

See discussions, stats, and author profiles for this publication at: <https://www.researchgate.net/publication/311704805>

Individual isotopic specialisations predict subsequent inter-individual variation in movement in a...

Article in *Ecology* · December 2016

DOI: 10.1002/ecy.1681

CITATIONS

0

READS

249

7 authors, including:



Phil M. Harrison

University of Waterloo

20 PUBLICATIONS 91 CITATIONS

[SEE PROFILE](#)



Lee F. G. Gutowsky

Ontario Ministry of Natural Resources & Fore...

49 PUBLICATIONS 277 CITATIONS

[SEE PROFILE](#)



Eduardo Martins

University of Waterloo

69 PUBLICATIONS 691 CITATIONS

[SEE PROFILE](#)

Some of the authors of this publication are also working on these related projects:



Toronto Region Telemetry Project [View project](#)



Collaboration for Environmental Evidence (CEE) [View project](#)

Reports

Ecology, 98(3), 2017, pp. 608–615
© 2016 by the Ecological Society of America

Individual isotopic specializations predict subsequent inter-individual variation in movement in a freshwater fish

P. M. HARRISON,^{1,2,5} L. F. G. GUTOWSKY,^{1,4} E. G. MARTINS,² T. D. WARD,¹
D. A. PATTERSON,³ S. J. COOKE,¹ AND M. POWER²

¹*Department of Biology, Fish Ecology and Conservation Physiology Laboratory, Carleton University, Ottawa, Ontario K1S 5B6 Canada*

²*Department of Biology, University of Waterloo, Waterloo, Ontario N2L 3G1 Canada*

³*Fisheries and Oceans Canada, Cooperative Research Management Institute, Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia V5A 1S6 Canada*

⁴*Aquatic Resource and Monitoring Section, Ontario Ministry of Natural Resources and Forestry, Peterborough, Ontario K9L1Z8 Canada*

Abstract. Despite many similarities and intuitive links between individual dietary specialization and behavioral inter-individual variation, these phenomena have been studied in isolation, and empirical data confirming relationships between these intraspecific variance sources are lacking. Here we use stable isotope analysis and acoustic telemetry to test the hypothesis that individual specialization in trophic ($\delta^{15}\text{N}$) and littoral/pelagic prey reliance ($\delta^{13}\text{C}$) covary with inter-individual variation in movement in a group of 34 free-swimming burbot (*Lota lota*). By performing stable isotope analysis on tissues with differing isotopic turnover rates (anal fin and dorsal muscle), in 24 lethally sampled burbot, we demonstrate that individual specialization in trophic niche ($\delta^{15}\text{N}$) and littoral/pelagic prey reliance ($\delta^{13}\text{C}$) occurred within the population. By performing stable isotope analysis on anal fins of a group of telemetry tagged burbot, we were able to show that interactions between trophic niche and littoral/pelagic prey reliance, explained a significant proportion of the subsequent between-individual variance in mean movement rates. These findings demonstrate an empirical connection between behavioral inter-individual variation and dietary specialization, thus providing a substantial expansion of our understanding of the wider ecological consequences of these interesting phenomena.

Key words: animal personality; burbot; individual differences; individual specialization; intraspecific variation isotope ecology; *Lota lota*; spatial ecology; telemetry.

INTRODUCTION

The ecological consequences of individual trophic and prey niche specialization and behavioral inter-individual variation are hypothesized to be far reaching (Réale et al. 2007, Dall et al. 2012, Sih et al. 2012). However, in comparison to the multitude of papers describing these phenomena (see Bolnick et al. [2003] and Bell et al. [2009] for reviews on individual dietary specialization and behavioral inter-individual variation respectively), demonstrations of how such variation influences the wider ecology of animals are scarce (Wolf and Weissing 2012). Given the central importance of diet and resource use in determining animal fitness (Smith and Blumstein 2008),

relationships among behavioral and dietary specializations have the potential to result in significant ecological consequences (Dall et al. 2012). However, despite many similarities and intuitive connections between behavioral and dietary specialization (Dall et al. 2012, Toscano et al. 2016), research among these phenomena has been isolated, and empirical data confirming connections among these individual variation sources are lacking.

Animal movement shapes ecosystems (Clobert et al. 2009). Accordingly, inter-individual variation in movement ecology, which is a common feature of spatial data sets (e.g., Cote et al. 2010, Harrison et al. 2015), likely plays an important role in mediating diet and resource use. Several theoretical pathways by which such inter-individual variation in movement ecology may influence diet and resource use specializations have been identified by Toscano et al. (2016). Individuals with varying space use patterns may have access to differing

Manuscript received 28 September 2016; revised 24 November 2016; accepted 6 December 2016. Corresponding Editor: Lorenzo Ciannelli.

⁵E-mail: pharriso@uwaterloo.ca

prey types in systems with spatially heterogeneous prey distributions (Wolf and Weissing 2012). Inter-individual variation in movement ecology has the potential to result in varying search and handling times among differing prey types, and thus optimal foraging theory (Stephens and Krebs 1986) would predict among individual heterogeneity in prey preference (Araújo et al. 2011). Moreover, individual differences in movement that are linked to individual differences in physiological requirements (including environmental tolerances) or social dominance hierarchies, have the potential to result in heterogeneity in optimal forage types (Toscano et al. 2016). Although there are many compelling theoretical connections between inter-individual variation in movement and individual dietary specialization, empirical tests of such relationships in wild contexts have rarely been attempted.

The stable isotopes ratios of predators consistently reflect the stable isotopes ratios of prey (Bearhop et al. 2004). Indeed, because $\delta^{15}\text{N}$ is enriched between consumers and diet, $\delta^{15}\text{N}$ is often used to estimate trophic position, with a 3.4‰ enrichment representative of one trophic level (Post 2002). In contrast, because $\delta^{13}\text{C}$ values are relatively constant between consumer and diet, yet differ among habitats, $\delta^{13}\text{C}$ analysis has proved a useful indicator of prey habitat. In aquatic systems, heterogeneity in $\delta^{13}\text{C}$ between pelagic (lowered $\delta^{13}\text{C}$) and littoral food webs (enriched $\delta^{13}\text{C}$), has proved to be particularly useful for determining lacustrine fishes' resource use (Post 2002), where resource partitioning is most commonly observed between littoral and pelagic zones (Svanbäck et al. 2008). Moreover, because metabolically inert tissues such as muscle reflect long-term diet, and more metabolically active tissues such as fins reflect more recent diet (Bearhop et al. 2004), within-individual temporal dietary consistency can be quantified from a single sampling occasion (Bolnick et al. 2003). Thus stable isotope analysis of multiple tissue types from multiple individuals, allows for the decomposition of the proportion of total isotopic variance (TNW, total niche width) explained by among-individual differences and the proportion of TNW explained by within-individual differences (WIC, within individual component). Accordingly, stable isotope analysis has proved to be a powerful tool for quantifying long-term trophic and foraging habitat niche specializations (e.g., Newsome et al. 2009).

Given the practicality of using telemetry to investigate inter-individual variation in behavior in wild contexts (Harrison et al. 2015, Killen et al. 2016, Nakayama et al. 2016); the large potential for relationships between movement and dietary and habitat niche (Cote et al. 2010); and the utility of stable isotope analysis to infer dietary and foraging habitat niche specialization, a study that combines the use of telemetry and stable isotope analysis has good potential to inform on the broader ecological consequences of intraspecific diversity. In this study, we investigate the hypothesis that long-term individual isotopic specialization explains a significant proportion of inter-individual variation in movement in the freshwater gadoid,

Lota lota. To test this hypothesis, we first determine the temporal consistency of specialization within the population through analysis of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of dorsal muscle and anal fin tissue of a lethally sampled group ($n = 24$). We then examine the relationship between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of anal fin tissue and subsequent mean movement rates in a group of 34 telemetry-tagged burbot previously found to exhibit temporally consistent inter-individual variation in movement rates.

METHODS

Study system and study species

The study took place in Kinbasket reservoir, British Columbia, Canada (Appendix S1: Fig. S1, 52°08' N 118°27' W). Kinbasket reservoir is a large (410 km²), deep (up to 190 m), steep sided, reservoir in the Columbia River watershed operated for storage and hydroelectricity production. For a full description of the reservoir, see Harrison et al. (2013). Burbot, *Lota lota*, are a winter active, benthic, piscivorous, top predator, and are common in lakes, rivers, and reservoirs (Stapanian et al. 2010, Harrison et al. 2016a) throughout much of their Holarctic range. Top predators in our study site included a large population of burbot (see Harrison et al. 2013, 2015, 2016b), and a population of bull trout, *Salvelinus confluentus* (Gutowsky et al. 2013) and rainbow trout, *Onchorynchus mykiss*. The study system contains a large population of kokanee, *Onchorynchus nerka*, which are thought to be burbot's main pelagic prey fish in the system, and Mountain whitefish, *Prosopium williamsoni*, the main littoral benthic forage fish species for burbot. Other species confirmed in reservoir include the longnose sucker *Catostomus catostomus*, large-scale sucker *Catostomus macrocheilus*, reidside shiner, *Richardsonius balteatus*, northern pikeminnow, *Ptychocheilus oregonensis*, and slimy sculpin, *Cottus cognatus* (Harrison et al. 2013).

Telemetry array

An array consisting of 42 omni-direction acoustic telemetry receivers (VR2W, VEMCO, Bedford, Nova Scotia, Canada) was deployed in the spring of 2010, retrieved, downloaded, and redeployed in the spring of 2011 and retrieved and downloaded in the spring of 2012, thus yielding a two-year study span. Full descriptions of the array design (Appendix S1: Fig. S1), receiver performance, and deployment procedure are given in (Harrison et al. 2013, 2015).

Capture, tagging and stable isotope sampling

A total of 75 burbot were captured using baited cod traps in the spring of 2010 ($n = 50$) and in the spring of 2011 ($n = 25$). Burbot were anesthetized, measured (total length, mm), and surgically implanted with acoustic telemetry transmitters. Further details of the capture and

surgery process can be found in [Harrison et al. \(2013, 2015\)](#). A small piece of anal fin tissue from each tagged fish was removed for isotopic analyses during surgery whenever possible. However, this procedure was not performed on individuals showing signs of barotrauma, to minimize additional stress. Dorsal muscle flesh was not collected from tagged fish due to infection risk. However, to test for the existence of dietary specialization within the population, an additional 24 burbot were captured and lethally sampled in the spring. For these fish, anal fin tissue and a small sample of dorsal muscle flesh were collected. All isotope samples were frozen at -18°C . Permitting restricted capture methods to cod-trapping and prescribed a decompression procedure (see [Harrison et al. \[2013, 2015\]](#) for full description). Accordingly, burbot were held in baited traps for 48–96 h prior to sampling and thus stomach content analysis was not possible.

Laboratory isotope analysis

Samples were dried for 48 h in a 50°C oven, ground, and weighed using a microbalance (readability 0.1 μg ; Mettler, Toledo GmbH, Greifensee, Switzerland). Samples were analysed at the Environmental Isotope Laboratory at the University of Waterloo using a Thermo-Finnigan Delta Plus continuous flow isotope mass spectrometer (ThermoFinnigan, Bremen, Germany) and coupled to a Carlo Erba Elemental Analyzer (CHNS-O EA1108, Carlo Erba, Milan, Italy). Machine analytical precision was $\pm 0.1\%$ and $\pm 0.2\%$ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively, and was determined by repeat analysis of duplicates (1 in 10). All resulting measurements are expressed using standard delta notation as parts per thousand (‰) differences with respect to the international reference standards, carbonate rock from the Peedee Belemnite formation for $\delta^{13}\text{C}$ ([Craig 1957](#)) and nitrogen gas in the atmosphere for $\delta^{15}\text{N}$ ([Mariotti 1983](#)).

Individual isotopic specialization

Trophic and littoral/pelagic resource use specialization were assessed in our lethally sampled group, using the within-individual variance in isotopic signatures ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$, respectively) between anal fin and dorsal muscle flesh samples, to estimate individual temporal consistency ([Araújo et al. 2007](#)). Variance components were estimated using a Gaussian linear mixed effects model, with individual burbot as the random intercept, and isotope values (two per fish) as the response. Thus the residual error term V_{res} , accounted for within-individual variation in isotope signatures, and the random effects variance V_{ind} the between-individual variation, with the sum of V_{res} and V_{ind} the total niche width (TNW). WIC was then expressed as the proportion of TNW accounted for by residual error. Thus low WIC values (near zero) indicate consistent among individual differences, i.e., specialization, and high WIC values (near one), suggest individually plastic diets, i.e., generalism.

Movement inter-individual variation

Significant, temporally consistent, repeatability of burbot monthly movement rates ($R = 0.32$ CI = 0.21, 0.5) was previously demonstrated in our tagged fish ([Harrison et al. 2015](#)) using Bayesian mixed effects models following the procedures outlined in [Dingemanse and Dochtermann \(2013\)](#). Individual mean monthly movement rates were calculated based on this data set. Of the 75 tagged burbot, 44 individuals yielded sufficient data to establish movement metrics ([Harrison et al. 2015](#)). While the array allowed us to estimate broad-scale movement metrics, individual receiver ranges were too large (~ 750 m radius) to allow for quantification of habitat use.

Relationship between movement and isotopic specializations

Of the 44 burbot that provided sufficient telemetry data to estimate movement, 34 provided sufficient tissue for isotope analysis. Using these 34 individuals, linear regressions were fitted to determine the relationship between our response variable, individual mean monthly movement rate, and our predictors; $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, and total length (cm) and all interactions. Prior to regression movement was cube root transformed to homogenize variances. Model selection was performed based on Akaike's information criterion adjusted for sample size (AIC_c) comparison using the package `AICmodavg` for R 3.2 (R Development Core Team 2016).

RESULTS

Individual isotopic specialization

Anal fin $\delta^{13}\text{C}$ values from our 24 lethally sampled burbot ranged by 10.9‰ (from -24.4% to -35.8%) and dorsal muscle samples ranged by 12.4‰ (-24.7% to -37.1%). Anal fin $\delta^{13}\text{C}$ explained a significant proportion of the variance in dorsal muscle $\delta^{13}\text{C}$ ($R^2 = 0.93$, $P < 0.0001$). WIC values for $\delta^{13}\text{C}$ were low (WIC 0.06), indicating high $\delta^{13}\text{C}$ specialization. Total length was not found to be a significant predictor of lethally sampled burbot dorsal muscle $\delta^{13}\text{C}$ (adjusted $R^2 = -0.03$, $F = 0.41$, $\text{df} = 1,22$, $P = 0.52$) or anal fin $\delta^{13}\text{C}$ (adjusted $R^2 = -0.01$, $F = 0.66$, $\text{df} = 1,22$, $P = 0.42$).

Anal fin $\delta^{15}\text{N}$ values from our lethally sampled burbot ($n = 24$) ranged by more than one trophic level (3.7‰) from 8.2‰ to 11.9‰, and dorsal muscle samples ranged by 4.2‰ (7.1–11.3‰). Anal fin $\delta^{15}\text{N}$ explained a significant proportion of the variance in dorsal muscle $\delta^{15}\text{N}$ ($R^2 = 0.69$, $P < 0.0001$). WIC values for $\delta^{15}\text{N}$ (WIC 0.42) were not as low as for $\delta^{13}\text{C}$, suggesting moderate $\delta^{15}\text{N}$ specialization. Total length was not found to be a significant predictor of lethally sampled burbot dorsal muscle $\delta^{15}\text{N}$ (adjusted $R^2 = -0.04$, $F = 0.12$, $\text{df} = 1,22$, $P = 0.72$) or anal fin $\delta^{13}\text{C}$ (adjusted $R^2 = 0.001$, $F = 1.036$, $\text{df} = 1,22$, $P = 0.32$). Total length of lethally sampled burbot ranged from 39.6 cm to 90.1 cm with a mean of 52.3 cm.

Tagged burbot ($n = 34$) anal fin $\delta^{13}\text{C}$ values ranged by a similar extent to our lethally sampled fish (range 9.1‰, -24.3 to -33.4 ‰). Furthermore tagged burbot anal fin $\delta^{15}\text{N}$ values ranged by a similar extent to our lethally sampled fish 3.4‰ (9.9–13.3‰ see Appendix S1: Fig. S1). Total length (cm) was not found to be a significant predictor of tagged burbot $\delta^{15}\text{N}$ (adjusted $R^2 = -0.03$, $F = 0.001$, $df = 1,33$, $P = 0.97$). Total length (cm) was found to be a marginally significant predictor of tagged burbot $\delta^{13}\text{C}$ (adjusted $R^2 = 0.08$, $F = 3.96$, $df = 1,33$, $P = 0.05$), with increased total length associated with a slight increase in $\delta^{13}\text{C}$ enrichment (estimate = 0.11, $SE = 0.06$, $T = 2.0$, $P = 0.05$). Tagged burbot total length was not found to be a significant predictor of a multivariate $\delta^{15}\text{N} \times \delta^{13}\text{C}$ response (Pillai test statistic = 0.11, $F = 1.92$, $df = 2,32$, $P = 0.16$). Tagged burbot total length ranged from 44.8 cm to 72.0 cm with a mean of 55.5 cm.

Relationship between isotopic and movement specialization

Our best model ($\text{AIC}_c = 86.35$, $R^2 = 0.49$, adjusted $R^2 = 0.44$, $P \leq 0.001$) to predict post sampling movement rates featured a significant interaction effect between $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($SS = 14.86$, $df = 1$, $F = 26.92$, $P \geq 0.001$), and provided a reasonable fit to our raw data (Fig. 1). Among individuals enriched in $\delta^{15}\text{N}$, a general pattern of decreased movement with increasing $\delta^{13}\text{C}$ enrichment was observed (Figs. 1 and 2). Among individuals with lowered $\delta^{15}\text{N}$, increased $\delta^{13}\text{C}$ enrichment was associated with a slight increase in movement. Total length and all interactions involving total length were not found to

significantly contribute to variance in movement (see Appendix S1: Table S1).

DISCUSSION

Our data reveal that interactions between $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ isotopic niches explained a significant proportion of subsequent inter-individual variation in movement, in a group of wild, free-swimming fish. These findings provide an intuitive, yet novel confirmation of our hypothesis that individual trophic and littoral/pelagic prey specialization, and individual variance in movement behavior are linked. Theoretical connections between individual dietary and behavioral specialization and have often been proposed (e.g., [Bolnick et al. 2011](#), [Dall et al. 2012](#)). Furthermore, behavioral inter-individual variation has been shown to influence many factors related to feeding ecology including food intake rates and growth (reviewed in [Biro and Stamps 2008](#)), community dynamics and species interactions ([Pruitt and Modlmeier 2015](#)), social dominance hierarchies (reviewed in [Toscano et al. 2016](#)), and predator-prey interactions ([Griffen et al. 2012](#), [Toscano and Griffen 2014](#)). Moreover a number of studies have shown that individual differences in behavior are linked to the occupation of habitats with differing forage opportunities (e.g., [Griffen et al. 2012](#), [Oudman et al. 2016](#)). However, our data are among the first to provide a direct empirical demonstration that individual differences in movement behavior are related to dietary specialization in a natural setting, and thus significantly advance our understanding of the wider ecological consequences of both phenomena.

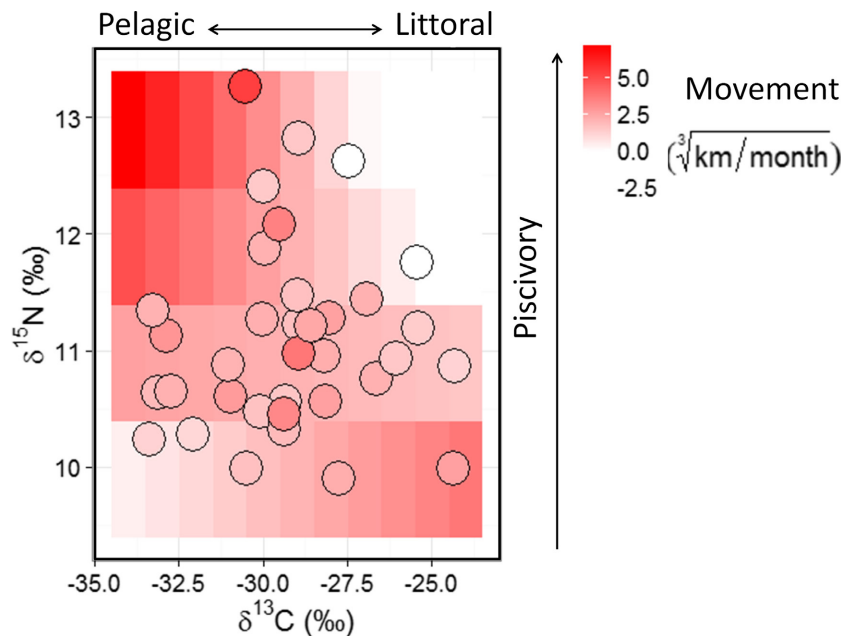


FIG. 1. Model estimates depicting the relationship between individual $\delta^{15}\text{N} \times \delta^{13}\text{C}$ interactions and subsequent cube-root-transformed movement rates of burbot, *Lota lota*. Solid circles depict raw data points and background grid depicts model estimates. Color gradients for raw data and model estimates reflect mean monthly movement.

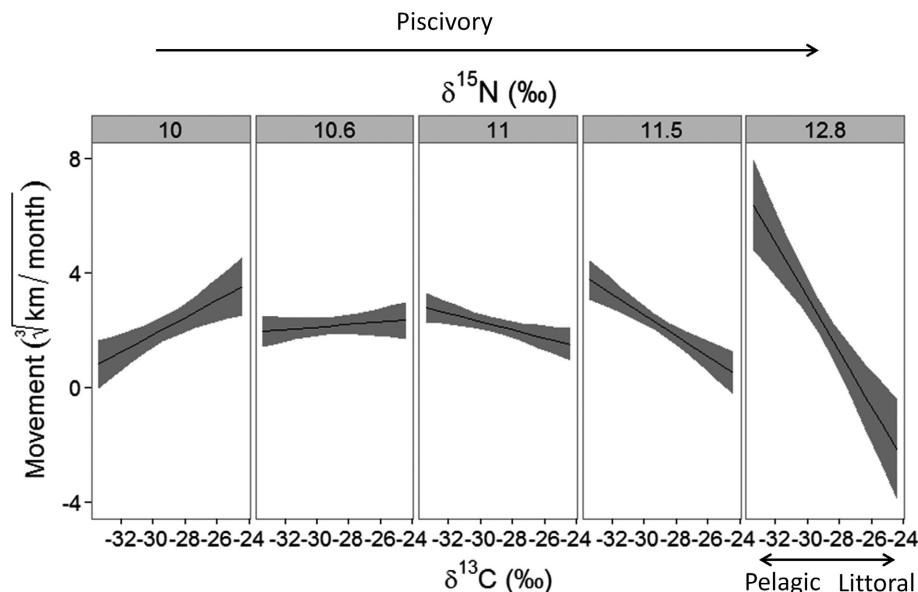


FIG. 2. Model estimates depicting the relationship between individual $\delta^{15}\text{N} \times \delta^{13}\text{C}$ interactions and subsequent cube-root transformed movement rates of burbot, *Lota lota*. Horizontal facets represent 0.05, 0.25, 0.5, 0.75, and 0.95 quantile $\delta^{15}\text{N}$. Shaded areas represent 95% confidence intervals.

Our data suggest that for the more piscivorous individuals (enriched in $\delta^{15}\text{N}$), a higher reliance on pelagic prey items (lower $\delta^{13}\text{C}$) was associated with increased monthly movement rates. In contrast, our data indicate that among the less piscivorous individuals (lowered $\delta^{15}\text{N}$), increasing movement was associated with increasing reliance on more littoral-based food items (enriched $\delta^{13}\text{C}$). These findings raise interesting questions about the directional causation of the covariation. Given that pelagic prey fish tend to be mobile, it is possible that a preference for pelagic prey may drive increased movement, with more resident tactics being suitable for ambush style capture of littoral fish. Indeed, in Red Knots *Calidris canutus*, a migratory shorebird, inter-individual differences in preference for prey nutritional quality have been shown to cause physiological differences in gizzard size and drive inter-individual variance in patch residence (Oudman et al. 2016). Alternatively, it has been argued that because behavioral variation can often be consistent across ontogeny, whereas diet preferences tend to be plastic, behavior is the more likely driver of prey choices (Toscano et al. 2016). In the case of our data, it is plausible that the differing physiological and energetic requirements of the resident and mobile behavioral types may drive prey choices. A third alternative is that both types of inter-individual variance are correlated with an unidentified covariate. Indeed, evidence that behavior, energy metabolism, stress physiology, and life history strategy are correlated under a pace-of-life-syndrome (POLS) is gaining ground (Réale et al. 2010). Thus it is also tenable that the inter-individual variation in movement and diet may be linked to a wider POLS type syndrome. Accordingly, we suggest that further work to empirically

test hypotheses about the causal direction of inter-individual variation covariance, and to establish whether dietary specialization should be included in the POLS, should be research priorities.

By performing isotopic analysis on anal fins as a proxy for diet, we were able to show that our tagged fish differed in their diets at a longer term scale than could have been established using stomach content analyses. Indeed, given the slow growing nature of the cold stenothermal burbot (Stapanian et al. 2010), isotopic turnover is likely relatively slow, and thus fin signatures may well represent a longer time period than for faster growing species (Hesslein et al. 1993). By utilizing multiple tissues from our terminal sample, we were able to show that a degree of temporal consistency in individual specializations occurred within the population. Tissue isotope turnover rates are not known for our study species, and thus low WIC could be driven by similarities in turnover rates among anal fin and dorsal muscle tissues. Nonetheless, differences in turnover rates among fin and muscle tissues have been experimentally established in a number of fish species (reviewed in Willis et al. 2013). Furthermore, observational relationships between fin and muscle have been estimated for a broad range of fish species and the rarity of 1:1 slopes suggest heterogeneity in turnover is common (reviewed in Willis et al. 2013). Moreover, while many confounding factors can mask specialization, in general false positive detections of dietary specializations are rare in multi-tissue stable isotope analysis (Bond et al. 2016). Accordingly we can be reasonably sure low WIC values, at least in part reflect temporally consistent isotopic specializations. Moreover, the temporal consistency of the combination of behavioral and dietary

specialization was highlighted by the ability of isotope samples to predict individual variability in behavior for up to two years following sampling. Accordingly, our results provide convincing evidence that the connected dietary and behavioral specializations we observed, occurred over ecologically relevant time scales.

While body-size is commonly reported as a predictor of animal movement (Radinger and Wolter 2013) body-size independent movement, such as we observed, is also commonly observed, particularly at the intra-specific scale, and among adult animals (Clobert et al. 2009). Likewise, no cross-species consensus exists concerning the relationship between littoral/pelagic foraging niche and body size, and indeed small-body-size effects such as we observed, and the complete absence of body size effects are commonly reported (Beaudoin et al. 1999). Furthermore, while one might intuitively expect individuals with larger body sizes to feed at higher trophic levels, body-size-independent $\delta^{15}\text{N}$ muscle tissue such as we observed, is also fairly commonly reported (Layman et al. 2014, O'Farrell et al. 2014). Together, these findings suggest that the combination of behavioral and dietary specialization we observed, were not likely to be a function of ontogeny or body size related heterogeneity, within the size ranges of fish tested herein.

While sex determination of tagged fish was not possible due to the necessary post-spawn capture timing, previous studies have shown that burbot isotopes and diet derived from stomach contents do not differ by sex (Recknagel et al. 2014). Furthermore there is little evidence to suggest burbot in this population exhibit sex-biased spatial ecology (Harrison et al. 2015). Accordingly, given the balance of evidence, our findings indicate that the inter-individual variation in diet and movement behavior are not likely a function of sexual heterogeneity.

The role of inter-individual variation in space use in determining habitat carrying capacity is increasingly being recognized (Cote et al. 2010). Our findings suggest that such diversity in behavior not only contributes to the carrying capacity of habitats by increasing the potential spatial niche available to a population, it is also likely increases the available trophic niche space available (Power et al. 2012). Similarly, the importance of inter-individual variation in space use is hypothesized to increase population resilience to environmental change, as the use of differing spatial locations and habitats provide an “insurance effect” to spatial or habitat specific threats (Wolf and Weissing 2012). Our findings suggest this population insurance effect may be amplified by the associated heterogeneity in diet and resource use, which likely results in a concurrent resilience to niche specific food-web collapse. Furthermore, inter-individual variation in diet and resource use (Michaud et al. 2010), habitat use (Power et al. 2012), and behavior (Duckworth 2009), are increasingly being recognized to contribute to diversification, speciation, and thus ultimately to biodiversity (Dall et al. 2012, Wolf and Weissing 2012). Our findings, along with the aforementioned work, suggest that the interconnectivity among these specializations may well further facilitate such divergence.

The study of inter-individual variation in behavior and the study of individual diet and resource specialization have often occurred in isolation and the literatures are fragmented (Dall et al. 2012). By providing an intuitive yet novel demonstration of inter-individual covariation in isotopic niche and movement rates, we have provided an important empirical demonstration of the interconnectivity between behavioral and dietary specializations in a group of free-swimming animals, observed in natural contexts. By combining stable isotope and telemetry methods, we were able to demonstrate that these covarying individual differences occur in ecologically relevant metrics at ecologically relevant timescales. Given that an improved understanding of the ecological consequences of inter-individual variation remains a major goal for contemporary food-web (Dall et al. 2012) and behavioral ecology (Wolf and Weissing 2012, Toscano et al. 2016), our findings highlight the promise of future work exploring the connectivity among dietary and behavioral specializations.

ACKNOWLEDGMENTS

Jamie Tippe of Grizzly Country Marine, Jayme Hills, Sean Landsman, Jeff Nitichoruk, Juan Molina, Mark Taylor, Glenn Crossin, Lisa Donaldson, and Taylor Nettles provided field assistance. Alf Leake, and the late Paul Higgins provided logistical support. 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 M. Power, BC Hydro, and the Center for Expertise on Hydropower Impacts of Fish and Fish Habitat of Fisheries and Oceans Canada. P. M. Harrison is supported by a MITACS accelerate fellowship in collaboration with Brent Mossop of BC Hydro. S. J. Cooke 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.

LITERATURE CITED

- Araújo, M. S., D. I. Bolnick, G. Machado, A. A. Giarretta, and S. F. Reis. 2007. Using $\delta^{13}\text{C}$ stable isotopes to quantify individual-level diet variation. *Oecologia* 152:643–654.
- Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. *Oikos* 14: 949–970.
- Bearhop, S., C. E. Adams, S. Waldron, R. A. Fuller, and H. Macleod. 2004. Determining trophic niche width: A novel approach using SIA. *Journal of Animal Ecology* 73: 1007–1012.
- Beaudoin, C. P., W. M. Tonn, E. E. Prepas, and L. I. Wassenaar. 1999. Individual specialization and trophic adaptability of northern pike (*Esox lucius*): an isotope and dietary analysis. *Oecologia* 120:386–396.
- Bell, A. M., S. J. Hankison, and K. L. Laskowski. 2009. The repeatability of behaviour: a meta-analysis. *Animal Behaviour* 77:771–783.
- Biro, P. A., and J. A. Stamps. 2008. Are animal personality traits linked to life-history productivity? *Trends in Ecology and Evolution* 23:361–368.
- Bolnick, D. I., R. Svanbäck, J. A. Fordyce, L. H. Yang, J. M. Davis, C. D. Hulsey, and M. L. Forister. 2003. The ecology of individuals: incidence and implications of individual specialization. *American Naturalist* 161:1–28.

- Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. W. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. *Trends in Ecology and Evolution* 26:183–192.
- Bond, A. L., T. D. Jardine, and K. A. Hobson. 2016. Multi-tissue stable-isotope analyses can identify dietary specialization. *Methods in Ecology and Evolution* 7:1428–1437.
- Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecology Letters* 12:197–209.
- Cote, J., J. Clobert, T. Brodin, S. Fogarty, and A. Sih. 2010. Personality-dependent dispersal: characterization, ontogeny and consequences for spatially structured populations. *Philosophical Transactions of the Royal Society B* 365:4065–4076.
- Craig, H. 1957. Isotopic standards for carbon and oxygen and correction factors for mass-spectrometric analysis of carbon dioxide. *Geochimica et Cosmochimica Acta* 12:133–149.
- Dall, S. R. X., A. M. Bell, D. I. Bolnick, and F. L. W. Ratnieks. 2012. An evolutionary ecology of individual differences. *Ecology Letters* 15:1189–1198.
- Dingemanse, N. J., and N. A. Dochtermann. 2013. Quantifying individual variation in behaviour: mixed-effect modelling approaches. *Journal of Animal Ecology* 82:39–54.
- Duckworth, R. A. 2009. The role of behavior in evolution: A search for mechanism. *Evolutionary Ecology* 23:513–531.
- Griffen, B. D., B. J. Toscano, and J. Gatto. 2012. The role of individual behavior type in mediating indirect interactions. *Ecology* 93:1935–1943.
- Gutowsky, L. F. G., P. M. Harrison, E. G. Martins, A. Leake, D. A. Patterson, M. Power, and S. J. Cooke. 2013. Diel vertical migration hypotheses explain size-dependent behaviour in a freshwater piscivore. *Animal Behaviour* 86:365–373.
- Harrison, P. M., L. F. G. Gutowsky, E. G. Martins, D. A. Patterson, A. Leake, S. J. Cooke, and M. Power. 2013. Diel vertical migration of adult burbot: a dynamic trade-off among feeding opportunity, predation avoidance, and bioenergetic gain. *Canadian Journal of Fisheries and Aquatic Sciences* 70:1765–1774.
- Harrison, P. M., L. F. G. Gutowsky, E. G. Martins, D. A. Patterson, S. J. Cooke, and M. Power. 2015. Personality-dependent spatial ecology occurs independently from dispersal in wild burbot (*Lota lota*). *Behavioral Ecology* 26:483–492.
- Harrison, P. M., L. F. G. Gutowsky, E. G. Martins, D. A. Patterson, S. J. Cooke, and M. Power. 2016a. Burbot and large hydropower in North America: benefits, threats and research needs for mitigation. *Fisheries Management and Ecology* 23:335–349.
- Harrison, P. M., L. F. G. Gutowsky, E. G. Martins, D. A. Patterson, S. J. Cooke, and M. Power. 2016b. Temporal plasticity in thermal-habitat selection of burbot. *Journal of Fish Biology* 88:2111–2129.
- Hesslein, R. H., K. A. Hallard, and P. Ramhal. 1993. Replacement of sulfur, carbon, and nitrogen in tissue of growing broad whitefish (*Coregonus nasus*) in response to a change in diet traced by S, C, and N. *Canadian Journal of Fisheries and Aquatic Science* 50:2071–2076.
- Killen, S. S., B. Adriaenssens, S. Marras, G. Claireaux, and S. J. Cooke. 2016. Context dependency of trait repeatability and its relevance for management and conservation of fish populations. *Conservation Physiology* 4:cow007.
- Layman, C. A., K. O. Winemiller, D. A. Arrington, and D. B. Jepsen. 2014. Body size and trophic position in a diverse tropical food web. *Ecology* 86:2530–2535.
- Mariotti, A. 1983. Atmospheric nitrogen is a reliable standard for natural ¹⁵N abundance measurements. *Nature* 303:685–687.
- Michaud, W. K., M. Power, and M. T. Kinnison. 2010. Trophically mediated divergence of Arctic charr (*Salvelinus alpinus* L.) populations in contemporary time. *Evolutionary Ecology Research* 10:1051–1066.
- Nakayama, S., K. L. Laskowski, T. Klefoth, and R. Arlinghaus. 2016. Between- and within-individual variation in activity increases with water temperature in wild perch. *Behavioral Ecology* 27:1676–1683.
- Newsome, S. D., M. T. Tinker, D. H. Monson, O. T. Oftedal, K. Ralls, M. M. Staedler, M. L. Fogel, and J. A. Estes. 2009. Using stable isotopes to investigate individual diet specialization in California sea otters (*Enhydra lutris nereis*). *Ecology* 90:961–974.
- O'Farrell, S., S. Bearhop, R. A. R. McGill, C. P. Dahlgren, D. R. Brumbaugh, and P. J. Mumby. 2014. Habitat and body size effects on the isotopic niche space of invasive lionfish and endangered Nassau grouper. *Ecosphere* 5:art123.
- Oudman, T., A. I. Bijleveld, M. M. Kavelaars, A. Dekinga, J. Cluderay, T. Piersma, and J. A. van Gils. 2016. Diet preferences as the cause of individual differences rather than the consequence. *Journal of Animal Ecology* 85:1378–1388.
- Post, D. M. 2002. Using stable isotopes to estimate trophic position: models, methods and assumptions. *Ecology* 89:703–718.
- Power, M., M. F. O'Connell, and B. Dempson. 2012. Determining the consistency of thermal habitat segregation within and among Arctic charr morphotypes in Gander Lake, Newfoundland. *Ecology of Freshwater Fish* 21:245–254.
- Pruitt, J. N., and A. P. Modlmeier. 2015. Animal personality in a foundation species drives community divergence and collapse in the wild. *Journal of Animal Ecology* 84:1461–1468.
- Radinger, J., and C. Wolter. 2013. Patterns and predictors of fish dispersal in rivers. *Fish and Fisheries* 15:456–473.
- Réale, D., S. M. Reader, D. Sol, P. T. McDougall, and N. J. Dingemanse. 2007. Integrating animal temperament within ecology and evolution. *Biological Reviews* 82:291–318.
- Réale, D., D. Garant, M. M. Humphries, P. Bergeron, V. Careau, and P.-O. Montiglio. 2010. Personality and the emergence of the pace-of-life syndrome concept at the population level. *Philosophical Transactions of the Royal Society B* 365:4051–4063.
- Recknagel, H., A. Amos, and K. R. Elmer. 2014. Morphological and ecological variation among populations and subspecies of Burbot (*Lota lota* [L., 1758]) from the Mackenzie River Delta, Canada. *Canadian Field-Naturalist* 128:377–384.
- Sih, A., J. Cote, M. Evans, S. Fogarty, and J. Pruitt. 2012. Ecological implications of behavioural syndromes. *Ecology Letters* 15:278–289.
- Smith, B. R., and D. T. Blumstein. 2008. Fitness consequences of personality: A meta-analysis. *Behavioral Ecology* 19:448–455.
- Stapanian, M. A., V. L. Paragamian, C. P. Madenjian, J. R. Jackson, J. Lappalainen, M. J. Evenson, and M. D. Neufeld. 2010. Worldwide status of burbot and conservation measures. *Fish and Fisheries* 11:34–56.
- Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, New Jersey, USA.
- Svanbäck, R., P. Eklöv, R. Fransson, and K. Holmgren. 2008. Intraspecific competition drives multiple species resource polymorphism in fish communities. *Oikos* 117:114–124.
- Toscano, B. J., and B. D. Griffen. 2014. Trait-mediated functional responses: Predator behavioural type mediates prey consumption. *Journal of Animal Ecology* 83:1469–1477.

- Toscano, B. J., N. J. Gownaris, S. M. Heerhartz, and C. J. Monaco. 2016. Personality, foraging behavior and specialization: integrating behavioral and food web ecology at the individual level. *Oecologia* 182:55–69.
- Willis, T. J., C. J. Sweeting, S. J. Bury, S. J. Handley, J. C. S. Brown, D. J. Freeman, D. G. Cairney, and M. J. Page. 2013. Matching and mismatching stable isotope ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) ratios in fin and muscle tissue among fish species: A critical review. *Marine Biology* 160:1633–1644.
- Wolf, M., and F. J. Weissing. 2012. Animal personalities: consequences for ecology and evolution. *Trends in Ecology and Evolution* 27:452–461.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at <http://onlinelibrary.wiley.com/doi/10.1002/ecy.1681/supinfo>