaby, Canada
[d] Fisheries and Oceans Canada, Cooperative Resource Management Institute, School of Resource and Environmental Management, Simon Fraser University, Burnaby, Canada
[e] Institute of Environmental Science, Carleton University, Ottawa, ON, Canada

ARTICLE INFO

Article history:
Received 26 January 2013
Initial acceptance 11 March 2013
Final acceptance 10 May 2013
Available online 24 June 2013
MS. number: A13-00095R

Keywords:
biotelemetry
bull trout
diel vertical migration
DVM
mixed models
Salvelinus confluentus

In aquatic organisms, diel vertical migration (DVM) is typically characterized as ascent at dusk and decent at dawn. Often several hypotheses are required to explain the sensory-mechanisms and ultimate causes of DVM. Currently, most of the research focused at the individual level has identified DVM functions as a response to light, feeding opportunities, predator avoidance and bioenergetics in small planktivores. However, there are no studies examining whether DVM hypotheses can explain and predict individual behavioural characteristics in top-level predators. In this study, we test whether bull trout, *Salvelinus confluentus*, a cold-water pelagic-cruising piscivore, show size-dependent daily and seasonal patterns in DVM consistent with light levels (proximate trigger) and feeding opportunities, predator avoidance and bioenergetics hypotheses. To test these hypotheses, free-swimming bull trout ($N = 187$, 358–881 mm total length) in a large, temperate reservoir were implanted with depth-sensing acoustic transmitters for 1 year. We found that swimming depths of bull trout were shallowest at night, deepest during the day and showed clear patterns of DVM across all seasons. In line with the predator avoidance hypothesis, large and small bull trout occupied different depths in all seasons except the spring, while the likelihood of depth change for large and small fish varied depending on season and diel period. The greatest depth difference among large and small bull trout occurred in the summer and less so in autumn. In the summer, small bull trout remained at greater depths (~15 m) than larger fish (~7 m) regardless of diel period. Our results indicate that light is a proximate trigger, and since there is no clear temperature-related bioenergetic advantage to changing depths during winter, feeding opportunities and predator avoidance are the most parsimonious DVM hypotheses to explain body-size-dependent behaviour in this top-level predator.

In fishes, diel vertical migration (DVM) is typically characterized as ascent at dusk and descent at dawn (Neilson & Perry 1990). Linked to a number of processes including thermoregulation (Brill et al. 1999; Cartamil & Lowe 2004; Sims et al. 2006), habitat selection (Pade et al. 2009; Plumb & Blanchfield 2009) and foraging (Sims et al. 2005; Fox & Bellwood 2011), the functional triggers and adaptive drivers of DVM currently explain patterns across daily and seasonal periods for planktivorous fish populations only (e.g. Bevelhimer & Adams 1993; Gjelland et al. 2009; Quinn et al. 2012). Although piscivores have been hypothesized to show DVM in relation to prey species (Jensen et al. 2006; Kahilainen et al. 2009), investigations of depth and vertical movement in relation to the mechanisms (e.g. size-dependent behaviour) thought to be responsible for DVM remain scant, and we are aware of no studies on individual DVM patterns in piscivorous fish.

Recently DVM has been related to both proximate triggers (i.e. sensory-motor and genetic developmental mechanisms) and ultimate causes (i.e. behaviours shaped by natural selection) (Mehner 2012). Proximate triggers include changes in light intensity and, to a lesser extent, changes in hydrostatic pressure and responses to thermal gradients (Levy 1990; Mehner 2012). Ultimate causes of DVM are hypothesized to be related to bioenergetic efficiency,

* Correspondence: L. F. G. Gutowsky, Fish Ecology and Conservation Physiology Laboratory, Ottawa-Carleton Institute for Biology, Carleton University, 1125 Colonel By Dr., Ottawa, ON K1S 5B6, Canada.
E-mail address: lee_gutowsky@carleton.ca (L. F. G. Gutowsky).

0003-3472/$38.00 © 2013 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.
http://dx.doi.org/10.1016/j.anbehav.2013.05.027

feeding opportunities and predator avoidance behaviour (Mehner 2012). Evidence to support these hypotheses, whether functional or adaptive, is often generated from observational studies, which are the most appropriate means of obtaining such information on migratory behaviour in free-living animals. For example, Levy (1990) used hydroacoustic sonar to infer that patterns of DVM in juvenile sockeye salmon, *Oncorhynchus nerka*, were related to changes in light and thermoregulation. In fishes, the most pervasive mechanism thought to reflect predator avoidance behaviour and prey detection is individual body size. Again using hydroacoustics, small planktivorous fish were shown to remain at greater depths (Levy 1991) or to ascend earlier and descend later (Busch & Mehner 2012) than larger conspecifics.

In this study we tested DVM hypotheses on adfluvial bull trout, *Salvelinus confluentus*, in a glacial-fed reservoir in British Columbia, Canada. Adfluvial bull trout are an excellent candidate species because they (1) possess a low thermal tolerance (Selong et al. 2001), (2) primarily feed on vertically migrating kokanee salmon, *Oncorhynchus nerka*, (3) show intra- and interspecific competitive behaviour (Beauchamp & Van Tassell 2001; Stewart et al. 2007) and (4) are similar to other cold-water pelagic-cruising predators (e.g. coaster brook charr, *Salvelinus fontinalis*; lake charr, *Salvelinus namaycush*). We used biotelemetry data to test hypotheses about DVM in bull trout across a wide size range (358–881 mm total length, TL) for 1 year. We hypothesized that putative factors related to DVM including diel period (proximate trigger), season (temperature-related bioenergetics efficiency) and body size (feeding opportunities and predator avoidance) would give rise to predictable patterns in depth distribution and vertical movement. Following the patterns observed in other salmonids (e.g. Levy 1990), we predicted that individuals' swimming depths would be shallowest at night. Since bull trout are a cold-water species (Selong et al. 2001) and the reservoir develops a thermal gradient (Bray 2012), swimming depths of bull trout were predicted to be deepest in the summer and shallowest in the winter and spring. While it was not possible to directly test individual interactions, any size-dependent depth distributions and vertical movements were predicted to result from competition and cannibalism risk among bull trout (Beauchamp & Van Tassell 2001).

METHODS

Study Site

The study was conducted in the Kinbasket Reservoir, a 190 km long impoundment of the Columbia, Wood and Canoe Rivers in the north Kootenay Rocky Mountain region of British Columbia (52°8′N, 118°28′W; Fig. 1). Kinbasket is one of the largest reservoirs in BC, covering an area of 43 200 ha and containing approximately 14.8 km^3 of water. The reservoir is fed by glacier melt-water streams and characterized by steep rocky shorelines, sand, rock and mud substrates, and little vegetation. Surface temperatures in the reservoir range from 2 to 15 °C in April–May, with summer surface temperatures typically in the 12–18 °C range (Bray 2012). In August through to mid-October, the reservoir typically has a gradual thermal gradient that reduces to 4 °C at a depth of 60 m (Bray 2012). The mean reservoir depth is 57 m, whereas the maximum depth is 160 m (RL&L Environmental Services Ltd 2001).

Kinbasket contains suitable habitat for native cold-water piscivores, including bull trout, rainbow trout, *Oncorhynchus mykiss*, burbot, *Lota lota*, and northern pike minnow, *Ptychocheilus oregonensis*. Kokanee salmon are a non-native planktivore that was stocked as a food source for bull trout and rainbow trout. Acoustic sonar and trawl-net surveys for kokanee salmon in the Kinbasket Reservoir are completed only during a brief period in August when kokanee are found in uniform abundance (10–25 m depth) and a limited mix of size classes (29–70 mm fork length and 193–221 mm fork length; Sebastian & Johner 2011). Although not studied in Kinbasket Reservoir, it is well established that kokanee may perform DVM (e.g. Levy 1990, 1991; Bevelhimer & Adams 1993). Diatoms (mainly *Asterionella formosa*) are the dominant primary producers, whereas cladocerans and chironomids are the most abundant zooplankton and benthic organisms, respectively (RL&L Environmental Services Ltd 2001; Bray 2012). Cladocerans are considered the preferred prey for kokanee in Kinbasket (Bray 2012). As with kokanee, cladocerans are well known for DVM (e.g. Bevelhimer & Adams 1993; Ringleberg 1999). The reservoir is oligotrophic, having low plankton biomass and low rates of primary productivity (RL&L Environmental Services Ltd 2001; Bray 2012).

Biotelemetry Receiver Deployment and Retrieval

Forty-two VR2W telemetry receivers (Vemco, Halifax, NS) were deployed in Kinbasket Reservoir between 1 May and 5 May 2010 (Fig. 1). Assuming a conservative receiver detection radius of 500 m, spatial coverage by the telemetry array was approximately 33 km^2. Four receivers placed proximal to the dam face (within 400 m) were securely fixed to a 2 m length of 0.6 cm thick wire rope that was hung from a log boom and weighted with a 2 kg cannon ball. All other receivers were stationed 10–30 m from the substrate and attached to a 1.6 cm thick floating rope that was anchored with sandbags and suspended by a yellow buoy. In 2011, receivers were retrieved and the data downloaded onto a laptop using the program VUE (Vemco, Halifax, NS).

Tagging

Since bull trout are commonly targeted by recreational anglers in the spring, capture was accomplished by trolling between 11 April and 25 May 2010 (Gutowsky et al. 2011). In late summer, bull trout were captured by angling at the mouths of known spawning tributaries (18 August–9 September 2010) where they congregate prior to spawning. Once captured, fish were placed in a 100-litre cooler filled with lake water that was regularly replaced. Bull trout were then moved into another 100-litre cooler that contained anaesthetic (40 mg/litre; one part clove oil emulsified in nine parts ethanol). Once anaesthetized (assessed by loss of equilibrium and no response to squeezing the caudal peduncle), bull trout were inverted and placed on a surgery table where a continuous supply of fresh water was pumped into the mouth and across the gills. Total length (to the nearest millimetre) and weight (to the nearest gram) were measured prior to surgery. A 3 cm long incision was made posterior to the pelvic girdle and a coded acoustic transmitter (model V13 TP; transmissions every 2–6 min, maximum depth 200 m, tag resolution 1.2 m) was inserted into the body cavity. Incisions were closed using three simple interrupted stitches. Postsurgery fish were placed in a recovery bath of fresh water, allowed to fully regain equilibrium, and released.

Our tagging procedures were approved by the Carleton University Animal Care Committee. Fish were obtained under scientific collection permits that were issued under the authority of the British Columbia Ministry of Environment (Permit No. CB-PG10-61414).

Database Management and Analysis

Biotelemetry data were sorted and stored in a Microsoft Access database. Bull trout detections were considered for analysis after the final receiver was deployed on 5 May 2010. Because the stress associated with tagging is believed to potentially affect fish