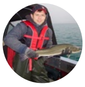
Temporal plasticity in thermal habitat selection of burbot, Lota lota, a diel-migrating winter-specialist. Journal of Fish Biology

Article *in* Journal of Fish Biology · March 2016

Impact Factor: 1.66 · DOI: 10.1111/jfb.12990



Journal of FISH BIOLOGY

fsbi An International Society for Fish Biology

Journal of Fish Biology (2016)
doi:10.1111/jfb.12990, available online at wileyonlinelibrary.com

Temporal plasticity in thermal-habitat selection of burbot *Lota lota* a diel-migrating winter-specialist

P. M. Harrison*†‡, L. F. G. Gutowsky†, E. G. Martins*†§,
D. A. Patterson§, S. J. Cooke† and M. Power*

**Department of Biology, University of Waterloo, Waterloo, ON, N2L 3G1 Canada, †Fish Ecology and Conservation Physiology Laboratory, Department of Biology, Carleton University, Ottawa, ON, K1S 5B6 Canadaand §Cooperative Research Management Institute, Fisheries and Oceans Canada, Simon Fraser University, Burnaby, BC, V5A 1S6 Canada*

(Received 30 June 2015, Accepted 16 February 2016)

In this study, animal-borne telemetry with temperature sensors was coupled with extensive habitat temperature monitoring in a dimictic reservoir, to test the following hypotheses: behavioural thermoregulation occurs throughout the year and temperature selection varies on a diel and seasonal basis, in a winter-specialist diel-migrating fish. Burbot *Lota lota* demonstrated nightly behavioural thermoregulation throughout the year, with a large seasonal shift between selection for very cold temperatures (<2° C) optimal for reproduction during the spawning period and selection for warmer temperatures (12–14° C) optimal for hunting and feeding during non-reproductive periods. During daylight hours, while *L. lota* avoided habitats warmer than optimal for reproduction and feeding during the spawning and non-reproductive periods, respectively, active selection was limited to selection for 4–6° C habitat during the prespawning period. Although behavioural thermoregulation explained the night-time migration, behavioural thermoregulation only partially explained daytime behaviour, indicating that diel migration is best explained by a combination of factors. Thus, thermal-habitat selection was a good predictor of night-time habitat occupancy in a diel-migrating species. Together, these results show that thermal-habitat selection by fishes may be important throughout the year and a more seasonally plastic behaviour than previously recognized.

Key words: acoustic telemetry; behavioural thermoregulation; diel migration; resource selection; thermal ecology.

INTRODUCTION

As obligate ectotherms, fish body temperature (T_B) reflects environmental temperature (T_E), with the result that T_E is the dominant environmental variable controlling the physiology and behaviour of fishes (Fry, 1971; Angilletta *et al.*, 2002). In T_E heterogeneous environments, temperature is competed for and exploited to maximize fitness and may be considered a niche resource (Magnuson *et al.*, 1979; Attrill & Power, 2004). Resource selection, the disproportionate use of a resource in relation to availability (Manly *et al.*, 2002) and its opposite measure, resource avoidance, are important

---

‡Author to whom correspondence should be addressed. Tel.: +1 519 888 4567 ext. 30166; email: pharriso@uwaterloo.ca

behaviours that allow animals to optimize fitness needs (Boyce & McDonald, 1999) and detection of resource selection patterns has often advanced understanding of the relationship between animals and their habitats (Boyce *et al.*, 2002). Thermal resource selection, where animals select and avoid thermal habitats to optimize fitness, is often referred to as behavioural thermoregulation (Huey & Stevenson, 1979; Hertz *et al.*, 1993).

In ectotherms, thermal optimum, the temperature at which a process is maximal, is dependent on physiological and behavioural states (Angilletta *et al.*, 2002). Thus, thermal optima vary between differing processes such as consumption, respiration, ova maturation and reproduction (Hasnain *et al.*, 2013). Bioenergetics theories suggest that animals can optimize fitness with temporal shifts in thermal-habitat selection in response to changes in physiological state, such as the diel pattern of 'hunt-warm rest-cool' (Sims *et al.*, 2006). The thermal optima of fishes are not static, they can shift seasonally in relation to reproductive and energetic state (Hasnain *et al.*, 2013) but research on behavioural thermoregulation in winter has been limited to thermal effluent studies (Cooke & McKinley, 1999; Cooke *et al.*, 2000). Few researchers have studied the role of behavioural thermoregulation outside of the summer period in systems with natural temperature regimes. In temperate aquatic systems, thermal heterogeneity is reduced in cooler periods compared with the summer. Nonetheless, where thermal-habitat heterogeneity exists, exploitation of heterogeneity seems likely, given the known importance of T_E to ectotherm physiology.

Diel migration (DM), cyclical movements in relation to light and dark periods, is a common behaviour in a broad range of taxa and environments and is important in the structuring of aquatic ecosystems (Lampert, 1989; Mehner, 2012). In aquatic systems, DMs are often vertical through the pelagic zone (DVM) (Scheuerell & Schindler, 2003). Benthic migrations between the profundal and littoral zone, known as diel bank migrations (DBM), have also been noted in several taxa (Gorman *et al.*, 2012) and horizontal migrations (DHM) have been reported in riverine fishes (Armstrong *et al.*, 2013). The leading hypotheses for the adaptive significance of diel migrations in fishes suggest that a fitness gain is achieved through a combination of improved feeding opportunity at night, increased predation shelter during the inactive daytime period and the use of thermal habitats optimal for feeding, hunting and resting states (Donner & Eckmann, 2011; Mehner, 2012; Harrison *et al.*, 2013). The multi-factor bioenergetics DM hypothesis is supported by evidence that fishes use thermal habitat similar to their final temperature preferendum (FTP) at night (Mehner *et al.*, 2010), with seasonal nightly fish depth distributions correlated with the depth of optimal thermal habitat (Busch & Mehner, 2009). To date, field-based empirical evidence has been based largely on thermal habitat use data (Andrews *et al.*, 2009), without reference to proportionate habitat availability or habitat use data, both of which are necessary to infer actual preference (Manly *et al.*, 2002).

Burbot *Lota lota* (L. 1758) is a useful model species for testing hypotheses regarding seasonal and diel patterns of thermal resource selection, because it is a diel migrating (Harrison *et al.*, 2013), stenothermic (Pääkkönen & Marjomäki, 2000), winter-specialist species (Shuter *et al.*, 2012) that inhabits thermally heterogeneous environments, such as dimictic lakes and reservoirs (Harrison *et al.*, 2016). In this study, animal-borne thermal biotelemetry and T_E logging was combined to investigate thermal-resource use, selection and avoidance in 18 *L. lota*, tracked for 1 year, in a large hydropower reservoir in British Columbia (BC), Canada. Zero-inflated mixed-effects resource-selection index models were used to test the following hypotheses: H1, behavioural thermoregulation occurs throughout the year; H2, temperatures selected differ on a diel and seasonal basis.

MATERIALS AND METHODS

STUDY SITE

Data were collected in Kinbasket Reservoir, a large (43 200 ha), deep (190 m) glacial-fed reservoir in the Kootenay–Rocky Mountain region of south-eastern BC. The reservoir is operated for storage and hydroelectric generation and was formed by the construction of the Mica Dam (52° 04′ 40″ N; 118° 34′ 00″ W) in 1976. The reservoir is fed by two major tributaries, the Canoe River and the Columbia River, which form the main two arms of the reservoir. During the study period, reservoir levels reached maximum elevation (754 m) on 4 November 2011 and the reservoir was drawn down to a minimum level (722 m) on 21 April 2011. Further details about the study site have been described (Gutowsky *et al.*, 2011, 2013; Harrison *et al.*, 2013, 2015; Martins *et al.*, 2013, 2014).

STUDY ORGANISM

Lota lota is a large-bodied benthic piscivore and top predator (Cott *et al.*, 2011, 2013) inhabiting both lake and river systems throughout their northern circumpolar distribution (Stapanian *et al.*, 2010). The species is most active during winter (Paragamian & Wakkinen, 2008) and is considered nocturnal (Müller, 1973; Harrison *et al.*, 2013). Typically, *L. lota* spawn in late winter to early spring, with spawning in the study region (Kootenay) thought to occur between February and April (McPhail & Paragamian, 2000). *Lota lota* are known to undergo DBM between the profundal and littoral zone (Cott *et al.*, 2015) and DM behaviour has been established in the study system (Harrison *et al.*, 2013) using a data set of which this paper is a sub-set.

THERMAL-HABITAT AVAILABILITY

Temperature logger chains featuring TidbiT thermistor temperature loggers (Onset Hobo Data Loggers UTBI 001; www.onsetcomp.com), accuracy of ±0·2° C, programmed to record temperatures at a minimum of every 5 min, were deployed at four sites within the reservoir (Fig. 1 for locations and Table I for details) at lowest reservoir fill levels, in April 2011. The Columbia and Canoe River sites were chosen because of their location on the two main tributary arms of the reservoir (Fig. 1). Encampment was chosen because of the high number of *L. lota* detections recorded at the station (Harrison *et al.*, 2013) and the Forebay site was chosen as the most downstream site relevant for the study. Together, the inclusion of sites on both main tributary arms, in the forebay and in a bay on the main confluence region, was chosen as a reasonably representative sample of reservoir thermal-habitat availability. In addition to the logger chains, a series of shore-based logger arrays were deployed at each site between the low-pool and high-pool marks to ensure coverage of the upper water column during periods of high reservoir fill (Fig. 1 for locations and Table I for details). Reservoir elevation data provided by the BC Hydro and Power Authority (www.bchydro.com) ensured that only data from submerged loggers were included in the thermal-habitat data set. Mean temperatures at depth for each diel period, on each day during the study period, were computed for each logger. Cubic spline interpolation (Livingstone, 2003; Jankowski *et al.*, 2006) at 5 m intervals was used to generate nightly and daily site-specific thermal profiles. Because of the varying reservoir levels, the number of loggers used to create a thermal profile varied (see Table I for details). Site-specific thermal profiles were estimated only on days when a minimum of three loggers were submerged. The number of days meeting the criterion at each location is given in Table I. The reservoir operational regime ensured that periods of high thermal heterogeneity, *i.e.* late summer, coincided with the maximum numbers of submerged loggers. The maximum depth use recorded by *L. lota* at each site during the study

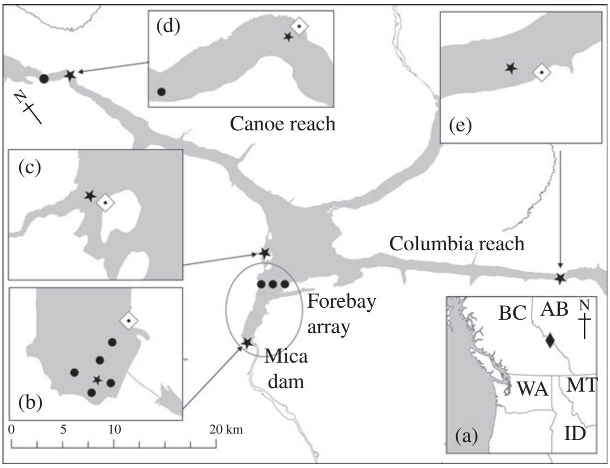


FIG. 1. Map of Kinbasket Reservoir telemetry and temperature logging array. Inset (a) ◆, the location of the reservoir in relation to provinces and states of western North America; (b) details of the Forebay Site near the dam face; (c) features the Encampment Site; (d) shows the Canoe Site; (e) details of the Columbia Site. ★, VEMCO VR2W receivers complete with thermistor chains; ●, VEMCO VR2W receiver only stations; ⊡, shore-based thermistor arrays.

period, with a daily correction for reservoir fill elevation, was used to define the lower limit of thermal-habitat availability.

CAPTURE AND TAGGING PROCEDURE

Seventy-five *L. lota* (50 during April to May 2010 and 25 during April to May 2011) were surgically implanted with temperature sensing acoustic telemetry tags (VEMCO V13TP; http://vemco.com/), 45 mm × 13 mm, 6 g in water, temperature signal transmission rate of 120–360 s, accuracy of ±0·5° C and average of 240 s and expected battery life of 1028 days. Complete details of the capture and tagging procedure can found in Harrison *et al.* (2013, 2015). Briefly, *L. lota* were captured using baited cod traps and decompressed to reduce risk of barotrauma (Neufeld & Spence, 2004). *Lota lota* were then anaesthetised in a 90 mg l^{-1} clove oil bath, an incision was made just offset to the mid-ventral line, the transmitter was inserted into the interperitoneal cavity and the incision was closed using three uninterrupted sutures. Recirculating lake water was applied to the gills throughout the surgery and the entire procedure

TABLE I. Summary of environmental temperature logger data and *Lota lota* detections by site (see Fig. 1)

Site	Maximum number of active loggers	Mean number of active loggers	Number of days when ≥3 loggers were submerged	Maximum *L. lota* depth recorded at site (m)	*L. lota* detections received (sample size)
Canoe	4	3·38	152	87·3	77 (2)
Columbia	4	3·41	137	100·1	41 (2)
Encampment	10	7·4	305	128·3	19 162 (9)
Forebay	37	24·2	366	188·3	10 104 (12)

was performed in <5 min. Recovered *L. lota* were released within 100 m of capture site. All experimental procedures were approved by the Carleton University Animal Care Committee.

TELEMETRY ARRAY

Single omnidirectional hydro-acoustic receivers (VEMCO VR2W) were positioned at the Columbia and Encampment logger stations (Fig. 1). The Canoe site featured an array of two VR2W receivers both within detection range (*c*. 750 m) of the temperature-logger array. The Forebay site featured six VR2Ws within detection range of the thermal-habitat loggers. Furthermore, 2 weeks of data from a thermal-logger chain installed at the outer Forebay site (Fig. 1) indicated isothermal conditions between this site and the inner Forebay and therefore the three VR2Ws placed at the outer Forebay were included in the Forebay group. VR2Ws were deployed as described in Gutowsky *et al.* (2013) in the spring of 2011 and data were downloaded in the spring of 2012.

THERMAL RESOURCE SELECTION

Resource selection was determined for the individual (i) at site (j) scale on a diel basis, with the thermal profile at a given logger chain used to represent the thermal habitat within detection range of the associated acoustic receivers. Diel period was defined by sunset and sunrise times at 52° 08′ N; 118° 28′ W. To ensure an adequate sampling period to estimate proportionate use and to reduce risk of false detections, selection indices were only calculated when individuals were detected 10 or more times within a diel period. Thermal habitat was categorized into 2° C bins. The resource selection index for a given thermal habitat bin W_{ij} was determined as $W_{ij} = O_{ij} A_{ij}{}^{-1}$, where O_{ij} is equal to the proportion of detections in a given thermal habitat for fish i at location j and A_{ij} represents the proportion of available habitat. W_{ij} index values <1 indicate avoidance, with W_{ij} equal to 1 indicating neutral selection and $W_{ij} > 1$ indicating active selection (Manly *et al.*, 2002). W_{ij} is often standardized (constrained between 0 and 1, B_{ij}) to ease the interpretation of preference, *i.e.* the likelihood of selection under equal availability. Standardization, however, relies on a fixed number of habitat categories (Manly *et al.*, 2002), because selection is interpreted as positive when $B_{ij} \geq n^{-1}$, where n is equal to the number of habitat categories. As the number of thermal habitats within and among seasons was variable in the data set, n could not be reliably estimated and standardization was avoided.

STATISTICAL FRAMEWORK

Mixed-effects models, which can account for correlations within repeatedly measured individuals, are a valuable tool for fitting resource selection models to telemetry data (Gillies *et al.*, 2006; Hebblewhite & Merrill, 2008). Typically, these methods use logistic regression to model presence (1) *v*. availability (0), where availability is estimated from a random sample of unused habitats (Boyce & McDonald, 1999; Boyce *et al.*, 2002). The approach is practical for data sets featuring infrequent detections (such as hourly or daily GPS fixes), but less practical for large data sets with fine-scale spatiotemporal coverage, such as high-frequency acoustic telemetry data sets, where the size of the data set may result in excessively long model convergence times (Hebblewhite & Merrill, 2008) and the inability to adequately capture intensity of use (Nielson & Sawyer, 2013). One alternative approach is to use short-term resource selection indices, such the W_{ij} of Manly *et al.* (2002), as the response variable in a generalized linear mixed effects model. The method ensures intensity of use is explicitly modelled and the precision at which habitat is measured can be fully utilized, rather than sampled, as is the case with the presence availability models. While the issue of temporal autocorrelation in resource selection modelling has been extensively explored (Cagnacci *et al.*, 2010; Fieberg *et al.*, 2010; Nielson & Sawyer, 2013), the issue of zero-inflation has received much less attention in regards to resource selection function (RSF) modelling. Excessive zeros associated with unused habitat are common in resource selection models (Manly *et al.*, 2002; Nielson & Sawyer, 2013) and have the potential to result in biased parameter estimation (Zuur *et al.*, 2009). Advances in zero-inflated modelling techniques, however, designed for count data (Zuur *et al.*, 2012) and continuous data (Pennington, 1983; Helser *et al.*, 2004) provide an excellent opportunity to incorporate zero-inflated distributions into resource selection modelling.

Generalized linear mixed model (GLMM) frameworks (Zuur *et al.*, 2009) were fitted with a delta-normal error distribution (Aitchison, 1955), to account for the high levels of zero inflation (75·9%) that occurred as a result of the frequency of unoccupied thermal habitat. The delta approach is a two-stage mixing process, suitable for zero-inflated data with a Gaussian non-zero response, that has been extensively applied to zero-inflated continuous fisheries data (Pennington, 1983; Helser *et al.*, 2004; Anlauf-Dunn *et al.*, 2014). The approach is similar to the zero-altered Poisson (ZAP) and hurdle models often used for count data (Zuur *et al.*, 2012), but the method allows for a continuous distribution of the non-zero data. Delta model selection estimates (Δ_{ij}) were derived using:

$$\Delta_{ij} = p_{ij}N_{ij}, \tag{1}$$

where p_{ij} is the probability of habitat occupancy and N_{ij} is the estimate of W_{ij} for the sub-set of non-zero data, *i.e.* occupied habitats. For all models, separate intercepts were used for each combination of individual *L. lota* × thermal-habitat category. This random effect structure was chosen over a crossed or nested structure (Pinheiro & Bates, 2000; Zuur *et al.*, 2009), for the ability to account for the correlation between successive visits to the same habitat, which would not be possible with a crossed or nested structure. Furthermore, separate intercepts for each combination of individual and thermal-habitat category make sense from a biological perspective, given that one would probably expect selection for differing habitats to be independent traits in a given fish. Correlation was modelled using a continuous autoregressive correlation structure (AR1), where the lag of 1 was used for consecutive diel periods (Pinheiro & Bates, 2000; Zuur *et al.*, 2009). Correlation structures were validated using autocorrelation function (ACF) plotting for the habitat occupancy model sets and a combination of ACF plotting and AIC comparison for the N_{ij} model. For both model sets, beyond optimal models used the following categorical fixed effects structure: thermal habitat (*T*, 2° C temperature bins starting at 0–1·99° C through to 18–20° C), season [*S*, prespawning (November to January), spawn and postspawning (February to April) and summer (May to October)], diel period (*D*, night and day), location (*L*, Forebay, Encampment, Canoe and Columbia) and all possible two- and three-way interactions.

PROBABILITY OF OCCUPANCY MODEL

Probability of occupation p_{ij}, or the probability of being detected at least once in a given thermal habitat, was modelled using a penalized quasi-likelihood generalized linear mixed effects logistic model, fitted using the glmmPQL function from the package MASS for R (http://cran.r-project.org/web/packages/mass/index.html). Backwards selection was performed using the wald.test function from the aod package for R (http://cran.r-project.org/web/packages/aod/index.html/), which is deemed an appropriate method for quasi-likelihood approximation (Breslow, 1990). Beyond optimal models took the form $it(p_{ij}) = \alpha + \beta_1\, T_{ij} + \beta_2\, S_{ij} + \beta_3\, D_{ij} + \beta_4\, L_{ij} + \beta_5\, I_{ij} + F_i$, where F_i is the random intercept represented by individual fish *i* in a given thermal habitat and is assumed to be *c.* $N\left(0, \sigma_F^2\right)$, p_{ij} represents the probability of a single detection for fish *i* at location *j* and I_{ij} is used to represent all possible two- and three-way interactions.

THERMAL-HABITAT SELECTION FOR OCCUPIED HABITATS MODEL

Non-zero selection estimates (N_{ij}) were computed using linear mixed effect models with a Gaussian error structure fitted using the package nlme for R (http://cran.r-project.org/web/packages/nlme/index.html/). Residual plotting was used to test for key model assumptions: heteroscedasticity between fixed effects levels, normality and independence (Zuur *et al.*, 2009). Where heterogeneity in variance between fixed effects levels was observed, the variance weighting function varIdent was applied and where residual plots indicated deviance from normality, cube-root transformations were used (Zuur *et al.*, 2009). Backwards selection was applied using the conditional F test approach (Pinheiro & Bates, 2000). Resulting beyond optimal models took the following form: $N_{ij} = \alpha + \beta_1 T_{ij} + \beta_2 S_{ij} + \beta_3 D_{ij} + \beta_4 L_{ij} + \beta_5 I_{ij} + F_i$.

DELTA THERMAL-HABITAT SELECTION MODEL

Model estimates were derived using equation (1). Conditional confidence intervals ($P < 0{\cdot}05$) for DW_{ij} estimates were derived using the parametric bootstrap approach (Efron & Tibshirani, 1994; Davison & Hinkley, 1997), based on the assumption of a near asymptotic distribution of estimates. Runs of 100 000 probable parameter estimates were drawn using the rmvnorm function from the mtvnorm package for R (http://cran.rproject.org/web/packages/mtvnorm/index.html/) and the variance–covariance matrices from the nlme model outputs for the best N_{ij} and probability of occupancy models. The product of the parameter estimates from each model were used to compute 100 000 fitted values from which the C.I. were estimated. The resulting C.I. from the delta model were then used to test hypotheses regarding thermal-habitat selection, where overlap with the W_{ij} value of 1 indicated neutral selection and non-overlapping intervals above or below 1 indicated positive selection or avoidance, respectively.

RESULTS

Eighteen of the 75 tagged *L. lota* were recorded at receivers within the vicinity of temperature-logger chains, resulting in 34 246 detections. Sixty-seven of the 75 tagged *L. lota* were detected at additional receivers employed in the reservoir for alternative studies (Harrison *et al.*, 2013, 2015). Individuals detected in this study had a mean total length (L_T) of 51·1 cm and ranged from 45·8 to 64·5 cm. Post-filtration, detections ranged from 35 to 12 910, with a median of 628 detections per individual over the study period. Environmental thermal-habitat availability profiles were calculated for 1913 diel period-based profiles across four stations (Table I). The combination of these environmental-habitat availability and thermal-habitat use estimates resulted in 4153 resource selection index observations, with individuals meeting the 10 detection per diel period criterion for diel W_{ij} observations on an average of 40 (not necessarily consecutive) days (range = 3–220 days). Eighteen *L. lota* were detected during the summer period, 16 during the prespawning period and 15 during the postspawning and spawning period. Diel depth distribution data in relation to thermal-habitat availability over the course of the year is shown in Fig. 2.

THERMAL-HABITAT AVAILABILITY

Seasonal and diel differences in overall thermal-habitat availability proportions were observed (Fig. 3), with >80% of available thermal habitat during the prespawning period falling between 2 and 6° C for both day and night periods and the range of thermal habitat available falling between 0 and 12° C (day) and 0 and 10° C (night). During the spawning and postspawning period, 2–4° C water accounted for up to 68·5 (day) and 67·7% (night) of the thermal habitat available and 0–2° C thermal habitat accounted for 31·6 and 31·0%, of thermal-habitat availability. In the summer period, 66·40% of the available thermal habitat fell between 2 and 6° C.

THERMAL-HABITAT OCCUPANCY

The best model featured a significant three-way interaction among diel period, season and thermal-habitat category ($X^2 = 238{\cdot}7$, d.f. = 26, $P < 0{\cdot}01$). Location and

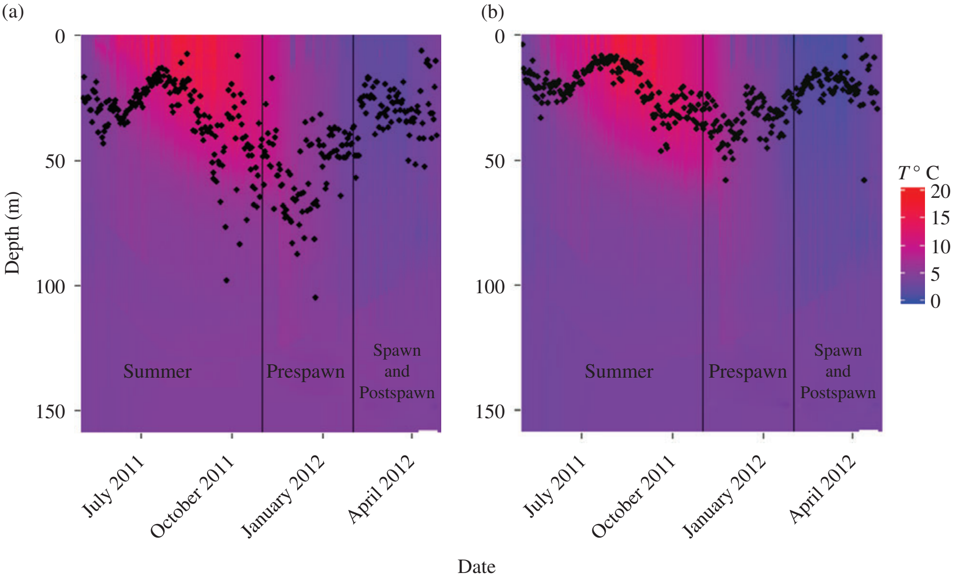


FIG. 2. (a) Daytime and (b) night-time diel thermal depth profiles of *Lota lota* in Kinbasket Reservoir. ●, the daily population mean depth ($n = 18$). Background colours indicate the mean temperature at depth across all sites.

all interactions involving location were not found to influence *L. lota* thermal habitat use (X^2, all $P \geq 0{\cdot}05$) and were subsequently removed from the final model. Model estimates C.I. are plotted in Fig. 4. Temporal correlation for the residual temporal autocorrelation was observed ($\Phi = 0{\cdot}54$) and accounted for. Individual differences accounted for 49% of the variance in the thermal-habitat use. Significant differences between diel periods within thermal-habitat categories (diagnosed by non-overlapping 95% C.I.) were observed in the spawn and postspawning periods, with increased probability of use of the 0–2° C thermal-habitat category at night and increased probability of use of the 2–4° C habitat during the day. During the prespawning period, 0–2° C habitat was available during day and night (4·74 and 4·21%, respectively), but never used. Habitat at 10–12° C was available (0·26%) during the day but never used. During the summer, 16–18° C habitat was available during the day and night (3·20 and 2·93%, respectively), but never used. Similarly, 18–20° C habitat was also available during the day (1·00%), but never occupied.

THERMAL-HABITAT SELECTION FOR OCCUPIED HABITATS

The model was populated with 1001 non-zero observations. Individuals produced enough data to calculate non-zero W_{ij} values for an average of 40, not necessarily consecutive days (range = 3–220 days). A significant season × diel period × thermal-habitat interaction effect was observed (Marginal F test, denominator $F_{25,906} = 10{\cdot}88$, $P < 0{\cdot}001$). Location and all interactions involving location were not found to significantly influence non-zero W_{ij} (Marginal F test, all $P > 0{\cdot}05$). In the final model, residual temporal correlation was observed and accounted for ($\Phi = 0{\cdot}82$).

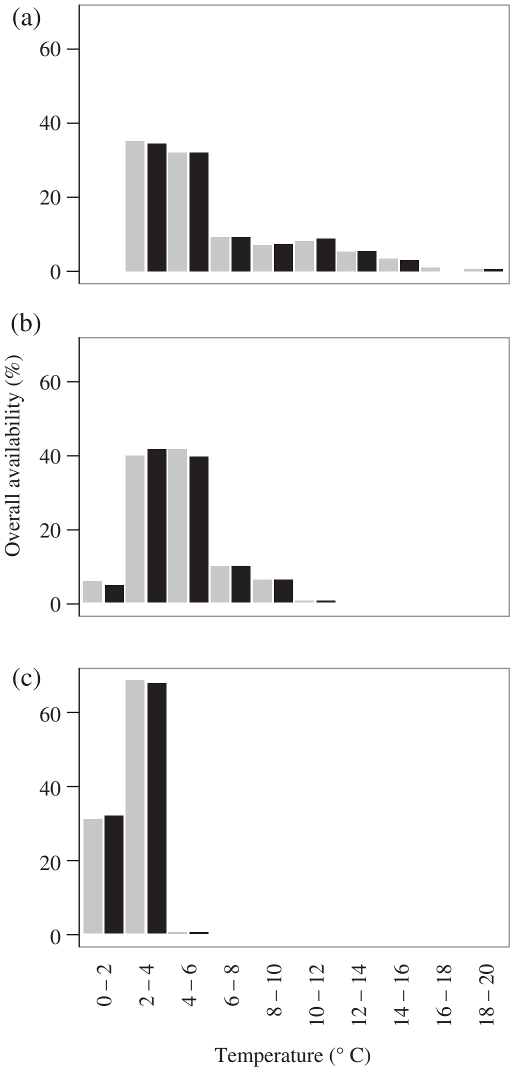


FIG. 3. Per cent availability of thermal habitat for *Lota lota* in Kinbasket Reservoir in (a) summer, (b) prespawn and (c) spawn and postspawn in the day (▨) and night (■).

Individual differences accounted for 10·1% of variation in non-zero thermal-habitat selection. Model estimates and confidence intervals are shown in Fig. 5.

DELTA THERMAL-HABITAT SELECTION MODEL

During the prespawning period *L. lota* showed significant selection for 4–6° C habitat during the day and 8–10° C habitat during the night (bootstrapped c.i. > 1, $P < 0·05$), *L. lota* avoided 0–2° C habitat during both diel periods and avoided 10–12° C habitat that was only available during the day (bootstrap c.i. < 1, $P < 0·05$) and showed neutral selection for all other habitats (c.i. = 1, $P < 0·05$).

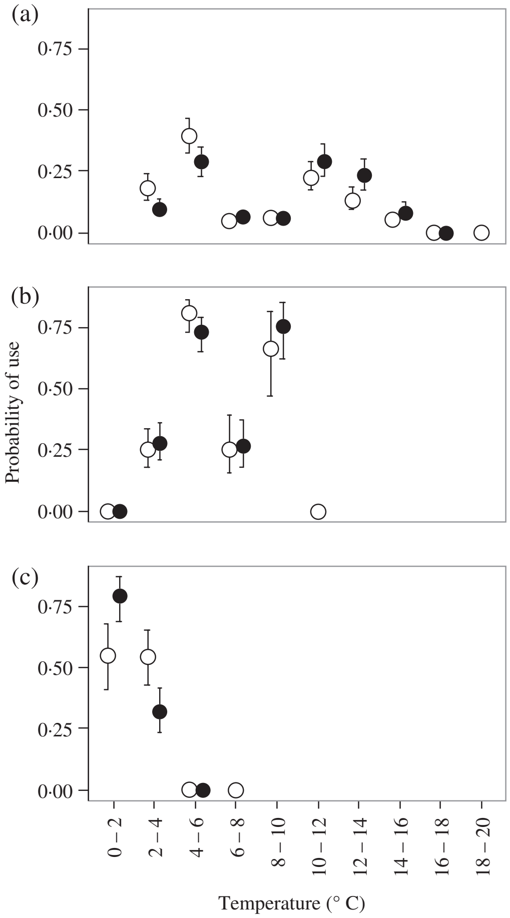


FIG. 4. Model estimates for probability of use by *Lota lota* within thermal-habitat categories for *L. lota* in Kinbasket Reservoir, Canada, in (a) summer, (b) prespawn and (c) spawn and postspawn in the daytime (○) and night-time (●); error bars represent conditional 95% C.I.

During the spawn and postspawning period, *L. lota* showed significant selection for 0–2° C habitat at night (bootstrapped C.I. > 1, $P < 0{\cdot}05$), neutral selection for 0–2° C habitat during the day (bootstrapped C.I. = 1, $P < 0{\cdot}05$) and avoided habitats >2° C during both day and night (bootstrapped C.I. < 1, $P < 0{\cdot}05$).

During the summer nights, *L. lota* showed positive selection for 12–14° C, neutral selection for habitats between 4–12° C and 14–16° C and avoided habitats <4 and >16° C. During summer daytime, *L. lota* showed neutral selection for 4–14° C and avoided thermal habitat >14 and <2° C. Model estimates and C.I. are shown in Fig. 6.

DISCUSSION

The data set used in this study comprised high frequency thermal-habitat availability and thermal-habitat selection measures of 18 *L. lota* tracked for a full year in a thermally

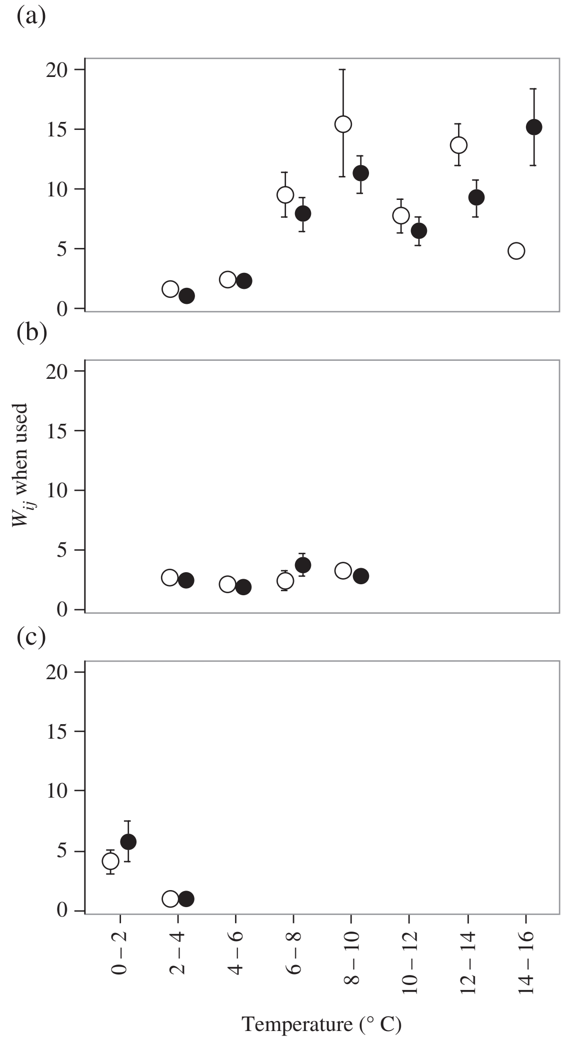


FIG. 5. Model estimates of *Lota lota* Manly's selection index (W_{ij}) values for thermal-habitat categories based on the sub-set of non-zero data, *i.e.* occupied habitats, in (a) summer, (b) prespawn and (c) spawn and postspawn in the daytime (○) and night-time (●). ___ is at the value $W_{ij} = 1$. Error bars represent conditional 95% C.I.

heterogeneous environment. Accordingly, these results provide a much more detailed and long-term data set of the thermal behaviour of *L. lota* than was previously available. These results provide empirical evidence confirming the hypotheses of year round behavioural thermoregulation (H1) and seasonal and diel patterns of thermal selection and avoidance (H2) in a stenothermic fish, inhabiting a thermally heterogeneous environment. Heterogeneity in diel patterns of thermal experience have previously been used to test hypotheses regarding physiological advantage (Brett, 1971; Sims *et al.*, 2006; Andrews *et al.*, 2009). These results, however, are among the first to utilize detailed thermal-habitat availability data sets to provide empirical evidence of a diel pattern of selection and avoidance during diel migrations. Furthermore, these results

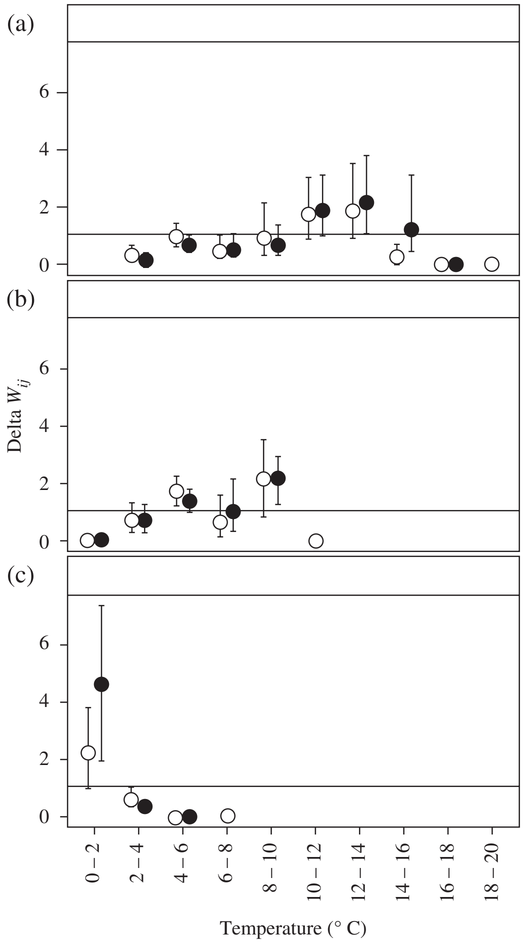


FIG. 6. Delta-normal model estimates for *Lota lota* Manly's selection index values (W_{ij}) by thermal habitat in (a) summer, (b) prespawn and (c) spawn and postspawn in the daytime (○) and night-time (●). ___ is at the value $W_{ij} = 1$. Error bars represent conditional 95% C.I.

are among the first to provide a field-based description of such a large seasonal temperature shift in the habitat selection (from 0–2° C to 12–14° C).

During the summer and prespawning periods, results suggest that night-time migration is associated with a pattern of behavioural thermoregulation towards optima for hunting, feeding and digesting in this night-active, nocturnal predator (Müller, 1973; Kavaliers, 1980; Harrison *et al.*, 2013). Summer night-time selected temperatures (12–14° C) were similar to thermal optima for consumption reported for *L. lota* (13·6–14·0° C; Rudstam *et al.*, 1995; Pääkkönen & Marjomäki, 2000; Pääkkönen *et al.*, 2003). The selected temperatures were also similar to optimal temperatures for gastric evacuation (12·6° C; Pääkkönen & Marjomäki, 1997), which would minimize stomach fullness to enable maximum nightly food intake (Jeschke *et al.*, 2002). In addition, the selected temperatures were close to the species' final temperature preferendum (FTP) (14·2° C; Hofmann & Fischer, 2002). Use of temperatures similar to FTP during nightly diel migrations has been noted in wild coregonids (Busch & Mehner, 2009; Mehner *et al.*, 2010) and these results confirm active selection for FTP. While the relationship between FTP and specific physiological thermal optima has not been quantitatively established for *L. lota*, FTP is often closely linked to an optimization of physiological and bioenergetic processes (Beitinger & Fitzpatrick, 1979; Reynolds & Casterlin, 1979; Jobling, 1981; Hasnain *et al.*, 2013) and closely matches temperatures that minimize the costs of swimming (Ohlberger *et al.*, 2008). The selection for the warmest available habitat (8–10° C) seen during the prespawning suggests a similar attempt to optimize thermal conditions for hunting, feeding and digesting.

The nightly selection for water <2° C during the spawn and postspawning may optimize thermal conditions for prespawning maturation and the spawning event and may have consequences for thermal-habitat available for developing embryos. *Lota lota* spawning maturation is strongly tied to temperature with Zarski *et al.* (2010) noting spawning maturation was fastest when temperatures rapidly declined to 1° C. *Lota lota* spawning has been observed at between 0 and 4° C (McPhail & Paragamian, 2000) and Wismer & Christie (1987) suggested an optimum spawning temperature of 1·2° C. Further, the selection for <2° C habitat may improve sperm motility, which was found to be optimal at <5° C (Lahnsteiner & Mansour, 2012). Lacustrine *L. lota* spawn at night in the littoral zone (McCrimmon, 1959) and while spawning takes place in the water column (Fabricius, 1954), eggs quickly sink and mature within the substratum (McPhail & Paragamian, 2000). *Lota lota* eggs have among the coldest optimum incubation temperatures of all freshwater temperate species (Teletchea *et al.*, 2009), thus nightly selection of <2° C during the spawning event may benefit eggs postspawn even though such temperatures are below those described as optimal for egg survival; 3·8° C (Vught *et al.*, 2008) and 3° C (Taylor & McPhail, 2000). Nonetheless, selection of these <2° C temperatures would ensure an avoidance of thermal habitat likely to cause mortality as 100% *L. lota* ova mortality has been recorded at >8·1° C (Vught *et al.*, 2008), >5° C (Zarski *et al.*, 2010) and >6° C (Taylor & McPhail, 2000). In winter, when temperatures fall below 4° C, available <2° C habitat tends to be located closer to the surface (Fig. 2) and it is possible that the selection of these very cold temperatures could be a function of selection for a non-thermal-habitat variable associated with shallow depth. Given the importance of temperature, however, in the reproductive processes of ectotherms (Huey, 1991; Van der Kraak & Pankhurst, 1996; Guderley & Pörtner, 2010), temperature is probably the most critical determinant of habitat selection.

The observations of a general daytime pattern of avoidance of thermal habitat >14 and <4° C during the summer and >2° C habitat during spawning and postspawning imply an avoidance of suboptimal thermal habitat for consumption and reproduction, respectively. With the exception of the selection observed for 4–6° C habitat during prespawning, significant active selection was not observed, indicating that selection for thermal habitat may not be as important during the day as at night. Together, these results suggest that while selection for physiological optima provides an effective explanation for the night-time migration, thermal-habitat selection only partly explains daytime behaviour. Accordingly, the data provide support for the contribution of behavioural thermoregulation in a multi-factor hypothesis for diel migration, similar to hypotheses proposed by Mehner (2012) and Harrison *et al.* (2013). The results, however, do not support a stand-alone bioenergetics diel migration hypothesis as proposed by Sims *et al.* (2006), under which one would expect to find a consistent pattern of selection for cooler habitat during the day.

Diel migration explanations have also been investigated using bioenergetics modelling exercises (Sims *et al.*, 2006; Busch *et al.*, 2011; Mehner *et al.*, 2011) and using experimental data to simulate diel thermal experience changes (Donner & Eckmann, 2011). Such models and experiments have proved useful for quantifying the theoretical bioenergetic fitness gains associated with diel migrations under a bioenergetics stand-alone diel migration hypothesis. Nonetheless, these methods are dependent on assumptions about activity levels and feeding rations, which are hard to estimate with precision (Hansen *et al.*, 1993; Mehner, 2012). Furthermore, these methods lack the ability to quantify fitness gain to predation vulnerability trade-offs, which are expected under a multifactor hypothesis. Indeed, given the close match with temperature selected at night and temperatures previously experimentally defined as optimum and the findings that suggest the daytime migration is not strongly tied to thermal-habitat selection, the field-based approach has provided data that is likely to be more valuable than could be provided by an experimental or modelling approach.

While seasonal shifts in thermal preference from experimental data have been described in a few species, *e.g.* Arctic charr *Salvelinus alpinus* (L. 1758) (Mortensen *et al.*, 2007) and cod *Gadus morhua* L.1758 (Clark & Green, 1991), the detection of a large seasonal temperature shift in the habitat selection (from 0–2° C to 12–14° C) is rare. Indeed, functional responses to availability, *i.e.* changes in selection strength in relation to changes in resource or habitat availability (Mysterud & Ims, 1998), are common in studies of non-thermal-habitat selection (Osko *et al.*, 2004; Hebblewhite & Merrill, 2008; Godvik *et al.*, 2009). Accordingly, it is suspected that temporal functional responses to thermal-habitat availability may be more common than previously acknowledged and the rarity of such findings reflects the lack of research into winter thermal ecology in general (Shuter *et al.*, 2012).The seasonal and diel shifts in temperature selection detected indicate that overall measures of thermal preference derived from a single season or single diel period may be reductive, particularly for winter-active or diel-migrating species. Thus, seasonal and diel thermal selection patterns warrant further investigation in additional species.

Behavioural thermoregulation still occurred during the winter period, despite the large reduction in reservoir thermal heterogeneity compared with summer. The findings that behavioural thermoregulation is an important tactic in winter in lake environments parallel previous work in river environments. Thermal-habitat selection is an important tactic used to survive winter in riverine salmonids (Cunjak, 1996), such as avoidance of freezing temperatures (Cunjak *et al.*, 1998) and the selection of warmer groundwater input (Cunjak & Power, 1986). Results from this study indicate that winter thermoregulation may also be important in lake environments. Furthermore, the fitness gains from behavioural thermoregulation in winter are probably amplified in a winter-feeding species (Hölker *et al.*, 2004; Shuter *et al.*, 2012). Accordingly, thermal heterogeneity in winter may be more important in structuring lake fish distribution than previously considered and more research is needed to understand how shorter winters might affect freshwater fishes, particularly winter specialists. Indeed, winter specialist species are already considered particularly vulnerable to winter temperature increases (Pörtner, 2006; Pörtner & Peck, 2010; Shuter *et al.*, 2012). The selection for very cold thermal habitat (<2° C) by *L. lota* during the late winter further highlights this vulnerability.

In conclusion, the results from this study are among the first to explicitly quantify the role of thermal-habitat selection in diel migration behaviour. Results show that behavioural thermoregulation towards optimal temperatures for reproduction, hunting and feeding consistently explain night-time behaviour throughout the year. Consistent patterns of selection, however, for cooler habitat during the daytime period, which would be expected from a bioenergetics-based 'hunt-warm rest-cool' diel migration strategy (Sims *et al.*, 2006), were not observed. Together, these results imply a partial role of behavioural thermoregulation within a multifactor DM hypothesis. Behavioural thermoregulation has long been acknowledged as an important tactic for maximizing fitness during summer periods (Huey & Stevenson, 1979). These findings have provided evidence that this tactic may also be important during winter periods and that selected temperatures can shift seasonally in response to reproductive state. Furthermore, the requirement for cold thermal habitat during the reproductive period highlights a potential vulnerability to increased winter temperatures. Given the importance of temperature for ectotherms, a thorough understanding of the relationship between fish and thermal habitat, particularly in winter, is essential for a complete understanding of fish ecology. Findings from the present study demonstrate that consideration of thermal ecology at the diel and seasonal scale has the potential to significantly advance knowledge in this area.

Thanks to J. Tippe of Grizzly Country Marine, J. Hills, S. Landsman, J. Nitichoruk, J. Molina, M. Taylor, G. Crossin and T. Nettles for field assistance. Additional thanks go to L. Donaldson for managing and populating the thermal-habitat database. Thanks to A. Leake and the late P. Higgins for logistical support. Thanks to two anonymous reviewers for their helpful comments that have improved the manuscript. Funding was provided by the Natural Sciences and Engineering Research Council of Canada (*via* NSERC HydroNet) and a Collaborative Research and Development Grant (http://www.nserc-crsng.gc.ca/Professors-Professeurs/RPP-PP/CRD-RDC_eng.asp) and a discovery grant to M.P., BC Hydro and Power Authority and the Center for Expertise on Hydropower Impacts of Fish and Fish Habitat of Fisheries and Oceans Canada. S.J.C. is supported by the Canada Research Chairs Program (http://www.chairs-chaires.gc.ca/home-accueil-eng.aspx). Some of the telemetry infrastructure was provided by the Canada Foundation for Innovation and the Ontario Ministry of Research and Innovation.

References

Aitchison, J. (1955). On the distribution of a positive random variable having a discrete probability mass at the origin. *Journal of the American Statistical Association* **50**, 901–908.

Andrews, K. S., Williams, G. D., Farrer, D., Tolimieri, N., Harvey, C. J., Bargmann, G. & Levin, P. S. (2009). Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. *Animal Behaviour* **78,** 525–536.

Angilletta, M. J., Niewiarowski, P. H. & Navas, C. A. (2002). The evolution of thermal physiology in ectotherms. *Journal of Thermal Biology* **27,** 249–268.

Anlauf-Dunn, K. J., Ward, E. J., Strickland, M., Jones, K. & Bradford, M. (2014). Habitat connectivity, complexity and quality: predicting adult coho salmon occupancy and abundance. *Canadian Journal of Fisheries and Aquatic Sciences* **71,** 1864–1876.

Armstrong, J. B., Schindler, D. E., Ruff, C. P., Brooks, G. T., Bentley, K. E. & Torgersen, C. E. (2013). Diel horizontal migration in streams: juvenile fish exploit spatial heterogeneity in thermal and trophic resources. *Ecology* **94,** 2066–2075.

Attrill, M. J. & Power, M. (2004). Partitioning of temperature resources amongst an estuarine fish assemblage. *Estuarine, Coastal and Shelf Science* **61,** 725–738.

Beitinger, T. L. & Fitzpatrick, L. C. (1979). Physiological and ecological correlates of preferred temperature in fish. *American Zoologist* **19,** 319–329.

Boyce, M. S. & McDonald, L. L. (1999). Relating populations to habitats using resource selection functions. *Trends in Ecology and Evolution* **14,** 268–272.

Boyce, M. S., Vernier, P. R., Nielsen, S. E. & Schmiegelow, F. K. (2002). Evaluating resource selection functions. *Ecological Modelling* **157,** 281–300.

Breslow, N. (1990). Tests of hypotheses in overdispersed Poisson regression and other quasi-likelihood models. *Journal of the American Statistical Association* **85,** 565–571.

Brett, J. R. (1971). Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *Integrative and Comparative Biology* **11,** 99–113.

Busch, S. & Mehner, T. (2009). Hydroacoustic estimates of fish population depths and densities at increasingly longer time scales. *International Review of Hydrobiology* **94,** 91–102.

Busch, S., Johnson, B. M. & Mehner, T. (2011). Energetic costs and benefits of cyclic habitat switching: a bioenergetics model analysis of diel vertical migration in coregonids. *Canadian Journal of Fisheries and Aquatic Sciences* **68,** 706–717.

Cagnacci, F., Boitani, L., Powell, R. A. & Boyce, M. S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philosophical Transactions of the Royal Society B* **365,** 2157–2162.

Clark, D. S. & Green, J. M. (1991). Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhua*), with evidence supporting an energetic basis for their diel vertical migration. *Canadian Journal of Zoology* **69,** 1302–1307.

Cooke, S. J. & McKinley, R. S. (1999). Winter residency and activity patterns of channel catfish, *Ictalurus punctatus* (Rafinesque) and common carp, *Cyprinus carpio* L., in a thermal discharge canal. *Fisheries Management and Ecology* **6,** 515–526.

Cooke, S. J., Bunt, C. M. & McKinley, R. S. (2000). Winter residency of smallmouth bass in a thermal discharge canal: implications for tempering pump operation. *North American Journal of Fisheries Management* **20,** 288–295.

Cott, P. A., Johnston, T. A. & Gunn, J. M. (2011). Food web position of burbot relative to lake trout, northern pike and lake whitefish in four sub-Arctic boreal lakes. *Journal of Applied Ichthyology* **27,** 49–56.

Cott, P. A., Johnston, T. A. & Gunn, J. M. (2013). Stability in life history characteristics among burbot populations across environmental gradients. *Transactions of the American Fisheries Society* **142,** 1746–1756.

Cott, P. A., Guzzo, M. M., Chapelsky, A. J., Milne, S. W. & Blanchfield, P. J. (2015). Diel bank migration of burbot (*Lota lota*). *Hydrobiologia* **757,** 3–20.

Cunjak, R. A. (1996). Winter habitat of selected stream fishes and potential impacts from land-use activity. *Canadian Journal of Fisheries and Aquatic Sciences* **53,** 267–282.

Cunjak, R. A. & Power, G. (1986). Winter habitat utilization by stream resident brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*). *Canadian Journal of Fisheries and Aquatic Sciences* **43,** 1970–1981.

Cunjak, R. A., Prowse, T. D. & Parrish, D. L. (1998). Atlantic salmon (*Salmo salar*) in winter: "the season of parr discontent"? *Canadian Journal of Fisheries and Aquatic Sciences* **55,** 161–180.

Davison, A. C. & Hinkley, D. V. (1997). *Bootstrap Methods and Their Applications*. Cambridge: Cambridge University Press.

Donner, M. T. & Eckmann, R. (2011). Diel vertical migration of larval and early-juvenile burbot optimises survival and growth in a deep, pre-alpine lake. *Freshwater Biology* **56,** 916–925.

Efron, B. & Tibshirani, R. J. (1994). *An Introduction to the Bootstrap*. New York, NY: CRC press.

Fabricius, E. (1954). Aquarium observations on the spawning behaviour of the burbot, *Lota vulgaris* L. *Report of the Institute of Freshwater Research, Drottningholm* **35,** 5–57.

Fieberg, J., Matthiopoulos, J., Hebblewhite, M., Boyce, M. S. & Frair, J. L. (2010). Correlation and studies of habitat selection: problem, red herring or opportunity? *Philosophical Transactions of the Royal Society B* **365,** 2233–2244.

Fry, F. E. J. (1971). The effect of environmental factors on the physiology of fish. In *Fish Physiology*, Vol. 6 (Hoar, W. S. & Randall, D. J., eds), pp. 1–98. New York, NY, and London: Academic Press.

Gillies, C. S., Hebblethwaite, M., Nielson, S. E., Krawchuk, M. A., Aldridge, C. L., Frair, J. L., Saher, D. J., Stevens, C. E. & Jerde, C. L. (2006). Application of random effects to the study of resource selection by animals. *Journal of Animal Ecology* **75,** 887–898.

Godvik, I. M. R., Loe, L. E., Vik, J. O., Veiberg, V., Langvatn, R. & Mysterud, A. (2009). Temporal scales, trade–offs and functional responses in red deer habitat selection. *Ecology* **90,** 699–710.

Gorman, O. T., Yule, D. L. & Stockwell, J. D. (2012). Habitat use by fishes of Lake Superior. II. Consequences of diel habitat use for habitat linkages and habitat coupling in nearshore and offshore waters. *Aquatic Ecosystem Health and Management* **15,** 355–368.

Guderley, H. & Pörtner, H. O. (2010). Metabolic power budgeting and adaptive strategies in zoology: examples from scallops and fish. *Canadian Journal of Zoology* **88,** 753–763.

Gutowsky, L. F. G., Harrison, P. M., Landsman, S. J., Power, M. & Cooke, S. J. (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. *Fisheries Research* **109,** 379–383.

Gutowsky, L. F. G., Harrison, P. M., Martins, E. G., Leake, A., Patterson, D. A., Power, M. & Cooke, S. J. (2013). Diel vertical migration hypotheses explain size-dependent behaviour in a freshwater piscivore. *Animal Behaviour* **86,** 365–373.

Hansen, M. J., Boisclair, D., Brandt, S. B., Hewett, S. W., Kitchell, J. F., Lucas, M. C. & Ney, J. J. (1993). Applications of bioenergetics models to fish ecology and management: where do we go from here? *Transactions of the American Fisheries Society* **122,** 1019–1030.

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Leake, A., Cooke, S. J. & Power, M. (2013). Diel vertical migration of adult burbot: a dynamic trade–off among feeding opportunity, predation avoidance and bioenergetic gain. *Canadian Journal of Fisheries and Aquatic Sciences* **70,** 1765–1774.

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J. & Power, M. (2015). Personality–dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). *Behavioral Ecology* **26,** 483–492.

Harrison, P. M., Gutowsky, L. F. G., Martins, E. G., Patterson, D. A., Cooke, S. J. & Power, M. (2016) Burbot and large hydropower in North America: Benefits, threats, and research needs for mitigation. *Fisheries Management & Ecology*. doi: 10.1111/fme.12178

Hasnain, S. S., Shuter, B. J., Minns, C. K. & Fraser, D. (2013). Phylogeny influences the relationships linking key ecological thermal metrics for North American freshwater fish species. *Canadian Journal of Fisheries and Aquatic Sciences* **70,** 964–972.

Hebblewhite, M. & Merrill, E. (2008). Modelling wildlife–human relationships for social species with mixed-effects resource selection models. *Journal of Applied Ecology* **45,** 834–844.

Helser, T. E., Punt, A. E. & Methot, R. D. (2004). A generalized linear mixed model analysis of a multi-vessel fishery resource survey. *Fisheries Research* **70,** 251–264.

Hertz, P. E., Huey, R. B. & Stevenson, R. (1993). Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *American Naturalist* **142,** 796–818.

Hofmann, N. & Fischer, P. (2002). Temperature preferences and critical thermal limits of burbot: implications for habitat selection and ontogenetic habitat shift. *Transactions of the American Fisheries Society* **131,** 1164–1172.

Hölker, F., Volkmann, S., Wolter, C., van Dijk, P. L. M. & Hardewig, I. (2004). Colonization of the freshwater environment by a marine invader: how to cope with warm summer temperatures. *Evolutionary Ecology Research* **6,** 1123–1144.

Huey, R. B. (1991). Physiological consequences of habitat selection. *American Naturalist* **137,** 91–115.

Huey, R. B. & Stevenson, R. (1979). Integrating thermal physiology and ecology of ectotherms: a discussion of approaches. *American Zoologist* **19,** 357–366.

Jankowski, T., Livingstone, D. M., Bührer, H., Forster, R. & Niederhauser, P. (2006). Consequences of the 2003 European heat wave for lake temperature profiles, thermal stability and hypolimnetic oxygen depletion: implications for a warmer world. *Limnology and Oceanography* **51,** 815–819.

Jeschke, J. M., Kopp, M. & Tollrian, R. (2002). Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* **72,** 95–112.

Jobling, M. (1981). Temperature tolerance and the final preferendum – rapid methods for the assessment of optimum growth temperatures. *Journal of Fish Biology* **19,** 439–455. doi: 10.1111/j.1095-8649.1981.tb05847.x

Kavaliers, M. (1980). Circadian locomotor activity rhythms of the burbot, *Lota Iota*: seasonal differences in period length and the effect of pinealectomy. *Journal of Comparative Physiology A* **136,** 215–218.

Lahnsteiner, F. & Mansour, N. (2012). The effect of temperature on sperm motility and enzymatic activity in brown trout *Salmo trutta*, burbot *Lota lota* and grayling *Thymallus thymallus*. *Journal of Fish Biology* **81,** 197–209.

Lampert, W. (1989). The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology* **3,** 21–27.

Livingstone, D. M. (2003). Impact of secular climate change on the thermal structure of a large temperate central European lake. *Climatic Change* **57,** 205–225.

Magnuson, J. J., Crowder, L. B. & Medvick, P. A. (1979). Temperature as an ecological resource. *Integrative and Comparative Biology* **19,** 331–343.

Manly, B. F. J., McDonald, L. L., Thomas, D. L., McDonald, T. L. & Erickson, W. P. (2002). *Resource Selection by Animals: Statistical Analysis and Design for Field Studies*. Dordrecht: Kluwer.

Martins, E. G., Gutowsky, L. F. G., Harrison, P. M., Patterson, D. A., Power, M., Zhu, D. Z., Leake, A. & Cooke, S. J. (2013). Forebay use and entrainment rates of resident adult fish in a large hydropower reservoir. *Aquatic Biology* **19,** 253–263.

Martins, E. G., Gutowsky, L. F. G., Harrison, P. M., Flemming, J. E. M., Jonsen, I. D., Zhu, D. Z., Leake, A., Patterson, D. A., Power, M. & Cooke, S. J. (2014). Behavioral attributes of turbine entrainment risk for adult resident fish revealed by acoustic telemetry and state–space modeling. *Animal Biotelemetry* **2,** 1–13.

McCrimmon, H. R. (1959). Observations on spawning of burbot in Lake Simcoe, Ontario. *Journal of Wildlife Management* **23,** 447–449.

McPhail, J. D. & Paragamian, V. L. (2000). Burbot biology and life history. In *Burbot: Biology, Ecology and Management* (Paragamian, V. L. & Willis, D. W., eds), pp. 11–23. Bethesda, MD: American Fisheries Society.

Mehner, T. (2012). Diel vertical migration of freshwater fishes: proximate triggers, ultimate causes and research perspectives. *Freshwater Biology* **57,** 1342–1359.

Mehner, T., Busch, S., Helland, I. P., Emmrich, M. & Freyhof, J. (2010). Temperature-related nocturnal vertical segregation of coexisting coregonids. *Ecology of Freshwater Fish* **19,** 408–419.

Mehner, T., Schiller, S., Staaks, G. & Ohlberger, J. (2011). Cyclic temperatures influence growth efficiency and biochemical body composition of vertically migrating fish. *Freshwater Biology* **56,** 1554–1566.

Mehner et al. (2012).

Mortensen, A., Ugedal, O. & Lund, F. (2007). Seasonal variation in the temperature preference of Arctic charr (*Salvelinus alpinus*). *Journal of Thermal Biology* **32,** 314–320.

Müller, K. (1973). Seasonal phase shift and the duration of activity time in the burbot, *Lota Iota* (L.) (Pisces, Gadidae). *Journal of Comparative Physiology* **84,** 357–359.

Mysterud, A. & Ims, R. A. (1998). Functional responses in habitat use: availability influences relative use in trade–off situations. *Ecology* **79,** 1435–1441.

Neufeld, M. D. & Spence, C. R. (2004). Evaluation of a simple decompression procedure to reduce decompression trauma in trap caught burbot. *Transactions of the American Fisheries Society* **133,** 1260–1263.

Nielson, R. M. & Sawyer, H. (2013). Estimating resource selection with count data. *Ecology and Evolution* **3,** 2233–2240.

Ohlberger, J., Staaks, G., Petzoldt, T., Mehner, T. & Hölker, F. (2008). Physiological specialization by thermal adaptation drives ecological divergence in a sympatric fish species pair. *Evolutionary Ecology Research* **10,** 1173–1185.

Osko, T. J., Hiltz, M. N., Hudson, R. J. & Wasel, S. M. (2004). Moose habitat preferences in response to changing availability. *Journal of Wildlife Management* **68,** 576–584.

Pääkkönen, J.-P. J. & Marjomäki, T. J. (1997). Gastric evacuation rate of burbot fed single-fish meals at different temperatures. *Journal of Fish Biology* **50,** 555–563.

Pääkkönen, J.-P. J. & Marjomäki, T. J. (2000). Feeding of burbot, *Lota lota*, at different temperatures. *Environmental Biology of Fishes* **58,** 109–112.

Pääkkönen, J.-P. J., Tikkanen, O. & Karjalainen, J. (2003). Development and validation of a bioenergetics model for juvenile and adult burbot. *Journal of Fish Biology* **63,** 956–969.

Paragamian, V. L. & Wakkinen, V. D. (2008). Seasonal movement of burbot in relation to temperature and discharge in the Kootenai River, Idaho, USA and British Columbia, Canada. In *Burbot*: *Ecology*, *Management and Culture* (Paragamian, V. L. & Bennett, D. H., eds), pp. 55–77. *American Fisheries Society Symposium* **59**.

Pennington, M. (1983). Efficient estimators of abundance, for fish and plankton surveys. *Biometrics* **39,** 281–286.

Pinheiro, J. & Bates, D. (2000). *Mixed–Effects Models in S and S–PLUS*. New York, NY: Springer.

Pörtner, H. O. (2006). Climate-dependent evolution of Antarctic ectotherms: an integrative analysis. *Deep Sea Research, Part II* **53,** 1071–1104.

Pörtner, H. & Peck, M. (2010). Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology* **77,** 1745–1779.

Reynolds, W. W. & Casterlin, M. E. (1979). Behavioral thermoregulation and the "final preferendum" paradigm. *American Zoologist* **9,** 211–224.

Rudstam, L. G., Peppard, P. E., Fratt, T. W., Bruesewitz, R. E., Coble, D. W., Copes, F. A. & Kitchell, J. F. (1995). Prey consumption by the burbot (*Lota lota*) population in Green Bay, Lake Michigan, based on a bioenergetics model. *Canadian Journal of Fisheries and Aquatic Sciences* **52,** 1074–1082.

Scheuerell, M. D. & Schindler, D. E. (2003). Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. *Ecology* **84,** 1713–1720.

Shuter, B. J., Finstad, A. G., Helland, I. P., Zweimüller, I. & Hölker, F. (2012). The role of winter phenology in shaping the ecology of freshwater fish and their sensitivities to climate change. *Aquatic Sciences* **74,** 637–657.

Sims, D. W., Wearmouth, V. J., Southall, E. J., Hill, J. M., Moore, P., Rawlinson, K., Hutchingson, N., Budd, G. C., Righton, D., Metcalfe, J. D., Nash, J. P. & Morrit, D. (2006). Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology* **75,** 176–190.

Stapanian, M. A., Paragamian, V. L., Madenjian, C. P., Jackson, J. R., Lappalainen, J., Evenson, M. J. & Neufeld, M. D. (2010). Worldwide status of burbot and conservation measures. *Fish and Fisheries* **11,** 34–56.

Taylor, J. L. & McPhail, J. D. (2000). Temperature, development and behavior in the early life history of burbot from Columbia Lake, British Columbia. In *Burbot*: *Biology*, *Ecology and Management* (Paragamian, V. L. & Willis, D. W., eds), pp. 30–37. *American Fisheries Society Symposium* **59**.

Teletchea, F., Gardeur, J., Kamler, E. & Fontaine, P. (2009). The relationship of oocyte diameter and incubation temperature to incubation time in temperate freshwater fish species. *Journal of Fish Biology* **74,** 652–668.

Van der Kraak, G. & Pankhurst, N. (1996). Temperature effects on the reproductive performance of fish. In *Global Warming: Implications for Freshwater and Marine Fish* (Wood, C. M. & McDonald, D. G., eds), pp. 159–176. Cambridge: Cambridge University Press.

Vught, I., Harzevilli, A. S., Auwerx, J., De Charleroy, D., Paragamian, V. L. & Bennet, D. H. (2008). Aspects of reproduction and larviculture of burbot under hatchery conditions. In *Burbot*: *Ecology*, *Management and Culture* (Paragamian, V. L. & Bennet, D. H., eds), pp. 167–178. *American Fisheries Society Symposium* **59**.

Wismer, D. A. & Christie, A. E. (1987). Temperature relationships of Great Lakes fishes: a data compilation. *Great Lakes Fishery Commission Special Publication* 87–3.

Zarski, D., Kucharczyk, D., Sasinowski, W., Targoska, K. & Mamcarz, A. (2010). The influence of temperature on successful reproductions of Burbot, *Lota lota* (L.) under hatchery conditions. *Polish Journal of Natural Sciences* **25,** 93–105.

Zuur, A. F., Ieno, E. N., Walker, N. J., Saveliev, A. A. & Smith, G. M. (2009). *Mixed Effects Models and Extensions in Ecology with R*. New York, NY: Springer.

Zuur, A. F., Saveliev, A. A. & Ieno, E. N. (2012). *Zero Inflated Models and Generalized Linear Mixed Models with R*. Newburgh, NY: Highland Statistics Limited.