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Partial diel migration: A facultative migration underpinned by long-term inter-individual variation

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Abstract

1. The variations in migration that comprise partial diel migrations, putatively occur entirely as a consequence of behavioural flexibility. However, seasonal partial migrations are increasingly recognised to be mediated by a combination of reversible plasticity in response to environmental variation and individual variation due to genetic and environmental effects.
2. Here, we test the hypothesis that while partial diel migration heterogeneity occurs primarily due to short-term within-individual flexibility in behaviour, long-term individual differences in migratory behaviour also underpin this migration variation.
3. Specifically, we use a hierarchical behavioural reaction norm approach to partition within- and among-individual variation in depth use and diel plasticity in depth use, across short- and long-term time-scales, in a group of 47 burbot (*Lota lota*) tagged with depth-sensing acoustic telemetry transmitters.
4. We found that within-individual variation at the among-dates-within-seasons and among-seasons scale, explained the dominant proportion of phenotypic variation. However, individuals also repeatedly differed in their expression of migration behaviour over the 2 year study duration.
5. These results reveal that diel migration variation occurs primarily due to short-term within-individual flexibility in depth use and diel migration behaviour. However, repeatable individual differences also played a key role in mediating partial diel migration.
6. These findings represent a significant advancement of our understanding of the mechanisms generating the important, yet poorly understood phenomena of partial diel migration. Moreover, given the pervasive occurrence of diel migrations across aquatic taxa, these findings indicate that individual differences have an important, yet previously unacknowledged role in structuring the temporal and vertical dynamics of aquatic ecosystems.

KEYWORDS
animal personality, behavioural reaction norms, diel migrations, hierarchical model, migration continuum, partial migration, telemetry

1 | INTRODUCTION

Partial migrations, where a proportion of a population performs alternative migratory tactics, are a pervasive phenomena among migrating animals (Chapman, Skov, et al., 2012). By facilitating a comparison of resident and migrant individuals, partial migrations provide a unique opportunity to improve our understanding of migration behaviour. Furthermore, the spatio-temporal variation in habitat occupancy that occurs as a function of partial migrations, has significant consequences for community and ecosystem dynamics (Chapman, Hulthén, et al., 2012). Accordingly, a determination of the repeatable or flexible nature of partial migrants, is a major, ongoing, goal for migration biology (Brodersen et al., 2014; Chapman et al., 2011; Dodson, Aubin-Horth, Thériault, & Páez, 2013). Diel migrations represent the largest and the most frequent discrete movement of biomass in the aquatic realm, and arguably, the dominant migration pattern on the planet (Mehner, 2012). Partial diel migration, a recently detected, poorly understood, diel form of partial migration, is hypothesised to be a widespread pattern among diel migrating organisms (Mehner & Kasprzak, 2011; Mehner & Magnan, 2015). Thus, the spatial and temporal variation in depth use associated with partial diel migration, has potentially large consequences for aquatic ecosystems. However, the underlying mechanisms generating this variation in diel migration behaviour are not well understood. Indeed, the individual-level data necessary to determine if partial diel migration variation occurs as a consequence of repeatable individual differences (obligate behaviour), or as a result of short-term migratory flexibility (facultative behaviour), have previously been lacking.

Like all non-breeding migrations, diel migrations occur in an attempt to optimise foraging/energetic gain to predation risk ratios (μ/g ratios, Werner & Gilliam, 1984). Nightly migrations into shallower, more productive habitats, maximise foraging opportunity (Hays, 2003), minimise predation risk from visual predators under the cover of darkness (Scheuerell & Schindler, 2003), and provide a warmer thermal habitat physiologically optimal for foraging (Mehner, 2012). Migration into deeper, cooler water during the day provides a thermal habitat beneficial for digestion, and optimises μ/g ratios through occupation of a predator-scarce environment during rest (Harrison et al., 2013; Mehner, 2012). In aquatic systems, the vertical distribution of prey, predators, and thermal habitat often vary at daily and seasonal scales. Moreover, individual energetic demand and satiation can fluctuate at daily and seasonal scales. Dynamic environments and variable intrinsic states promote facultative migrations (Chapman, Hulthén, et al., 2012). Thus, it has been generally assumed that partial diel migrants are entirely facultative and completely free to moderate their migration behaviour in response to variation in predator and prey density, thermal habitat, and energetic and satiation status (Busch, Johnson, & Mehner, 2011; Mehner, Kasprzak, & Holker, 2007; Mehner & Magnan, 2015).

However, repeatable individual differences are a common feature of non-migratory labile behaviours (Bell, Hankison, & Laskowski, 2009). Furthermore, individual differences often explain a significant proportion of variation in the labile spatial behaviours of wild fish (Harrison et al., 2015; Nakayama, Laskowski, Klefoth, & Arlinghaus, 2016; Villegas-Ríos, Réale, Freitas, Moland, & Olsen, 2017). Thus, it seems probable that a degree of repeatable among-individual variation also underpins diel migration behaviour. However, despite the potentially large eco-evolutionary implications of individual variation (Wolf & Weissing, 2012), the idea that facultative migrations such as diel migration, are underpinned partly by repeatable individual variation, has been largely ignored. Indeed, given than aquatic systems are vertically heterogeneous (Hays, 2003), the existence of repeatable inter-individual variation in diel migration behaviour, has potentially large consequences for individual fitness and community interactions. Moreover, given that selection occurs at the individual level, individual variation in depth use and diel depth plasticity, have potential implications for the evolution of diel migratory behaviour (Nussey, Wilson, & Brommer, 2007).

Traditionally, partial migrations were discretely classified as obligate, or facultative behaviours. However, the recent environmental threshold theory for partial seasonal migrations (ETP, Pulido, 2011; Dodson et al., 2013; Brodersen et al., 2014), suggests migration heterogeneity is controlled by a combination of; variation in environmental conditions and intrinsic status, and individual differences in migratory responsiveness to the conditions and status which promote migration. These individual differences in migratory responsiveness are thought to result in within-population variation in migratory responses to homogenous conditions (Brodersen et al., 2012; Dingle & Drake, 2007). Thus, large shifts in average environmental conditions can result in individually reversible shifts between obligate and facultative migration status. The ETP was originally developed in relation to the traditional view of seasonal migration, where behaviour was discretely classified as resident or migrant (Dingle & Drake, 2007). However, contemporary research has revealed that migration actually often consists of a continuous distribution of differing individual migration distances and directions (the migratory continuum, Cagnacci et al., 2011; Singh et al., 2012). Diversity in diel migratory strategy, such as reverse migration (daytime ascent), along with variation in general depth use, has been observed in a number of systems exhibiting diel migrations (Mehner, 2012). Furthermore, a discrete categorisation of habitat by depth is often not practical in a vertically and temporally dynamic animal community. Accordingly, the treatment of diel migration behaviour as a continuous trait (plasticity in depth among diel periods), that is potentially correlated with general depth use, may better capture individual nuances in complex migration behaviour. Nonetheless, we posit that the ETP theory also likely has relevance to the continuous view of migration behaviour. Indeed, under an ETP one would predict that underlying individual differences in migratory responsiveness, would continue to influence the continuous extent and direction of diel migration behaviour, even in a highly flexible, facultative migration.

Advances in animal telemetry technology have allowed for an unprecedented individual scale insight into the spatial behaviour of animals (Hussey et al., 2015). However, the technology to estimate continuous measures of energetic state and satiation from multiple individuals, while simultaneously quantifying daily, vertical variation in potential predation risk, foraging opportunity and thermal habitat, is not yet available for free-swimming wild aquatic animals. Nonetheless, an identification of the precise combinations of the variables known to promote a diel migration response (Mehner, 2012) is not necessary to determine the repeatable or flexible nature of a migration behaviour. The detection of short-term within-individual flexibility in depth use and diel migration behaviour alone, is sufficient to determine that the response is flexible, and not a purely obligate behaviour. Furthermore, individual repeatability, if co-occurring with short-term flexibility, would demonstrate that partial diel migration variation is mediated by a combination of facultative and repeatable behaviours. Moreover, the persistence of individual differences in migratory behaviour over long periods, and thus multiple contexts, would suggest that this individual variation occurred as a function of permanent environmental effects or genetic variation (Araya-Ajoy, Mathot, & Dingemanse, 2015; Biro & Stamps, 2015).

In this study, we used acoustic depth telemetry to track the depth distribution of 47 wild, free-swimming individual burbot, *L. lota*, over 2 years in a reservoir in British Columbia, Canada. We hypothesised that the variations in diel depth plasticity and general depth use that constitute a partial diel migration, occur as a combination of long-term repeatable among-individual variation and short-term flexibility. To test this hypothesis, we used a hierarchical behavioural reaction norm approach to partition among- and within-individual variation in depth use and diel migration at short-term (among-dates-within-seasons, and among-seasons) and long-term (across all detection) scales. We predict that daily and seasonal within-individual flexibility in migration behaviour will occur, indicative of a flexible, facultative migration response. Moreover, we predict that long-term repeatable individual variation will also be detected, indicative of a facultative partial migration that is also partially governed by among-individual variation.

2 | MATERIALS AND METHODS

2.1 | Study species

Burbot, a freshwater, piscivorous fish (Harrison, Gutowsky, Martins, Ward, et al., 2017), are common in lakes, rivers and reservoirs throughout much of their large northern circumpolar distribution (Harrison et al., 2016a; Stapanian et al., 2010). As a nocturnal, benthic species, burbot perform diel migrations, using deeper depths during the day and migrating, while maintaining close proximity to benthic habitats, towards shallower habitat at night (Carl, 1995; Cott, Guzzo, Chapelsky, Milne, & Blanchfield, 2015). The depth distribution of burbot in our study system, Kinbasket Reservoir, is well researched, with diel migration behaviour at the population level, explained by a combination of thermal bioenergetics optimisation (Harrison et al., 2016b), predation avoidance and feeding opportunity (Harrison et al., 2013). In a previous study, we detected a partial migration with 27% of individuals remaining resident on average at night (Harrison et al., 2013). Using the same data, we now investigate whether the variation in migratory behaviour that comprised partial diel migration, occurred as a function of individual variation, environmental variation or a combination of both.

2.2 | Study site and telemetry array

The study data were collected from Kinbasket Reservoir (52°08′N 118°27′W), a 410 km^2 hydropower storage reservoir in South Eastern British Columbia, Canada. This cold deep (up to 190 m) reservoir is primarily fed by glaciers and snow melt (for a full description of the reservoir, see Gutowsky et al., 2013; Martins et al., 2013). An array of 42 omni-directional acoustic telemetry receivers (VR2W; VEMCO Halifax, Nova Scotia, Canada; see Donaldson et al., 2014) were deployed in the spring of 2010, data were downloaded in the spring of 2011 and data were downloaded and receivers retrieved in the spring of 2012. Further details on the array and mooring procedure can be found in Harrison et al. (2013).

2.3 | Capture and tagging

Burbot were captured in the spring of 2010 (n = 50) and the spring of 2011 (n = 25) using baited cod traps and decompressed to minimise barotrauma risk, following the procedure outlined by Neufeld & Spence (Neufeld & Spence, 2004). Burbot were surgically implanted with acoustic depth-sensing telemetry tags (V13TP, 45 mm × 13 mm, 6 g in water, signal transmission rate 60–180 s, average 120 s, expected battery life 1,028 days; VEMCO Halifax, Nova Scotia, Canada). Identification of sex was not possible due to post-spawn capture, however, total length was recorded. Full details of the capture and surgical procedure can also be found in Harrison et al. (2013, 2015).

2.4 | Data analysis

Long-term (over the entire study), medium-term (across seasons × years) and short-term (across dates) repeatability of average depth use (intercept) and long-term and medium-term individual repeatability of diel migration (slope) were assessed using linear hierarchical random regression models fitted with a Gaussian error distribution. Measures of repeatability at these three hierarchical scales allowed discrimination between: individual repeatability in depth use and diel migration behaviours at the daily and seasonal scale, indicative of a facultative migration response to temporally correlated environmental conditions; and long-term individual variation indicative of a repeatable behavioural trait.

Models were fitted using the package LME4 (Bates, Maechler, Bolker, & Walker, 2015) following the methods described in Araya-Ajoy et al. (2015). Our response variable depth (m), was cube root transformed to achieve normality in the residuals (Zuur, Ieno, Walker, Saveliev, & Smith, 2009), and to homogenise variance across our fixed effects levels. In field data, where individuals are free to choose their context, the inclusion of fixed effects terms is important to ensure between individual differences in experience of fixed effects levels do not artificially inflate repeatability estimates (Dingemanse & Dochtermann, 2013; Nakagawa & Schielzeth, 2010). Thus, we included the following fixed effects: diel period (DE), season by year (SY), reservoir distance (RD) and total fish length (TL). All continuous variables were mean centred and divided by two standard deviations, ensuring zero means. The 0,1 coding of our binary variables diel period and year allowed us to also mean centre and divide by two standard deviations, ensuring zero means in perfectly balanced datasets (Araya-Ajoy et al., 2015; Gelman & Hill, 2007). Two-way interactions were fitted for all possible combinations of fixed effects, and the full model was presented without backwards selection, following Whittingham, Stephens, Bradbury, and Freckleton (2006). Details of all fixed effects estimation are given below.

Diel period was calculated using sunset and sunrise times at 52°08′N 118°27′W, to ensure that factor levels respond to light and dark periods, the time of which varies considerably over a year at this northern latitude. Days and nights when individual fish were recorded <10 times were removed from the data prior to analysis. This ensured an adequate sampling period for a representative depth estimate. Day was coded as 0 and night was coded as 1.

Seasons were combined with years as a single variable (SY), to account for known interaction effects on burbot depth use (Harrison et al., 2013). Seasons were categorised as Summer—May to October, Pre-Spawn—November to January, and Spawn and Post-Spawn—February to April. Sampling year was categorised as Year 1, May 2010 to April 2011, and Year 2, May 2011 to April 2012, again coded as 0 for year 1 and 1 for year 2 respectively.

Reservoir distance, was calculated as the linear distance from the point of detection on a given date, to the confluence region (km). The RD variable was designed to capture the broad-scale pattern of decreasing depth availability that occurs in the reservoir as individuals move away from the dam and into the more riverine shallower habitats to the northwest and southeast of the confluence area (Harrison et al., 2015). Total length was based on the measured total length of fish in cm on the day of capture.

Random effects were fitted using a random regression approach (Araya-Ajoy et al., 2015), with intercepts representing the average depth use between day and night and slopes representing the individual plasticity in depth use between day and night. The hierarchical random effects structure included the following nested random effects: Ind, representing the individual burbot, $\text{series}_{\text{season}\times\text{year}}$, a unique factor combination of individual and season × year level, $\text{series}_{\text{dates}}$, a unique combination of individual and full date (dd/mm/yy), which is inherently nested within a season × year level (see Supporting Information for lme4 code for random effects).

The final model took the following form:

$$\begin{aligned} y_{ijk} = {} & \left(\beta_0 + \text{Ind}_{0k} + \text{series}_{\text{season}\times\text{year}_{0jk}} + \text{series}_{\text{dates}_{0jk}}\right) \\ & + \left(\beta_1 + \text{Ind}_{1k} + \text{series}_{\text{season}\times\text{year}_{1jk}} + \text{series}_{\text{dates}_{1jk}}\right) + \text{DE}_{ijk} \\ & + \text{TL}_k + \text{RD}_{ijk} + \text{SY}_{ijk} + \text{DE}\times\text{TL}_{ijk} + \text{DE}\times\text{RD}_{ijk} + \text{DE}\times\text{SY}_{ijk} \\ & + \text{TL}\times\text{RD}_{ijk} + \text{TL}\times\text{SY}_{ijk} + \text{RD}\times\text{SY}_{ijk} + e_{0ijk} \end{aligned} \tag{1}$$

where y_{ijk} represents a single phenotypic response by burbot k, at series j, at instance i as a function of DE_{ijk} (the diel period). Accordingly, we were able to calculate individual-mean intercepts ($\beta_0 + \text{Ind}_{1k}$) and reaction norm slopes ($\beta_1 + \text{Ind}_{1k}$) over the entire period, along with series deviations from the intercept ($\text{series}_{\text{dates}_{0jk}}$) and ($\text{series}_{\text{season}\times\text{year}_{0jk}}$), and slope ($\text{series}_{\text{dates}_{1jk}}$) and ($\text{series}_{\text{season}\times\text{year}_{1jk}}$). The fixed effect interaction term between season × year (SY) and diel period (DE) allowed for uneven sampling of individuals across levels, and thus accounted for the population-level effects of SY that induce variation in our nested level, that is within-individual variation in diel depth plasticity (Araya-Ajoy et al., 2015). Furthermore, two-way interaction terms between our fixed effects levels (RD, reservoir distance, TL total length) ensured the model captured all population-level multidimensional plasticity.

The support for a given random effects structure was established by AIC comparison, using REML fits (Zuur et al., 2009). Marginal and conditional R^2 values were also computed for all alternative random effects structure models, following the methods described in Johnson (2014). Residuals were plotted against all fixed effects levels (including between day and night levels) to confirm variance homogeneity assumptions (Zuur et al., 2009). REML-based posterior distributions for parameter estimates were simulated using the ARM package following the methods described in Gelman and Hill (2007).

Long-term (over the entire study period), medium-term (across seasons) and short-term (within seasons across dates) individual repeatability of average depth use (intercepts), and long-term and medium-term repeatability of diel migration (slopes), and intercept–slope correlations were calculated following the procedures given in Araya-Ajoy et al. (2015) and detailed in Appendix S1. All variance estimates for average depth use (intercepts) are given as proportions of total phenotypic variation (the sum of all fixed effects, all random intercepts and residual variance). In the case of diel migration variation (slopes), a single slope was estimated for a given day. Thus, residual variation (i.e. the within date variation) needed to estimate repeatability at the short-term scale is not estimable. Nonetheless, we were still able to estimate individual diel migration variation among dates.

3 | RESULTS

In total, 481,337 burbot depth detections were received. Of the 75 tagged fish (50 in year 1, and 25 in year 2), 47 met the detection quality criteria. The final random regression model was populated by a total of 373,439 post-filter observations of depth from 47 burbot over a period spanning 2 years (May 2010 to May 2012). Total lengths of fish included in the analysis ranged from 44.8 to 71.4 cm. Individuals averaged 7,946 depth detections and ranged from a minimum of 383 to a maximum of 52,893 detections per fish. In total, burbot were recorded at 5,214 $\text{series}_{\text{dates}}$ levels, with an average of 110 dates per fish, a minimum of 7 and a maximum of 540. Burbot were recorded in a total of 218 $\text{series}_{\text{season}\times\text{year}}$ levels averaging 4.6 season × year level combinations with a maximum of 6, and a minimum of 1.

While all fixed effects and interactions were retained in our predictive model (Table S1 for full fixed effects estimates), only the interactions between diel period and confluence distance ($F = 6.45$, $p = .01$, $ndf = 1$, $ddf = 2{,}952$) and the interaction between confluence distance and season × year ($F = 3.22$, $p = .006$, $ndf = 5$, $ddf = 1{,}958$) variables were identified as statistically significant. Total length and all interactions containing total length were not found to be significant

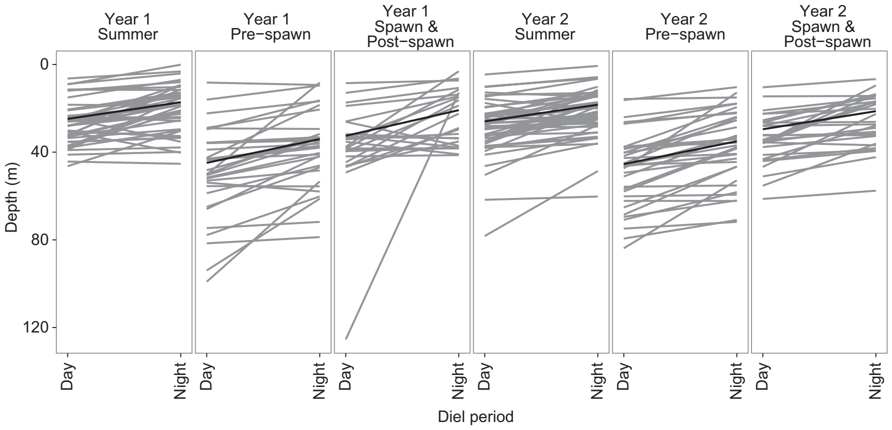

FIGURE 1 Visualization of random regression results for burbot seasonal and diel depth behaviour over 2 years. Grey lines depict individual intercepts and slopes. Solid lines indicate population-level means

TABLE 1 Comparison of alternate random effects structure for linear mixed-effects models of burbot depth use, fitted using REML methods (Zuur et al., 2009), with random intercepts (I) and random slopes (I × E). Full fixed effects structures were included in all models (see equation 1). Hierarchical random effects levels included individual burbot (Ind), the unique combination of burbot ID and date (series$_{\text{dates}}$), and the unique combination of burbot ID and season × year levels (series$_{\text{season×year}}$). Marginal and conditional R^2 values were calculated using the methods described in Johnson (2014)

	Ind	Series$_{\text{dates}}$	Series$_{\text{season×year}}$	AIC	R^2_{marginal}	$R^2_{\text{conditional}}$
1	I × E	I × E	I × E	−73,269	.142	.925
2	I × E	I × E	I	−73,040.78	.145	.923
3	I × E	I × E		−72,369.15	.137	.922
4	I × E	I		57,150.97	.131	.888
5	I × E			579,740	.151	.461
6	I			592,406	.162	.443

predictors of depth use (all $p > .05$). At the population scale, a pattern of diel migration, that is, decreasing depth use at night, was seen in all season × year levels (Figure 1).

In our final model, the fixed effects explained a relatively small proportion of variance in our dataset, in comparison to our random effects components (marginal R^2 .18, conditional R^2 .91). The best random effects structure included a hierarchical random slope and intercept at all three series levels (Table 1). Significant diversity in individual-level intercepts and slopes was detected, with diel migration, residency (i.e. remaining deep), reverse migration (increased depth use at night) and reverse residency (i.e. remaining shallow) all evident at seasonal (Figure 1) and daily scales (Figure 2).Repeatable individual differences in plasticity in depth use over the diel cycle, that is, diel migration behaviour, were found at multiple temporal scales (Table 2). Within-individual among-season × year (series$_{\text{season×year}}$) variation accounted for the largest proportion of phenotypic variation in diel migration behaviour (Table 1 for significance and Table 2 for estimate). Repeatability was highest at this medium scale, with individual burbot demonstrating a degree of repeatability in their diel behaviour within season × year levels and plasticity in their diel migration behaviours among seasons × year levels (Table 2; Figure 1). Within-individual, among-dates-within-seasons variation also accounted for a significant proportion of phenotypic variation in diel migratory behaviour, indicating that individuals also demonstrated a degree of flexibility in migration strategy at the daily scale (Table 2). An example of the degree of within-individual among-dates flexibility can be seen in Figure 2, where burbot 1,867 is seen to perform migration behaviour, residency strategy and reverse migration in a given week. Moreover, all individuals displayed flexibility in migration amplitude (Figure 3). However, our findings show that despite considerable within-individual flexibility in diel migration behaviour at the among-dates-within-season and among-season levels, individuals repeatedly differed in their diel migration strategy, when assessed over the entire study period (Tables 1 and 2). Repeatable individual differences in general depth use were also found at all measured temporal scales (Table 2). Individual repeatability in depth use was highest at the short-term scale, with individuals demonstrating highly repeatable depth use within a given date and large differences in depth use among-dates-within-seasons. Series$_{\text{season×year}}$ also accounted for a significant proportion of phenotypic variation in depth (Table 2), with individuals demonstrating a degree of repeatability within a season and a degree of plasticity in depth use among-seasons (Figure 1). However, despite a degree of individual flexibility in depth use among-seasons and among-dates-within-seasons, individuals repeatedly differed in their depth use over the entire study period (Table 2).

Diel migration behaviour and general depth use were found to be positively correlated, with individuals that use deeper habitats on

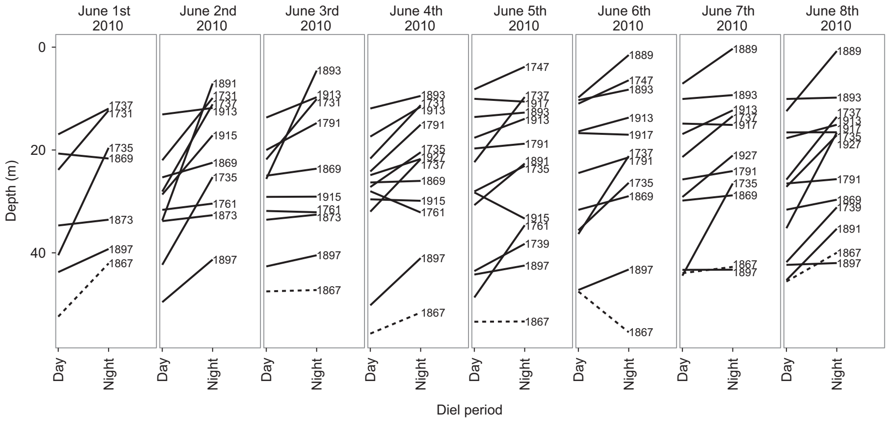

FIGURE 2 An example of within-individual among-dates flexibility in diel migration strategy based on a sample of data from 8 days from individual burbot. Labels represent individual fish ID numbers, with individual 1,867 discussed in the text highlighted with a dashed line

TABLE 2 Sources of variation in burbot depth use and diel migration behaviour derived from linear mixed effects model with random intercepts (individual burbot $n = 47$) and slopes (diel period, day −0.5, night +0.5). Among-individual components use the subscript ("ind"), among-dates components use the subscript ("dates") and among-season × year levels use the subscript ("season × year"), R_p represents the proportion of total variance in reaction norm components inclusive of fixed effects, residual and random effects variance

	Average depth (intercept)	Depth plasticity (slope)
Variance components	R_p (CI_{lower}, CI_{upper})	R (CI_{lower}, CI_{upper})
Fixed effects	0.18 (0.13, 0.25)	na
Residuals	0.089 (0.088, 0.090)	na
$\text{Series}_{\text{ind}}$	0.18 (0.17, 0.20)	0.15 (0.12, 0.19)
$\text{Series}_{\text{season×year}}$	0.104 (0.101, 0.107)	0.67 (0.65, 0.68)
$\text{Series}_{\text{dates}}$	0.44 (0.43, 0.45)	0.19 (0.17, 0.20)
Long-term	0.18 (0.16, 0.18)	0.15 (0.12, 0.19)
Medium-term	0.28 (0.27, 0.31)	0.81 (0.77, 0.87)
Short-term	0.73 (0.70, 0.75)	na

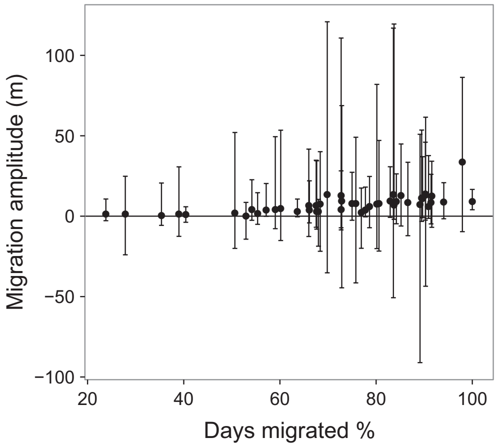

FIGURE 3 Mean, maximum and minimum migration amplitudes of individual burbot. Amplitude was calculated as the difference between mean daily depth and mean nightly depth on a given day. Percentage of days migrated was calculated as percentage of days when migration amplitude was >0

average, also performing the largest diel migrations (Table 3). Positive correlations were also observed at the within-individual level, with individuals performing larger diel migrations on days when they used deeper depths and in seasons when they used deeper depths (Table 3).

4 | DISCUSSION

Our data reveal that individual, wild, free-swimming burbot were plastic in their depth use and diel migration behaviour among-seasons, and among-dates-within-seasons. The large proportion of phenotypic variation explained by this short-term within-individual flexibility, indicates that partial diel migration variation occurred primarily as a consequence of individual plasticity in response to environmental variation. However, our results also show that individual burbot repeatedly differed in their depth use and diel migration behaviour, over the entire study period. Together, these findings provide empirical support for our hypothesis that partial diel migration variation occurs as a combination of facultative responses, and repeatable individual differences in migratory responsiveness. These findings represent a significant advancement of our understanding of the mechanisms generating diel migration variation, which was previously hypothesised to be governed entirely by short-term environmental and endogenous variation. Furthermore, given that partial diel migrations are a pervasive phenomena among diel migrating animals (Mehner & Kasprzak, 2011), our findings suggest that these repeatable individual differences in diel migratory behaviours, play an important, yet previously unrecognised role, in structuring the vertical distribution of aquatic communities.

Repeatable individual differences are a common feature of non-migratory labile behaviours (Bell et al., 2009; Dall, Bell, Bolnick, & Ratnieks, 2012). Repeatability is implied by seasonal partial migration studies that document migration status heredity (Berthold, 1991; Pulido, 2011; Pulido, Berthold, & van Noordwijk, 1996). Repeatability is a defining feature of obligate partial seasonal migrations (Chapman,

TABLE 3 Intercept Slope Correlations (I × E cor), with 95% credibility intervals in parentheses for diel depth use behavioural reaction norms, derived by hierarchical random regression

	Among-individuals	Within-individuals (among-dates-within-seasons)	Within-individuals (among-season × year levels)
I × E cor	0.36 (0.23, 0.45)	0.22 (0.21, 0.24)	0.37 (0.32, 0.41)

Skov, et al., 2012). Furthermore, seasonal partial migration variation is often mediated by a combination of repeatable individual variation in migratory responsiveness and environmental variation (the ETP reviewed in Dodson et al., 2013; Pulido, 2011). While our findings may be intuitive, the data we present provides the first demonstration that long-term individual repeatability can underpin a labile, facultative migration such as diel migration. Similarly, while our demonstration of the ETP's relevance to more frequently occurring continuous migration behaviours such as diel migration is novel, these findings are also intuitive, given the evidence for ETP among seasonal migrations.

Our data show that within-individual plasticity, both among-seasons and among-dates-within-seasons, explained the dominant proportion of phenotypic variation in depth use and diel migration behaviours. These findings demonstrate that diel migration behaviour was largely facultative, that is, flexible and condition dependent, and not a purely obligate, fixed behaviour. The ultimate causes of diel migration behaviour have been identified through general comparisons of temperature, predator threat and prey density, between shallow night-time and deep daytime habitats (Busch et al., 2011; Mehner, 2012). Indeed, we previously demonstrated that the population-level pattern of diel migration of burbot in this system, represents a complex trade-off among predation avoidance, foraging opportunity and a seasonal hunt-warm rest-cool, thermal bio-energetic advantage (Harrison et al., 2013, 2016b). However, simultaneous quantification of short-term variation in the vertical availability of these habitat features for each tagged, free-swimming burbot, is more challenging. Moreover, it is currently difficult to repeatedly estimate within-individual variation in endogenous variables such as satiation and energetic demand, which also have the potential to influence proximate migration decisions (Brodersen, Nilsson, & Hansson, 2008).

Nonetheless, temporal scaling of among- and within-individual variation, provide clues to the proximate factors influencing individual migration decisions. Daily variation in energetic demand and satiation are common in fish (Strubbe & Van Dijk, 2002). Seasonal variation in energetic demand is frequently observed in temperate iteroparous ectotherms, such as burbot (Ultsch, 1989). Energetic demand and satiation status are well known to influence willingness to forage under predation risk (reviewed in Milinski, 1993) and are important determinants of facultative seasonal migration variation (Brodersen et al., 2008; Olsson, Greenberg, Bergman, & Wysujack, 2006). Accordingly, it is probable that within-individual variation in energetic demand and satiation plays an important role in the daily and seasonal within-individual variation in diel migration behaviour observed in this study. Indeed, the alternative strategy of night-time residency in cooler, deeper, predator-free water likely represents an optimisation of μ/g ratios for a satiated fish or a fish with low energetic demand (Harrison et al., 2013). Likewise, the alternative strategy of daytime occupancy of the shallow, predator risky, food-rich, shallow zone during the day, may also represent an optimal μ/g ratio for an individual with high energetic demand and an empty stomach.

Large daily variations in vertical thermal habitat distribution were rare in our study system (Harrison et al., 2016b). Accordingly, daily variation in the bio-energetic advantage that accrued from a hunt-warm rest-cool strategy, was likely small and thus played a limited role in the daily variation in diel migration behaviour. In contrast, seasonal variation in the vertical distribution of thermal habitats is common in temperate lakes and was reservoirs, and was pronounced in this system (Harrison et al., 2016b). Thus, there is a high probability that variation in the thermal bio-energetic advantages accrued by diel migration, contributed to the seasonal plasticity in depth use and diel migration seen in this study. Similarly, seasonal and daily variation in prey and predator depth distributions, are common feature of aquatic systems (Gutowsky et al., 2013; Hays, 2003). Accordingly, there is a strong possibility that the resulting temporal variation in potential μ/g ratios of migration, also contributed to the observed daily and seasonal plasticity in migration behaviour.

Together, these findings suggest that temporal variation in the vertical distribution of thermal habitat, predation threat and prey opportunity, along with seasonal and daily within-individual variation in energetic demand, all potentially influence the proximate diel migration response. The precise combinations of these factors that result in a μ/g ratio that promotes diel migration remain elusive. However, the precise quantification of a combination of these factors that promotes a diel migration response, would likely have limited applicability to heterogeneous systems or species, given that μ/g ratios are dependent on predator and prey community composition. In contrast, given the ubiquity of individual variation in non-migratory labile behaviours, the existence of individual variation in diel migrations, may well have broad applicability to alternative diel migrating species and systems, and even alternative facultative migration types.

By taking a multi-level approach, we have shown that the population-level pattern of nightly migration into shallower waters, is actually comprised of a remarkable diversity of migration patterns that vary in direction and extent both within and across individuals. These findings demonstrate that diel migration is a much more complex behavioural phenomenon than has previously been acknowledged through population-level research. Moreover, these results suggest that the costs and benefits associated with diel migration behaviour are not homogeneously partitioned across individuals or temporal contexts. Accordingly, our findings suggest multi-level approaches such as that we have adopted, will be essential for future insight into the fitness benefits of this poorly understood migration phenomena.

By adopting a reaction norm approach, we have demonstrated that a relationship exists between general depth use and diel migration behaviour, with individuals that occupy deeper habitats on average, also the most plastic in depth use over the diel cycle. These findings may reflect a physical restriction of vertical migration opportunity associated with shallow water use. Alternatively, given that depth use and diel depth plasticity can be considered behavioural traits, these correlations may occur due to shared genetic, maternal or permanent environmental origins (Brommer, 2013b; Dingemanse & Dochtermann, 2013). Our detection of within-individual depth use and diel migration correlations, suggest a degree of correlation also exists at the short-term scale (Brommer, 2013a), with diel migration within individuals constrained on days and in seasons when an individual is located at shallower average depths. These correlations, along with the individual variation in general depth use observed, provide a novel demonstration that diel migration behaviour is not independent of general depth use. Accordingly, our findings suggest that research that focuses entirely on diel migration amplitude, is likely an over simplification of this complex behaviour, and future work should adopt our more nuanced, reaction norm precedent.

By excluding short-term repeatability from our measure of individual variation and tracking fine-scale depth use over a long time-frame, over multiple seasonal conditions, we showed that the individual differences observed were not an artefact of short-term individual differences in environmental conditions, nor an artefact of biased sampling design. By including a spatial variable, RD, which serves as a broad-scale proxy for habitat depth, we demonstrated that individual differences in diel migration were not a function of individual differences in habitat depth. By accounting for body length, we showed that the individual variation observed was not a function of differing body size. Accordingly, our results provide convincing evidence that individual differences in depth use and in diel migration strategy occur as a function of either genetic differences or unmeasured permanent environmental effects.

Our findings raise interesting questions regarding the causes of these individual differences in migratory behaviour. Diel migration is risky (Busch et al., 2011; Mehner, 2012) and individual differences in willingness to forage in the presence of predators are common (Dammhahn & Almeling, 2012; McArthur, Banks, Boonstra, & Forbey, 2014; Mella, Ward, Banks, & McArthur, 2015). Accordingly, it is plausible that the repeatable individual differences in diel migratory behaviour, are linked to individual differences in willingness to forage under predation risk. Indeed, individual variation in seasonal migrations has been directly linked to the shy–bold personality axis (Chapman et al., 2011). Alternatively, it is also possible that individual variation in diel migration behaviour is linked to the fast–slow activity personality axis, and more broadly to metabolic, hormonal and life-history variation (the-pace-of-life-syndrome Réale et al., 2010). Indeed, fast–slow life-history variation is thought to be correlated with risk taking (Wolf, van Doorn, Leimar, & Weissing, 2007), activity and foraging behaviour (Nakayama, Rapp, & Arlinghaus, 2017). A third alternative is that this migration variation is linked to dietary specialisation. Dietary specialisation has been shown to covary with individual variation in horizontal movement patterns in our model species (Harrison, Gutowsky, Martins, Ward, et al., 2017), and vertical heterogeneity in prey types are a common feature of aquatic systems. Accordingly, investigations into correlations between diel migration responsiveness and personality axes, life-history variation and dietary specialisations are all promising directions for future research.

Individual variation in spatial ecology and migration behaviours are important components of population resilience and stability, habitat carrying capacity, diversification and speciation (Kerr, Cadrin, & Secor, 2010; Réale, Reader, Sol, McDougall, & Dingemanse, 2007; Wolf & Weissing, 2012). Accordingly, the idea that “individuals matter” is increasingly recognised in the conservation and management of fisheries and aquatic ecosystems (see Killen, Adriaenssens, Marras, Claireaux, & Cooke, 2016; Ward et al., 2016 for reviews). Indeed, there is a growing consensus that variation in behaviour can influence vulnerability to fisheries capture and thus reduce population behavioural diversity and ultimately resilience and stability (e.g. Uusi-Heikkilä, Wolter, Kleforth, & Arlinghaus, 2008). Similarly, individual variation in diel migration behaviour has potentially important implications for vulnerability to depth-specific capture fisheries. Furthermore, the vertical and temporal segregation that occurs as a consequence of individual variation in diel migration, may reduce intraspecific competition, and thus influence habitat carrying capacity. Moreover, given the importance of depth use in the development of phenotypic diversity in aquatic species (Power, O’Connell, & Dempson, 2005; Zimmerman, Krueger, & Eshenroder, 2006), individual differences in diel migration and depth use likely have a role in morphotype development and speciation. Furthermore, given the important role of diel migrations in trophic interactions and bentho-pelagic nutrient pathways (Euclide, Hansson, & Stockwell, 2016), individual variation in diel migration behaviour has potential community- and ecosystem-wide consequences.

The degree of plasticity in diel migration behaviour observed in this study, also likely has ecological consequences. The ability of individuals to modify their behaviour in response to environmental change is increasingly recognised as an important component of population stability and resilience to environmental change (Sih, Ferrari, & Harris, 2011). Indeed, the high degree of within-individual flexibility in diel migration seen in this study is likely important in dynamic aquatic environments. Furthermore, the temporal plasticity of the diel migration response seen in this study highlights the potential for environmental change to contribute to the global decline of migratory behaviour (Wilcove & Wikelski, 2008). Indeed, such flexibility in diel migration and depth use is likely to prove increasingly important for the persistence of aquatic organisms in light of human-induced rapid environmental change (Sih et al., 2011).

5 | CONCLUSIONS

Multi-level analysis is critical for an understanding of the processes that shape and maintain partial migration (Brodersen et al., 2008; Chapman et al., 2011) and research into individual differences in behaviour has increased significantly in recent years (Wolf & Weissing, 2012). Nevertheless, the sophisticated techniques and methodologies designed for investigating individual differences in behaviour and in behavioural plasticity have never before been adopted for the study of partial diel migration. In this study, we demonstrated the utility of the integration of inter-individual variation, behavioural plasticity and partial migration concepts, through the treatment of partial migration as a behavioural reaction norm. Accordingly, we were able to show that partial diel migration, is actually comprised of a complex pattern of within- and among-individual diversity of migratory directions, migratory extents and residency depths, which are not independent of general depth use. Moreover, we showed that the variation in migratory behaviour that constitutes that partial diel migration, primarily occurs as a consequence of short-term within-individual flexibility. However, our findings also showed that partial diel migration variation was also mediated by repeatable individual differences. These findings represent a significant improvement in our understanding of the mechanisms generating this common, yet poorly understood migration phenomenon. Moreover, these findings suggest that repeatable individual variation in diel migration behaviour has an important, yet previously unrecognised role in shaping the temporal depth distribution of aquatic organisms.

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AUTHORS' CONTRIBUTIONS

The study was designed by S.J.C., M.P., D.P. and P.M.H., data were collected by L.F.G.G., E.G.M. and P.M.H., the data were analysed by P.M.H., the paper was written by P.M.H., and all authors contributed significantly to revisions.

DATA ACCESSIBILITY

All data have been deposited in the MacOdrum Library Data Repository, Carleton University Dataverse https://doi.org/10.5683/sp/97a0dy (Harrison, Gutowsky, Martins, Patterson, et al., 2017).

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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