

Diel vertical migration of adult burbot: a dynamic trade-off among feeding opportunity, predation avoidance, and bioenergetic gain

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Abstract: Diel vertical migration (DVM) of pelagic organisms is typically attributed to bioenergetic gain, foraging opportunity, predator avoidance, and multifactor hypotheses. While a number of benthic species perform nightly migrations into shallower waters, the function of these DVMs has largely been ignored in benthic fishes. We used depth and temperature sensing telemetry to investigate DVM function in burbot (*Lota lota*), a freshwater benthic piscivore. We modeled the influence of season, diel period, and body size on the depth, vertical activity, migration probability, and thermal experience of 47 adult burbot over 2 years in a reservoir in British Columbia, Canada. Burbot were found to occupy significantly shallower water at night than during the day. Our results, which showed elevated nightly activity and a seasonal size-structured depth distribution during DVMs, suggest these migrations likely provide a feeding opportunity “window” for this nocturnal predator, constrained by predation or cannibalism threats to smaller individuals. The observed thermal experience patterns suggest DVM may also provide a seasonal bioenergetic advantage. Our detection of within-individual plasticity in migration strategy is indicative of a partial migration. Taken together, our results suggest a multifactor DVM hypothesis: a dynamic trade-off among bioenergetic advantage, foraging opportunity, and predation threat.

Résumé : La migration verticale journalière (DVM) chez les organismes pélagiques est normalement attribuée à des gains bioénergétiques, des possibilités d'alimentation, l'évitement de prédateurs ou des hypothèses plurifactorielles. Si un certain nombre d'espèces benthiques effectuent des migrations nocturnes vers des eaux moins profondes, la fonction de ces DVM chez les poissons benthiques n'a pas vraiment été étudiée. Nous nous sommes servis de la télémétrie de mesure de la profondeur et de la température pour étudier la fonction des DVM chez la lotte (*Lota lota*) adulte, un poisson piscivore benthique d'eau douce. Nous avons modélisé l'influence de la saison, de la période du jour et de la taille du corps sur la profondeur, l'activité verticale, la probabilité de migration et l'expérience thermique de 47 lottes adultes dans un réservoir en Colombie-Britannique (Canada), sur une période de deux ans. Nous avons constaté que les lottes occupaient des eaux significativement moins profondes la nuit que le jour. Nos résultats, qui font ressortir une activité accrue pendant la nuit et une répartition saisonnière de la profondeur structurée par taille durant les DVM, portent à croire que ces migrations offrent vraisemblablement une « fenêtre » propice à l'alimentation à ce prédateur nocturne, contraint par la menace de prédation ou de cannibalisme en ce qui concerne les petits individus. Les motifs d'expérience thermique observés donnent à penser que les DVM peuvent également conférer un avantage bioénergétique saisonnier. La détection d'une certaine plasticité individuelle sur le plan de la stratégie de migration indique une migration partielle. Ensemble, nos résultats appuieraient une hypothèse plurifactorielle, soit un compromis dynamique entre un avantage bioénergétique, des possibilités d'alimentation et la menace de prédation. [Traduit par la Rédaction]

Introduction

Diel vertical migrations (DVMs) are common among a range of aquatic organisms (Blaxter 1974; Lampert 1989). DVM research has focused on pelagic organisms such as zooplankton (Loose and Dawidowicz 1994; Hays 2003), zooplanktivorous fishes (Clark and Levy 1988; Scheuerell and Schindler 2003), and pelagic piscivores (Stockwell et al. 2010). Benthic species can also perform DVM between shallow water at night and deeper water during the day (Sims et al. 2006; Gorman et al. 2012), but the DVM of adult freshwater benthic species has received little attention in the DVM literature.

The proximate cause of DVMs is generally accepted to be the change in light conditions during light–dark cycles (Mehner 2012). In pelagic organisms, the ultimate function of DVM is thought to be a combination of bioenergetic gain, predation avoidance, foraging opportunity optimization, and multifactor explanations. However, with the exception of Sims et al.'s (2006) study of the function of DVM in benthic sharks, the function of DVMs in adult benthic organisms has rarely been studied.

The decision to migrate among habitats can be seen as an attempt to optimize the mortality rate to foraging gain ratio (μ/f) (Werner and Gilliam 1984; Gilliam and Fraser 1987). Interspecific,

Received 25 March 2013. Accepted 30 July 2013.

Paper handled by Associate Editor Keith Tierney.

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interpopulation, and within-individual dimorphism in migration tactics have long been observed in ecology. With the advent of new technologies that allow the tracking of individuals, these “partial migrations” are now recognised as being the norm (Chapman et al. 2012b). DVMs are no exception and the term “partial DVM” has recently been used to describe DVMs that include <100% of the population (Mehner and Kasprzak 2011).

Bioenergetic theory suggests DVM is driven by fitness gains associated with foraging in warmer water at night and digesting in cooler, deeper waters during the day (Brett 1971; Sims et al. 2006; Busch et al. 2011). Under a bioenergetics scenario, DVMs cease during periods when no thermal advantage is apparent (Sims et al. 2006). While DVMs driven solely by bioenergetics have been described in benthic sharks (Sims et al. 2006), no similar empirical evidence has been provided for freshwater species.

Predation avoidance DVM theories (Scheuerell and Schindler 2003; Hrabik et al. 2006) suggest movement occurs in response to predator threat (Busch et al. 2011). Because prey size is limited by predator gape size, in the absence of direct observation of predation, predation-driven DVMs may be identified by body size-related differences in migration behaviour, such as size-structured depth distributions (Busch and Mehner 2012). Similarly, where DVMs are identified as partial migrations (Mehner and Kasprzak 2011; Busch and Mehner 2012), size-related differences in the probability of migration among individuals have been shown to reflect size-related differences in predation risk (Busch et al. 2011).

Feeding opportunity optimization DVM strategies, where predator migrations reflect prey migration, have been described among zooplankton (Levy 1990) and fishes (Janssen and Brandt 1980). In the absence of prey data, activity rates can provide a useful surrogate for analysing foraging opportunity (Andrews et al. 2009). For example, elevated activity rates have been linked to increased foraging in brook trout, *Salvelinus fontinalis* (Boisclair and Leggett 1989; Boisclair 1992).

Multifactor DVM explanations, where DVMs are a function of a combination of factors, are increasingly being recognised for their ability to explain DVM better than simplistic single-factor hypotheses (Stockwell and Johnson 1999; Mehner 2012). The most common multifactor explanation is the “anti-predation window” strategy (Clark and Levy 1988), where differences in the visual ranges of predators and prey allow animals to remain undetected by predators while foraging in the upper water column at night (Scheuerell and Schindler 2003).

As a benthic fish (Stapanian et al. 2010), burbot (*Lota lota*) provide an interesting model species in which to explore the function of DVM outside the traditional pelagic organism focus. Burbot have been shown to exhibit DVM during larval and juvenile stages (Donner and Eckmann 2011) and are thought to perform DVM as adults. However, empirical evidence of adult burbot DVM is limited to a study by Yule et al. (2008), who noted a nightly increase in burbot biomass in shallower water, and two telemetry studies that anecdotally observed an adult burbot DVM (Bergersen et al. 1993; Carl 1995). Given that lentic burbot are known to be benthic (Fischer 2000a, 2000b) and are often found in profundal or littoral habitats (Fischer 1999; McPhail and Paragamian 2000), it seems likely that they follow basin topography during DVM, rather than migrating through the water column. Burbot are a top piscivore (Cott et al. 2011), with fish forming 60% to 99% of the adult diet (Rudstam et al. 1995; Fratt et al. 1997; Mittelbach and Persson 1998). Burbot are also nocturnal (Müller 1973; Kavaliers 1980; Fischer 2000a), slow-swimming animals (Jones et al. 1974) and possess a highly developed olfactory system (Brown 1982; Hinkens and Cochran 1988).

In this study, we utilised acoustic telemetry over a 2-year period to monitor the depth and thermal experience of 47 adult burbot in Kinbasket Reservoir, British Columbia, Canada. We investigated the influence of season, diel period, and body size on the depth distribution, vertical activity, probability of migration, and ther-

mal experience. We tested the hypothesis that burbot depth distribution and activity differ between day and night, and investigated whether DVMs were consistently performed by all individuals. We then explored burbot DVM in the context of a number of possible explanatory hypotheses, including bioenergetics, thermal experience, antipredation response, foraging opportunity optimization, and multifactor explanations.

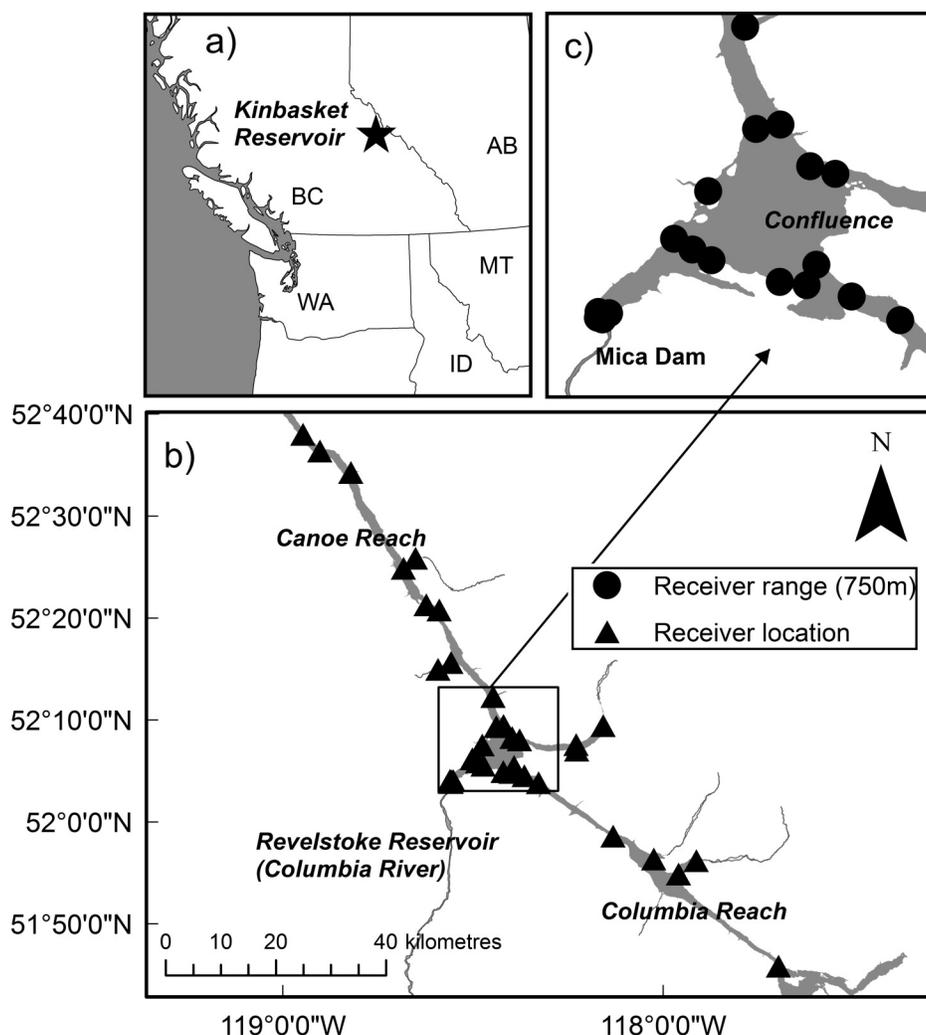
Materials and methods

Data for the study were collected from May 2010 to May 2012 in Kinbasket Reservoir, a deep (~190 m maximum depth, 57 m average depth), steep-sided, oligotrophic, 410 km² hydroelectric storage reservoir (Bray 2011). The reservoir is situated 147 km north of Revelstoke, British Columbia, Canada (52°08'N, 118°27'W; Fig. 1). The reservoir was formed by the construction of the Mica Hydroelectric Dam in 1973 and resulted in the impoundment of the Columbia and Canoe reaches of the upper Columbia River system. Kinbasket Reservoir is characterized by a drawdown routine where water levels typically vary up to 30 m seasonally. Dissolved oxygen concentrations have been shown to be consistently >80% saturated throughout the reservoir (Bray 2011). Typically, a broad thermocline with no surface mixing layer begins to be observed in spring. In May 2010, the broad thermocline extended from the surface to 15 m, with surface waters varying between 2 and 13 °C. Over the summer this broad thermocline increased to a maximum depth of 64 m in July, when surface temperatures reached ~15 °C (Bray 2011). Large-bodied predators confirmed to occur in the reservoir include burbot, bull trout (*Salvelinus confluentus*), rainbow trout (*Oncorhynchus mykiss*), and northern pikeminnow (*Ptychocheilus oregonensis*) (Westslope 2005). The pelagic fish community is dominated by kokanee, *Oncorhynchus nerka*, with a recent survey suggesting a density of 600 kokanee per hectare in the confluence region of the reservoir (Sebastian and Johner 2011). Other species confirmed to occur in the reservoir include mountain whitefish (*Prosopium williamsoni*), longnose sucker (*Catostomus catostomus*), large-scale sucker (*Catostomus macrocheilus*), redside shiner (*Richardsonius balteatus*), and slimy sculpin (*Cottus cognatus*) (Westslope 2005).

Burbot capture and tagging procedure

Burbot were captured using baited cod traps following methods described by Spence (2000). To avoid barotrauma, decompression procedures were carried out as described by Neufeld and Spence (2004). A spring capture period (April–May) was chosen to coincide with low water temperatures (~2 °C), which have been shown to reduce capture stress and maximize capture rates (Bernard et al. 1991). Minimum size for tagging (300 g) was established by using the 2% tag mass in water rule (Brown et al. 1999). Captured burbot were anaesthetised in a 90 ppm clove oil bath. Following loss of equilibrium, fish were measured to the nearest millimetre. Seventy-five burbot (50 in 2010 and 25 in 2011) were surgically implanted with pressure- and temperature-sensing acoustic transmitters (VEMCO V13TP-1L, 45 mm × 13 mm, 6 g in water, signal transmission rate 60–180 s, average 120 s, expected battery life 1028 days, VEMCO, Halifax, Nova Scotia, Canada). Surgical methods were as described by Cooke and Schreer (2003) and Wagner et al. (2009), with 20 mm incisions made approximately 30–50 mm anterior to the vent, slightly offset from the midventral line. The postspawn timing of the sampling period generally precluded sexing of fish. Throughout the surgery, recirculating lake water was applied to the gills. Incisions were closed using 3/0 monofilament absorbable sutures (PDS II, Ethicon Inc., Somerville, New Jersey). The entire surgical procedure took <5 min and fish were released once they regained equilibrium, or recompressed at depth ($n = 13$, 22.6%) if showing any significant signs of barotrauma (Neufeld and Spence 2004).

Fig. 1. (a) Kinbasket Reservoir location. (b) Map of the study site, Kinbasket Reservoir, British Columbia, showing the location (triangles) of receivers where burbot were detected. (c) The confluence region (where >95% of burbot detections occurred), featuring 750 m receiver ranges (circles).



Telemetry array

Forty-two independent omnidirectional hydrophone acoustic telemetry receivers (VR2W, VEMCO, Halifax, Nova Scotia, Canada) were deployed throughout the reservoir in the spring of 2010. Receivers were situated throughout the reservoir to ensure an adequate, representative sample of habitats (Fig. 1). Average receiver range was ~750 m radius, yielding acoustic coverage of approximately 8% (35 km²) of the reservoir (Fig. 1). Receivers were deployed at minimum reservoir drawdown in late April 2010; they were moored using three sandbags as anchors, tied to polypropylene rope, positioned at approximately one-third of the depth using cable ties and electrical tape, and tied to partially submerged marker buoys, following the methods described by Roscoe et al. (2010). This enabled us to minimize disturbance from recreational reservoir users and provide for easy retrieval. Receivers were retrieved and data were downloaded in the spring of 2011 and 2012. In 2011, all 42 receivers were retrieved, but in 2012, only 37 receivers were successfully retrieved, as lowered water levels and shifting ice prevented access to five remote receiver locations. This presence-absence telemetry array does not allow for triangulation of position and therefore while we can detect fish depth, we cannot determine the position of fish in relation to the lake bottom. However, given that burbot are well known to be benthic (Fischer 2000a, 2000b), we expect that depth detections likely reflect benthic behaviour.

Statistical analyses

Depth detection time-series plots were used to eliminate from the data set fish that appeared to have either shed their tag or died after surgery. Accordingly, minimum criteria for individual fish inclusion in statistical analyses were a 3 month detection span and a minimum of 1000 detections per fish. To eliminate code collisions or incomplete code transmissions, and to ensure an adequate sampling period, a preanalysis filtration included a minimum criterion of 10 detections per diel period. To ensure that behaviour was not affected by surgery, detections within 14 days of surgery (a conservative period) were removed from the analysis (Rogers and White 2007).

Model details

Model 1 was fitted with a response variable of depth (mean depth per diel period, minimum of 10 detections, in metres) and fixed effects of diel period, season, year, and total length.

Model 2 was fitted with a response variable of rate of vertical movement (ROVM, i.e., the sum of the absolute change in depth divided by the detection duration, per diel period in metres per hour, again with a minimum of 10 detections per diel period) and fixed effects of diel period, season, and year.

Model 3 was fitted with a response variable of temperature experience (mean temperature per diel period derived from a

minimum of 10 detections in degrees Celsius) and fixed effects of diel period, season, and year.

Model 4 was fitted with a response variable of probability of migration (binary response variable for DVM occurrence, where DVM was deemed to have definitely not occurred when mean nightly depths were <1 m shallower than mean daytime depths in a given 24 h period) and fixed effects of diel period, season, year, and total length.

In all four models, the random intercept was represented by individual burbot. Models 1–3 were fitted using linear mixed effects (LMM) methods and Model 4 was fitted using generalized linear mixed effects (GLMM) methods. The fixed effects terms were defined by the following: season, identified by Paragamian and Wakkinen (2008) as biologically relevant to burbot (i.e., prespawn and spawn (November to January), postspawn (February to April), and summer (May to October)); diel period (day and night), derived from the time between sunset and sunrise at 52°8'N, 118°28'W; year (year 1, April 2010 to May 2011 and year 2, May 2011 to May 2012); and total length (cm), which was centred to facilitate model convergence. All four models (prior to backward selection) included all possible two-way and three-way interaction terms.

Temporal autocorrelation was assessed using ACF plots of residuals (Pinheiro and Bates 2000; Zuur et al. 2009). In the LMMs, temporal autocorrelation was accounted for using autoregressive moving-average (function corARMA in R) correlation structures, which allow combinations of autoregressive (AR) and moving-average (MA) components, with the model order represented by p and q , respectively. Temporal sequences were constructed that allowed a lag of 1 (at order 1) to represent the correlation between one diel period and the next. The autoregressive component uses a linear regressing coefficient at order p , and the moving-average component uses an unweighted moving-average coefficient at order q (Pinheiro and Bates 2000; Zuur et al. 2009). The optimum correlation model structures were chosen based on AIC and ACF plotting of residuals (Zuur et al. 2009). The optimum structure identified had p and q order values defined as Model 1 ($p = 1, q = 1$), Model 2 ($p = 1, q = 1$), and Model 3 ($p = 0, q = 3$). For our probability of migration model (Model 4), a compound symmetry correlation structure was applied that assumed a uniform correlation between observations. All analyses were carried out in R-15.0 (R Development Core Team 2012), and the nlme package version 3.1-100 (Pinheiro and Bates 2000; Pinheiro et al. 2012) and lme4 R package version 0.999375-42 (Bates et al. 2011) were used to fit LMMs and GLMMs, respectively.

Backward selection was performed using marginal conditional F tests for LMMs (Zuur et al. 2009) and log-likelihood ratio tests for GLMMs (Zuur et al. 2009). Normality assumptions for LMMs were checked graphically using Q-Q plots and histograms of standardized residuals (Zuur et al. 2009). Where significant deviations from normality occurred, as in our depth model and the ROVM model, cube root and inverse hyperbolic transformations (Burbidge et al. 1988) were used, respectively. Where heteroscedasticity was detected in graphical residual analyses, different variances for each level of a categorical fixed effect were accounted for in the model using the varIdent variance structure available in package nlme (Zuur et al. 2009).

Post hoc multiple comparisons tests were applied using the Tukey method using the multcomp package version 1.2-13 for R (Bretz et al. 2010). Model predictions and standard errors for plotting were derived using the predict. SE function from the AICcmodavg package version 1.24 for R (Mazerolle 2011). For plotting, our continuous variable total length was predicted at the 0.25, 0.5, and 0.75 quantile values (51.2, 54.4, and 61.0 cm total length, respectively).

The hypothesis that burbot depth distribution and activity differ between day and night was tested by post hoc comparison of response variables between day and night from our depth model (Model 1) and ROVM (Model 2) models, respectively. Partial migra-

tion was investigated using the probability of migration model (Model 4). The bioenergetic efficiency strategy explanation was explored using post hoc comparisons of mean thermal experience between night and day from the temperature model (Model 3), with the expectation that under a solely bioenergetic DVM scenario, DVM would occur only during seasons when a clear difference in body temperature between diel periods was observed. Furthermore, we would expect that if nightly thermal experience means were found to be different than daytime means, this would indicate the presence of a possible bioenergetic advantage (Sims et al. 2006; Andrews et al. 2009). Evidence of a predation avoidance DVM was explored using a post hoc comparison of the slopes of higher-order interactions involving total length from our depth model (Model 1) and with log-likelihood ratio tests on the inclusion of our total length variable in our probability of DVM model (Model 2). Observation of a pattern of size structure in nighttime depth distribution or migration probability would be expected to be indirect evidence of predation avoidance (Busch et al. 2011). The foraging optimization strategy DVM explanation was explored using post hoc comparison of daytime and nighttime activity rates from our ROVM model (Model 2), with the expectation that increased nighttime activity might reflect increased foraging activity in a nocturnal predator. The multifactor DVM explanation was investigated with the expectation that we would find partial support for more than one previous DVM explanation.

Results

Of the 75 adult burbot tagged over 2 years (50 in year 1 and 25 in year 2), 47 different burbot (30 in year 1 and 27 in year 2) met the minimum detection criteria for use in statistical analyses. Accordingly, 930 282 postfilter burbot sensor detections were recorded, comprising 481 337 depth detections and 448 945 temperature detections. Burbot were detected at 37 of our 42 receivers (Fig. 1). More than 95% of detections were recorded at receivers in the confluence area (Fig. 1a). Detections were recorded between 29 April 2010 and 26 April 2012 (i.e., over a period of 727 days). Total length of tagged burbot ranged from 44.8 to 74.1 cm. Observed postsurgical mortality was limited to one individual (0.75%).

Depth (Model 1)

A total of 7893 mean depth (per diel period per fish) response variable observations were calculated from a total of 481 337 postfilter depth detections. Overall mean depth \pm SE was 37.09 ± 1.30 m during the day and 25.9 ± 1.52 m at night. A variety of DVM amplitudes and behaviours were observed; four individual burbot DVM behaviours are shown in Fig. 2. In the reduced depth model, significant effects were found for the season \times diel period \times year and the season \times diel period \times total length interactions (see Table 1 for full model details). A strong DVM pattern was found, with burbot occupying significantly shallower depths at night than during the day in all seasons and years (Tukey's test, all $P < 0.01$, Fig. 3). Back-transformed model predictions at median total length (54.4 cm) revealed DVM amplitudes of 6.7–8.7 m, 6.1–10.6 m, and 7.3–13.1 m for summer, prespawn and spawn, and postspawn seasons, respectively, in years 1 and 2 (Fig. 3). Significant effects were found for the season \times diel period \times total length interaction ($F = 12.44, P < 0.01$; Table 1). Post hoc testing revealed no significant relationship between burbot size and burbot depth distribution during the day in all seasons (Fig. 4, all $P > 0.05$). However, during the nighttime, a significant effect of body size was found (see Fig. 4), with larger burbot occupying significantly shallower depths than smaller burbot in the prespawn and spawning period ($Z = -3.27, P = 0.01$) and in the summer ($Z = 0.04, P = 0.04$). No body size effect was found during the postspawn nighttime period ($Z = 2.09, P = 0.15$).

Table 1. Model 1. Higher-order linear mixed-effects model estimates of cube-root-transformed burbot depth occupation (m), showing parameter significance based on conditional *F* tests (ndf, numerator degrees of freedom; ddf, denominator degrees of freedom), and fixed effect level estimates with standard errors (SE), degrees of freedom (df), and *t* and *P* values based on Wald *t* tests.

Parameter (conditional <i>F</i> test)	Fixed effect levels	Estimate	SE	df	<i>t</i>	<i>P</i>
Season × Diel period × Year (ndf = 2, ddf = 7828, <i>F</i> = 49.85, <i>P</i> < 0.0001)	Prespawn and spawn × Night × Year 2	-0.369	0.038	7829	-9.765	<0.01
	Summer × Night × Year 2	-0.141	0.031	7829	-4.523	<0.01
Season × Diel period × Total Length (ndf = 1, ddf = 7828, <i>F</i> = 12.44, <i>P</i> < 0.0001)	Prespawn and spawn × Night × Total Length	-0.016	0.003	7829	-4.942	<0.01
	Summer × Night × Total Length	-0.008	0.003	7829	-2.854	<0.01

Note: Standard deviations of random effects (fish ID) variance: intercept = 0.14, residual = 0.62. Autoregressive correlation estimate at parameter 1 = 0.81, moving-average correlation estimate at parameter 1 = -0.64.

Fig. 2. An example of raw depth detection data from four burbot during a week in March 2011, with nighttime periods in grey and daytime periods in white.

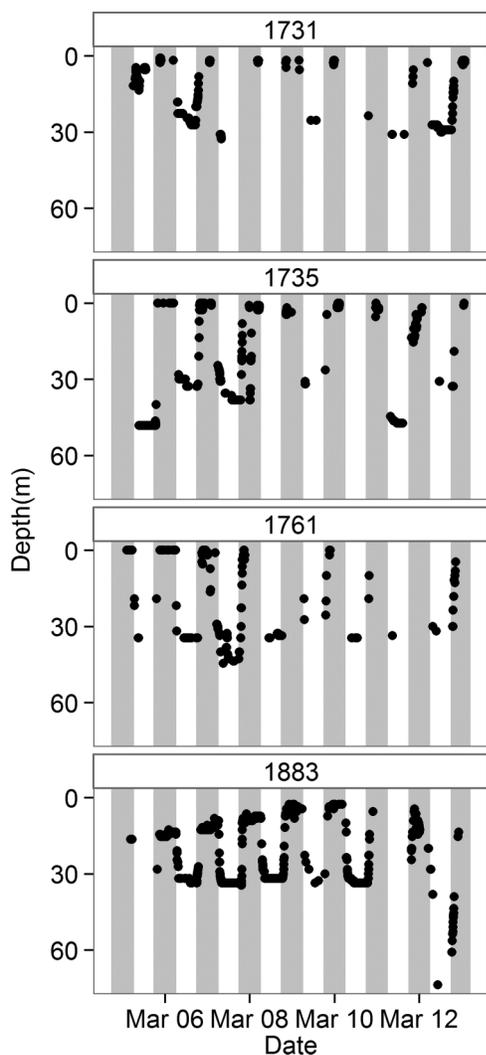


Fig. 3. Model 1. Back-transformed reduced linear mixed model burbot depth (m) estimates for median total length (54.4 cm). Open circles represent daytime depth occupation, and closed circles represent nighttime depth occupation. Error bars represent standard errors. Significant differences between diel periods were found for all season and year combinations (Tukey's test, all *P* < 0.05).

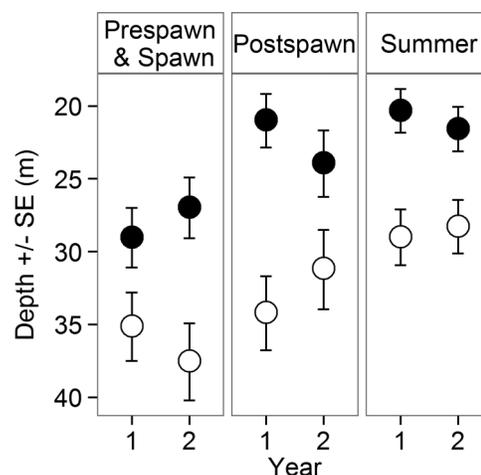
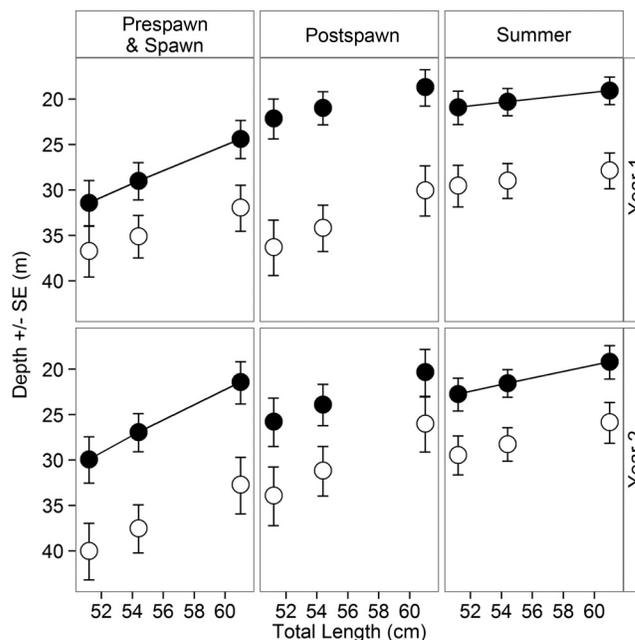


Fig. 4. Model 1. Back-transformed reduced linear mixed model burbot depth (m) estimates at 0.25, 0.5, and 0.75 quantiles of total length among seasons and years. Error bars represent standard errors. Solid lines represent slopes identified as significant (all *P* < 0.05).



Rate of vertical movement (Model 2)

The ROVM model was constructed using 7893 ROVM (per diel period per fish) response variable observations calculated from 481 337 postfilter depth detections. Mean ROVM ± SE was observed to be 4.27 ± 0.34 m·h⁻¹ during the day and 6.58 ± 0.44 m·h⁻¹ at night. In the reduced model, significant effects were observed for the season × diel period × year interaction (Table 2). A clear nightly pattern of vertical movement was found, with burbot being significantly more vertically active at night than during the day in all year and season combinations (Fig. 5; Tukey's test, all *P* < 0.05), except in year 1 during the prespawn and spawning

Table 2. Model 2. Higher-order reduced linear mixed-effects model estimates of inverse hyperbolic sine-transformed burbot rate of vertical movement ($\text{m}\cdot\text{h}^{-1}$), showing parameter significance based on conditional F tests (ndf, numerator degrees of freedom; ddf, denominator degrees of freedom), and fixed effect level estimates with standard errors (SE), degrees of freedom (df), and t and P values based on Wald t tests.

Parameter (conditional F test)	Fixed effect levels	Estimate	SE	df	t	P
Season \times Diel period \times Year (ndf = 2, ddf = 7489, $F = 23.16$, $P < 0.0001$)	Prespawn and spawn \times Night \times Year 2	0.83	0.12	7489	6.79	<0.01
	Summer \times Night \times Year 2	0.40	0.10	7489	3.93	<0.01

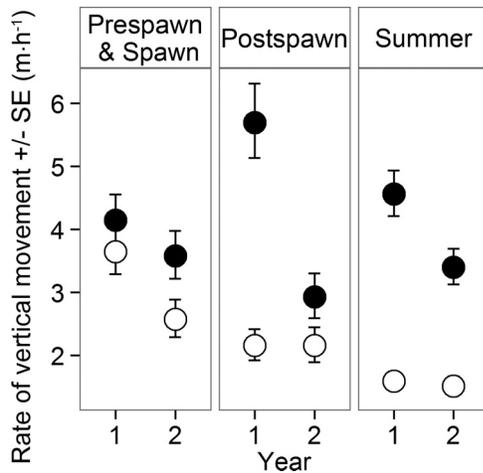
Note: Standard deviations of random effects (fish ID) variance: intercept = 0.32, residual = 0.95. Autoregressive correlation estimate at parameter 1 = 0.86, moving-average correlation estimate at parameter 1 = -0.83.

Table 3. Model 3. Higher-order reduced linear mixed model estimates of burbot thermal experience occupancy ($^{\circ}\text{C}$), showing parameter significance based on marginal conditional F tests (ndf, numerator degrees of freedom; ddf, denominator degrees of freedom), and fixed effect level estimates with standard errors (SE), degrees of freedom (df), and t and P values based on Wald t tests.

Parameter (conditional F test)	Fixed effect levels	Estimate	SE	df	t	P
Season \times Diel period \times Year (ndf = 2, ddf = 7510, $F = 26.99$, $P < 0.0001$)	Prespawn and spawn \times Night \times Year 2	-0.26	0.1	7510	-2.61	<0.01
	Summer \times Night \times Year 2	-0.61	0.08	7510	-7.15	<0.01

Note: Standard deviations of random effects (fish ID) variance: intercept = 0.92, residual = 2.52. Seasonal variance structure parameter estimates: summer = 1.00, prespawn and spawn = 0.68, postspawn = 0.23. Moving-average correlation estimate at parameter 1 = 0.78, parameter 2 = 0.94, parameter 3 = 0.38.

Fig. 5. Model 2. Back-transformed reduced linear mixed effects model estimates of burbot rate of vertical movement ($\text{m}\cdot\text{h}^{-1}$). Open circles represent day, and closed circles represent night. Error bars represent standard errors of predictions. Significant differences between day and night were found in all season and year combinations (Tukey's test, all $P < 0.05$) except during the prespawn and spawn season in year 1.

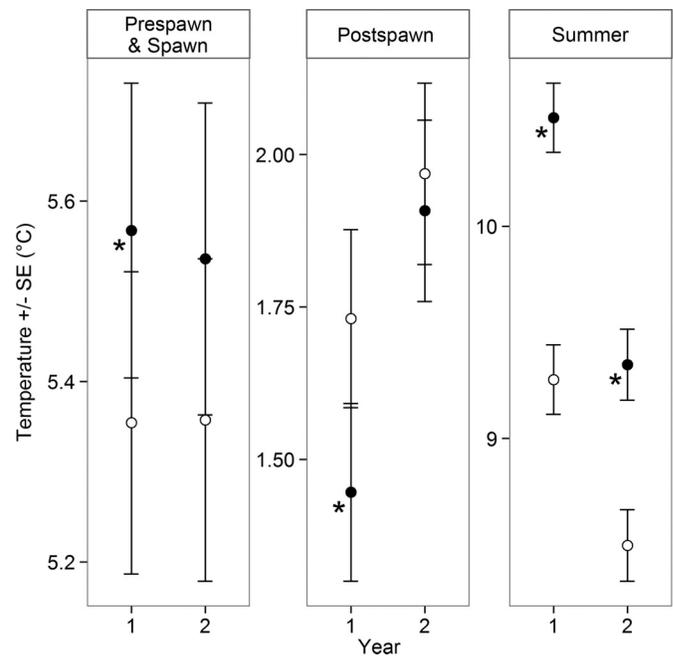


period. Summer daytime vertical activity rates were found to be significantly lower in both years when compared with all other seasons (Tukey's test, all $P < 0.5$).

Temperature experience (Model 3)

The thermal experience model was produced using 7567 mean temperature experience (per diel period per fish) response variable observations calculated from 448 945 postfilter raw detections. Observed seasonal temperature experience means \pm SE (for day and night, respectively) were as follows: summer, 8.32 ± 0.29 $^{\circ}\text{C}$ and 10.00 ± 0.30 $^{\circ}\text{C}$; prespawn and spawn, 5.44 ± 0.20 $^{\circ}\text{C}$ and 5.86 ± 0.23 $^{\circ}\text{C}$; and postspawn, 1.80 ± 0.08 $^{\circ}\text{C}$ and 1.78 ± 0.09 $^{\circ}\text{C}$. In the reduced model, significant effects of the season \times diel period \times year interaction were found (see Table 3). In the summer period, burbot consistently experienced warmer water at night than during the day in year 1 (Tukey's test, estimate = +1.2 $^{\circ}\text{C}$, $Z = 22.17$, $P < 0.01$) and in year 2 (Tukey's test, estimate = +0.9 $^{\circ}\text{C}$, $Z = 15.46$, $P < 0.01$). No consistent pattern of thermal experience was detected in the prespawn and spawn period or the postspawn period across the two years. In the prespawn and spawn period, burbot used significantly warmer water at night in year 1 (Tukey's

Fig. 6. Model 3. Reduced linear mixed model estimates of burbot thermal experience ($^{\circ}\text{C}$). Open circles represent daytime and closed circles represent nighttime. Error bars represent standard errors. Asterisks indicate significant differences between night and day within season and year (Tukey's test, all $P < 0.05$).



test, estimate = +0.21 $^{\circ}\text{C}$, $Z = 3.6$, $P < 0.01$), and no difference in diel thermal experience was seen in year 2. In the postspawn period, burbot were found to be experiencing significantly cooler water at night in year 1 (Tukey's test, estimate -0.29 $^{\circ}\text{C}$, $Z = -12.75$, $P \leq 0.01$), although there were no significant differences in year 2 (Tukey's test, estimate = -0.06 $^{\circ}\text{C}$, $Z = -2.51$, $P = 0.07$, see Fig. 6).

Probability of migration (Model 4)

Our model was constructed using 2888 binary observations, where individuals were detected during both diel periods in a 24 h cycle starting at sunrise. Burbot were observed to migrate on 2121 occasions (73% of the time). Migration was observed in all individuals, with the proportion of days when migration was observed ranging from 20% to 100%. Burbot body size and sampling year and all associated interactions were not found to significantly influence the probability of DVM and were removed from

Table 4. Model 4. Reduced binomial generalized linear model estimates of DVM probability, showing Z value and associated P value based on χ^2 test.

Parameter	Fixed effect levels	Estimate (logit)	SE	Z	P
Season	Postspawn (intercept)	0.66	0.19	3.45	<0.01
	Prespawn and spawn	0.32	0.16	2.01	0.04
	Summer	0.35	0.13	2.63	<0.01

Note: Standard deviations of random effects (fish ID) variance: intercept = 1.01.

the reduced model (log-likelihood ratio test, all $P > 0.05$). In the reduced model, only season was found to significantly influence the probability of migration (log-likelihood ratio test, $P = 0.02$, see Table 4). Post hoc multiple comparison showed the probability of migration differed significantly only between the postspawn period and summer, with the probability of migration in the summer being 7% higher than during the postspawn period (Tukey's test, $Z = 2.63$, $P = 0.02$).

Discussion

Data from this study provide support for the hypothesis that adult burbot depth distribution and activity differ at a diel scale, with burbot displaying a clear pattern of DVM and nocturnal activity. Furthermore, while we observed DVM behaviour in all individuals at times throughout our study period, our observations of resident behaviours and within-individual plasticity in migration strategy suggest a partial migration pattern. While we showed that thermal experience coupled with diel activity shifts was consistent with a bioenergetics efficiency DVM strategy for at least 6 months a year (May–October), the continuation of DVM throughout seasons when no difference in thermal experience between diel periods was observed (November to April) indicates the bioenergetic efficiency strategy alone cannot fully explain DVM. Our observations of size-structured depth distribution in the summer and the prespawn and spawning period provide indirect evidence that predation threat may play a part in modulating DVM behaviour among smaller individuals on a seasonal basis. In addition, our observations of significantly lowered daytime activity are consistent with the sedentary daytime behaviour reported in the burbot literature (Paragamian et al. 2005; Paragamian and Wakkinen 2008). This may in part represent a predation avoidance mechanism for a slow-swimming, nocturnal benthic animal and likely amplifies any bioenergetic gains. However, the evidence of migration of larger individuals suggests predation avoidance alone does not fully explain DVM behaviour. Adult burbot nocturnal activity and feeding combined with daytime sedentary behaviour and a reluctance to feed are well documented (Müller 1978; Kavaliers 1980; Fischer 2004). We therefore suggest that the most likely explanation for elevated nighttime activity is an increase in foraging activity, consistent with the feeding opportunity optimization hypothesis. In light of the partial support for all three hypotheses and our observations of resident behaviours and within-individual plasticity in migration strategy not being completely explained by any one of our models, we conclude that a multifactor hypothesis is the best explanation for DVM in adult burbot. The decision to migrate, therefore, may be a dynamic strategy, reappraised on a daily basis.

The detection of a distinct diel pattern of depth distribution provides empirical evidence of adult burbot DVM and confirms several earlier preliminary investigations (i.e., Bergersen et al. 1993; Carl 1995). As noted in our Materials and methods section, our data set does not allow us to compute depth in relation to the lake bottom; however, given that burbot are well known to exhibit strongly benthic behaviours (Fischer 2000a, 2000b), we believe burbot remain benthic and follow basin topography during migration, rather than migrating through the water column.

Our data indicate that DVM coincides with the use of warmer water at night and cooler water during the day throughout the summer season. While the temperature gradient observed was modest (1.2 and 0.9 °C in years 1 and 2, respectively), Sims et al. (2006) demonstrated bioenergetic gains of up to 4% with a similar gradient (0.4 and 0.9 °C). Indeed, this pattern of thermal experience, when coupled with our evidence of elevated nighttime activity and daytime sedentary behaviour, seems to suggest a “hunt warm, rest cool” strategy (Sims et al. 2006), consistent with a bioenergetic advantage for at least 6 months a year. Our observation of a slightly increased probability of migration during the summer season when compared with the postspawn season, where no thermal advantage was detected in both years, also indicates bioenergetic advantage may influence the decision to migrate. DVM as a strategy for bioenergetic efficiency gain has been described in juvenile burbot (Donner and Eckmann 2011) and marine predators (Sims et al. 2006). Nevertheless, the absence of a temporally consistent diel pattern of thermal experience and the continuation of DVM through the postspawn period, when no diel difference in thermal experience was apparent, suggests selection of thermal experience for bioenergetic advantage does not fully explain adult burbot DVM.

Predator avoidance has been suggested as a possible ultimate function of DVM in a number of freshwater species (Scheuerell and Schindler 2003; Hrabik et al. 2006). Our detection of a nighttime size-structured depth distribution during the prespawn and spawn period and the summer suggests predation avoidance may play a part in modulating depth distributions during these periods. Accordingly, an optimization of the μ/f ratio for smaller burbot may be achieved through a more risk-averse strategy of deeper depth distribution during nightly migrations in the summer and the prespawn and spawn period. In contrast, predation risk for larger individuals during the migration is expected to be negligible and thus foraging may occur without constraint.

While the observed size-structured depth distribution could also be indicative of prey size distribution, we consider predation or cannibalism risk to be the more likely explanation, given the large size of burbot and other predators in the system. While burbot tagged in the present study had a maximum length of 74.0 cm and a median length of 54.4 cm, our trapping method may be downward size selective because in this system we have captured burbot up to 101.0 cm long, with four fish over 100 cm (P.M. Harrison and L.F.G. Gutowsky, unpublished data). Furthermore, a 2010 sturgeon set-line study on the reservoir recorded an incidental catch of 297 burbot with a maximum total length of 103.0 cm and an average length of 72.2 cm (Prince 2011). If, in the absence of a burbot-specific equation to predict maximum prey length, we apply Damsgard's (1995) widely used model (see Stockwell et al. 2010 for an application example) to predict prey size vulnerabilities, where maximum prey length (cm) = $0.535 \times$ predator length (cm) – 0.487, then a burbot of 1010 mm would be capable of preying on burbot up to 530 mm. Of our 47 tagged burbot, 18 were less than 530 mm. Burbot have a relatively large mouth to total length ratio (Scott and Crossman 1973) and consequently Damsgard's Arctic char (*Salvelinus alpinus*) predator based model may underestimate prey size for burbot predators. Furthermore, body depth is often a better predictor of maximum prey size than total length (see Nilsson and Bronmark 2000). Given that Damsgard's equation is based on fusiform prey (Arctic char) and burbot are an elongate species (Scott and Crossman 1973), we expect this equation to also underestimate maximum length of burbot as prey. In addition, we suspect that unsuccessful predation attacks, which likely occur above the maximum prey size thresholds, also play a part in modulating antipredation response. Indeed, Damsgard (1995) makes this point explicitly: “it is however important to stress that the existence of prey size refuges does not necessarily mean that predation is unimportant as a regulatory factor”. In light of the above evidence, and evidence of burbot cannibalism in the liter-

ature (Schram et al. 2006), we believe that intraspecific predation may indeed be playing a role in the size-structured depth distribution we observed.

Bull trout are also large-bodied (maximum size in the reservoir of 88.1 cm; Gutowsky et al. 2011; Nitychoruk et al. 2013), aggressive predators that perform a clear pattern of DVM in this system (Gutowsky et al. 2013). Again, using Damsgard's (1995) equation, the largest bull trout is capable of consuming burbot up to 46.6 cm long. Four of our 47 tagged burbot were less than 46.6 cm and 28 were within 10 cm of this size. Furthermore, in a concurrent bull trout study in this system (Gutowsky et al. 2013), we witnessed a cannibalism attempt on a 56.0 cm angled bull trout (L.F.G. Gutowsky and P.M. Harrison, personal observation). As stated above, we expect Damsgard's equation to underestimate length for burbot as prey, and as a consequence, interspecific predation seems, although to a lesser degree than cannibalism, a likely possibility in this system.

Our detection of an elevated nightly activity provides empirical evidence of adult burbot nocturnal behaviour and confirms the lab-based observations of Müller (1973), Kavaliers (1980), and Pääkkönen et al. (2000). We suspect the failure to detect nocturnal behaviour in the prespawn and spawn period in year 1 is an artifact of the lower sample sizes within receiver range during this period (year 1, $n = 23$ and year 2, $n = 20$). Elevated activity rates have been linked to increased foraging in brook trout (Boisclair 1992), and a linear relationship between activity and foraging is an assumption integral to many bioenergetics models (Boisclair and Leggett 1989). Therefore, the elevated nocturnal activity rates we found may in part reflect increased foraging activity at night and suggest foraging opportunity optimization may be playing a part in the upwards migration. While elevated nightly vertical activity and much reduced daytime activity could also indicate a diel diet shift, we could find no burbot literature to support this hypothesis. In contrast, adult burbot are well known to exhibit strongly nocturnal behaviours (Kavaliers 1980), showing daytime sedentary behaviours accompanied by a reluctance to feed during the day (Fischer 2000a, 2004). Burbot are top-level piscivores (Cott et al. 2011), and stomach content and stable isotope studies suggest that pelagic fish often form up to 100% of adult burbot diet; for example, Wagner (1972) found burbot diet consisted of 100% alewife (*Alosa pseudoharengus*) in Lake Michigan, and Schram et al. (2006) showed burbot stomachs in Lake Superior contained 64% *Coregonus* spp. and 17% *Osmerus mordax*. Black et al. (2003) showed that in a large Columbia River reservoir quite similar in size to our study site, burbot preyed almost exclusively on introduced kokanee and lake whitefish (*Coregonus clupeaformis*). Unfortunately we do not have site-specific burbot diet data. However, we suspect that kokanee, which are the most abundant pelagic fish in our study system (Sebastian and Johner 2011), may, along with other potential burbot forage fishes in this system such as mountain whitefish and slimy sculpin, provide a nightly foraging opportunity for adult burbot. Kokanee were distributed at between 10 and 35 m at night in August 2010 (Sebastian and Johner 2011) and perform a well-documented DVM in many systems (Levy 1990; Stockwell and Johnson 1999; Scheuerell and Schindler 2003), and therefore it seems likely that burbot would encounter kokanee during the DVM. Furthermore, our data suggest that burbot show a strong affinity for tributary mouth vicinities, as >50% of burbot detections were received at tributary mouth vicinities (P.M. Harrison, unpublished data), where burbot are likely to encounter staging kokanee. Burbot possess a highly developed olfactory system (Hinkens and Cochran 1988) and are known to show a strong preference for nocturnal feeding (Brown 1982; Fischer 2004). Therefore, migration into shallow water at night may provide a "window" of feeding opportunity where the nocturnal feeding burbot have an advantage over visual feeding prey such as kokanee or mountain whitefish. While feeding opportunity optimization may account for the occupation of shallower water at

night, reduced daytime activity rates, consistent with burbot's well-documented nocturnal behaviour, suggest daytime foraging was minimal. Consequently, we suggest that feeding opportunity optimization cannot fully explain adult burbot DVM, as it is likely not imparting a significant influence on the "decision" to emigrate to deeper waters during the day.

When foraging opportunity is minimal, optimization of the μ/f ratio may be achieved by a complete negation of predation threat. Fischer (2004) showed that for slow-swimming benthic species such as stone loach, *Barbatula barbatula*, minimal daytime activity and an occupation of predator-free habitat may be an important strategy for avoiding predation risk. Indeed, for slow-swimming animals such as burbot (Jones et al. 1974), which often display daytime sedentary behaviours (Carl 1995; Paragamian and Wakkinen 2008), daily emigration into the profundal zone may represent a complete negation of predation threat from co-occurring, fast-swimming visual feeders such as bull trout and rainbow trout.

Given the partial evidence for bioenergetic efficiency, predation avoidance, and feeding opportunity optimization strategies, we suggest that the DVM of adult burbot is most likely a dynamic multifactor strategy. Indeed, our data suggest that DVM behaviour may be a strategy whereby the μ/f ratio is optimized by multiple factors. Nightly migration into shallow water likely provides a "window" of feeding opportunity for a nocturnal animal adapted to feeding under low light conditions. Our data suggest this "window" may be seasonally modulated by predation risk in smaller individuals. Our data also indicate daytime occupation of deeper water, coupled with low activity rates, may provide a modest bioenergetic advantage for at least 6 months a year and may be an important strategy for predation avoidance. However, the emigration likely provides little improvement in foraging opportunity for a nocturnal feeding predator. Dynamic DVM ultimate hypotheses have been suggested for pelagic species and typically feature trade-offs between foraging opportunity and predation risk (Levy 1990; Scheuerell and Schindler 2003; Jensen et al. 2006). While multifactor DVM explanations that feature all three factors have been described for coregonids (Jensen et al. 2006) and juvenile burbot (Donner and Eckmann 2011), our data suggest that multifactor strategies may be more common among benthic adult fishes than previously thought.

Although DVM behaviour was observed in all individuals, the detection of a resident behaviour (27% of the time, on average) suggests that the DVM is a within-individual "partial DVM" or "partial migration" consistent with those described by Mehner and Kasprzak (2011) and Chapman et al. (2012a, 2012b). Our detection of weak correlations between migration probability and season and our failure to detect size-structured patterns of migration probability suggests that migration is not a "fixed" behaviour; instead, the "decision" to migrate may be reappraised on a daily basis. While our data do not provide a mechanistic explanation for the resident behaviour, we believe that trade-offs among foraging gain, bioenergetic gain, and predation risk likely play a role. Stomach fullness (satiation) has been identified as a major determinant in the decision to forage in fishes (Hart and Gill 1992; Strubbe and van Dijk 2002; Gill 2003) and has been indicated as playing a role in DVM in zooplankton (Pearre 2003). Indeed, for satiated fish, resident behaviour in deeper water would likely provide a bioenergetic advantage and minimize predation threat.

Our study provides empirical evidence of adult burbot DVM, nocturnal activity, and a partial migration pattern. Our results suggest that the nightly migration into shallow water may provide a foraging opportunity "window" for a nocturnal predator and this "window" may be constrained by predation threats to smaller individuals. For a nocturnal animal, the daily emigration into deeper water appears to provide little improvement in foraging opportunity, but it may be important for the minimization of predation threat in a slow-swimming benthic fish and may provide a bioenergetic advantage during the summer period. Taken

together, the evidence presented here suggests the observed DVM is a dynamic partial migration, whereby the μ/f ratio is optimized through a complex dynamic daily trade-off among feeding opportunity optimization, avoidance of predation, and bioenergetic gain.

Acknowledgements

We thank Jamie Tippe of Grizzly Country Marine, Juan Molina, Jayme Hills, Taylor Nettles, Glenn Crossin, Jeff Nitychoruk, Mark Taylor, and Sean Landsman for assistance in the field. Funding was provided by the Natural Sciences and Engineering Research Council of Canada (via NSERC HydroNet and a Collaborative Research and Development Grant and a discovery grant to MP), BC Hydro, and the Center for Expertise on Hydropower Impacts of Fish and Fish Habitat of Fisheries and Oceans Canada. We thank three anonymous reviewers whose comments helped to improve the document. SJC is supported by the Canada Research Chairs Program. Some of the telemetry infrastructure was provided by the Canada Foundation for Innovation and the Ontario Ministry of Research and Innovation. We also thank Paul Higgins and Karen Smokrowski for supporting the project.

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